

Growth, production and carbon demand of macrofauna in Young Sound, with special emphasis on the bivalves *Hiatella arctica* and *Mya truncata*

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Abstract

Composition, abundance and biomass of macrobenthos in the outer part of a NE Greenland fjord, Young Sound (74°18'N, 20°18'W) were examined by grab sampling and photography along six transects, each with a depth range of 10 to 60 m. We found a species-rich fauna, dominated by brittle stars and bivalves. Annual growth and production of two bivalve species, *Mya truncata* and *Hiatella arctica*, were estimated by analysis of shell increments. Both species exhibited growth patterns typical of the Arctic, i.e. long life span and low annual growth. To investigate the exceptionally slow growth of *H. arctica*, laboratory experiments were conducted. Food availability was identified as the primary constraint on annual growth, whereas low temperature caused lower energy requirements and hence prolonged the growth season for bivalves. The strong influence of food limitation was also demonstrated in a study of the year-to-year variation in growth of *M. truncata*. A relative growth index was constructed for the period 1962–2000 based on measurements of individual increments. The index demonstrated a significant influence of ice cover on growth of bivalves, suggesting that the length of the ice-free season, which determines phytoplankton production, affects the growth pattern. Carbon demands of dominant species were estimated by three empirical models available in the literature and used to evaluate the role of the benthos in carbon cycling. Modelled carbon demands for *M. truncata* and *H. arctica* were well above those derived from actual production estimates from Young Sound. A conservative approach was adopted based on minimum estimates yielding an average of 15 mg C m⁻² d⁻¹ for the macrobenthos. Taking into account the different approaches used, the carbon demand of macrobenthos in Young Sound is among the highest reported from the Arctic.

7.1 Introduction

Benthic macrofauna species are an important component of coastal ecosystems. They consume a significant fraction of the available production and are in turn an important source of food for fish, seabirds and mammals. This is also the case in the Arctic, where approximately 20% of the world's shelf areas are located (Menard & Smith, 1966) and where a high

standing stock of benthic macrofauna is found in spite of a low and highly seasonal input of food. This is possible because large areas of the Arctic consist of relatively shallow shelf areas with a tight benthic-pelagic coupling. Also, the low temperature reduces the energy requirements of the benthos, allowing a relatively large biomass to be supported by a low

primary production. Finally, in areas with a stable physical environment, the long life span of benthic species will allow a large biomass to accumulate over decades in spite of low annual production. Brittle stars have been found to be the most characteristic group of the Arctic shelf. Abundances of 100–200 individuals m^{-2} have been reported from the Barents Sea, the Laptev Sea, the Greenland Sea (Piepenburg, 2000) and the Chuckchi Sea (Ambrose et al., 2001) with single observations of up to 500 ind. m^{-2} . The biomass of brittle stars is typically in the range 400–600 mg C m^{-2} (Piepenburg, 2000). Food availability is one of the major driving forces influencing the biomass and composition of benthic assemblages in the Arctic. Hence, maximum biomass is found in the highly productive Chuckchi Sea with biomass values of up to 60 g C m^{-2} (Grebmeier et al., 1988). In East Greenland fjords, Thorson (1933, 1934) reported benthic biomass in the range 200–500 g wet weight m^{-2} (approximately 15–40 g C m^{-2} converted).

Compared with plankton, which show high spatial and temporal variability in biomass, the macrobenthos are a predictable food source for higher trophic levels such as grey whale (Highsmith & Coyle, 1990), walrus (Born et al., 2003), bearded seal (Hobson et al., 2002) and eider (Richman & Lovvorn, 2003). Despite their obvious importance for the marine food web, very little is known about the life history traits of benthic populations; growth rates, mortality, reproductive strategies etc. Such information is critical since estimates of consumption and production of populations are significant for the description of the trophic flow through an ecosystem (Brey, 1999). Studies of populations are also important when it comes to quantifying biological consequences of the predicted changes in the Arctic climate in the near future.

Extensive fjord systems are a characteristic feature of the East Greenland coast, but compared with the East Greenland shelf these areas have received relatively little attention. In this chapter we try to evaluate the role of the macrobenthos in the carbon flow in Young Sound. We do this based on information on the composition and abundance of the benthic community combined with data on growth and production of two dominant bivalves (*Hiatella arctica* and *Mya truncata*). In addition, we estimate production and carbon demand of dominant species by applying empirical models available in the literature.

7.2 Methods

7.2.1 Study area

This study was conducted in the outer part of Young Sound, NE Greenland (74°18'N, 20°18'W) between 1999 and 2003. The fjord is approximately 90 km long and 2–7 km wide. The maximum depth is c. 340 m and near the entrance is a sill at a depth of 40 to 50 m. The fjord is ice-covered 9 to 10 months of the year. The phytoplankton production is primarily confined to the ice-free period, when bloom conditions rapidly deplete nutrients above the halocline, causing production to sink to subsurface levels at about 20 m. (Rysgaard et al., 1999; Chapter 5). Above the halocline, the temperature can reach 5°C during summer, while it stays below -1°C below the halocline (Rysgaard et al., 2005). Details on sediment composition and carbon content can be found in Sejr et al. (2000) and in Chapter 8.

7.2.2 Composition, abundance and biomass of fauna

Identification and quantification of the entire macrobenthic fauna was performed at Transect 2 (Fig. 7.1). Ten van Veen grabs (0.04 m^2) were collected at each of the following depths: 20, 35, 60 and 85 m and sieved through a 0.5-mm screen (Sejr et al., 2000). Collected specimens were identified to species level if possible and counted. At the remaining transects photography was used to study the abundance of large dominant groups only, such as brittle stars, bivalves and sea urchins. Transects 1–6 were studied in August 1999 using a digital video camera covering 0.7 m^2 . In 2003, Transects 1, 3 and 5 were studied again using a high-resolution digital still camera covering approximately 0.3 m^2 (Fig. 7.2). The image quality allowed positive identification of brittle stars with a disc diameter down to 2 mm. Abundances of dominant groups identified from photos were transformed into biomass by multiplying abundance values with mean individual biomass. Specimens used for assessing size distribution and individual biomass were collected from dredge hauls (brittle stars, sea urchins) or by suction sampling (*Mya truncata*) at 20 to 30 m along Transect 2. In addition to photography, the abundance and biomass (shell-free dry weight) of *Hiatella arctica* was estimated by van Veen grab sampling (0.04 m^2) at Transects 1–6 (Sejr et al., 2002a).

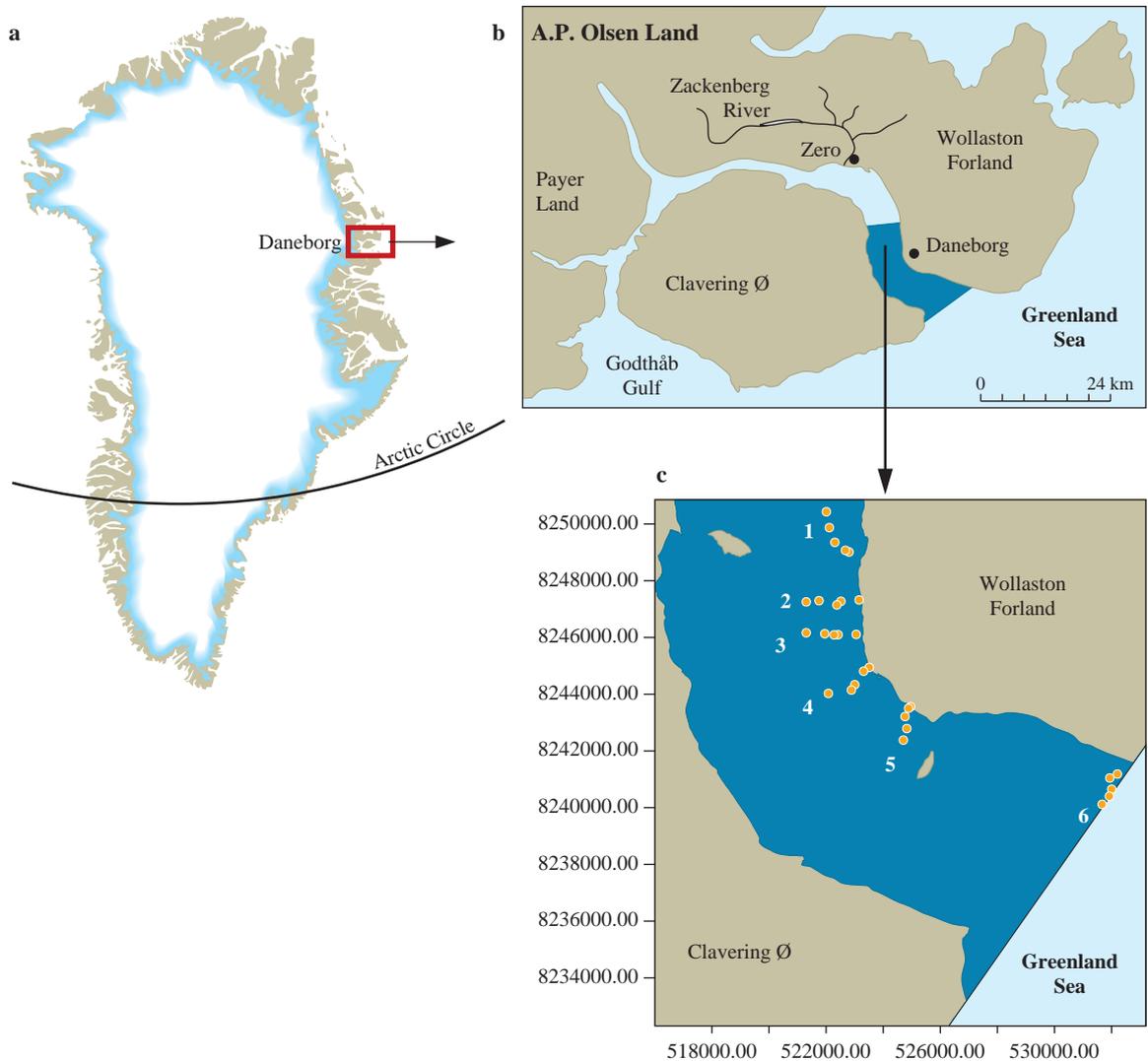


Fig. 7.1 Map of the area studied in Young Sound showing transects where benthos were sampled.

Fig. 7.2 Photo from Transect 2, 40 m from Young Sound, showing abundance of bivalves and brittle stars.

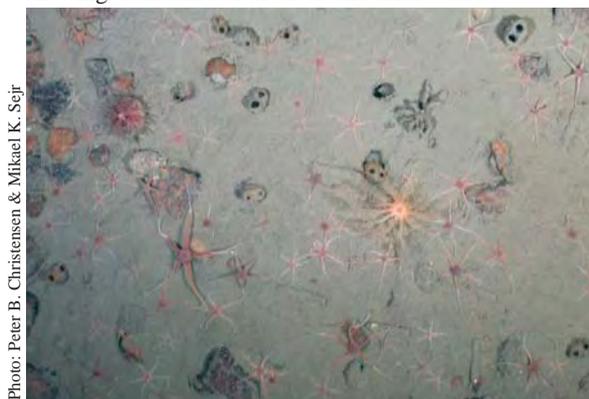


Photo: Peter B. Christensen & Mikael K. Sej

7.2.3 Population dynamics of bivalves

Annual growth of *Hiatella arctica* and *Mya truncata* was studied by using growth increments in the shell (Fig. 7.3) to estimate individual age (see Sej et al. (2002a) for details and references on the method). A mark-recapture study showed growth increments to be produced annually for *Hiatella arctica* (Sej et al., 2002b) and this was assumed to be the case for *Mya truncata*. The number of increments could thus be used as a proxy for individual age. Annual increments have previously been shown for *Mya arenaria* (MacDonald & Thomas, 1980) and other polar bivalves (Brey & Meckensen, 1997) and seem to

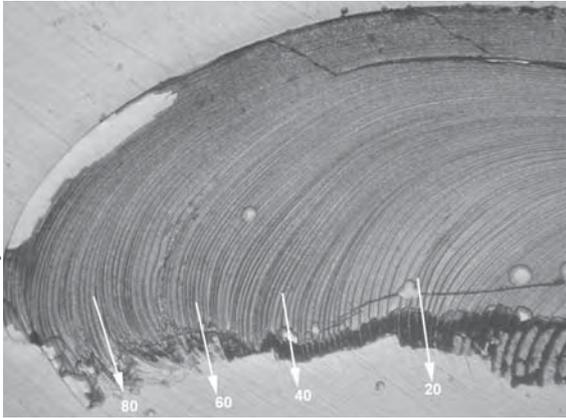


Fig. 7.3 Cross-section of the umbo region of *Mya truncata* showing growth increments at c. 40 magnification.

be a general feature in polar areas with pronounced seasonality. The specialised Von Bertalanffy growth function was fitted to length-at-age data for both species. Individual production was then calculated using the weight-specific method (Brey, 2001). Mortality of each bivalve population was estimated from the size-converted catch curve using a single negative exponential model (Brey, 2001).

To study long-term changes in bivalve growth, the width of individual growth bands was measured in 28 *M. truncata* individuals. Actual growth (in μm) was log_e transformed before the ontogenetic trend in growth was removed by applying a common smoothing spline. The residuals from the spline were then used as an estimate of relative growth for each individual.

7.2.4 Physiology of bivalves

To study the physiological effects of low temperature on bivalve filtration rate the response to changes in temperature was determined (Petersen et al., 2003). Filtration rate was determined using the clearance method (Riisgård, 2001) from the exponential reduction of added *Rhodomonas* sp. cells. Measurements were conducted on specimens of *Hiatella arctica* and *Mya truncata* from Young Sound and compared with values for *Hiatella* sp. collected in Sweden.

To further study the physiological basis for the observed growth pattern, rates of filtration, assimilation, respiration and ammonia excretion were measured in individuals of *H. arctica* from Young Sound kept at $-1.5\text{ }^{\circ}\text{C}$ and fed different concentrations of the algae *Rhodomonas* sp. (Sejr et al., 2004). From these

measurements the amount of assimilated energy at different food levels could be calculated and converted into tissue growth by applying estimated growth efficiencies.

7.2.5 Carbon demand of benthos

Estimates of carbon demand of dominant groups were obtained by three different empirical models: 1. The model of Brey (1999), which predicts the production-to-biomass ratio (P/B) of benthic populations based on inputs of water depth, temperature, individual size, biomass and taxonomic and functional group. 2. The model of Tombiolo & Downing (1994), which estimates annual production based on inputs of temperature, maximum individual biomass, population biomass per m^2 and depth. 3. Individual respiration rates of brittle stars were estimated using the formula developed by Mahaut et al. (1995) and used to estimate respiration rate and carbon demand in Arctic brittle stars (Piepenburg, 2000). For models 1 and 2 estimates of production were converted into total carbon demand assuming an assimilation efficiency of 80% and a growth efficiency of 30% (Piepenburg, 2000). In addition, the carbon demands of *M. truncata* and *H. arctica* were estimated from production estimates in Young Sound, and the production of the sea urchin *Strongylocentrotus* sp. was calculated using the growth model for *Strongylocentrotus pallidus* from the northern Barents Sea (Bluhm et al., 1998).

7.3 Results & discussion

7.3.1 Benthic composition, abundance and biomass

In spite of the long seasonal ice cover and limited production, a relatively high macrobenthic biomass dominated by bivalves has built up in outer Young Sound. High sediment heterogeneity and little disturbance from ice and particles from land have allowed populations of slow-growing infaunal and epifaunal species to develop, resulting in a diverse community. On average, 47 (range 43–52) different species are found per 201 specimens in Young Sound (Table 7.1) compared with an average of 38 (range 33–43) from Svalbard and 33 and 35–44 from the Java Sea and the North Sea, respectively (Kendall, 1996). Polychaetes dominated the infauna, constituting up to 80% of the total abundance. The ten most abundant species in 56 grab samples (0.04 m^2) collected at 20 to

Table 7.1 Total infaunal abundance (individuals per m²) in grab samples (0.04 m²) at Transect 2 in outer Young Sound. Diversity is given by Shannons diversity index (H'). Number of species is per grab sample. ES₂₀₁ gives the number of species per 201 individuals using Hurlberts rarefaction term. Median and 95% confidence limits (CL) are given for all except ES₂₀₁. Redrawn from Sejr et al. (2000).

Depth (m)	20	35	60	85
Abundance (ind. m ⁻²)				
Median	2675	1125	1075	863
CL	1575–3625	650–1575	675–1850	775–1125
Diversity (H')				
Median	2.8	2.6	2.8	2.6
CL	2.6–3.0	2.2–2.8	2.6–2.9	2.4–2.7
Number of species				
Median	26	17	19	17
CL	23–32	13–20	18–28	14–20
ES ₂₀₁	47	48	49	43

Table 7.2 List of most abundant infaunal species found in 56 grab samples (0.04 m²) at Transect 2. Total abundance in all samples and relative contribution are given. Redrawn from Sejr et al. (2000).

	Total (individuals)	Proportion (%)	Cumulative (%)
<i>Cirratulus cirratus</i>	398	13.5	13.5
<i>Lumbriclymene minor</i>	228	7.7	21.2
<i>Maldane sarsi</i>	161	5.5	26.7
<i>Terebellides stroemi</i>	145	4.9	31.6
<i>Lumbrineris fragilis</i>	145	4.9	36.5
<i>Hamothoe</i> spp.	126	4.8	41.3
<i>Aricidae suecica</i>	121	4.3	45.6
<i>Polydora quadrilobata</i>	118	4.0	49.6
<i>Hiatella arctica</i>	81	2.7	52.3
<i>Astarte</i> spp.	45	1.5	53.8

85 m depth at transect 2 are presented in Table 7.2. Some of the most abundant infaunal species include the polychaetes *Cirratulus cirratus*, *Maldane sarsi* and *Terebellides stroemi* and the bivalve *Astarte* spp. Deposit feeders constituted about 75% of all specimens in grab samples. Infaunal abundance decreased from a median of 2675 ind. m⁻² at 20 m to 863 ind. m⁻² at 85 m (Table 7.1) combined with a clear shift in faunal composition (Sejr et al., 2000), most likely due to depth-related changes in food supply and sediment characteristics. Both in terms of total abundance and dominant species, the fauna in Young Sound is very similar to that of other fjords in East Greenland (Thorson, 1933; Thorson, 1934), Svalbard (Holte & Gulliksen, 1998) and eastern Canada (Thomson et al., 1982). On the East Greenland shelf, mean abun-

Table 7.3 Depth-specific abundance (mean ± 95% CI) of selected benthos in Young Sound across 6 transects.

Depth (m)	<i>Mya truncata</i> (ind. m ⁻²)	<i>Hiatella arctica</i> (ind. m ⁻²)	<i>Strongylocentrotus</i> sp. (ind. m ⁻²)	<i>Ophiuroidea</i> spp. (ind. m ⁻²)	<i>Cucumaria</i> sp. (ind. m ⁻²)
10	2.4 ± 1.5	2.7 ± 0.8	0.02 ± 0.05	4.9 ± 1.3	0
20	18.3 ± 3.3	33.7 ± 6.3	0.9 ± 0.5	36.2 ± 8.0	0
30	18.0 ± 3.3	59.3 ± 12.3	2.3 ± 0.8	120 ± 12.2	0.1 ± 0.2
40	15.5 ± 7.5	17.0 ± 6.1	0.6 ± 0.3	125 ± 19.5	0.9 ± 0.4
50	1.0 ± 0.8	8.1 ± 3.6	0.2 ± 0.2	144 ± 20.1	0.9 ± 0.5
60	0.1 ± 0.2	1.3 ± 0.8	0.1 ± 0.1	216 ± 17.6	1.2 ± 0.7

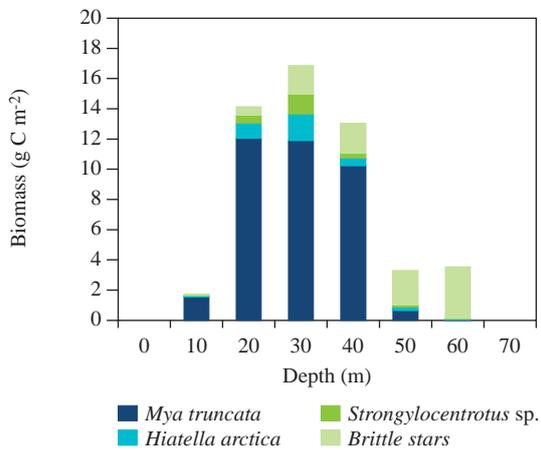


Fig. 7.4 Mean depth-specific biomass (g C m⁻²) of abundant species of macrofauna in Young Sound.

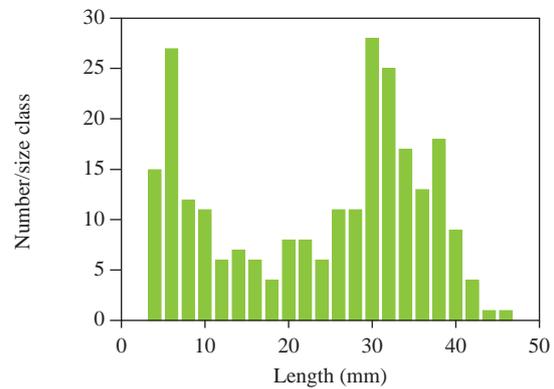


Fig. 7.5 Size distribution (shell length; mm) of the bivalve *Hiatella arctica* in Young Sound. N=244.

dances of 5000–9500 ind. m⁻² have been reported in ice-free waters of the Northeast Water Polynya, whereas the abundance in nearby ice-covered areas dropped to 1200–3500 ind. m⁻² (Ambrose & Renaud, 1995), which is comparable with the abundance in Young Sound. The high biomass of bivalves in outer Young Sound seems to be a characteristic feature of the fjords compared with the deeper shelf along the East Greenland coast.

The epifauna was dominated by brittle stars, with a maximum abundance of 216 ind. m⁻² at 60 m (Table 7.3). The different species of brittle stars could not be distinguished with certainty in photos but three species were found in dredge samples from 50 m; *Ophiacantha bidentata*, *Ophiura robusta* and *Ophiocten sericeum*. Of the three species, *O. sericeum* was the most numerous, constituting 53% of the total abundance in dredges. Brittle stars are the most characteristic epibenthic animals of the Arctic seabed, and the species *O. sericeum* is abundant in shallow parts of the Greenland, Barents and Laptev Seas (Piepenburg, 2000). The mean abundance of 216 ind. m⁻² with a biomass of 3.42 g C m⁻² is among the highest reported in the Arctic. As in Young Sound, brittle stars typically exhibit a depth-related zonation in abundance, the maximum being found typically between 50 and 100 m (Piepenburg, 2000). Unfortunately, we were unable to estimate brittle star abundance at depths below 60 m in Young Sound, but a considerable biomass is most probably present in deeper parts of the fjord. In addition to brittle stars, echinoderms such as the sea urchin *Strongylocentrotus* sp., the feather star

Heliometra glacialis and the sea cucumber *Cucumaria* sp. were abundant (Table 7.3).

In terms of biomass, bivalves are clearly dominant (Fig. 7.4). Abundant species in the Young Sound study area include *Mya truncata*, *Hiatella arctica*, *Astarte* spp. and *Macoma calcarata*, all of which are characteristic of shallow (<50 m) areas of fjords in East Greenland, Svalbard and NE Canada. The high biomass is attained through a combination of longevity and low mortality as shown for *Hiatella arctica*. Clear bimodal size distribution indicates dominance of small (<10 mm) and large (>30 mm) individuals (Fig. 7.5). The relatively narrow peak in bivalve abundance at 20 to 40 m observed in Young Sound is most likely a result of a combination of depth-related differences in mortality and food supply. The slow growth of *H. arctica* and *M. truncata* (see below) makes them vulnerable to disturbance from ice, which limits their biomass in the upper 0–10 m. At depths down to c. 35 m a combination of benthic diatoms and subsurface phytoplankton blooms ensures access to high-quality food, whereas at greater depths specimens have to rely on sedimenting carbon of lower quality. Decreasing food availability was also identified by Ockelmann (1958) as the primary reason for the decline in bivalve biomass with distance from the sea in several East Greenland fjords. That food availability should influence patterns of bivalve biomass within East Greenland fjords is in good agreement with observations of large-scale variations of total benthic biomass reflecting productivity of overlying water masses (Grebmeier et al., 1988).

7.3.2 Growth and production of the bivalves

Hiatella arctica and *Mya truncata*

Age estimated from growth increments showed bivalves to be very long-lived (Fig. 7.6). The oldest specimen of *H. arctica* was 126 years old, whereas *M. truncata* reached ages of up to 50 years. Although specimens of *Arctica islandica* can live even longer (Ropes, 1985) it is a good example of the longevity often observed in polar benthos. From the size-converted catch curve the mortality can be estimated for the small and large size groups of *Hiatella arctica* (Fig. 7.7). Small individuals are subject to an annual mortality of $Z = 0.58$ which drops to $Z = 0.15$ for large individuals. Due to the extreme longevity of this species, the number of individuals surviving

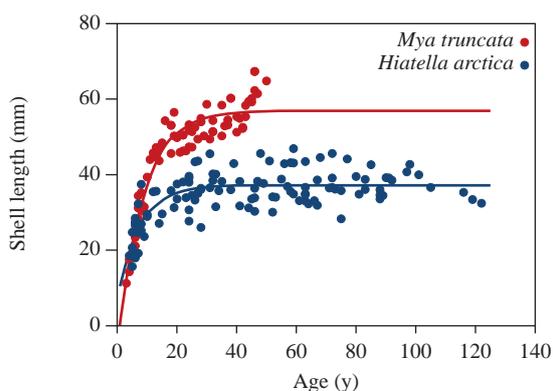


Fig. 7.6 Von Bertalanffy growth function fitted to length-at-age data for *Mya truncata* and *Hiatella arctica* from Young Sound. *H. arctica*: $L_{\infty} = 37.2$ mm, $K = 0.14$ yr⁻¹, $t_0 = -1.4$ yr, $n = 117$, $r^2 = 0.56$. *M. truncata*: $L_{\infty} = 56.8$ mm, $K = 0.12$ yr⁻¹, $t_0 = 1.1$ yr, $n = 77$, $r^2 = 0.83$.

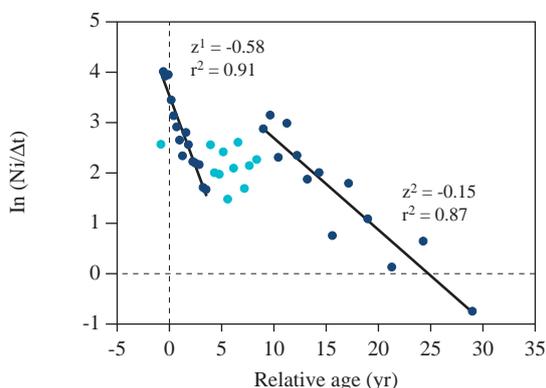


Fig. 7.7 Size-specific mortality of the bivalve *Hiatella arctica* in Young Sound obtained using a single negative exponential mortality model on size distribution. The model was fitted on part of the data (dark blue dots) while intermediate age stages were excluded (light blue dots).

the first critical phase will accumulate over almost a century, causing high biomass and dominance of old individuals. The growth model fitted to age-at-length data shows a distinct difference between the two species; *M. truncata* continues to increase in shell length throughout its entire life span whereas *H. arctica* stops increasing shell length after 40–45 years. Also, because of the difference in size, the individual annual production of *H. arctica* is much smaller than that of *M. truncata*; 0.03 g dw yr⁻¹ for *H. arctica* compared with 0.28 g dw yr⁻¹ for *M. truncata* (Fig. 7.8).

The extremely slow growth of *H. arctica* was studied in two sets of laboratory experiments. First, the influence of temperature on clearance rates was compared in two populations of *Hiatella*, one from Young Sound and one from Tjärnö, Sweden (Petersen et al., 2003). The Arctic population showed adaptation to low temperatures by being fully active even at a temperature of -1°C . The size-specific clearance rates were much lower than those of the Swedish population at 12°C . In a second study (Sejr et al., 2004), specimens of *H. arctica* from Young Sound were kept at -1.2°C and exposed to different food concentrations. By combining measurements of clearance rates with measurements of assimilation efficiency the amount of assimilated energy could be estimated at a maximum of 3 J h^{-1} or 12–25% of that of other species of similar size at higher temperature (Sejr et al., 2004). The low temperature in Young Sound thus clearly limits the growth potential of *H. arctica* by reducing clearance rates and, hence, the amount of energy available for growth. However, the low

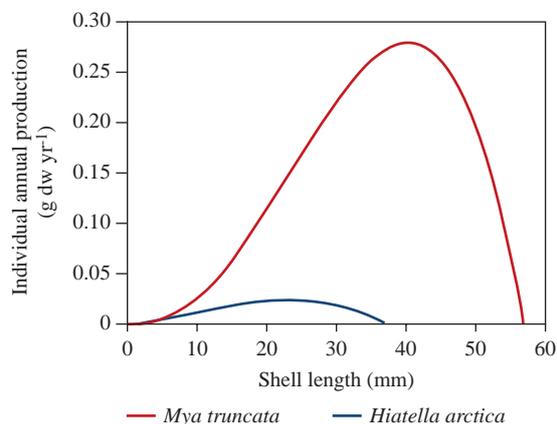


Fig. 7.8 Relationship between size (shell length; mm) and annual individual production (g dw yr⁻¹) of the bivalves *Hiatella arctica* and *Mya truncata* in Young Sound.



Marking bivalves (*Hiatella arctica*) for a recapture study on annual growth bands in Young Sound.

temperature also reduces metabolism and, thereby, energy requirements. From the laboratory studies it was estimated that individual *H. arctica* require algae concentrations of only $0.34 \mu\text{g Chl } a \text{ l}^{-1}$ at -1.3°C to maintain a positive energy budget (Sejr et al., 2004), whereas individuals of *Mytilus edulis* of similar size require $1.03 \mu\text{g Chl } a \text{ l}^{-1}$ at 15°C (Clausen & Riisgård, 1996). Low food levels are therefore sufficient to cover basic metabolic expenses – a great advantage in an environment where food supply is limited most of the year. Estimated laboratory growth of *H. arctic* from Young Sound fed on a monoalgal diet was further compared with the annual growth of the natural population of *H. arctica* in Young Sound (Sejr et al., 2004). Specimens kept in the laboratory at optimal food conditions and at a temperature similar to that prevailing in Young Sound were able to achieve a growth equivalent to the *in situ* annual production in just 23 days. This shows that despite the limiting effect of temperature on the growth potential of *H. arctica* in Young Sound, the growth potential is not fully realized because food is limiting through long periods of the year in Young Sound. Phytoplankton production in Young Sound is usually concentrated within a two-month period in July and August (see Chapter 5) and the energy budgets of bivalves in

Young Sound are most likely positive only during the three to four months of open water. During the rest of the year, bivalves rely on resuspended material and stored energy. A good example of the seasonal energy budget of a polar bivalve was given by Brockington (2001) in a study on the Antarctic bivalve *Laternula elliptica*. Here, individuals stopped feeding for four months during winter and reduced metabolism to a minimum of just 33% of their summer metabolism. During the non-feeding season, energy requirements were covered by catabolism of stored energy.

In addition to studying individual growth at a seasonal level, it is of interest to look at year-to-year variation in growth in the population. Analogously to the growth rings in trees, increments in the shells of bivalves can be used to reconstruct past variations in growth. Analysis of year-to-year variation in each individual revealed a significant autoregressive component, indicating that conditions in one year affect the growth in the following year. Most likely this is because of the strong dependence on stored energy, which allows individuals to carry the effects of a good year into the next in the form of extra stored energy. For *M. truncata* the standardised growth index shows clear variation in time (Fig. 7.9), a significant part of which could be explained by variations in the duration of the open-water period during summer (Schmidt et al., *submitted*). Primary producers in Young Sound are clearly limited by light during spring when ice cover reduces incoming sunlight (Rysgaard et al., 1999; Borum et al., 2002; Glud et al., 2002; Chapters 4, 5 & 9). In years when sea ice disappears early, increased

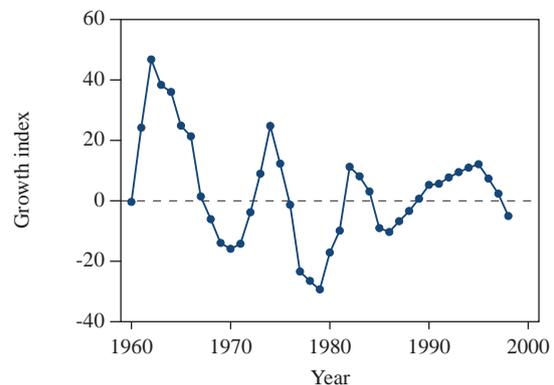


Fig. 7.9 Three-year moving average of growth index for the bivalve *Mya truncata* showing the long-term variation in annual growth in Young Sound. Index is based on measurements of growth increments in the shell.

production of phytoplankton can thus be expected. As bivalves apparently are food-limited, their growth will reflect food conditions, and changes in ice conditions will cascade down and influence growth of bivalves. A similar relationship has been observed in the North Sea. Here, long-term growth patterns of the bivalve *Arctica islandica* are influenced by the climatic effect on copepods (Witbaard et al., 2003). During years with high NAO index values in winter, water-column stratification develops later, depressing the copepod population and, hence, resulting in higher vertical flux of phytoplankton. This produces better food conditions and increased growth rates for *A. islandica*. The copepods in Young Sound also play an important part in the vertical flux of carbon (Chapter 5). However, subsurface blooms in Young Sound make primary production directly available to benthic populations at depths of 20–30 m. Since the individuals of *M. truncata* studied here were collected at 20 m depth, they have access to phytoplankton, resulting in a direct link between climate, sea-ice cover, primary production and bivalve growth.

7.3.3 Carbon demand of benthos

Carbon demand calculated from benthic biomass combined with conversion factors and empirical models from the literature only yield a rough estimate of the role of macrobenthos. However, it is often the only possible way, as measurements of species-specific rates are very sparse for Arctic macrobenthos.

Hence, this approach has been used by several authors (Klages et al., 2003; Piepenburg, 2000). In our study, we can evaluate the output from the models by comparing their results with the actual production estimates for *H. arctica* and *M. truncata* in Young Sound (Table 7.2). The predicted carbon demand based on the model of Tombiolo & Downing is a factor of 5 to 6 higher than that predicted by Brey's model, which in turn is twice the value of the carbon demand estimated from actual production estimates for *M. truncata* and *H. arctica*. This discrepancy is due to the uncertainties associated with the model output and also the fact that Young Sound is a low-productive area and, therefore, bound to show production values below the "average" predicted by such models. An alternative method was employed by Piepenburg et al. (1995) who used shipboard measurements to estimate respiration rates of benthic groups. Rates from that study were used to estimate the carbon demand of polychaetes in Young Sound (Glud et al., 2000). In the case of molluscs, Piepenburg et al. (1995) used a mean mass-specific respiration rate of $0.05 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$ for individuals with mass $>1 \text{ g}$ wet weight (ww) and $0.15 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$ for individuals with mass $<1 \text{ g}$ ww. When transformed into daily carbon demands, these rates are equivalent to 0.077 and $0.57 \text{ mg C ind}^{-1} \text{ d}^{-1}$ for average-sized *H. arctica* and *M. truncata*, respectively. For equal-sized individuals, carbon demands based on actual production estimates are 0.045 and $0.74 \text{ mg C ind}^{-1} \text{ d}^{-1}$ for *H. arc-*

Photo: Göran Ehlme



Sea anemones (Class Anthozoa) at 36 m depth in outer Young Sound.

Table 7.4 Estimated carbon demand ($\text{mg C m}^{-2} \text{d}^{-1}$) for dominant species of benthos in Young Sound at 10–60 m depth.

Method	<i>Mya truncata</i> ($\text{mg C m}^{-2} \text{d}^{-1}$)	<i>Hiatella arctica</i> ($\text{mg C m}^{-2} \text{d}^{-1}$)	<i>Ophiuroidea</i> spp. ($\text{mg C m}^{-2} \text{d}^{-1}$)	<i>Strongylocentrotus</i> sp. ($\text{mg C m}^{-2} \text{d}^{-1}$)
Ind. production				
Mean	6.81	0.92		0.16
Max	13.50	2.69		0.54
Min	0.08	0.05		0.01
Brey et al. 1999				
Mean	12.70	1.92	3.21	0.68
Max	25.27	5.59	6.42	2.27
Min	0.14	0.12	0.12	0.02
Tombiolo et al. 1994				
Mean	32.22	6.29	8.09	3.01
Max	66.06	17.76	15.10	10.96
Min	0.41	0.40	0.52	0.16
Mahaut et al. 1995				
Mean			6.04	
Max			12.09	
Min			0.27	

Table 7.5 Carbon demand ($\text{mg C m}^{-2} \text{d}^{-1}$) of Arctic benthos.

Study	Location	Depth (m)	Organisms	Carbon demand ($\text{mg C m}^{-2} \text{d}^{-1}$)
This study	Young Sound	10–60	Mega and macrobenthos	Mean 15
Klages et al. (2003)	Kara Sea	10–68	Macrobenthos	3.5–43.2
Piepenburg et al. (1995)	NW Barents Sea	80–240	Mega and macrobenthos	16.5
Klages et al. (2004)	Central Arctic ocean	150–4500	Macrobenthos	Median 0.7
Ambrose et al. (2001)	NE Chuckchi Sea	36–50	Brittle stars	Median 3.4
Piepenburg (2000)	NE Greenland shelf banks	40–150	Brittle stars	Median 5.3
Piepenburg (2000)	Barents Sea shelf banks	80–100	Brittle stars	Median 3.6
Piepenburg (2000)	Laptev Sea	30–45	Brittle stars	Median 6.2

tica and *M. truncata*, respectively. This comparison illustrates the uncertainties associated with estimating carbon demand using different methods. Here we use a conservative approach and base our estimate on minimum values, i.e. actual production estimates or predicted production values (for brittle stars). It is important to keep in mind that carbon demand estimates based on somatic production neglect the energy expended during reproduction, which for old individuals often exceeds the amount invested in growth. In an extreme example, a population of the Antarctic sea urchin *Sterechinus neumayeri* invested 95% of its total production in reproduction (Brey et al., 1995).

Macrobenthic carbon demand in Young Sound is dominated by bivalves and brittle stars (Table 7.4). The carbon demand of *M. truncata* and *H. arctica*

reaches $16 \text{ mg C m}^{-2} \text{d}^{-1}$ at 30 m whereas the demand of brittle stars peaks at 60 m with an estimated consumption of $6 \text{ mg C m}^{-2} \text{d}^{-1}$. The importance of brittle stars for the remineralisation of carbon in the Arctic has been noted in several studies (Piepenburg, 2000; Ambrose et al., 2001). Our study highlights the fact that in shallow coastal areas the carbon demand of bivalves can exceed that of brittle stars, at least at shallow depths, but also that bivalves can contribute significantly when values are integrated across the entire area. It is important to remember that several other species of bivalves are present in Young Sound. Specifically species such as *Astarte* spp., *Macoma calcareea* and *Portlandia* spp. may, combined, reach biomass values equivalent to those of *M. truncata* and *H. arctica* (Thorson, 1933, 1934). Their contribution is not included in our estimate of carbon



Bivalve *Hiatella arctica* from outer Young Sound.

demand. Additionally, based on the importance as prey for walrus (Chapter 10) the species *Serripes groenlandicus* could also be expected to contribute significantly to total carbon demand of bivalves.

To our knowledge, only one other study has attempted to estimate the carbon demand of Arctic bivalves. In a study from the Lancaster Sound region, Welch et al. (1992) estimated the carbon demand of *Mya truncata* based on annual production from 0–100 m depth at 634 kJ m⁻² yr⁻¹ equivalent to 38 mg C m⁻² d⁻¹. The higher carbon demand of *M. truncata* in Lancaster Sound compared with Young Sound was predominantly due to higher abundance of clams. Since bivalves have been found to be numerous and attain high standing stocks in several other coastal areas, we believe that the relative importance of bivalves in our study should be representative of other regions.

The average carbon demand of brittle stars (10–60 m) based on predicted annual production was 3.2 mg C m⁻² d⁻¹. Typically, median values for shallow shelf

areas range between 3 and 6 mg C m⁻² d⁻¹ (Table 7.5). The latter values are obtained using respiration rates for deep-sea organisms, which results in higher carbon demands than when predicted production is used based on Brey's model. The carbon demand of brittle stars in Young Sound is therefore among the highest reported for Arctic areas. Unfortunately, estimates of brittle star abundance are not available from depths below 60 m and a considerable biomass is likely to be present in deeper parts of the area. The overall contribution of brittle stars to the remineralisation of carbon in Young Sound is thus even higher and their relative contribution compared with bivalves more important, which underlines the importance of brittle stars not only in shelf areas but also in the vast fjord systems of East Greenland.

The grand mean carbon demand (across depths and taxa), including that of polychaetes (Glud et al., 2000), is 15 mg C m⁻² d⁻¹, ranging from 2 mg C m⁻² d⁻¹ at 10 m to 23 mg C m⁻² d⁻¹ at 30 m. This is comparable with estimates for both the Kara and Barents Seas (Table 7.5), where, however, carbon demand was calculated based on biomass measurements comprising the entire zoobenthic fauna. Despite the conservative estimate, the fauna in Young Sound was found to account for 20% of the total mineralisation at 60 m depth, while the estimate at 40 m was 30%. This shows that the fauna directly influences carbon cycling by ingesting a significant fraction of the available carbon. Shallow depth and low levels of physical disturbance are probably important factors causing the high carbon demand of benthos in the present study. At depths of 10 to 30 m macrofaunal organisms have direct access to subsurface blooms of phytoplankton as well as a considerable production of benthic diatoms (Glud et al., 2002). At 30 to 60 m depth a considerable vertical export of carbon (Chapter 6) allows a high biomass of especially bivalves to build up despite low annual production.

Although both bivalves and brittle stars ingest an important proportion of the produced carbon, they probably have different roles in the trophic net. Both *H. arctica* and *M. truncata* are filter feeders and at their preferred depths (20–30 m) they can effectively exploit the subsurface peak of phytoplankton biomass. Walrus in Young Sound feed almost exclusively on bivalves during summer to build up their energy stores (Chapter 10). Hence, bivalves are a direct trophic link between microscopic algae and large mammals, creat-

ing a short and energetically efficient food chain that allows a population of large mammals to persist in a low-productive environment. Bivalves are also the favored prey of seals, eiders and scavenging amphipods. Therefore, they are important structuring components of the marine food web. On the other hand, brittle stars are thought to be generalists (Piepenburg, 2000). Few if any predators prey on brittle stars, which therefore become a trophic dead end.

In the calculation of macrobenthic carbon demand in Young Sound an assimilation efficiency of 80% was applied (Piepenburg, 2000; Klages et al., 2003), which is in good agreement with actual measurements of *Hiatella arctica* feeding on *Rhodomonas* sp. (Sejr et al., 2004). This implies that c. 20% of the carbon ingested by zoobenthos is not assimilated and that the benthos therefore exert an indirect influence on the carbon flow in the system. Large infaunal filter feeders such as *H. arctica* and *M. truncata* increase sedimentation by filtering phytoplankton from the water column, and, in addition, 20% of the filtered material passes through the gut and is excreted 5 to 20 cm into the sediment, where it is further decomposed by bacteria. Faunal activity thereby changes the relative importance of different oxidation pathways and indirectly increases the importance of the anaerobic bacteria.

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