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Abundance, oxygen consumption and carbon demand of brittle stars in Young Sound and the NE Greenland shelf

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ABSTRACT: We used sea floor photography to estimate brittle star abundance in Young Sound, NE Greenland and the adjacent shelf. From photos covering a total area of 78 m^2 and spanning a depth range from 20 to 310 m we found maximum average densities of >400 ind. m^{-2} at 40 to 80 m depth. *Ophiocten sericeum* was the dominant species. However, gradual changes in species and size composition with depth were observed. Average biomass was ~600 mg C m^{-2} with highest values at sites dominated by the large *Ophiopleura borealis* (up to 2190 mg C m^{-2}). We measured average individual oxygen consumption of 3 dominant species at ambient temperature (–1.0°C) and salinity in incubation chambers using a fiber-optic oxygen sensor enabling continuous measurements. We established a general relation between individual disc diameter (*D*, mm) and oxygen consumption (*R*, µmol O_2 h^{-1} ind.$^{-1}$): $R = 6.0 \times 10^{-4} \times D^{2.60}$ ($R^2 = 0.96$, n = 33), which facilitated the estimation of community respiration and carbon demand from sea floor images. Peaks in total carbon demand were found in the fjord at 30 m (14 mg C m^{-2} d^{-1}) and 160 m depth (13 mg C m^{-2} d^{-1}), resulting from high densities of medium sized (10 to 15 mm disc diameter) *O. sericeum*, and the presence of the very large (20 to 35 mm disc diameter) *O. borealis*, respectively. At the other stations values ranged from 0.5 to 8 mg C m^{-2} d^{-1}. Overall, our results demonstrate that brittle stars, despite very low individual energy requirements, contribute significantly to marine carbon cycling in Young Sound as well as in the shelf areas off NE Greenland.

KEY WORDS: Arctic · Macrobenthos · Epifauna · Respiration · Sea floor photography · Megafauna · Benthos

INTRODUCTION

Brittle stars (Echinodermata; Ophiuroidea) form dense assemblages in several marine habitats and in the deep sea around the world (e.g. Tyler 1980, Smith 1983, Brey & Clarke 1993, Quiroga & Sellanes 2009). Despite their widespread occurrence in coastal areas in the Arctic (Piepenburg 2000) few studies have focused on the ecology of brittle stars and therefore little is known about the significance of brittle stars in ecosystem carbon cycling. Respiration is a very fundamental parameter that can be used to estimate the population energy demand and importance in ecosystem carbon cycling. To our knowledge, only 3 studies have estimated respiration rates of Arctic brittle stars. In the Beaufort Sea, Renaud et al. (2007) measured oxygen consumption of several dominant species, including several species of brittle stars, but specific oxygen consumptions rates for brittle stars were not presented. In the Chukchi Sea, Ambrose et al. (2001) estimated oxygen consumption of *Ophiura sarsi* with a mean disc diameter of 2.2 cm with and without the addition of algae, but relied on a general relation between mass-specific respiration and biomass (Mahaut et al. 1995) to calculate population respiration due to uncertainties as to the reliability of their measurements. The most detailed study was performed by Schmid (1996), who estimated oxygen consumption of 33 specimens belonging to 4 different species within a relatively narrow size interval.

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In Young Sound, NE Greenland, brittle stars have been registered as a dominant epifaunal group at shallow depths (<60 m) with densities up to several hundred individuals per square meter (Sejr et al. 2000). In this study, we complement previous studies by estimating abundance of brittle stars in the deeper part of the fjord and along a transect into the Greenland Sea. We then measure oxygen consumption of the dominant species and produce an estimate of the daily carbon demand by brittle stars in the study area.

MATERIALS AND METHODS

Study area. The study was conducted in the outer part of Young Sound (74° 18′ N, 20° 15′ W) and outside the fjord entrance on the continental shelf in the Greenland Sea, NE Greenland, in August 2009. Young Sound is a 90 km long and 2 to 7 km wide sill fjord, with a mean depth of 100 m. The fjord is ice-covered from October/November to July and water temperatures never exceed –1.0°C below the subsurface layer (>20 m) (Bendtsen et al. 2007). Phytoplankton production is confined to the ice-free period, and characterised by a peak subsequent to the break-up of sea ice, usually lasting a few weeks until nutrients are depleted in the surface layer.

Abundance, biomass and size frequency. A series of high-resolution digital photos (Ocean Imaging Systems) of the sea floor were taken along 3 depth-transects in Young Sound at 20, 30, 40, 50, 60, 80, 100 and 160 m depth, and at 4 stations on the Greenland Sea shelf ranging in depth from 200 to 310 m. Ten photos from each station (26 stations in total, each photo covering 0.3 m^2) were used to quantify the abundance of brittle stars. Using the image processing software ImageJ 1.43r, we measured the disc diameter of brittle stars in the photos in order to describe the size frequency distribution. Biomass was estimated on the basis of the allometric relationship between disc diameter, D (mm) and individual body mass, M (mg organic C) for *Ophiocten sericeum* in the Barents Sea: $M = 0.016 \times D^{2.622}$. The relationship for *Ophiura sarsi*: $M = 0.019 \times D^{2.796}$ was used to convert disc diameter to biomass for *Ophiopleura borealis* (Piepenburg 2000).

Oxygen consumption. Brittle stars were collected with a small dredge at 20, 60 and 160 m depth in Young Sound. Specimens were transferred to an aquarium containing bottom water and returned quickly to the laboratory, where they were carefully sorted with respect to species and size. After an immediate escape response due to handling, brittle stars quickly returned to a normal, rather slow-moving, activity pattern. To allow recovery from handling, they were held in open incubation chambers in aerated seawater at ambient temperature (–1.0°C) and salinity for ~1 h before metabolic measurements were initiated. Due to the relatively short recovery periods specimens were assumed to have been actively feeding until shortly before the beginning of our measurements. We measured oxygen consumption, R (μmol O_2 h^{-1}), of *Ophiocten sericeum*, *Ophiura robusta* and *Ophiopleura borealis* in closed incubation chambers kept in the dark, using a fiber-optic oxygen sensor (FIBOX, PreSens) and oxygen-sensitive optode patches calibrated to zero oxygen (sodium dithionite solution) and air saturated water. This system enabled continuous measurements of oxygen concentration in the closed chambers. Chamber volumes ranged from 240 to 360 ml. The water was stirred by a 20 mm Teflon-coated magnet (60 rpm) fixed at the centre of the chambers. To reduce incubation times (average of the experiments was ~4 h), we measured total oxygen consumption of batches of 4 to 13 individuals of similar disc diameter (~1 mm), corresponding to previous observations of brittle star densities in the Arctic (Piepenburg 2000, Sejr et al. 2009). Thus, we obtained an average estimate of individual R (corrected for a control without brittle stars). For the large *O. borealis*, only one specimen was included in each incubation chamber.

Carbon demand. Total oxygen consumption of the brittle star community, R_{total}, was calculated by a combination of (1) the size frequency, (2) the abundance (ind. m^{-2}), and (3) the relation between disc diameter and individual oxygen consumption:

$$R_{\text{total}} = \sum N_i \times R_i \quad (1)$$

where N_i and R_i are the number of brittle stars and the average individual oxygen consumption, respectively, in size class i (1 mm intervals). Thus, an average R_{total} was estimated for each station.

Oxygen consumption was converted to carbon mineralisation by assuming a respiratory coefficient, RQ, of 0.7 (Grebmeier et al. 2006). An assimilation efficiency of 0.8 and a net growth efficiency of 0.3 (e.g. Navarro & Thompson 1996, Sejr et al. 2004) result in 56% of the ingested carbon being mineralised. Thus, estimates of carbon requirements could be obtained by multiplying the respiration-derived mineralisation rates by a factor of 1.79.

RESULTS

Abundance and biomass

Peak abundance of brittle stars was found at 40 to 80 m depth in Young Sound (Fig. 1a) with an average abundance of at least 200 ind. m^{-2}. Maximum abundance was 445 ind. m^{-2} at 60 m. At depths <100 m *Ophiocten sericeum* prevailed. *Ophiura robusta* was occasionally found at 30 to 60 m in the fjord but never constituted more than 1 to 2% of total abundance. At 2 stations (100 and 160 m) only the very large *Ophiopleura borealis* was observed. On the shelf, abundance decreased steadily with depth, from 162 ind. m^{-2} at 200 m to 9 ind. m^{-2} at 310 m, coinciding with a change in dominance from *O. sericeum* to *Ophiacantha bidentata* and *O. borealis*. Maximum biomass (average 2190 mg C m^{-2}) was found at 160 m in Young Sound due to the dominance of the very large species *O. borealis* (Fig. 1b). High biomass was also found at 30 m (1088 mg C m^{-2}) due to high abundance of relatively large *O. sericeum*. Lowest biomass was found at the deepest station in the Greenland Sea (36 mg C m^{-2}).

Size frequency

The size distribution of the dominant species, *Ophiocten sericeum*, changed with depth. Median *D* in Young Sound ranged from 10.3 mm at 20 to 30 m depth to 5.0 mm at 40 to 80 m (Fig. 2a) and was 9.9 mm at 100 to 160 m. Median *D* in the Greenland Sea was 6.9 mm at 200 to 310 m depth. The occurrence of *Ophiopleura borealis* is seen in the bi-modal distribution of size frequencies (Fig. 2b) at the 100 to 160 m depth interval. The median *D* of *O. borealis* was 27.6 mm.

Oxygen consumption

We measured oxygen consumption (R, µmol O_2 h^{-1} $ind.^{-1}$) of 33 batches of brittle stars (226 specimens in total). In all cases we observed a linear decrease in O_2 concentration in the incubation chambers ($R^2 > 0.95$). The average individual oxygen consumption rate ranged from 0.04 µmol $ind.^{-1}$ h^{-1} in *Ophiocten sericeum* with an average disc diameter of 5.0 mm (13 ind. in chamber) to 4.7 µmol $ind.^{-1}$ h^{-1} for *Ophiopleura borealis* with a disc diameter of 29.6 mm (Fig. 3a). In the 3 species investigated, no apparent difference in the relationship between consumption rate and size were observed. Hence, R increased allometrically with increasing D across species according to: $R = 6.0 \times 10^{-4} \times D^{2.60}$ (R^2 = 0.96, n = 33).

Carbon demand

Maximum carbon demand was found in the fjord at 30 m (14 mg C m^{-2} d^{-1}) and at 160 m (12.9 mg C m^{-2} d^{-1}). At the remaining stations, values ranged from 3 to 8 mg C m^{-2} d^{-1} except at the deepest station (310 m) where carbon demand was 0.5 mg C m^{-2} d^{-1} (Fig. 4).

DISCUSSION

The estimated carbon demand for brittle stars in Young Sound and the nearby shelf in August 2009 is among the highest reported from the Arctic (Table 1).

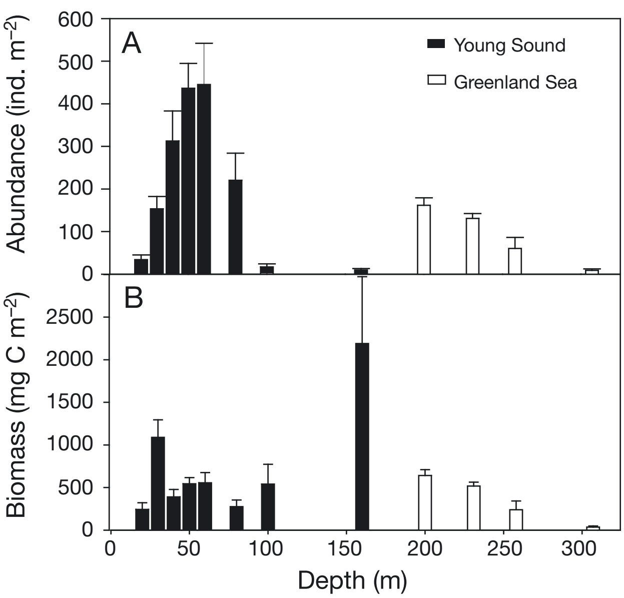

Fig. 1. (A) Average abundance (± 95% CI) of brittle stars in Young Sound and the Greenland Sea obtained from sea floor photography, and (B) estimated biomass (average ± 95% CI)

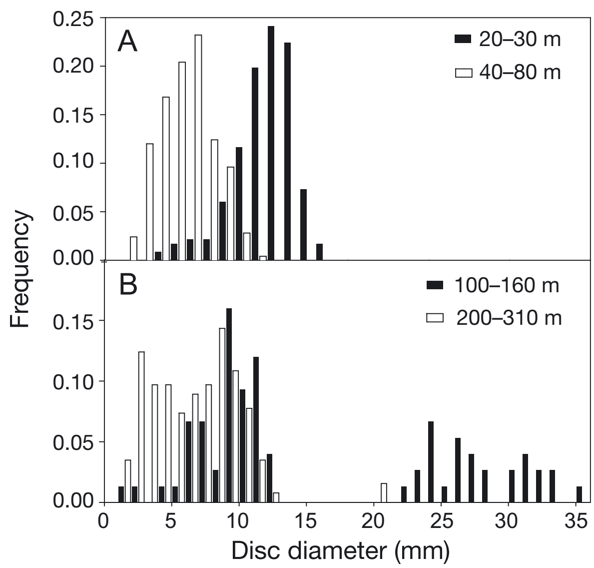

Fig. 2. Size frequency distributions of brittle stars from (A) 20 to 80 m depth, and (B) 100 to 310 m depth in Young Sound and the Greenland Sea. All specimens >20 mm are *Ophiopleura borealis*

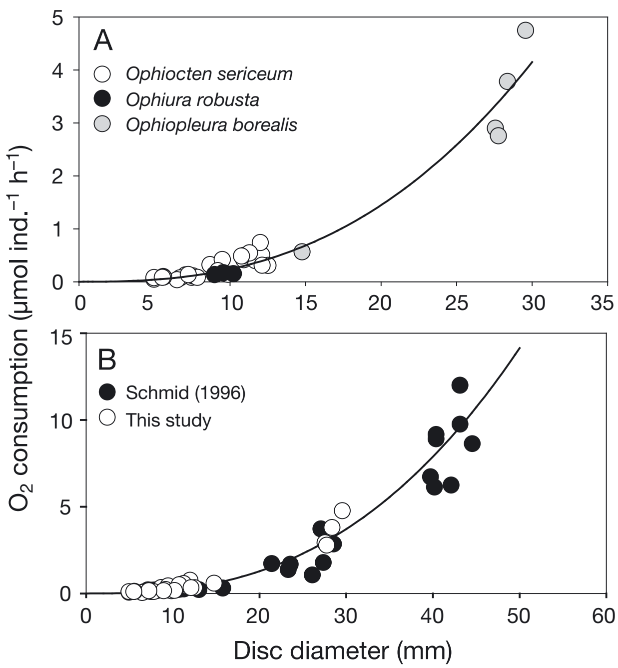

Fig. 3. (A) Average individual oxygen consumption rate, R (µmol O_2 h^{-1}), of 3 different species of brittle stars as a function of disc diameter, D (mm): $R = 0.006 \times D^{2.60}$. (B) General relationship between D and individual R in 6 species of Arctic brittle stars: $R = 0.0005 \times D^{2.62}$

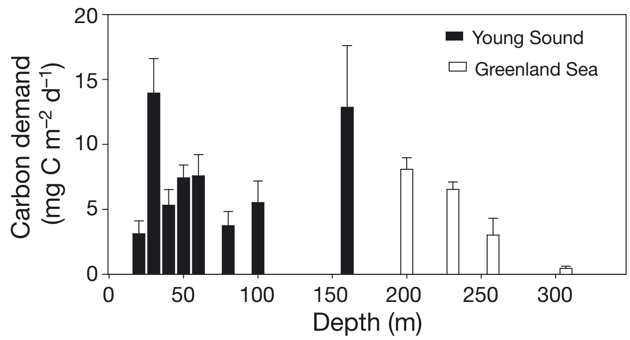

Fig. 4. Average carbon demand (±95% CI) of brittle stars, estimated from individual respiration rates, abundance and size frequency distribution

Table 1. Estimates of average carbon demand of brittle stars in the Arctic and of other dominant macrobenthic species in Young Sound

Species/site	Depth (m)	Carbon demand (mg C m^{-2} d^{-1})	Reference
Arctic brittle stars			
Young Sound	20–30	8.5	This study
	40–80	6.0	This study
	100–160	9.2	This study
NE Greenland			
Shelf	200–310	4.5	This study
Banks	40–150	5.3	Piepenburg (2000)
Trough slopes	100–580	1.0	Piepenburg (2000)
Trough bottoms	180–440	0.4	Piepenburg (2000)
Upper slope	80–770	<0.1	Piepenburg (2000)
Barents Sea	80–100	3.6	Piepenburg (2000)
	150–360	1.8	Piepenburg (2000)
Laptev Sea	14–23	0.1	Piepenburg (2000)
	30–45	6.2	Piepenburg (2000)
Chukchi Sea	29–212	6.7[a]	Ambrose et al. (2001)
Beaufort Sea	32–420	8.8	Renaud et al. (2007)
Other species in Young Sound			
Hiatella arctica	0–60	2.5	Sejr et al. (2002)
Mya truncata	10–60	6.8	Sejr & Christensen (2007)
Strongylocentrotus sp.	5–65	4.2	Blicher et al. (2007)

[a]Carbon demand estimate obtained by multiplying respiration rates by 1.79 (see 'Materials and Methods')

Average carbon demand for the depth intervals studied range from 4.5 to 9.2 mg C m^{-2} d^{-1}. Estimates of total mineralisation in the sediment in summer, as obtained from sediment cores (5.3 cm diameter), range from ~30 mg C m^{-2} d^{-1} (100 to 165 m depth) to 240 mg C m^{-2} d^{-1} (20 m) (Glud et al. 2000). Thus, brittle stars contribute an additional 1 to 25% (average of all stations = 8%) to the sediment exchange estimated by Glud et al. (2000), which predominantly included bacterial mineralisation. This is comparable to the contribution from brittle stars in the Barents Sea (depths <200 m, Piepenburg et al. 1995) and the maximum contributions in the Chukchi and Beaufort Seas (Ambrose et al. 2001, Renaud et al. 2007). Besides their direct contribution to ecosystem carbon transport, brittle stars are likely to stimulate bacterial mineralisation by bioturbation (e.g. Vopel et al. 2003) and fractionation of organic material through ingestion and excretion (Mamelona & Pelletier 2005). Moreover, sub-lethal predation on brittle stars can be significant (Aronson 1992, Sköld & Rosenberg 1996). Estimates of the annual average carbon demand of 3 other dominant macrobenthic species are available from Young Sound (Table 1). Although their carbon demands are significant, their distribution is limited to shallow depths (<60 m). In Young Sound, approximately 70% of the sea floor is found at depths >60 m (Bendtsen et al. 2007). When the shelf areas in the Greenland Sea are taken into account, our results demonstrate that brittle stars in NE Greenland are clearly a dominant macrofaunal group in terms of abundance and carbon mineralisation, and an important contributor to marine carbon cycling as such.

Due to the large standing stock of brittle stars, their carbon demand in Young Sound was relatively high despite low individual respiration rates. The grand average biomass across all depths (600 mg C m^{-2}) is comparable to maximum values from shelves and slopes in NE Greenland and the Laptev Sea, and exceeds values from the Barents Sea (Piepenburg 2000). However, the maximum biomass of 2190 mg C m^{-2} at 160 m depth is well below the 3388 mg C m^{-2} reported from a single station in the Chukchi Sea (Ambrose et al. 2001). The other component used to estimate carbon demand is the average individual respiration rate. To compare our rates with those of Schmid (1996), we converted individual biomasses (ash-free dry weight, AFDW) given in that study to disc diameter using the allometric relationships between disc diameter and body mass (organic C) provided by Piepenburg (2000). The individual respiration rates measured by Schmid (1996) are comparable to our estimates and indicate a general relationship between disc diameter and individual respiration across 6 species of brittle stars encompassing a wide range in size (Fig 3b). It should be noted that values are approximate as they rely on general assumptions regarding the organic C:AFDW ratio and the allometric relationship between biomass and disc diameter to make data directly comparable. Moreover, a general relationship such as this does not consider the potential seasonal variation in macrobenthic activity, which has been reported in other studies in polar areas (Brockington & Clarke 2001, Blicher et al. 2010). However, it can be used to produce a preliminary estimate of the carbon requirements of this abundant taxon in the Arctic using a more general approach based on size structure and abundance, which can be effectively described using sea-floor images.

Different sediment composition or water mass characteristics are likely to be responsible for the observed patterns in the general abundance of brittle stars as well as the depth zonation of species. *Ophiocten sericeum*, *Ophiura robusta* and *Ophiopleura borealis* are cold-water species mainly occurring in the Arctic (Piepenburg 2000 and references therein). Hence, entrainment of relatively warm Atlantic Water (>2°C) across the shelf break (Sejr et al. 2009, J. Mortensen unpubl.) might be responsible for the abundance of *O. bidentata* at the deep stations in the Greenland Sea. However, at present our knowledge of the factors controlling the distribution of different species of brittle stars in the Arctic is very limited. Piepenburg (2000) combined data from several Arctic and sub-Arctic regions and found brittle star biomass to peak in the range of 40 to 150 m with peak abundance at 50 to 100 m, and our data does not deviate from this very general pattern. The dominance of the species *O. sericeum* has also been found at depths <150 m in NE Greenland at 78 to 81°N, and in the Barents Sea and the Laptev Sea (Piepenburg 2000).

In summary, the data presented add to existing examples of how macrofauna in general and brittle stars in particular are important components of benthic carbon cycling in Arctic fjords and shelves, potentially adding up to 25% to the mineralisation of bacteria and meiofauna. Also, the general relationship between disc diameter and individual respiration across 6 species of brittle stars may prove useful to future studies, as it allows a preliminary estimate of brittle star oxygen consumption, mineralisation and carbon demand to be made from sea floor photos.

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