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Oxygen isotope ratios in the shell of Mytilus edulis: archives of glacier meltwater in Greenland?

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Melting of the Greenland Ice Sheet (GrIS) is accelerating and will contribute significantly to global sea level rise during the 21st century. Instrumental data on GrIS melting only cover the last few decades, and proxy data extending our knowledge into the past are vital for validating models predicting the influence of ongoing climate change. We investigated a potential meltwater proxy in Godthåbsfjord (West Greenland), where glacier meltwater causes seasonal excursions with lower oxygen isotope water ($\delta^{18}O_w$) values and salinity. The blue mussel (*Mytilus edulis*) potentially records these variations, because it precipitates its shell calcite in oxygen isotopic equilibrium with ambient seawater. As M. edulis shells are known to occur in raised shorelines and kitchen middens from previous Holocene warm periods, this species may be ideal in reconstructing past meltwater dynamics. We investigate its potential as a palaeomeltwater proxy. First, we confirmed that M. edulis shell calcite oxygen isotope ($\delta^{18}O_c$) values are in equilibrium with ambient water and generally reflect meltwater conditions. Subsequently we investigated if this species recorded the full range of $\delta^{18}O_{w}$ values occurring during the years 2007 to 2010. Results show that $\delta^{18}O_w$ values were not recorded at very low salinities (<~ 19), because the mussels appear to cease growing. This implies that M. edulis $\delta^{18}O_c$ values are suitable in reconstructing past meltwater amounts in most cases, but care has to be taken that shells are collected not too close to a glacier, but rather in the mid region or mouth of the fjord. The focus of future research will expand on the geographical and temporal range of the shell measurements by sampling mussels in other fjords in Greenland along a south-north gradient, and by sampling shells from raised shorelines and kitchen middens from prehistoric settlements in Greenland.

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Introduction

Many biomineralising organisms faithfully record environmental variability in the chemistry of growth increments in their skeletons, e.g. corals (Watanabe et al., 2011; Swart, 1983), coralline algae (Williams et al., 2011; Halfar et al., 2008), land snails (Yanes et al., 2011; Goodfriend and Ellis, 2002), freshwater snails (Stevens et al., 2012; Abell and Hoelzmann, 2000), freshwater bivalves (Versteegh et al., 2011, 2010b; Kaandorp et al., 2003) and marine bivalves (Santos et al., 2012; Jones and Quitmyer, 1996; Schöne et al., 2005). The oxygen isotope composition (δ^{18} O values) of marine bivalves is often used as a proxy for temperature (Wanamaker Jr. et al., 2011; Carré et al., 2005). It can, however, also be applied to reconstruct $\delta^{18}O_w$ values (Freitas et al., 2012; Khim, 2002), which usually directly relate with salinity (Ingram et al., 1996).

The marine bivalve Mytilus edulis (blue mussel) produces prominent annual growth increments (Richardson et al., 1990) and precipitates its shell in oxygen isotopic equilibrium with the environment (Wanamaker et al., 2006, 2007), In combination with its wide geographic distribution, this makes the species highly suitable for reconstructing pre-instrumental temperatures or salinities. These applications, however, have so far been limited. Donner and Nord (1986) showed that *M. edulis* $\delta^{18}O_c$ values reflect water composition, and can be used to estimate past temperatures. Ingram et al. (1996) demonstrated that the amount of freshwater discharge into San Francisco Bay is accurately reflected in shell $\delta^{18}O_c$ values, and that *M. edulis* shells can be used to reconstruct pre-instrumental freshwater fluxes. Here we investigate the potential of δ^{18} O, records of M. edulis in the reconstruction of past glacier meltwater fluxes in a Greenland fjord.

The GrIS is the world second largest ice mass. Current global warming causes accelerated melting (Rignot and Kanagaratnam, 2006; Howat et al., 2005; Andresen et al., 2012), resulting in increased runoff since the early 1990s (Hanna et al., 2011; Box et al., 2006) and significantly contributing to global sea level rise (Price et al., 2011; IPCC, 2007; Krabill et al., 2000). The natural variability in GrIS mass balance over time

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is reconstructed by means of modelling studies, using instrumental data (covering the most recent decades) and proxy data (Alley et al., 2010; Israelson et al., 1994). Uncertainties in model projections are still considerable (Applegate et al., 2012; IPCC, 2007). In order to reduce these uncertainties and validate models, it is vital to collect proxy data on past ice sheet behaviour, such as surface mass balance and runoff (Hanna et al., 2011; Applegate et al., 2012; Alley et al., 2010).

 $M.\ edulis$ shell $\delta^{18}{\rm O_c}$ values may provide additional information regarding past meltwater conditions in Greenland. Although $M.\ edulis$ is common in West and South Greenland, it is currently absent north of Central East Greenland. Subfossil shells, however, can be found in kitchen middens of prehistoric people, and raised palaeoshorelines dating to 5500–8000 before present (BP) (McGovern et al., 1996; Hjort and Funder, 1974). As such there is a rich supply of shells from previous Holocene warm periods, potentially giving insight in GrIS dynamics during those time intervals.

We aim to establish if the shell $\delta^{18}O_c$ composition of M. edulis can be used as a proxy for ambient $\delta^{18}O_w$ values, reflecting the amount of meltwater, in Godthåbsfjord, West Greenland. We pose the following research questions:

- 1. Does the mixing of seawater and meltwater in the fjord yield a linear relationship between salinity and $\delta^{18}O_w$?
- 2. Do seasonal $\delta^{18}O_c$ records accurately reflect the full seasonal $\delta^{18}O_w$ cycle, including $\delta^{18}O_w$ excursions that are coincident with glacier meltwater input?

2 Material and methods

2.1 Study area

The Godthåbsfjord is situated in the sub-Arctic SW Greenland (64° N, 51° W; Fig. 1). The fjord system is made up of a number of fjord branches. Tidal range varies from 1 to 5 m (Richter et al., 2011). The inner part of the main fjord is in contact with three tidal 12022

outlet glaciers. The distance from the mouth to the head of the fjord is 187 km. A general description of bathymetry and water masses in the fjord is provided by Mortensen et al. (2011).

2.2 Shell collection and water monitoring

In May 2010 and June 2011, 10 *M. edulis* specimens were collected in the low intertidal on rocky shores along a transect from the glacier to the mouth of Godthåbsfjord. They were all adults and varied between 55 and 81 mm in length (Fig. 1, Table 1). Soft tissue was removed and the rinsed shells were dried at 50 °C for 24 h.

At time intervals of 2 to 4 weeks, water samples were collected for δ^{18} O analyses at 1 m depth. Water temperature and salinity were measured using a Sea-Bird Electronics SBE19plus SEACAT Profiler CTD (conductivity, temperature and depth). The SBE19plus were calibrated by the manufacturer every 1–2 yr and uncertainties of the salinities after calibration were typically within the range 0.005–0.010. Temperature uncertainties were near to the initial accuracy of the instrument of 0.005 °C. At location GF3 monitoring started on 5 October 2005; at locations GF10 and GF5 measurements started on 9 January 2009 and 16 May 2009, respectively (Fig. 1). For δ^{18} O analysis, 2 ml water samples from each station were collected in gas-tight vials and analysed for δ^{18} O values on a Picarro Isotopic Water Analyzer, L2120-/ (Picarro, Sunnyvale, CA, USA). Water samples were introduced into the vaporization chamber using an attached PAL autosampler (Leap Technologies, Carrboro, NC, USA). Each sample was analysed three times (three consecutive replicate injections; σ = 0.005–0.007 ‰) alongside a set of three laboratory reference materials, which had previously been calibrated to the VS-MOW scale (Coplen, 1994).

2.3 Genetic identification

In the North Atlantic two species of *Mytilus* can be found: *M. edulis* and *M. trossulus* (Varvio et al., 1988; McDonald et al., 1991), sometimes occurring together and

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interbreeding (Riginos and Cunningham, 2005). Since these species cannot be distinguished solely on morphological grounds, DNA fingerprinting was performed using four PCR-based nuclear markers (two RFLP markers) to determine the species of the shells collected. These markers are diagnostic for *M. edulis*, *M. trossulus*, and *M. galloprovincialis*. Prior to DNA extraction, shells were washed in sterile deionised water and dried at 100 °C in an incubator for 4 h (Doherty et al., 2007). DNA was extracted using the E.Z.N.A. kit (Omega Biotek, Norcross, GA, USA) following the manufacturer's protocol except for increased digestion time from 5 to 30 h (Doherty et al., 2007). The protocol for the two RFLP markers, Mal-1 treated with restriction enzyme *Spel* and ITS followed by restriction with *Hhal*, is outlined in Rawson et al. (2001) and Heath et al. (1995), respectively. The applications of Glu-5 and Me 15/16 markers are outlined in Rawson et al. (1996a) and Inoue et al. (1995), respectively (Table 2). For three of the PCR-based markers products were visualized on 2 % agarose gels, while Me15/16 was

analysed using an automated sequencer (ABI 3130 Genetic Analyser; Applied Biosys-

tems, Foster City, CA, USA) due to relatively small differences in allele sizes (Inoue

et al., 1995; Kijewski et al., 2009). For all four markers it was consistently confirmed,

2.4 Shell sampling and $\delta^{18}O_c$ analyses

that all 10 samples belong to *M. edulis*.

One valve of each shell was embedded in epoxy resin and a slab of ${\sim}2\,\text{mm}$ thickness was cut along the longest growth axis. Powder samples for $\delta^{18}O_c$ analysis were drilled from the calcite outer layer, parallel to the internal growth lines, using a New Wave Micromill.. Drill bit diameter was $80\,\mu\text{m}$; sampling resolution varied between 250 and $1000\,\mu\text{m}$, and drilling depth was ${\sim}\,500\,\mu\text{m}$.

Samples were measured via a Finnigan MAT Delta Plus XL mass spectrometer in continuous flow mode connected to a GasBench with a CombiPAL autosampler at Iowa State University (Department of Geological and Atmospheric Sciences). Reference standards (NBS-18, NBS-19, LSVEC) were used for isotopic corrections, and to assign the data to the appropriate isotopic scale. At least one reference standard was

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2.5 Calculation of predicted $\delta^{18}O_c$ values

Many bivalve species precipitate their shells in oxygen isotopic equilibrium with the ambient water (Hickson et al., 1999; Freitas et al., 2012; Chauvaud et al., 2005), following the equation for inorganic calcite (Kim and O'Neil, 1997):

$$1000 \ln \alpha_{\text{(calcite-water)}} = 18.03 \left(10^3 T^{-1} \right) - 32.42 \tag{1}$$

For *M. edulis*, a species-specific equation has been established, which is not significantly different from the above equilibrium equation (Wanamaker et al., 2007):

1000 ln
$$\alpha_{\text{(calcite-water)}} = 18.02 \left(10^3 T^{-1}\right) - 31.84$$
 (2)

In both equations T is the temperature in K and α is the isotope fractionation factor:

$$\alpha_{c-w} = \frac{\left(1000 + \delta^{18}O_c(VSMOW)\right)}{\left(1000 + \delta^{18}O_w(VSMOW)\right)}$$
(3)

For calculation of predicted $\delta^{18}O_c$ ($\delta^{18}O_{pred}$) values we use the species specific Eq. (2).

2.6 Alignment of $\delta^{18}O_{pred}$ and $\delta^{18}O_{c}$ values

In order to align measured $\delta^{18} O_c$ values with $\delta^{18} O_{pred}$ values, seasonal shell $\delta^{18} O_c$ records were separated into calendar years, allowing for a growth cessation at the peak $\delta^{18} O_c$ value as well as at the summer low $\delta^{18} O_c$ value (Versteegh et al., 2009; Goodwin et al., 2003; Goewert et al., 2007). Peaks and troughs of the $\delta^{18} O_{pred}$ and

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 δ^{18} O_c records were first aligned, and subsequently the points in between, using point-by-point time-axis shifting of δ^{18} O_c values towards δ^{18} O_{pred} values (Freitas et al., 2006; Goewert et al., 2007; Versteegh et al., 2010a).

3 Results

3.1 Water data

Water temperature varied between minima of around $-1\,^{\circ}\text{C}$ and maxima of 6 to $9\,^{\circ}\text{C}$ in all three locations. Salinity and $\delta^{18}\text{O}_{\text{W}}$ values are close to those of full marine conditions (33.5 and $-0.7\,\%$, respectively) during the first half of the year (January–June), and show sharp excursions towards much lower values during the following months. Salinity minimum values vary between \sim 19 at GF3 and GF5, down to 4.6 at GF10. Minimum $\delta^{18}\text{O}_{\text{W}}$ values show a similar behaviour with -9.1 and $-9.8\,\%$, for GF3 and GF5 respectively, and a very low $-18.6\,\%$ at GF10 (Fig. 2a–c).

3.2 Measured $\delta^{18}O_c$ values in shells

Microsampling of the 2 to 3 last growth increments, counted from the ventral margin, yielded between 14 and 40 samples per shell. Bulk shell composition is shown as the range of data in a box whisker diagram (Fig. 3). Shell $\delta^{18} \rm O_c$ values vary between 3.7 and -8.0% (VPDB). In proximity of the glacier, seasonal $\delta^{18} \rm O_c$ minima are $\sim 9.0\%$ lower than nearer the coast (-8.0% in Ice Fjord north 3a vs. 1.0% in Godthåbsfjord Archipelago 1a); maximum $\delta^{18} \rm O_c$ values differ by only 2.9% (0.8% in Ice Fjord north 3a vs. 3.7% in Godthåbsfjord Archipelago 1a; Fig. 3).

Shell $\delta^{18}O_c$ compositions along the growth axis are plotted as a function of distance from the ventral margin. The ventral margin represents the shell material precipitated immediately before shell collection. The distance axis is therefore reversed. These $\delta^{18}O_c$ records show typical sinusoid patterns of seasonal growth, influenced by

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seasonally varying temperature and $\delta^{18} O_w$ values. Winters are represented by peaks in $\delta^{18} O_c$ values, because of low temperatures and low meltwater input. Summers are troughs in $\delta^{18} O_c$ values, because of higher temperatures and higher meltwater input (see also Discussion). Winter peaks are sharper than $\delta^{18} O_w$ summer troughs, and are therefore likely truncated by seasonal growth cessation (Fig. 4a–j) (Goodwin et al., 2003; Goewert et al., 2007).

Conspicuous dark lines (under reflected light) within the shells, correspond to a slowing down of growth prior to growth cessation, and roughly correspond to winter growth cessations in the $\delta^{18} \rm O_c$ records (Fig. 4a–j). The number of years counted by dark growth lines and the number of $\delta^{18} \rm O_c$ peaks are the same in all shells, except Ice Fjord north 3a, which has insufficient resolution to discern annual cycles, and Kapisillit 13a, which appears to have one extra growth cessation during the summer of 2008 (Fig. 4g,i). Lighter growth lines than the annual ones can be seen in several specimens (Godthåbsfjord Archipelago 1a and 1b, Ice Fjord south 4b, Ice Fjord north 3b, Kapisillit 13a; Fig. 4a, b, f, h and i). These lighter lines apparently correspond with troughs in the $\delta^{18} \rm O_c$ records, and are probably caused by an additional cessation of growth during maximum meltwater input (see Discussion). Using growth lines and $\delta^{18} \rm O_c$ values, calendar years can be assigned in all but one shell (Ice Fjord north 3a; Fig. 4g). This specimen is therefore excluded from subsequent analysis.

4 Discussion

4.1 Relationship $\delta^{18}O$ – salinity

Regression analysis yields a linear relationship between $\delta^{18} O_w$ and salinity, following:

$$\delta^{18}O_{w} = 0.631 \cdot S - 21.84 \tag{4}$$

where S is salinity ($R^2 = 0.9778$; p < 0.0005; n = 202). An ANOVA showed there is no significant difference in regression coefficient between locations (Fig. 5). From this 12027

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relationship it follows that glacier meltwater has a $\delta^{18}O_w$ value of -21.8% (VSMOW) and seawater has a salinity of ~ 33.5 and a $\delta^{18}O_w$ value of $\sim -0.7\%$ (VSMOW). From the linear mixing of freshwater and seawater, it follows that there is a direct and simple relationship between glacier meltwater amounts and salinity ($\delta^{18}O_w$) at any point in the fjord.

4.2 Equilibrium precipitation of calcite

Although it is known from experiments that *M. edulis* precipitates its shell in δ^{18} O equilibrium with the ambient water (Wanamaker et al., 2006, 2007), we aimed to confirm this for the specimens presented here in a field setting. A valid approach is to compare the δ^{18} O_c value of the ventral margin with δ^{18} O_{pred} values calculated from δ^{18} O_w and temperature on the date of shell collection (Versteegh et al., 2010a). Five shells were selected that were collected closest to the water monitoring locations. δ^{18} O_{pred} values were calculated using Eq. (2) and δ^{18} O_w values calculated from salinity (Eq. 5). δ^{18} O_{pred} and δ^{18} O_c values are presented in Table 3. There is a good correspondence between δ^{18} O_{pred} and δ^{18} O_c values. They differ only by 0.1 to 0.3%, with the exception of shell Ice Fjord north 3b, which differs by 0.7% from δ^{18} O_{pred} values. It is likely that this shell did not precipitate any calcite immediately before it was collected.

4.3 Predicted and measured shell $\delta^{18}O_c$

 $\delta^{18} O_{pred}$ values were calculated using Eq. (2) and $\delta^{18} O_{w}$ based on salinity (Eq. 4). The influence of $\delta^{18} O_{w}$ on $\delta^{18} O_{pred}$ is dominant over that of temperature, resulting in $\delta^{18} O_{pred}$ curves that are similar in shape to $\delta^{18} O_{w}$ curves (Fig. 2a–c).

Seasonal $\delta^{18} O_c$ records of the five shells selected above can now be compared with seasonal $\delta^{18} O_{pred}$ values. As the shell $\delta^{18} O_c$ peaks are sharper than the $\delta^{18} O_{pred}$ records, it is likely that shells cease growing during winter. Similarly, during several

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summer seasons, the shell $\delta^{18} O_c$ records appear "dampened" and do not record low $\delta^{18} O_w$ values (see further discussion below), suggesting and additional summer growth cessation. The $\delta^{18} O_{pred}$ and $\delta^{18} O_c$ records were aligned by first matching peaks and troughs, and subsequent point-by-point time-axis shifting (Freitas et al., 2006; Goewert et al., 2007; Versteegh et al., 2010a).

At the locations GF3 and GF5 $\delta^{18}O_{pred}$ and $\delta^{18}O_{c}$ correspond well, with the shells faithfully recording almost the entire range of $\delta^{18}O_{pred}$ values. In the shell Nipisat Sound 2 the meltwater peaks of 2007 and 2008 do not seem to be picked up entirely, probably due to time-averaging within one shell powder sample (Goodwin et al., 2003). The same is true for the very low $\delta^{18}O_{pred}$ values at GF5 and in the shell Akia 10a during 2010.

This difference of up to 1.9% can alternatively be caused by a summer growth cessation, occurring when ambient water becomes too fresh for the mussel to thrive (Qiu et al., 2002). This certainly seems to be the case in the three shells collected near GF10. None of them recorded the very low $\delta^{18}O_w$ during 2010. Many shells also show a faint dark line (slow growth prior to growth cessation) during periods of low δ^{18} O_c values (Fig. 4a-j). It is known that marine bivalves, including M. edulis, have a reduced size and growth rate in low-salinity conditions (Westerborn et al., 2002; Schöne et al., 2003), and that salinities lower than 9.6 are lethal to the mussels within 10 days (Almada-Villela, 1984; Qiu et al., 2002). In response to a sudden drop in salinity, M. edulis withdraw their mantle and siphons, and close their shells (Qiu et al., 2002). It is likely that the mussels in Godthåbsfjord show this behaviour when exposed to very low salinities and as such cease growing and fail to record large meltwater pulses. δ^{18} O_c values suggest that the threshold salinity value for shell growth is at \sim 19. However, the abrupt decrease in salinity/ $\delta^{18}O_w$ values at the beginning of the melt season, combined with the limitations given by the resolution of data, make it difficult to establish a precise threshold for growth.

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Observations on salinity and $\delta^{18}O_w$ show that there is linear mixing of seawater and meltwater in Godthåbsfjord, implying that the meltwater contributions and $\delta^{18}O_w$ values follow a simple and predictable relationship at any location in the fjord. This indicates that glacier meltwater is the absolutely dominant source of freshwater in the fjord system.

Our results corroborate previous findings, that *M. edulis* precipitates shell calcite in oxygen isotopic equilibrium with the ambient water, not only under controlled laboratory conditions (Wanamaker et al., 2006, 2007), but also under natural conditions. Oscillating $\delta^{18} O_w$ values in Godthåbsfjord are faithfully recorded, at least at salinities $\sim>$ 19, below which shell growth apparently ceases.

Comparison of $\delta^{18}O_c$ values and growth lines, visible in shell cross-section, show that conspicuous dark lines are winter growth cessations, whereas growth cessations caused by low salinities are visible as a thinner and lighter growth lines within annual bands.

We conclude that this species can be suitable for reconstructing past meltwater amounts in ice sheet influenced fjords, and may offer an opportunity to investigate GrIS melting during previous Holocene warm periods. Care has to be taken, however, that individuals are used that lived not too close to a glacier, but rather in the centre or mouth of a fjord, so the full amplitude of local $\delta^{18}O_w$ variations is captured.

Future research will focus on expanding the geographical and temporal range of these shell δ^{18} O_c records, by sampling modern mussels from other fjords in Greenland along a south-north gradient. In addition shell will be sampled from raised shorelines (6000–8000 BP) and kitchen middens from prehistoric settlements in Greenland.

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Table 1. Specifications of shell samples.

Sample ID	Location	Collection date	Shell length (mm)
Godthåbsfjord Archipelago 1a	64° 02.003′ N 51° 45.592′ W	14/05/2010	71
Godthåbsfjord Archipelago 1b	64° 02.003′ N 51° 45.592′ W	14/05/2010	68
Nipisat Sound 2	64° 11.088′ N 51° 55.127′ W	14/05/2010	68
Ice Fjord north 3a	64° 38.679′ N 51° 01.114′ W	01/06/2011	53
Ice Fjord north 3b	64° 38.679′ N 51° 01.114′ W	01/06/2011	61
Ice Fjord south 4a	64° 38.354′ N 50° 47.766′ W	01/06/2011	77
Ice Fjord south 4b	64° 38.354′ N 50° 47.766′ W	01/06/2011	81
Akia 10a	64° 15.812′ N 51° 43.908′ W	02/06/2011	73
Kapisillit 13a	64° 26.648′ N 50° 13.397′ W	04/06/2011	56
Kapisillit 13b	64° 26.648′ N 50° 13.397′ W	04/06/2011	55

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Table 2. PCR-based nuclear markers for Mytilus.

Marker	Enzyme	Fragment sizes (bp)			References
		M. edulis	M. trossulus	M. gallopro- vincialis	
Mal-1	Spel	~ 650	~ 425/350/275		Rawson et al. (1996b, 2001)
ITS	Hhal	200	200/450	200	Heath et al. (1995)
Glu-5'	_	350/380	240	300/500	Rawson et al. (1996a)
Me 15/16	-	180	168	126	Inoue et al. (1995), Kijewski et al. (2009)

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Table 3. Comparison of ventral margin $\delta^{18} {\rm O_c}$ and $\delta^{18} {\rm O_{pred}}$ values.

Sample ID	Collection date	Station	δ^{18} O _{pred} (% VPDB)	Ventral margin $\delta^{18}O_c$ (‰ VPDB)
Nipisat Sound 2	14/05/2010	GF3	2.50	2.82
Akia 10a	02/06/2011	GF5	1.85	1.73
Ice Fjord north 3b	01/06/2011	GF10	0.67	1.39
Ice Fjord south 4a	01/06/2011	GF10	0.67	0.73
Ice Fjord south 4b	01/06/2011	GF10	0.67	0.49



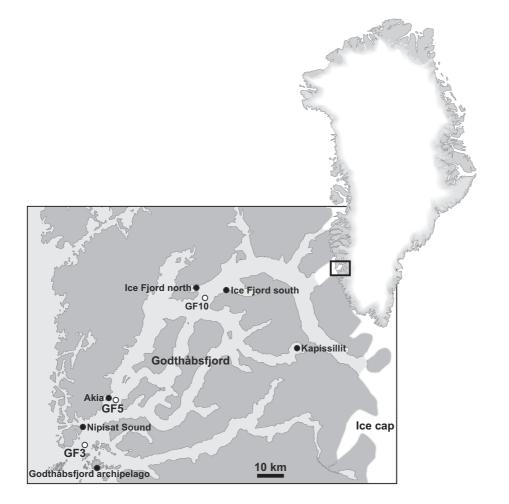


Fig. 1. Map of Godthåbsfjord with locations of shell collections (black circles) and water measurements (open circles).

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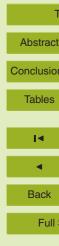
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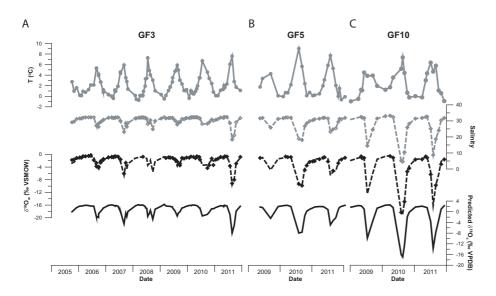


Fig. 2. (A-C) Environmental data at water monitoring locations. Solid grey circles and lines are temperature; open grey diamonds and dashed lines are salinity. Black diamonds are $\delta^{18}O_w$ measurements; dashed black lines show $\delta^{18}O_w$ values calculated from the linear relationship between salinity and $\delta^{18}O_w$ (Eq. 4). Solid black lines indicate $\delta^{18}O_{pred}$ values based on temperature and $\delta^{18}O_w$ calculated according to Eq. (2).

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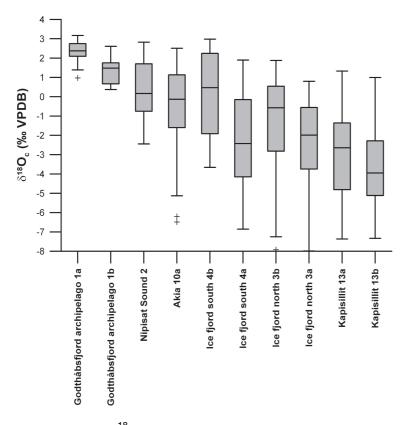


Fig. 3. Box-whisker diagram of δ^{18} O values of all shells. Grey boxes are 50 % of data, whiskers 25% of data each, outliers are indicated with + symbols. At the left side of the graph are the shells that were collected closest to the open ocean and show least influence of freshwater in their δ^{18} O_c values. At the right side are the shells collected closest to the glacier, with most profound freshwater influence on their $\delta^{18}O_c$ values.

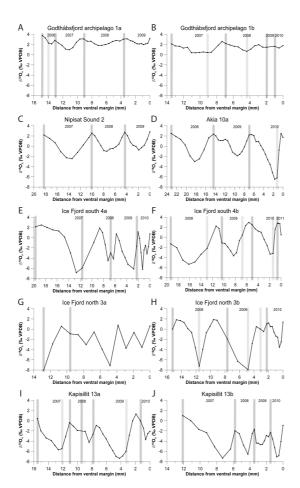


Fig. 4. (A–J) Seasonal δ^{18} O_c graphs of shells. In dark grey distinct dark growth lines (expected to be annual growth cessations) are indicated, in light grey less profound dark lines observed in the shell.

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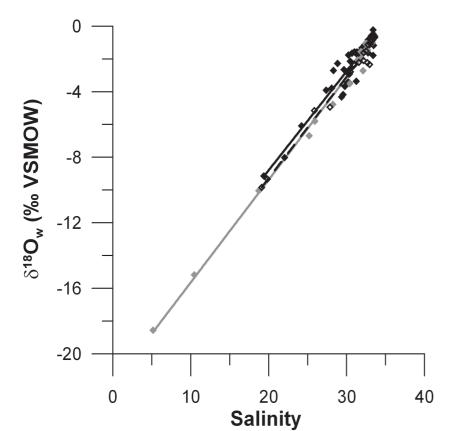


Fig. 5. Scatter plot showing the relationship between $\delta^{18}O_w$ and salinity for the three sampling locations: $\delta^{18}O_w = 0.631 \cdot S - 21.84$ ($R^2 = 0.9778$; p < 0.0005; n = 202). Black diamonds and solid line are GF3, open diamonds and black dashed line are GF5 and grey diamonds and solid line are GF10.

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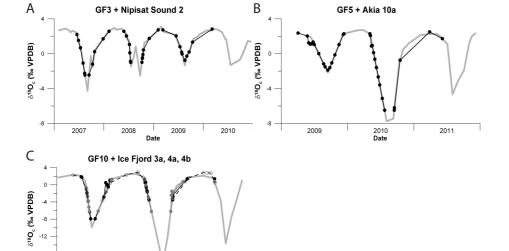


Fig. 6. (A–C) Comparison of $\delta^{18} O_{pred}$ and $\delta^{18} O_{c}$ values for three different sites. In addition to a winter growth cessation that is visible in most shells, a summer growth cessation appears to occur when $\delta^{18} O_{w}$ values (i.e. salinity) get too low.

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