

Carbon source and trophic structure along a depth gradient in Isfjorden, Svalbard

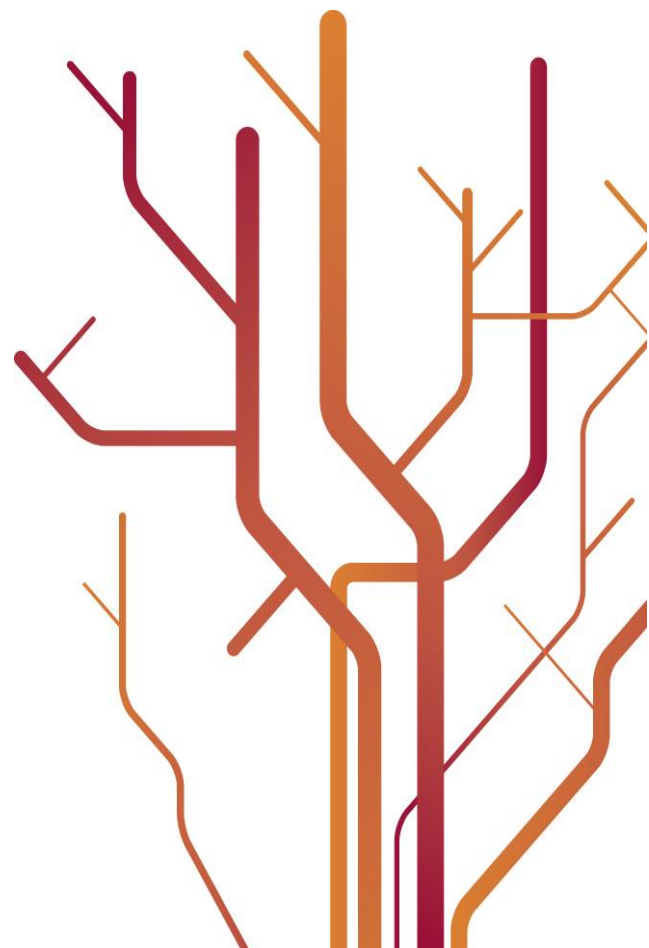


Therese Smelror Løkken

Master's thesis in Biology

BIO-3950 (60 ECT)

August 2013



FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

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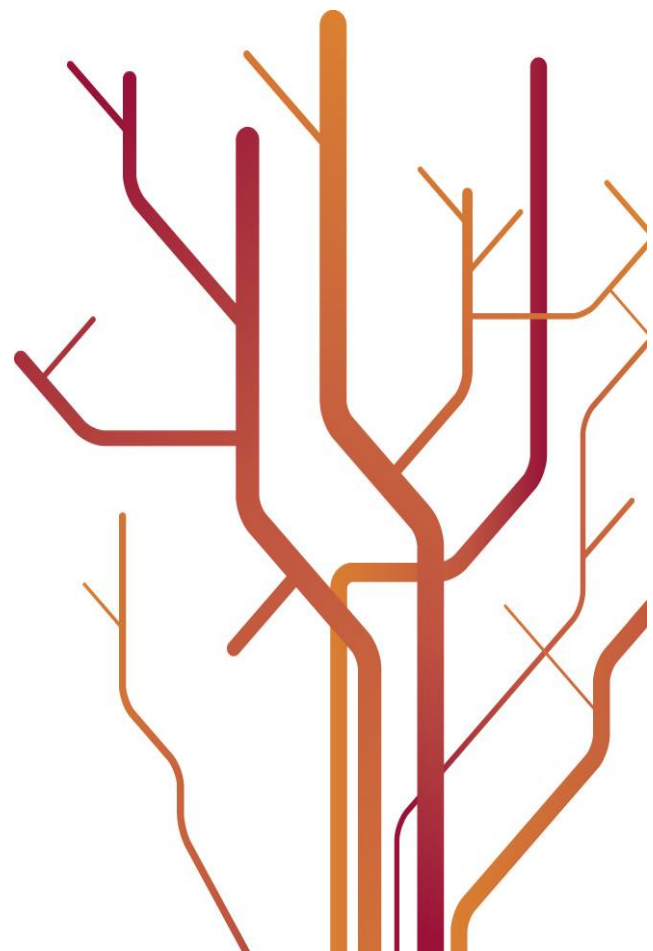


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Abstract

Stable isotope analysis has been used to examine marine food webs since the 1980s and has become a valuable tool for studying carbon sources and trophic structures in benthic food chains in the Arctic. Prior to the present study, no one has used stable isotope analysis to test for a difference in the main carbon source or trophic structure along a depth gradient in the Arctic. Carbon sources (pelagic POM, sediment POM and macroalgae) and consumers (benthic filter feeders, deposit feeders, grazers, scavengers and predators and grazing zooplankton) were collected from Isfjorden, Svalbard, at depths ranging from 0 – 400 m. There was a big overlap in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for most of the carbon sources sampled, making it difficult to identify one single food source to any of the depths. Most benthic primary consumers (filter-feeding bivalves and grazers) were enriched in $\delta^{13}\text{C}$ relative to pelagic POM, sediment POM and the brown algae *Chorda filum* at all depths. Most primary consumers fell in between the fractionation rates of the two groups of brown algae (filter-feeding bivalves), or were enriched in $\delta^{13}\text{C}$ relative to the isotopically lightest carbon source sampled in this study (grazers). This suggests that a) a mixture of multiple carbon sources constitute the diets of most primary consumers, and possibly the entire benthic food web, and b) the benthic primary consumers utilize one or more carbon sources not sampled in this study. The $\delta^{15}\text{N}$ among primary consumers varied somewhat between stations, but this was not reflected higher up in the food chain. The biggest difference in $\delta^{15}\text{N}$ was found for the sea urchin *Strongylocentrotus* sp., which is likely caused by different feeding strategies among specimens inhabiting shallow and deep waters.

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1. Introduction

1.1 Background

Arctic marine ecosystems are influenced by a multitude of biotic (inter- and intraspecific competition, primary production and food availability) and abiotic (temperature, salinity, light, radiation, pollution) factors (Wassmann et al. 2006). Food-web structures, including primary food source, trophic pathways and food web members' relative trophic position can provide information which may help predict the relative stability of the system when changes to biotic or abiotic factors are introduced to the system (Renaud et al. 2011). Numerous studies of Arctic food web structures focusing on benthic organisms has been conducted (Iken et al. 2001, McMahon et al. 2006, Beuchel & Gulliksen 2008, Kedra et al. 2010, Renaud et al. 2011, Kedra et al. 2012), partially because marine benthic macrofauna communities are considered suitable for monitoring environmental long-term changes in an ecosystem. Benthic macrofaunal organisms are relatively immobile and are therefore representative for the area from which they are sampled. Additionally, many benthic taxa are relatively long-lived, with life span of 2 to 5 or longer, making surveys of the same organisms or communities spanning over multiple years possible (Beuchel & Gulliksen 2008, Kedra et al. 2010).

Stable isotope analysis has been used to examine marine food webs since the 1980s (Peterson & Fry 1987, Fry 1988) and has become a valuable tool in ecological studies of the Arctic, where continuous sampling throughout the year is logistically challenging due to ice conditions and the light regime of the polar night (Dunton et al. 1989, Lovvorn et al. 2005, Tamelander et al. 2006a, Renaud et al. 2011). This method holds an advantage over more traditional food web study techniques (stomach content analysis, feeding experiments and *in situ* observations), as it reflects assimilated rather than potential carbon sources. Where the more traditional techniques provide a *snapshot* of an ecosystem, a stable isotope analysis may provide a longer integrated history of feeding strategies. As an example, this method has been important in investigating to which degree benthic consumers are coupled to pelagic primary production (Hobson et al. 1995, Iken et al. 2001, Tamelander et al. 2006a). Tissues of consumers tightly linked to pelagic primary production are generally less enriched in ^{13}C compared to tissues of consumers linked to detrital-based food webs. This has been shown in the Northeast Water Polynya off northeastern Greenland (Hobson et al. 1995). Here, similar $\delta^{13}\text{C}$ values between pelagic POM-based feeders (*Calanus* spp. and *Themisto* spp.) and benthic filter feeders (*Similipecten groenlandicus* and *Heliometra* sp.) were found, showing that a major component of the benthic community was supported by freshly-deposited

material from pelagic primary production. Moreover, Kedra et al. (2012) reports similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in consumers in March and August, showing that the strong seasonality of the primary production in the Arctic does not influence the structure of the shallow benthic food web in Kongsfjorden, Svalbard. This adds to the study of Renaud et al. (2011) in the same fjord, where no significant differences in carbon source and trophic structure were found between the different locations or between July and October.

Where two or several different sources of primary production are present in a system, stable isotope analysis may contribute information on the relative importance of each source (Post 2002, Tamelander et al. 2006a). Gilles et al. (2012a) found well-separated $\delta^{13}\text{C}$ signatures in several different carbon sources and consumers in East Antarctica, enabling the identification of three main carbon pathways; pelagic POM, macroalgae/epiphytic/benthic diatoms and sediment POM/diatoms.

Potential organic sources in Arctic marine food chains are typically derived from phytoplankton (pelagic POM), pelagic carbon sinking to the bottom (sediment POM), benthic macroalgae, ice algae/ice POM (Hobson et al. 1995, Tamelander et al. 2006b) and terrestrial carbon via freshwater discharges or coastal erosion (Dunton et al. 2006, Feder et al. 2010, Iken et al. 2010). At the outer parts of Isfjorden, the ice cover is normally rare (Nilsen et al. 2008a), which should exclude sea ice POM as an important food source for the food web. Terrestrial carbon can also likely be disregarded as an important food source, as production on land is low. Although the marine benthic algal vegetation of Spitsbergen is generally poorly studied, Fredriksen & Kile (2012) found a total number of 83 algal taxa in the other parts of Isfjorden, and a particularly dense kelp community (*Alaria esculenta*, *Laminaria digitata* and *Saccharina latissima*) on the south side of the fjord. Macroalgal distribution, however, is limited by light penetration in the water column, and usually does not grow below 50 m (Nielsen et al. 2002). Although Nerot et al. (2012) reports a decreasing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ pattern with increasing depth in four filter feeding mollusc species, no study so far has attempted to test for a difference in the main carbon source along a depth gradient, at least in the Arctic.

Although several Arctic benthic species are known to switch between feeding types and therefore have the potential to move between trophic levels in space and time (Kedra et al. 2012), Renaud et al. (2011) found little spatial difference in the food-web structure of the soft-sediment benthos in Kongsfjorden, and Kedra et al. (2012) found little variability between seasons in the same fjord. Kongsfjorden is located north of Isfjorden, and is also an open fjord (without a sill at the mouth of the fjord). Isfjorden is therefore influenced by similar oceanographic processes as Kongsfjorden. Based on the findings of Renaud et al. (

2011) and Kedra et al. (2012) I therefore suggest that there is little spatial (and depth) difference in the food-web structure of Isfjorden.

Hypotheses

H₀₁: There is no difference in carbon source to the benthic food webs of Isfjorden regardless of water depth.

H₀₂: There is no difference in trophic structure of the benthic food webs of Isfjorden regardless of water depth.

2. Material and Methods

2.1. Study area

Isfjorden is the largest fjord in the Svalbard archipelago. It is 170 km long, 24 km at its widest and up to 425 m deep (Figure 1). It is located on the west side of the Spitsbergen island and oriented in a South-West ($78^{\circ}7'N$) – North-East ($78^{\circ}27'N$) direction. The fjord is linked directly to the shelf and slope area along West Spitsbergen as it has no distinctly shallow sill at its mouth, permitting inflow of Atlantic Water from the West Spitsbergen Current (Nilsen et al. 2008a, Forwick & Vorren 2009). However, the inflow of Atlantic Water varies among years, with along-shore wind components being an important factor controlling this (Berge et al. 2005). The hydrography of Isfjorden is also characterized by water masses of local origin, with surface waters from melting glaciers and river runoff, local waters (increased salinity due to sea-ice formation) and winter-cooled waters originating in the fjord (Nilsen et al. 2008a, Forwick & Vorren 2009).

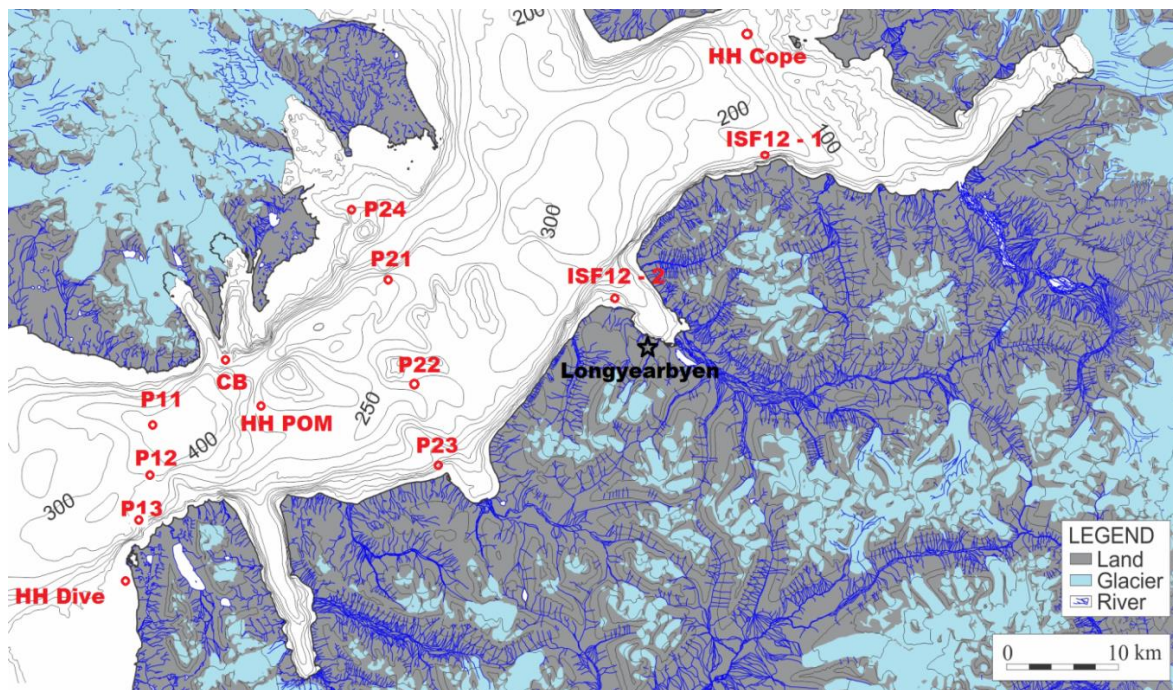


Figure 1. Map of Isfjorden, with the “RV Johan Hjort stations” P11 – P24, the “RV Viking Explorer station ISF12-1 and ISF12-2, the “RV Helmer Hansen” stations HH Dive, HH Cope and CB. The station CB shows where the buoy was deployed in June 2012. Map courtesy of Matthias Forwick, UiT.

2.2. Sample collection

All samples were collected during the summer and autumn of 2012 (Figure 1, Table 1) during cruises with the ships RV “Viking Explorer” (August 4 - 7th), RV “Johan Hjort” (August 17 – 23rd) and RV “Helmer Hansen” (September 22nd – October 5th), or hand-picked from the shore (August 4 – 6th and October 18th). Pelagic particulate organic matter (Pelagic POM) from 420 – 5 m depth was sampled using a rosette water sampler and filtered on Munktell MG/F filters (0.7 µm pore size, 250 mL sea water pr. sample) between August 17-23rd (Stations P11 – P24) and on Whatman GF/F filters (0.7 µm pore size, 800 – 1500 mL sea water pr. sample) on September 22nd (Station HH POM). The filters were first examined under a stereo microscope to remove copepods and other conspicuous zooplankton. The samples were then wrapped in aluminum foil and frozen until analysis. Macroalgae were collected by hand, using a triangular dredge or an algal rake August 4 – 7th (Station ISF12-1 and ISF-2) and October 18th (Station ISF12-2). One additional macroalgal sample was collected from a untethered buoy deployed at Sagaskjæret in June (Station CB) and retrieved September 22nd. Epiphytes were scraped off the algae and the samples were frozen in aluminum foil until analysis. Particulate organic matter from the sediment (Sediment POM) was collected from the top 1-2 cm layer of van Veen grab samples during August 17 – 23rd and frozen until analysis. Benthos, fish and zooplankton were collected by triangular dredge, a 0.1 m² van Veen grab, a 2 m beam trawl (4 mm mesh size), a Campelen 1800 bottom trawl towed on double warps with a 22 mm cod-end mesh size, a pelagic Harstad trawl (8 mm mesh size) August 17-23rd (stations P11 – P24), hand-picked from the Sagaskjæret bouy (station CB), and collected by SCUBA divers (October 4th, station HH Dive). The animals were sorted, identified and frozen whole (or parts) until analysis. Zooplankton samples (*Calanus* spp. and Copepoda) were collected with a WP2 net (0.25 m² opening, mesh size 180 µm) August 17-23rd and October 5th (Station HH Cope).

The samples were collected as a part of the Fram Center project “Arctic and Boreal Benthic Process and Function” (ArcProFun), where two Norwegian fjords systems Isfjorden-Billefjorden and Porsangerfjorden have been investigated. The overall goal of the project was to achieve increased knowledge on Arctic and Boreal fjord systems and establish a monitoring program for studying the effects of climate change on bottom communities in Arctic and Boreal fjords.

Table 1. Sampling sites and collection information. The longitude and latitude for the CB station refers to when and where the buoy was deployed. The buoy was retrieved August 22nd near the HH POM station.

Station name	Substrate	Latitude (°N)	Longitude (°E)	Date	Sampling gear	Depth (m)
ISF12-1	Rocky bottom	78° 33.7'	016° 32.2'	4 August	Δ-Dredge	14 - 10
ISF12-2	Rocky bottom	78° 25.3'	015° 40.4'	5 August	Algae rake	2 - 1
				6 August	Hand-picked	Littoral
				18 October	Hand-picked	Littoral
P11	Soft bottom	78° 11.0'	013° 42.3'	17 August	Beam trawl	180
					CTD w/ Rosette	180 - 5
					Grab	182
					WP2	182 - 5
P12	Soft bottom	78° 08.7'	013° 46.5'	18 August	Beam trawl	414
					Campelen trawl	410
					CTD w/ Rosette	422 - 5
					Grab	410
					Harstad trawl	60 - 0
					WP2	422 - 5
P13	Soft bottom	78° 06.8'	013° 47.4'	17 August	Beam trawl	198
					CTD w/ Rosette	226 - 5
					Grab	271
					WP2	270 - 5
P21	Soft bottom	78° 16.0'	014° 33.3'	20 August	Beam trawl	273
					Campelen trawl	272
					CTD w/ Rosette	220 - 5
					Grab	272
					Harstad trawl	60 - 0
					WP2	270 - 5
P22	Soft bottom	78° 11.1'	014° 43.2'	17 August	Beam trawl	214
					Campelen trawl	209
					CTD w/ Rosette	220 - 5
					Grab	226
					Harstad trawl	60 - 0
					WP2	226 - 5
P23	Soft bottom	78° 08.9'	014° 46.8'	17 August	Beam trawl	198
					CTD w/ Rosette	226 - 5
					Grab	271
					WP2	270 - 5
P24	Soft bottom	78° 17.5'	014° 30.7'	18 August	Beam trawl	120
					CTD w/ Rosette	148 - 5
					Grab	152
					WP2	100 - 5
CB	Buoy	78° 21.3'	013° 09.3'	June	Buoy	-
HH Dive	Rocky bottom	78° 05.9'	013° 48.1'	4 October	Scuba diving	0 - 25
HH Cope	Pelagic	78° 48.2'	016° 10.6'	5 October	WP2	70 - 100
HH POM	Pelagic	78° 12.5'	013° 57.1'	22 September	CTD w/ Rosette	15

2.3. Stable isotope analysis and sample treatment

Stabile isotope

Isotopic compositions in the tissues of animals are closely related to dietary isotopic distribution (Peterson and Fry 1987, Fry 1988). Naturally occurring stable isotopes of carbon and nitrogen show a stepwise enrichment between prey and consumer tissue during assimilation process. Selective metabolic fractionation leads to a preferential loss of lighter isotopes during excretion (nitrogen) and respiration (carbon). This stepwise isotopic enrichment in consumer tissue compared to prey tissue allows the establishment of relative trophic position of the food web members. The established mean enrichment steps for ^{13}C and ^{15}N between subsequent trophic levels in marine systems is ~ 1 ‰ and 3 - 4 ‰, respectively (Iken et al. 2001, Sørense et al. 2006a, Renaud et al. 2011). However, the fractionation rate for $\delta^{13}\text{C}$ between carbon source and primary consumer is shown to be significantly larger than the ~ 1 ‰ found higher up in the food chain (Hobson et al. 1995, Nadon & Himmelman 2006). A 4 ‰ enrichment factor for $\delta^{13}\text{C}$ between the two first levels of the food web is therefore suggested by Nadon & Himmelman (2006). Nitrogen isotopic ratio ($\delta^{15}\text{N}$) is generally used to establish the trophic position for the organism because of the 3 - 4 ‰ enrichment, whereas the carbon isotopic ratio ($\delta^{13}\text{C}$), which remains relatively stable amongst trophic levels, is used to link carbon sources at the bottom of the food web to consumers. Stable isotope values are reported in parts per thousand differences from a standard (δ values):

$$\delta X = [(R_{\text{Sample}}/R_{\text{Standard}}) - 1] \times 1000 \quad (\text{Eq. 1})$$

where X equals ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$. The δ -value is a measure of the amount of heavy and light isotopes in the sample. An increase in the δ -value means an increase in the heavy isotope component (^{13}C or ^{15}N) and a corresponding decrease in the light isotope component (^{12}C or ^{14}N). Standard references are carbon from the PeeDee Belemnite limestone and nitrogen gas from atmospheric air (Peterson and Fry 1987).

Analysis

POM filters were freeze-dried at -60°C for 24 h. Sediment POM, animals and macroalgae were dried at 60°C for 48 – 120 h. Muscle tissue was analyzed for fish, mollusks (except for *Sepiolo* sp. where whole tentacles were used) and large crustaceans (e.g. decapods). Most of the fish samples were dissected in the field, and the remaining animals were dissected in the lab before drying. Where pure muscle tissue was hard to obtain (*Strongylocentrotus* sp.),

gonads were used. For ophiuroids and asteroids, one or several whole arms were analyzed. One or several whole organisms were used for small crustaceans (e.g. cumaceans, amphipods, isopods) and polychetes. For sponges, tunicates and cnidarians, whole organisms or a piece of $\sim 1\text{cm}^2$ was used.

Carbonates are isotopically enriched in ^{13}C relative to other organic matter and are not representative of assimilated carbon from potential food sources. Therefore, carbonates were removed from all ophiuroid and asteroid specimens, and also from sediments by soaking the samples in 0.2 M H_3PO_4 for 4 hours at 4°C and then rinsing with distilled water. Because acidification of samples may lead to changes in stable nitrogen isotope values of the organic matter, the $\delta^{15}\text{N}$ values were obtained from non-acidified samples, whereas $\delta^{13}\text{C}$ data came from acidified echinoderm and sediment samples (Søreide et al. 2006b, Mateo et al. 2008). The stable carbon and nitrogen isotope composition of all samples were measured using a ThermoFinnigan Delta V Advantage isotope ratio mass spectrometer coupled to a Costech elemental analyzer via the ConFlo III combustion interface in the Environmental Geochemistry Laboratory, Department of Geology, Bates College, USA between January and July 2013. The internal standards (acetanilide, caffeine and fish muscle) were run every 8 to 10 samples. The reproducibility, as determined by the standard deviation of the internal standards, was $\pm 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Samples containing less than 0.9 μMole carbon or nitrogen were considered unreliable and therefore disregarded (section 3.1.2).

Lipid normalization

Lipid content varies among type of organisms and tissues in both space and time (Sweetling et al. 2006). Because lipids are depleted in ^{13}C relative to other major biochemical compounds (proteins and carbohydrates) the difference in lipid content in different organisms or tissues may lead to considerable bias in comparison of stable isotope values if not taken into account. However, lipid extraction prior to analysis may lead to the loss of non-lipid compounds that can alter the $\delta^{15}\text{N}$ value of a sample (Sweetling et al. 2006, Post et al. 2007). Therefore, lipid correction was performed after sample analysis using the lipid normalization equation (Equation 2) and the measured carbon-to-nitrogen ratio (C:N) for all samples with a C:N ratio higher than 3.5 (e.g. all animal tissue samples except for Rajidae in this study), as suggested by Post et al. (2007).

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \cdot \text{C:N} \quad (\text{Eq. 2})$$

Trophic level (TL)

Trophic levels (TLs) were calculated using the equation (Equation 3) suggested by Peterson and Fry (1987):

$$TL_{\text{consumer}} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}) / \Delta\delta^{15}\text{N} + TL_{\text{base}} \quad (\text{Eq. 3})$$

Where $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ of the animal samples, $\delta^{15}\text{N}_{\text{base}}$ is the $\delta^{15}\text{N}$ of the baseline organism, TL_{base} is the trophic level of the base line organism and $\Delta\delta^{15}\text{N}$ is the fractionation of $\delta^{15}\text{N}$. In this study, the average $\delta^{15}\text{N}$ of all Copepod samples (collected from stations P11 – P24) was used as a baseline (defined as trophic level 2), since it is assumed that samples primarily consist of *Calanus* spp. which graze on phytoplankton (Tamelander et al. 2006b, Nilsen et al. 2008b). The fractionation rate ($\Delta\delta^{15}\text{N}$) used was 3.4 ‰, as it is widely used in stable isotope analysis performed in the Arctic (Søreide et al. 2006a, Renaud et al. 2011, Kedra et al. 2012).

2.4. Statistical analysis

All statistical analyses (one-way ANOVA, Tukey's honest significance test and tests for correlation (Pearson's r)) were performed with SYSTAT 13. All figures, plots and tables were made in Microsoft Excel 2010 and SYSTAT 13. Simple calculations (Standard Deviations, averages, lipid corrections and trophic level calculations) were performed with Microsoft Excel2010.

3. Results

A table of all results ($\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm \text{SD}$) is presented in Appendix 1.

3.1. Carbon sources

A total of 10 macroalgal species or species complexes were collected, in addition to pelagic POM and sediment POM. The isotopic distributions of each sampled carbon source (maximum and minimum $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measured) are shown in Figure 2. The $\delta^{15}\text{N}$ isotopic distribution for POM August are *weighted average* values only (explained in section 3.1.2).

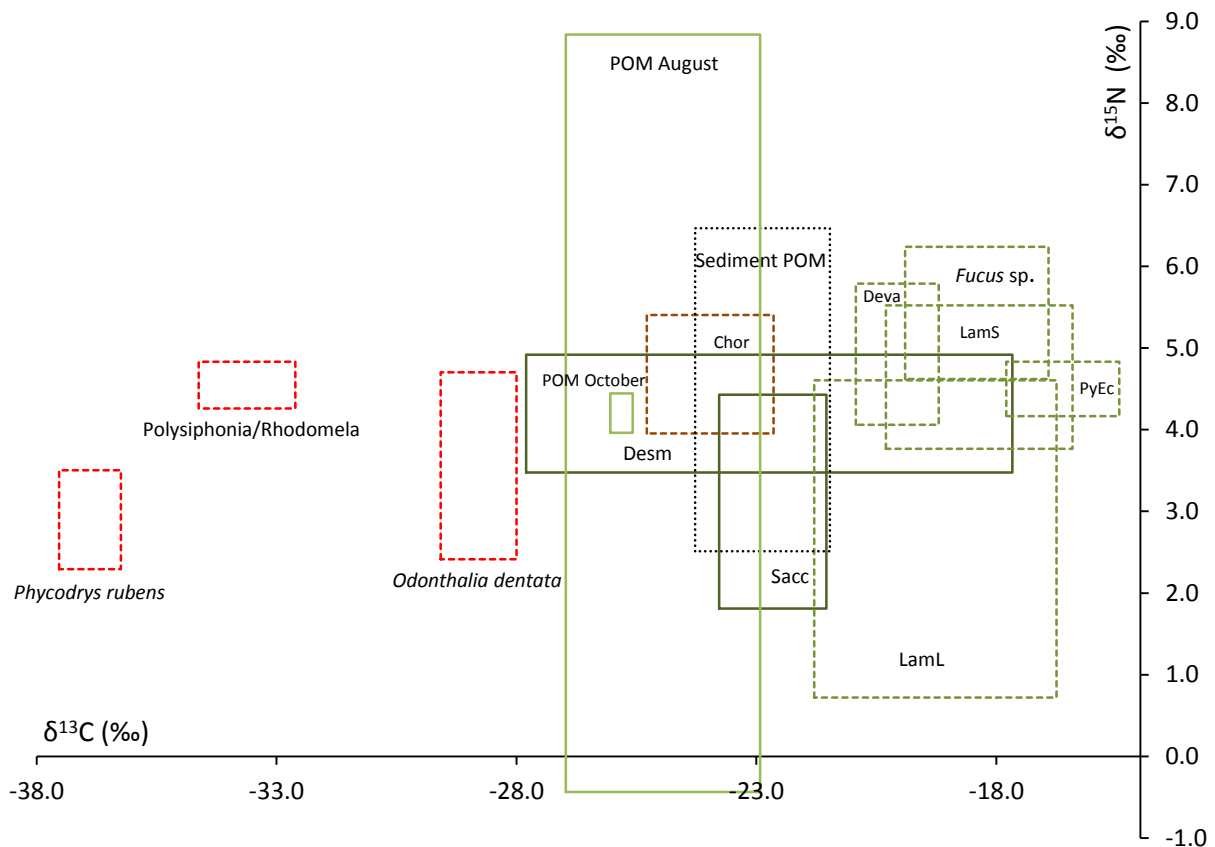


Figure 2. Isotopic distribution of all carbon sources. The boxes represent the full range of data from replicates of the respective carbon sources (maximum and minimum $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Abbreviations are as follows Chor: *Chorda filum*, Desm: *Desmarestia acuelata*, Deva: *Devaleraea ramentacea*, LamL: lamina of *Laminaria digitata*, LamS: stipe of *Laminaria digitata*, PyEc: *Pylaiella littoralis/Ectocarpus fasciculatus* and Sacc: *Saccharina latissima*.

3.1.1. Macroalgae

There was considerable variability in $\delta^{13}\text{C}$ among the different macroalgal taxa, ranging from -37.0 ‰ for the red alga *Phycodrys rubens* to -16.9 ‰ for the brown algal complex *Pylaiella littoralis/Ectocarpus fasciculatus*. The largest within-species range was found for the brown alga *Desmarestia aculeata* with $\delta^{13}\text{C}$ ranging from -27.8 ‰ and -17.7 ‰ (Figure 2). Results from the ANOVA showed a significant difference in the $\delta^{13}\text{C}$ values for the different macroalgae taxa ($F_{10,44} = 59.48$, $p < 0.01$). A Tukey's test (Tukey's honest significance test) based on all $\delta^{13}\text{C}$ values identified all three red algae (Rhodophyta) taxa as outliers from the dataset, but not as members of the same group (Figure 2). The same test divided the brown algae (Phaeophyceae) into three distinct groups. Group 1 consisted of only *Chorda filum*, Group 2 consisted of *Desmarestia aculeata* and *Saccharina latissima* and Group 3 consisted of the remaining species; *Devaleraea ramentacea*, *Fucus* sp., *Pylaiella littoralis/Ectocarpus fasciculatus* and both *Laminaria digitata* samples (Figure 2, Figure 5).

Two samples were collected from each *Laminaria digitata*; one from the blade and one from the lamina (Figure 2). The ANOVA showed no significant difference between the $\delta^{13}\text{C}$ for the samples from the lamina and the stipe ($F_{1,8} = 0.56$, $p < 0.5$) but a significant difference for $\delta^{15}\text{N}$ ($F_{1,8} = 6.74$, $p > 0.01$).

The $\delta^{15}\text{N}$ values varied less than $\delta^{13}\text{C}$, ranging from 2.2 ‰ for the *Laminaria digitata* lamina to 5.2 ‰ for the brown algae *Chorda filum*.

3.1.2. Pelagic POM

No significant difference in $\delta^{13}\text{C}$ was found among samples collected in August and samples collected in October or among stations in August ($F_{7,63} = 1.15$, $p = 0.34$). For the POM collected August, $\delta^{13}\text{C}$ increased with depth (Figure 3). Only one individual data point is available for the depths 300 m and 400 m (station P12), because this was the only station with deeper than 250 m. Because of variable nitrogen content in the POM samples collected in August, a *weighted average* of $\delta^{15}\text{N}$ was calculated for each station (method explained in Appendix 2). A plot of $\delta^{15}\text{N}$ in relation to depth was not made, as too few reliable $\delta^{15}\text{N}$ values ($\mu\text{mole N} < 0.9$) were measured.

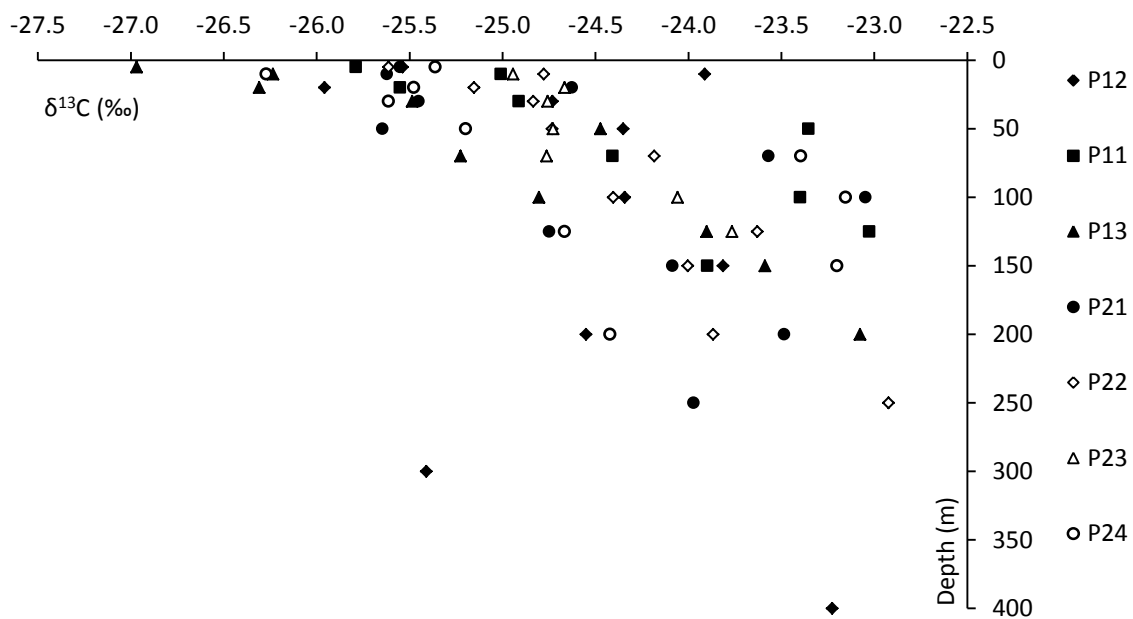


Figure 3. $\delta^{13}\text{C}$ (‰) at different depths for the stations P11 – P24. Values for depths below 250 m are only available for station P12.

3.1.3. Sediment POM

No correlation between depth and $\delta^{13}\text{C}$ (Figure 4a) or $\delta^{15}\text{N}$ (Figure 4b) was found for the sediment POM (Pearsons $R = 0.35$, $p > 0.4$ and $R = 0.41$, $p > 0.3$, respectively). Station P11 (depth 182 m) had both the most enriched value for $\delta^{13}\text{C}$ (-21.5‰) and the most depleted value for $\delta^{15}\text{N}$ (2.5 ‰). For the remaining stations, the $\delta^{13}\text{C}$ values were similar; ranging from -24.3 ‰ for station P22 (depth 226 m) and -23.6 ‰ for station P12 (depth 410 m). The $\delta^{15}\text{N}$ varied more for these stations ranging from 3.5 ‰ for station P24 (152 m) to 6.5 ‰ for Station P21 (271 m). No $\delta^{13}\text{C}$ is available for station P24 (152 m). No sediment was collected for the diving station (HH Dive), as the substrate was rocky bottom.

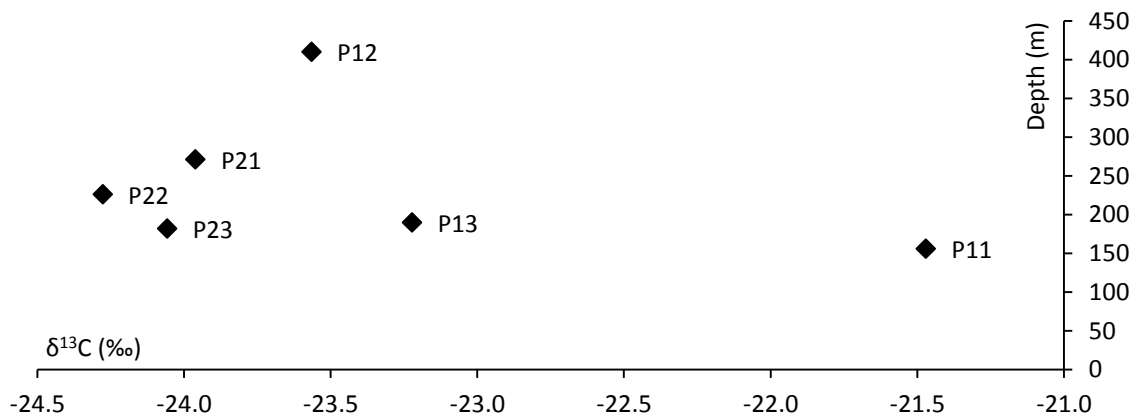


Figure 4a. $\delta^{13}\text{C}$ measured for sediment POM at different depths. The data labels name the stations. No $\delta^{13}\text{C}$ is available for station P12.

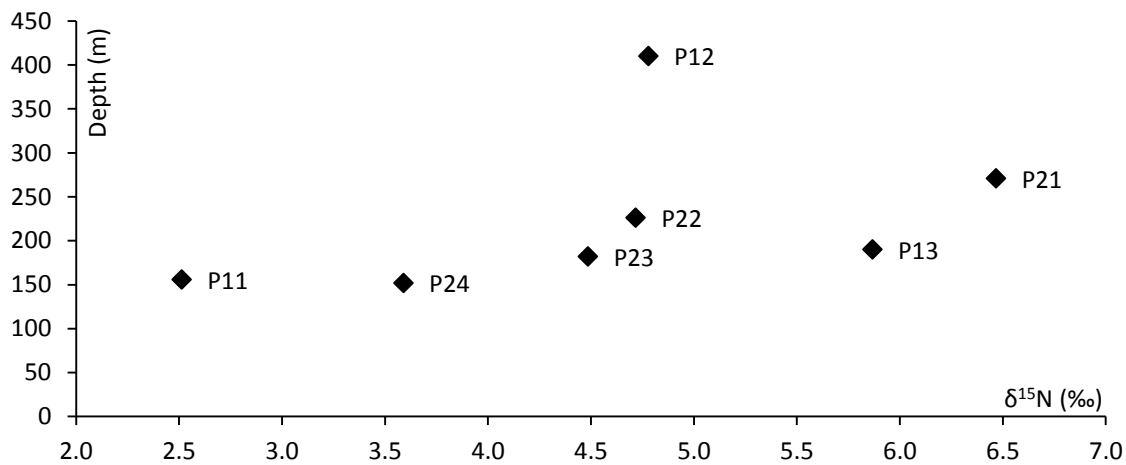


Figure 4b. $\delta^{15}\text{N}$ measured for sediment POM at different depths. The data labels name the stations.

3.1.4. Primary carbon source at the depth gradient

There was little difference to the primary carbon sources at different depths. Although the ANOVA found a significant difference in the $\delta^{13}\text{C}$ of the primary consumer (filter-feeding bivalves and *Strongylocentrorus* sp., $F_{6,67} = 2.4$, $p > 0.03$), the average $\delta^{13}\text{C}$ of the primary consumers did not vary more than about 1 ‰ among depths (ranging from -18.2 ‰ to -17.2 ‰, Figure 5), with the exception of the depth 190 – 200 m (average $\delta^{13}\text{C} = -15.8$ ‰). However, at this depth only three values were measured (one replicate of *Chlamys islandica* and two replicates of *Balanus* sp.). All three values at this station were enriched in $\delta^{13}\text{C}$ compared to the same species at the other depths.

Figure 6 shows the average of all carbon sources and their corresponding fractionation rates (dotted lines). The brown algae (*Chorda filum*, Phaeophyceae 2 and Phaeophyceae 3) are grouped according to the Tukey's test as explained above (section 3.1.1). The Rhodophyta are pooled together in this figure, although not identified as a group by the

Tukey's test. A fractionation rate of 4 ‰ for $\delta^{13}\text{C}$ for the first trophic level (between carbon source and primary consumer) as suggested by Nadon & Himmelmann (2006) and a fractionation rate of 1 ‰ between trophic level 2 and trophic level 3 has been used. The fractionation rate used for $\delta^{15}\text{N}$ was 3.4 ‰. Pelagic grazers (Copepoda and *Calanus* spp.) fell within the fractionation trajectories for pelagic POM both in August and October, although *Calanus* spp. was enriched in $\delta^{13}\text{C}$ by 4.8 ‰ relative to the pelagic POM collected in October. The $\delta^{13}\text{C}$ enrichment between Copepoda and pelagic POM collected in August was 1.4 ‰. All benthic primary consumers (with the exception of *Bathyarca glacialis* from the depth 260 – 270 m), were more enriched in $\delta^{13}\text{C}$ than Rhodophyta, pelagic POM, sediment POM and *Chorda filum*. They did, however, have signatures consistent with some contributions of the brown algal groups Phaeophyceae 2 and Phaeochycaea 3. Some of the benthic consumers (*Strongylocentrotus* spp. at the depths 180 – 182 m and 0 – 25 m, *Balanus* sp. at 190 – 200 m and *Chlamys islandica* at 190 – 200 m) was enriched in $\delta^{13}\text{C}$ relative to the isotopically lightest carbon source measured in this study (Phaeophyceae 3).

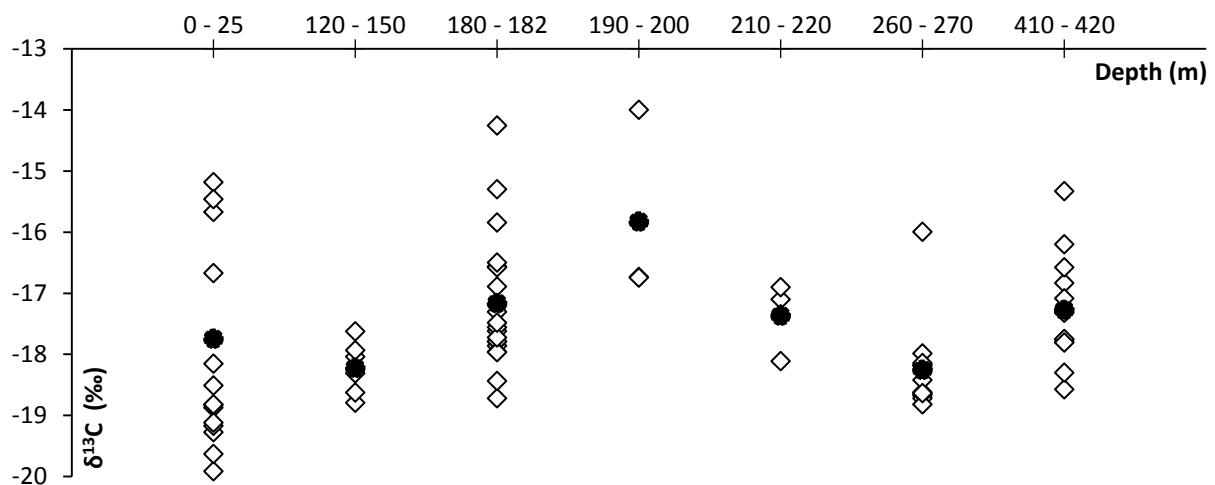


Figure 5. Distribution of $\delta^{13}\text{C}$ of all primary consumers collected. The black circles show the average primary consumer $\delta^{13}\text{C}$ for each depth.

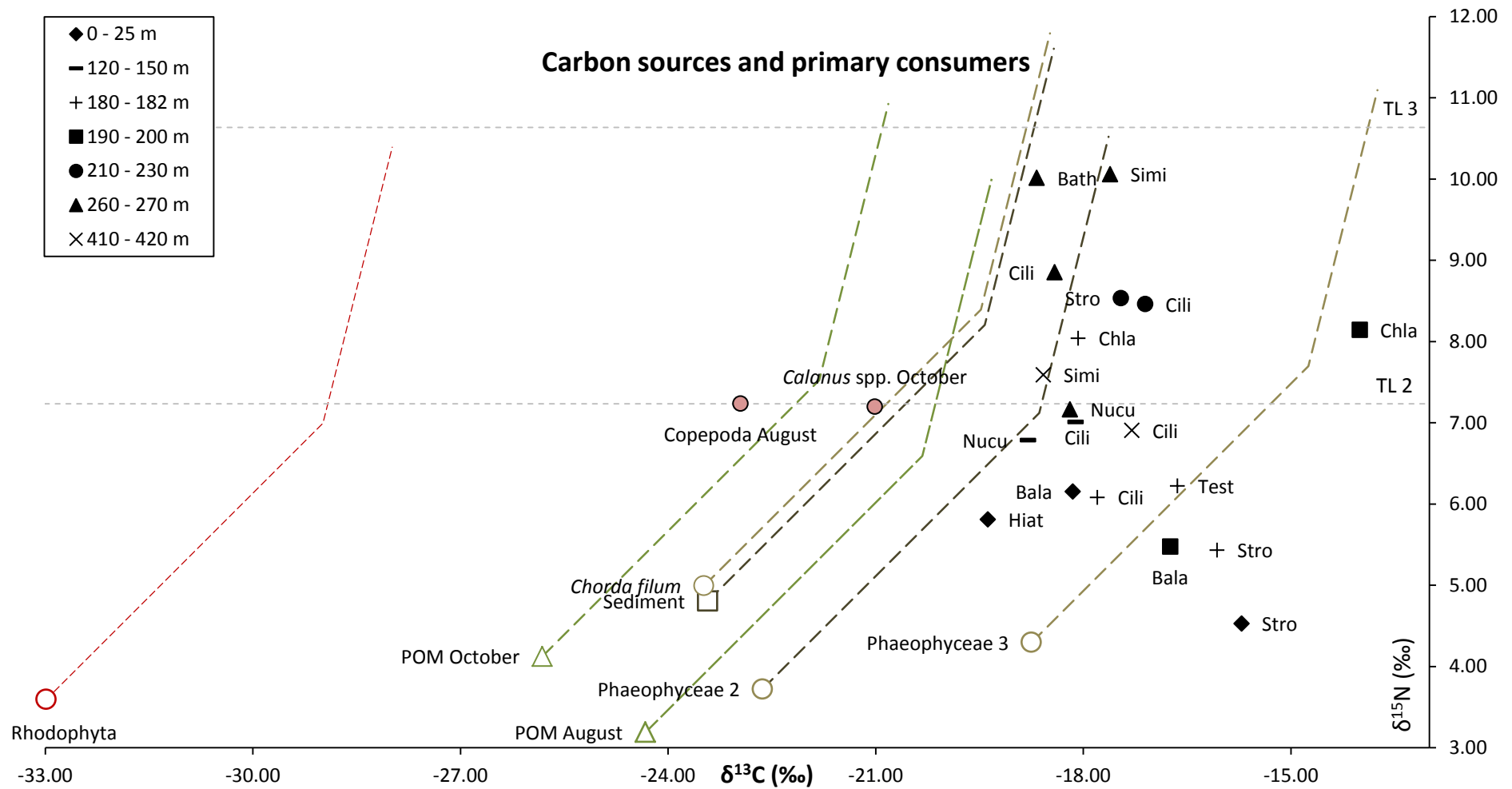


Figure 6. Carbon sources (average values), corresponding fractionation rates and primary consumers. Copepoda is the average of all Copepoda samples from station P11 – P24 (collected in August), and is set as trophic level 2. *Calanus* spp. is the average of the *Calanus* from station HH Cope (collected in October). Copepoda is set as trophic level 2 (TL 2). Abbreviations are as follows; Bala: *Balanus balanus* or *Balanus* sp., Bath: *Batharca glacialis*, Chla: *Chlamys islandica*, Cili: *Ciliatocardium ciliatum*, Hiat: *Hiatella arctica*, Nucy: *Nuculana pernula*, Stro: *Strongylocentrotus* sp and Test: *Testidunalia testidunalis*. Phaeophyceae 2 consists of the algal species *Desmarestia acuelata* and *Saccharina latissima* and Phaeophyceae 3 consists of *Devaleraea ramentacea*, *Fucus* sp., *Pylaiella littoralis/Ectocarpus fasciculatus* and *Laminaria digitata*.

3.2. Trophic structure of consumers

Figures 7a – d show the $\delta^{15}\text{N}$ values of the consumers sampled at different depths. Because few of the same species or taxa were obtained from multiple depths, the samples were divided into feeding categories in order to detect differences in trophic structure. The biggest difference in $\delta^{15}\text{N}$ found among depths was for the primary consumers (*Strongylocentrotus* sp., Bivalvia, Porifera and Ophiuroidea). At all depths, the categories of primary consumers were located at the lowest trophic levels and predators were occupying the highest trophic levels. The categories of deposit feeders were located in between. No feeding categories at any depths had a trophic level higher than 4, suggesting that the trophic levels are of approximately the same length at all depths. However, at depth 210 – 270 m the error bar reaches beyond trophic level 4, due to one replicate of the snail *Admete viridula* ($\delta^{15}\text{N} = 15.5$ ‰). In general, there was a big range in $\delta^{15}\text{N}$ values for most feeding categories at all depths, especially for predators and scavengers. A description of the content of each feeding category at each depth is given in Appendix 3. At some stations, very few samples were collected. Therefore, stations with similar depths have been pooled together in these plots; P11, P13, P24 and P23 (140 – 200 m) and P21 and P22 (210 – 270 m).

The $\delta^{15}\text{N}$ values of the species or taxa found at multiple depths are shown in Figure 8. No significant difference among depths were found for *Sabinea septemcarinata*, *Buccinum* sp. and Polynoida ($F_{3,16} = 1.2$, $p = 0.34$, $F_{3,9} = 0.4$, $p = 0.76$, $F_{3,10} = 3.7$, $p = 0.05$, respectively). For *Ciliatocardium ciliatum* a significant difference was found among depths ($F_{4,19} = 29.4$, $p < 0.01$), but no correlation between depth and $\delta^{15}\text{N}$ was found ($r = 0.07$, $n = 24$). For *Strongylocentrotus* sp., a small significant difference was found between depths ($F_{3,10} = 8.7$, $p < 0.01$), but no strong correlation between depth and $\delta^{15}\text{N}$ ($r = 0.46$, $n = 14$).

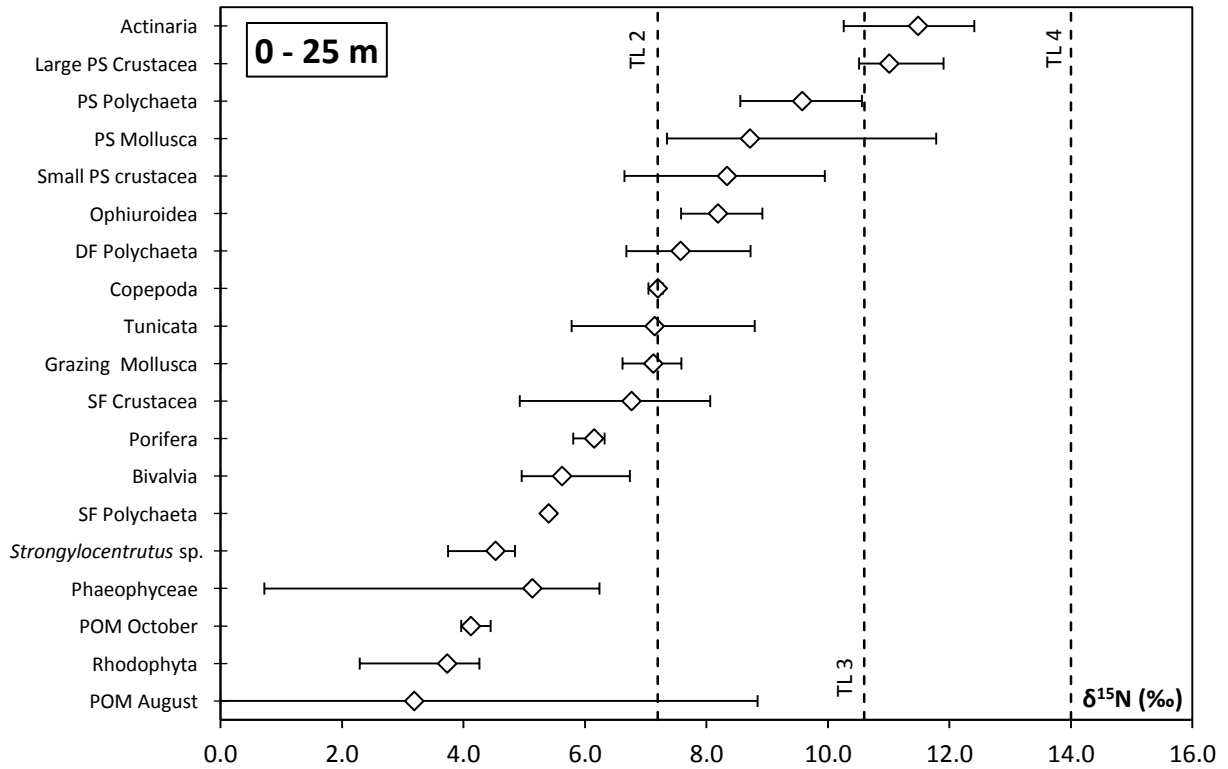


Figure 7a. $\delta^{15}\text{N}$ values for feeding groups at 0 – 25 m depth (stations HH Dive). The dotted lines show trophic level 2 (Copepoda), 3 and 4. The error bars show the full range of the $\delta^{15}\text{N}$ for the respective feeding category. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger.

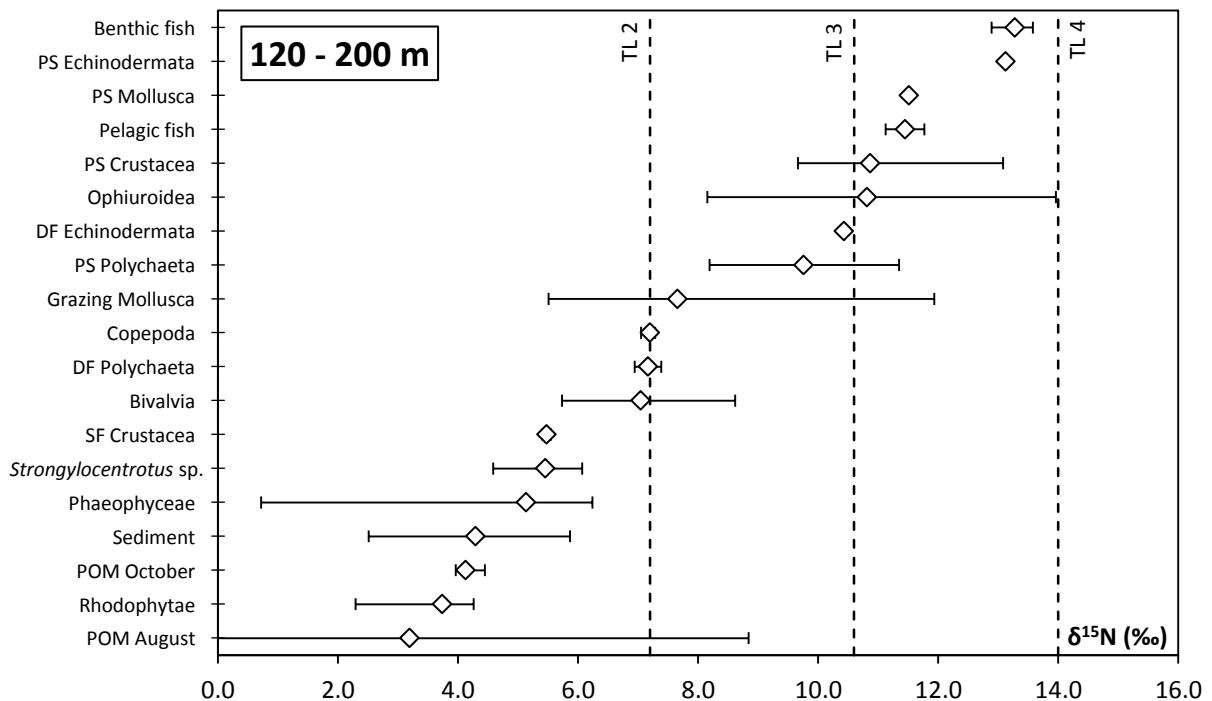


Figure 7b. $\delta^{15}\text{N}$ values for feeding groups at 120 - 200 m depth (stations P11, P13, P23 and P24). The dotted lines show trophic level 2 (Copepoda), 3 and 4. The error bars show the full range of the $\delta^{15}\text{N}$ for the respective feeding category. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger.

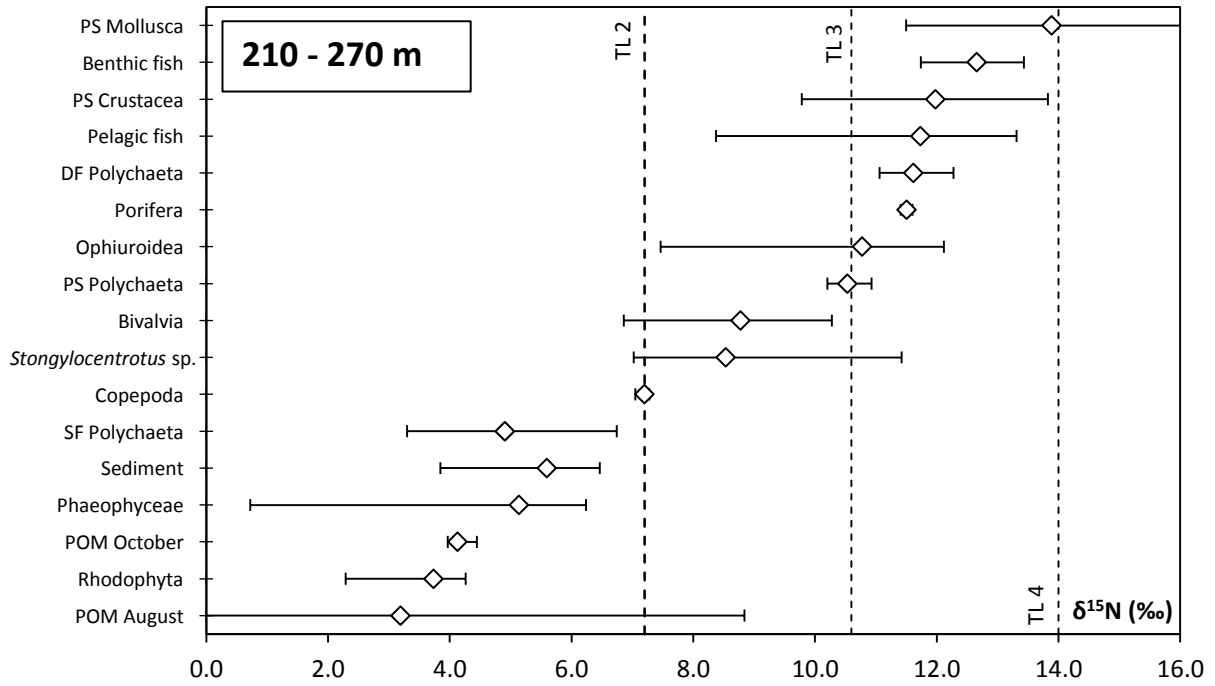


Figure 7c. $\delta^{15}\text{N}$ values for feeding groups at 210 - 270 m depth (stations P21 and P22). The dotted lines show trophic level 2 (Copepoda), 3 and 4. The error bars show the full range of the $\delta^{15}\text{N}$ for the respective feeding category. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger.

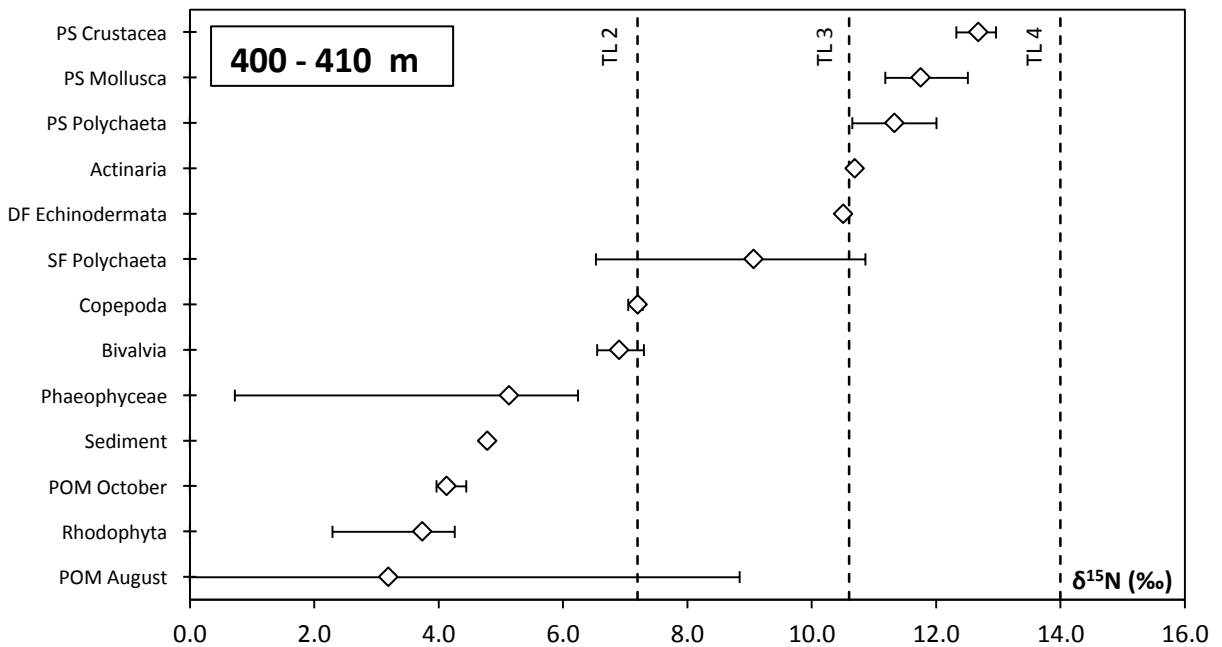


Figure 7d. $\delta^{15}\text{N}$ values for feeding groups at 400 - 410 m depth (station P12). The dotted lines show trophic level 2 (Copepoda), 3 and 4. The error bars show the full range of the $\delta^{15}\text{N}$ for the respective feeding category. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger.

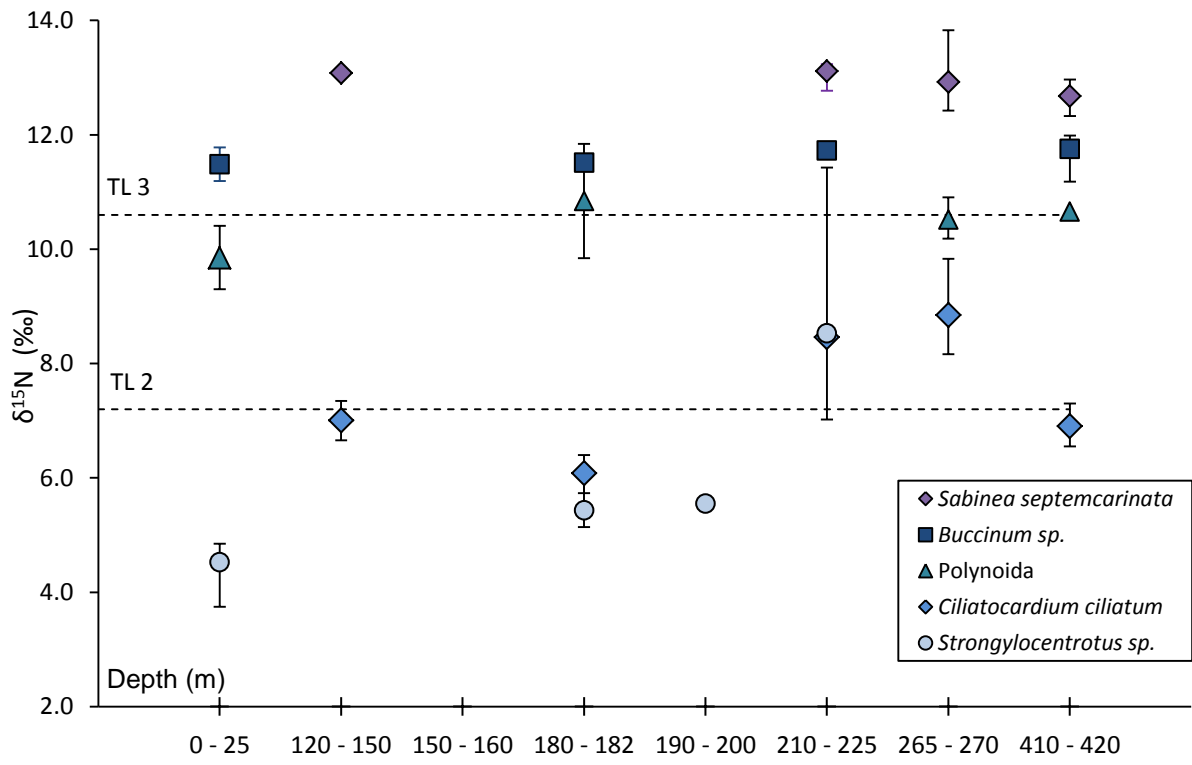


Figure 8. $\delta^{15}\text{N}$ for the species or taxa *Sabinea septemcarinata*, *Buccinum sp.*, Polynoida, *Ciliatocardium ciliatum* and *Strongylocentrotus sp.* at different depths. The error bars show the full range (maximum and minimum value measured) of the respective $\delta^{15}\text{N}$ values.

4. Discussion

4.1. Primary carbon sources at water depth

There was a considerable overlap in the isotopic distribution of most of the carbon sources sampled in this study, both for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figure 2, Figure 5), which generally made it difficult to distinguish among the sources in the food web. Although the Rhodophyta had well-separated isotopic distributions, they were all strongly depleted in $\delta^{13}\text{C}$ relative to all animal samples, and can therefore be disregarded as an important carbon source at all depths examined. The strongly depleted values of $\delta^{13}\text{C}$ are consistent with other isotope analysis of red algae in the Arctic and Antarctic (Hobson et al. 1995, Gilles et al. 2012a, Gilles et al. 2012b). None of the primary consumers collected did fit exactly with any of the calculated fractionation rates of the carbon sources (Figure 5), although Copepoda and *Calanus* spp. fell within the fractionation range of pelagic POM. The low $\delta^{13}\text{C}$ enrichment between Copepoda and pelagic POM collected in August (1.4 ‰) could be caused by the turnover rate for ^{13}C . The values of Copepoda in August could be influenced by the pelagic POM signatures up to several months before they were sampled, when $\delta^{13}\text{C}$ of the phytoplankton could be significantly different (Tamelander et al. 2006b). Most of the primary consumers had isotopic values that placed them between the two groups of brown algae (Phaeophyceae 2 and Phaeophyceae 3), or even to the right of these two groups (having $\delta^{13}\text{C}$ enriched relative to the lightest carbon source in this study). This may suggest that a) a mixture of multiple carbon sources constitute the diets of the primary consumers, and possibly the entire benthic food web, and b) the benthic primary consumers utilize one or more carbon sources not sampled in this study. There are a number of studies reporting important contributions to diets of benthic organisms from carbon sources with enriched $\delta^{13}\text{C}$ values, such as sea-ice POM (Hobson et al. 1995, McMahon et al. 2006, Søreide et al. 2006a, Tamelander et al. 2006a, Gilles et al. 2012a, Gilles et al. 2012b), terrestrial carbon (Dunton et al. 2006, Iken et al. 2010, Kedra et al. 2012) and benthic/epiphytic diatoms (Gilles et al. 2012a). Although Kedra et al. (2012) reports some input of terrestrial carbon to the benthic food chain in Kongsfjorden, the latter is a likely explanation for the enriched $\delta^{13}\text{C}$ values in this study. The organisms with the most enriched $\delta^{13}\text{C}$ values were *Strongylocentrotus* sp., *Tonicella marmorea* and *Testudinalia testudinalis*, which are all known to be grazers (Nadon & Himmelman 2010) and are likely to feed on benthic/epiphytic diatoms, whereas the enriched organisms discussed by Kedra et al. (2012) were deposit feeding polychaetes or cirratulids.

At the depth 0 – 25 m, both filter/suspension feeders, predator/scavengers and Ophiuroidea were slightly more depleted in $\delta^{13}\text{C}$ relative to the same feeding categories at other depths (Appendix 5). It is unlikely that this is due to a higher contribution of pelagic POM in the shallower compared to deeper waters. However, pelagic POM did show an increasingly higher $\delta^{13}\text{C}$ value with increasing depth. The POM available to filter feeders at shallower depths could therefore be depleted in $\delta^{13}\text{C}$ relative to the POM available at greater depths. However, since pelagic POM was not collected at the shallow station, no clear conclusion can be made. There are several possible reasons why the $\delta^{13}\text{C}$ values increase with depth for the POM collected in August. POM is a mixture of several carbon sources and does not necessarily contain only phytoplankton. The composition of bacteria, zooplankton, feces and other dead organic material, and even species composition of autotrophs could be different at different depths. Another explanation could be a difference in the availability of inorganic carbon and dissolved CO_2 in different water layers (Hobson et al. 1995, Gilles et al. 2012b, Nerot et al. 2012). However, the increased $\delta^{13}\text{C}$ values with increasing depth suggests that POM values measured at the surface or at the chlorophyll *a* maximum are not necessarily representative values for the POM available to benthic organisms (Hobson et al. 1995, Nerot et al. 2012).

Deposit feeding animals (DF Polychatea, DF Echinodermata) were on average enriched in $\delta^{13}\text{C}$ relative to sediment POM by 4.87 – 7.46 ‰ (Appendix 5). This mismatch between the isotopic values of deposit feeders and sediment POM could be due to the fact that the isotopic values represent bulk carbon, whereas deposit feeders may selectively feed on particles from the sediment. This is supported by the fact that most deposit feeders were located at a relatively high trophic level (trophic level 2, 3 or higher, Figures 7a - d), which could indicate organic material reworked into the sediment (Kedra et al. 2011). The same trend with enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for deposit feeders is reported by Kedra et al. (2012) from Kongsfjorden.

Moreover, it is important to note that the isotopic values of primary producers may be influenced by various environmental factors (light intensity, temperature and depth), and may therefore vary among locations (Gilles et al. 2012b). Each macroalgal taxa in this study were collected from one single location (ISF12-1, ISF12-2 and CB), and is therefore not necessarily representative for, or even found at, all stations or depths. Additionally, there are very few, if any, of the sampled species that feed directly on any of the macroalgae included in this study (Nadon & Himmelman), and by the time these carbon sources are available to the

benthos via filter feeders, they will most likely have a different isotopic signature than fresh plant material.

4.2. Trophic structure at water depth

There was considerable range in $\delta^{15}\text{N}$ values of the primary consumers sampled with values spanning almost 3 trophic levels (Figure 5, Figure 7a - d). This could be due to several reasons. First of all, there was a sizeable range in the $\delta^{15}\text{N}$ values for most of the sampled carbon sources, especially pelagic POM (Figure 2). Secondly, $\delta^{15}\text{N}$ is usually correlated to size (and age) of the animal because larger animals are able to feed on larger particles or prey (Nadon & Himmelmann 2010). Although the size of the animals varied considerably between depths and stations, no accurate measure of size or age was made in this study. Although there was a big range in $\delta^{15}\text{N}$ values for primary consumers, this did not seem to be reflected higher up in the food chain. Where the same species were sampled at multiple depths, there were little difference in the $\delta^{15}\text{N}$ values among depths for the predator/scavengers (Figure 8). This is consistent with the findings of Renaud et al. (2011), who found little spatial differences between locations in Kongsfjorden, and could be explained by the high level of omnivory among Arctic marine benthic taxa (Kedra et al. 2012). This is further supported by the fact that most feeding groups at all depths had a large range in $\delta^{15}\text{N}$ in this study, spanning over one whole trophic level or more (Figures 7a – b), suggesting that their food sources were derived from multiple trophic levels.

The biggest difference in $\delta^{15}\text{N}$ values among depths was found for the sea urchin *Strongylocentrotus* sp. One likely explanation for the enriched $\delta^{15}\text{N}$ values at greater depths compared to shallower depths could be a change in feeding strategy (Nadon & Himmelmann 2010). It is likely a herbivore at shallower depths where primary producers are available, and acting more as a scavenger or omnivore on deeper waters where primary production might be low. However, the replicate numbers at each depth are very low (1 – 5 individuals). Further testing with larger sample sizes are needed in order to draw any strong conclusions.

Bivalves are often chosen as baselines when calculating the trophic levels (Nadon & Himmelmann 2010, Nerot et al. 2012, Kharlamenko et al. 2013) in stable isotope analysis. The large range among $\delta^{13}\text{C}$ values for bivalves found in this study draw attention to the importance of taking small scale spatial variation in primary consumers into consideration when choosing a baseline.

4.3. Limitations of stable isotope analysis

Although stable isotope analysis are widely used in the study of marine food chains, it has certain limitations. For example, exoskeleton tissue may have a significant lower $\delta^{15}\text{N}$ than soft tissue, which in turn may lead to an underestimation of trophic level by 0.5 – 1.0 TL (Søreide & Nygård 2012). For many animals, such as amphipods and Cumaceans, where pure muscle is difficult to obtain, this could lead to a misinterpretation of trophic position if unaccounted for. For example, the assumed detritivore *Diastylis goodsiri* had much lower $\delta^{15}\text{N}$ values compared to sediment POM than expected (Appendix 1), which is likely due to the thick exoskeleton of this species. Values for species where this could cause a bias in the data has therefore not been included in the figures.

C:N ratios are shown to be correlated with lipid content, and is therefore used to correct for biases high lipid contents might have on animal tissue (Post et al. 2007). High C:N ratios might therefore indicate correspondingly high contents of lipids. For the *Stongylocentrotus* sp. sampled in this study, there was a big range in the C:N ratio between replicates (Appendix 5). This could partly be due to dissection errors, where different types of tissue with various amounts of lipids were included in each replicate. A Pearson's r test showed a strong correlation between the measured $\delta^{13}\text{C}$ and C:N ratio (Pearson's $r = 0.83$, $n = 14$). This could indicate that the differences in C:N ratios between replicates could be explained by a difference in lipid contents. However, the lipid normalization equation (Equation 2) did not correct this correlation, and the lipid corrected $\delta^{13}\text{C}$ values showed an even stronger correlation with the C:N ratio (Pearson's $r = 0.92$, $n = 14$), indicating that the high C:N ratio values might not be caused by lipids, or that the correlation between lipid content and C:N ratio is not what Post et al. (2007) suggests. The lipid normalization equation by (Post et al. 2007) should therefore be used with caution.

The fact that most of the sampled carbon sourced displayed an overlap in their isotopic distributions suggests that this method alone might not be strong enough to answer the hypotheses in this study. In order to draw stronger conclusions, other methods, such as fatty acid composition (Graeve et al. 1997, Budge et al. 2008, Kharlamenko et al. 2013), genetics of stomach contents, feeding experiments, direct observations and modelling (Nilsen et al. 2008b) could be used in addition to stable isotope analysis.

4.4. Data set

Although the dataset in this study is relatively large, there are few replicates for each species at each depth. A small data set (smaller than 20 – 30 replicates) provide a low statistical power and therefore conclusions are more based on biological reasoning than statistical evidence.

Where several stations have been pooled together according to depth (e. g. the plots showing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of different feeding categories) the locations along the fjord axis (east-west, north-south, figure 1) has not been taken into consideration. The north and the south side of the fjord are known to be influenced by different water masses (Nilsen et al. 2008a), which may lead to differences in POM $\delta^{13}\text{C}$ and $\delta^{15}\text{C}$ which in turn may influence the isotopes of filter feeders (Nerot et al. 2012). This has, however, not been tested here, as it is beyond the scope of the hypotheses in this study.

5. Conclusion

Although several feeding categories at the depth 0 – 25 m were somewhat depleted in $\delta^{13}\text{C}$ compared to the same categories at greater depths, there seemed to be little difference to the main carbon sources among depths tested in this study. The fact that most of the primary consumers had isotopic values that placed them in between the two groups of brown algae (Phaeophyceae 2 and Phaeophyceae 3), or even to the right of these two groups (having $\delta^{13}\text{C}$ enriched relative to the lightest carbon source in this study), suggests that a) a mixture of multiple carbon sources constitute the diets of the primary consumers, and possibly the entire benthic food web, and b) the benthic primary consumers utilize one or more carbon sources not sampled in this study, likely benthic/epiphytic diatoms.

Although primary although there was a significant difference among depths for the two primary consumers (*Ciliatocardium ciliautum* and *Strongylocentrotus* sp.) sampled at multiple stations, this trend did not seem to be reflected higher up in the food chain. There was a similar trend in the distribution of feeding categories, and none of these feeding categories had $\delta^{15}\text{N}$ values ranging over trophic level 4 at any depths.

The overlap in the isotopic distribution suggests that stable isotope analysis might not be a strong enough tool to answer the hypotheses in this study. In order to draw stronger conclusions, other methods, such as fatty acid composition genetics of stomach contents, feeding experiments, direct observations and modelling (Nilsen et al. 2008b) could be used in addition to stable isotope analysis.

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Appendix 1

Table A.1a shows all the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm$ Standard deviation of all species or taxa sampled at the stations HH (here CB is included), ISF12 (ISF12-1 and ISF12-2 pooled together) and P24 and P23. The $\delta^{13}\text{C}$ presented are lipid corrected values. Table A.1b shows the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm$ Standard deviation of all species or taxa sampled at the stations P11, P13, P22, P21 and P12. The $\delta^{13}\text{C}$ presented are lipid corrected values.

Table A.1a. Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm$ Standard deviation of all species or taxa sampled at the stations HH (here CB is included), ISF12 (ISF12-1 and ISF12-2 pooled together) and P24 and P23. The $\delta^{13}\text{C}$ presented are lipid corrected values. Replicate numbers are given in the parentheses.

	HH (1 - 25 m)		ISF12 (0 - 14 m)		P24 (120 - 150 m)		P23 (150-160 m)	
	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$
Crustacea								
<i>Balanus balanus</i> (Linnaeus, 1758)	6.1 ± 0.74 (n = 5)	-18.1 ± 1.52 (n = 5)						
<i>Calanus</i> spp.	7.2 ± 0.09 (n = 6)	-21.0 ± 0.25 (n = 5)						
<i>Caprella</i> sp.	6.2 ± 0.13 (n = 6)	-17.4 ± 0.53 (n = 6)	6.9 ± 0.18 (n = 4)	-17.3 ± 1.07 (n = 4)				
Copepoda					9.5	-23.9		
<i>Eualus gaimardii</i> (H. M. Edwards, 1837)							10.6 ± 0.28 (n = 5)	-18.0 ± 0.42 (n = 5)
<i>Gammarillus homari</i> (Fabricius, 1779)	6.3 ± 0.54 (n = 3)	-18.3 ± 0.13 (n = 3)						
<i>Hyas araneus</i> - large (Linnaeus, 1758)	11.0 ± 0.63 (n = 3)	-19.1 ± 0.73 (n = 3)						
<i>Hyas araneus</i> - small	8.4 ± 0.49 (n = 4)	-18.0 ± 1.61 (n = 4)						
<i>Ischyrocercus anguipes</i> (Krøyer, 1838)	7.4 ± 0.20 (n = 5)	-21.3 ± 0.24 (n = 4)						
<i>Lebbeus polaris</i> (Sabine, 1824)	9.6 ± 0.24 (n = 3)	-19.3 ± 0.07 (n = 3)						
<i>Pagurus pubescens</i> (Krøyer, 1838)	7.1 ± 0.41 (n = 6)	-14.5 ± 0.53 (n = 6)						
<i>Sabinea septemcarinata</i> (Sabine, 1824)					13.1	-17.9		
<i>Semibalanus balanoides</i> (Linnaeus, 1767)	7.4 ± 0.57 (n = 5)	-19.0 ± 0.89 (n = 5)						
<i>Socarnes</i> sp.	9.1 ± 0.09 (n = 3)	-15.1 ± 0.43 (n = 3)						
<i>Spirontocaris spinus</i> (Sowerby, 1805)	9.4 ± 0.36 (n = 3)	-19.7 ± 0.28 (n = 3)						
Chordata								
<i>Dendrodoa aggregata</i> (Müller, 1776)	7.10 ± 0.21 (n = 6)	-19.78 ± 1.11 (n = 6)						
<i>Gadus morhua</i> (Linnaeus, 1758)							11.8	-20.6
<i>Halocynthia pyriformis</i> (Rathke, 1806)	8.4 ± 0.42 (n = 5)	-19.6 ± 1.56 (n = 5)						
<i>Hippoglossoides platessoides</i> (Fabricius, 1870)							13.6	-19.1
<i>Hippoglossoides platessoides</i> - small							12.9	-18.3
<i>Lycodes</i> sp.							13.4	-17.4
<i>Sebastes mentella</i> (Travin, 1951)							11.1	-20.6
<i>Syncoicum turgens</i> (Phipps, 1774)	5.9 ± 0.18 (n = 5)	-18.7 ± 0.33 (n = 5)						
Cnidaria								
<i>Actinia equina</i> (Linnaeus, 1758)	11.4	-19.0						
<i>Homothia nodosa</i> (Fabricius, 1780)	12.1 ± 0.22 (n = 5)	-20.1 ± 0.48 (n = 5)						
<i>Sagartia troglodytes</i> (Price in Johnston, 1847)	10.6 ± 0.33 (n = 2)	-20.6 ± 0.56 (n = 2)						
<i>Urticina eques</i> (Gosse, 1858)	11.0 ± 0.32 (n = 2)	-20.1 ± 0.19 (n = 2)						
Echinodermata								
<i>Heliopecten</i> sp.							10.4	-18.5
<i>Ophiacantha bidentata</i> (Bruzéus, 1805)					11.5 ± 0.21 (n = 5)	-18.5 ± 0.59 (n = 6)		
<i>Ophiopholis aculeata</i> (Linnaeus, 1767)	8.2 ± 0.51 (n = 5)	-19.2 ± 0.95 (n = 5)						
<i>Ophiura sarsii</i> (Lütken, 1855)					8.5 ± 0.21 (n = 5)	-17.2 ± 2.46 (n = 5)		
<i>Strongylocentrotus</i> sp.	4.5 ± 0.40 (n = 5)	-15.7 ± 1.95 (n = 5)						
Mollusca								
<i>Buccinum</i> sp.	11.5 ± 0.29 (n = 2)	-16.4 ± 1.05 (n = 2)						
<i>Ciliatocardium ciliatum</i> (Fabricius, 1780)					7.0 ± 0.23 (n = 5)	-18.1 ± 0.38 (n = 5)		
<i>Dendronotus frondosus</i> (Ascanius, 1774)	10.7	-19.3						
<i>Hiattella arctica</i> (Linnaeus, 1767)	5.8 ± 0.64 (n = 5)	-19.4 ± 0.41 (n = 5)						
<i>Margarites</i> sp.	7.2 ± 0.37 (n = 6)	-11.3 ± 2.74 (n = 6)						
<i>Musculus</i> sp.	5.2 ± 0.13 (n = 2)	-21.0 ± 0.14 (n = 2)						
<i>Nuculana pumila</i> (O. F. Müller, 1779)					6.8	-18.8		
<i>Sepiella</i> sp.							12.0	-18.1
<i>Tonicella marmorea</i> (O. Fabricius, 1780)	8.3	-19.7						
<i>Velutina</i> sp.	7.6 ± 0.32 (n = 5)	-20.5 ± 0.30 (n = 5)						
Polychaeta								
<i>Nereis zonata</i>	9.3 ± 0.79 (n = 4)	-20.7 ± 0.35 (n = 4)						
Nereididae							8.7 ± 0.52 (n = 3)	-19.0 ± 0.04 (n = 3)
<i>Nothria</i> sp.					10.2 ± 0.50 (n = 5)	-19.0 ± 0.30 (n = 5)		
<i>Phyllodoce groenlandica</i> (Ørsted, 1842)	9.4	-23.3						
Polynoidae	9.8 ± 0.40 (n = 5)	-18.4 ± 0.75 (n = 5)						
Sabellidae	5.4	-19.6						
<i>Thelepus cincinnatus</i> (Fabricius, 1780)	7.6 ± 0.73 (n = 6)	-19.1 ± 0.44 (n = 6)						
Porifera								
<i>Grantia</i> sp.	6.1 ± 0.18 (n = 5)	-11.6 ± 1.21 (n = 5)						
Carbon sources								
<i>Chorda filum</i>			5.0 ± 0.53 (n = 5)	-23.5 ± 0.99 (n = 5)				
<i>Desmarestia aculeata</i>			4.1 ± 0.50 (n = 5)	-22.7 ± 4.43 (n = 5)				
<i>Devaleraea ramentacea</i>			4.7 ± 0.57 (n = 5)	-20.2 ± 0.70 (n = 5)				
<i>Fucus</i> sp.			5.2 ± 1.11 (n = 5)	-18.3 ± 1.26 (n = 5)				
<i>Laminaria digitata</i> - blade			2.2 ± 1.67 (n = 5)	-19.5 ± 1.83 (n = 5)				
<i>Laminaria digitata</i> - stipe			4.5 ± 0.60 (n = 5)	-18.5 ± 1.63 (n = 5)				
<i>Odontalia dentata</i>			3.4 ± 0.93 (n = 5)	-28.5 ± 0.61 (n = 5)				
<i>Phycodius rubens</i>			2.8 ± 0.40 (n = 5)	-36.9 ± 0.46 (n = 5)				
<i>Polysiphonia/rhodomera</i>			4.6 ± 0.20 (n = 5)	-33.5 ± 0.74 (n = 5)				
<i>Pylorella littoralis / Ectocarpus fasciculatus</i>	4.5 ± 0.28 (n = 5)	-16.9 ± 1.00 (n = 5)						
<i>Saccharina latissima</i>			3.3 ± 0.85 (n = 5)	-22.6 ± 0.81 (n = 5)				
Particulate Organic Matter (POM)	4.2 ± 0.28 (n = 3)	-25.8 ± 0.23 (n = 5)			-0.4	-24.7	0.4	-24.5
Sediment					3.6	-19.0	4.5	-24.1

Table A.1b. Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ \pm Standard deviation of all species or taxa sampled at the stations P11, P13, P22, P21 and P12. The $\delta^{13}\text{C}$ presented are lipid corrected values.

	P11 (180 - 182 m)		P13 (190 - 198 m)		P22 (209 - 226 m)		P21 (266 - 270 m)		P12 (410 - 422 m)	
	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	$\delta^{13}\text{C} \pm \text{SD}$
Arthropoda										
<i>Amrhis phyllonyx</i> (Sars, 1858)										
<i>Balanus balanus</i> (Linnaeus, 1758)			5.5 \pm 0.07 (n=2)	-16.7 \pm 0.01 (n=2)						
<i>Calanus</i> spp.										
Copepoda	7.6 \pm 0.57 (n=2)	-23.0 \pm 0.31 (n=2)	7.6 \pm 0.21 (n=2)	-23.0 \pm 0.51 (n=2)					7.7	-23.5
<i>Diatylis goodisiri</i> (Bell, 1855)							6.6 \pm 0.22 (n=3)	-22.4 \pm 0.50 (n=3)		
<i>Eualus gaimardi</i> (H. M. Edwards, 1837)							7.4 \pm 1.52 (n=4)	-14.7 \pm 1.68 (n=4)		
<i>Hyas araneus</i> (Linnaeus, 1758)							10.4 \pm 0.41 (n=5)	-17.7 \pm 0.36 (n=5)		
<i>Lepidopetrum umbra</i> (Goes, 1866)							10.9 \pm 0.63 (n=5)	-17.5 \pm 0.35 (n=5)		
<i>Nymphon</i> sp.							10.1	-12.7		
<i>Pagurus pubescens</i> (Krøyer, 1838)					10.1	-14.8		-18.8		
<i>Pandalus borealis</i> (Krøyer, 1838)					11.4 \pm 0.26 (n=4)	-18.4 \pm 0.20 (n=4)	11.3 \pm 0.41 (n=5)	-18.1 \pm 0.37 (n=5)		
<i>Rhachotropis inflata</i> (Sars, 1883)							10.9 \pm 0.82 (n=3)	-17.7 \pm 1.36 (n=3)		
<i>Sabinea septemcarinata</i> (Sabine, 1824)					13.1 \pm 0.20 (n=4)	-17.1 \pm 0.15 (n=4)	12.9 \pm 0.40 (n=10)	-17.2 \pm 0.48 (n=10)	12.7 \pm 0.24 (n=5)	-17.3 \pm 0.36 (n=5)
<i>Spirontocaris spinus</i> (Sowerby, 1805)	10.9 \pm 0.1 (n=3)	-17.9 \pm 0.42 (n=3)								
<i>Spirontocaris</i> sp.			10.6 \pm 0.58 (n=4)	-17.3 \pm 0.55 (n=4)						
<i>Themisto abyssorum</i> (Boeck, 1870)							8.9	-20.4	8.1	-21.4
<i>Themisto libellula</i> (Lichtenstein, 1822)					8.6 \pm 0.18 (n=4)	-21.00 (n=4)				
<i>Themisto</i> sp.									9.0	-21.5
Chordata										
<i>Artediiellus atlanticus</i> (Jordan & Evermann, 1898)					13.0 \pm 0.22 (n=3)	-18.4 \pm 0.12 (n=3)				
<i>Boreogadus saida</i> (Lepechin, 1774)					12.2 \pm 0.46 (n=3)	-20.2 \pm 0.07 (n=3)				
<i>Gadus morhua</i> (Linnaeus, 1758)					11.0 \pm 1.37 (n=5)	-20.6 \pm 0.52 (n=4)				
<i>Gadus morhua</i> - small							11.1	-20.3		
<i>Gadus morhua</i> - medium							11.9	-20.2		
<i>Gadus morhua</i> - large							13.2	-19.7		
<i>Leptoichthys maculatus</i> (Fries, 1776)					14.1 \pm 0.11 (n=3)	-18.1 \pm 0.07 (n=3)				
<i>Lumpenus lampretaeformis</i> (Walbaum, 1972)					13.0 \pm 0.28 (n=3)	-18.3 \pm 0.11 (n=3)				
<i>Mallotus villosus</i> - small (Müller, 1776)							11.4	-20.1		
<i>Mallotus villosus</i> - medium							12.4	-20.2		
<i>Mallotus villosus</i> - large							11.6	-20.0		
<i>Melanogrammus aeglefinus</i> - small (Linnaeus, 1758)							11.8	-20.0		
<i>Melanogrammus aeglefinus</i> - medium							13.3	-19.3		
<i>Melanogrammus aeglefinus</i> - large							12.9	-20.5		
<i>Reinhardtius hippoglossoides</i> - small (Walbaum, 1792)							12.0	-21.1		
<i>Reinhardtius hippoglossoides</i> - medium							11.7	-20.9		
<i>Reinhardtius hippoglossoides</i> - large							12.7	-20.4		
<i>Sebastes mentella</i> (Travin, 1951)					11.0 \pm 0.31 (n=3)	-20.7 \pm 0.22 (n=3)				
Rajidae - small							12.02	-16.6		
Rajidae - medium							12.36	-18.7		
Rajidae - large							12.86	-18.3		
<i>Synoicum turgens</i> (Phipps, 1774)										
Cnidaria										
<i>Actinia equina</i> (Linnaeus, 1758)									10.7	-19.1
Actinaria										
<i>Hormathia nodosa</i> (Fabricius, 1780)										
<i>Sagaritia troglodytes</i> (Price in Johnston, 1847)										
<i>Urticina eques</i> (Gosse, 1858)										
Echinodermata										
<i>Ctenodiscus crispatus</i> (Retzius, 1805)	10.4	17.0							10.5	-16.1
<i>Crossaster papposus</i> (Linnaeus, 1767)			13.1	-15.9						
<i>Helmetaria</i> sp.										
<i>Henricia</i> sp.							14.3 \pm 0.14 (n=2)	-15.6 \pm 0.39 (n=2)		
<i>Ophiacantha bidentata</i> (Brüzelius, 1805)			12.0 \pm 1.87 (n=3)	-17.6 \pm 1.45 (n=3)			11.6 \pm 0.35 (n=5)	-19.1 \pm 0.34 (n=5)		
<i>Ophiopholis aculeata</i> (Linnaeus, 1767)	9.5 \pm 0.39 (n=5)	-18.7 \pm 0.18 (n=5)	9.9 \pm 2.70 (n=3)	-17.9 \pm 0.45 (n=3)						
<i>Ophiura sarsii</i> (Lütken, 1855)	9.7 \pm 0.17 (n=4)	-18.0 \pm 0.18 (n=4)			11.7	-13.9	9.5 \pm 0.11 (n=3)	-17.3 \pm 1.53 (n=3)		
<i>Ophiocollex glacialis</i> (Müller & Tröschel, 1842)							11.4 \pm 0.44 (n=4)	-18.9 \pm 0.45 (n=4)		
<i>Ophiocten sericeum</i> (Forbes, 1852)							9.4 \pm 0.04 (n=2)	-18.9 \pm 0.19 (n=2)		
<i>Pteraster</i> sp.										
<i>Strongylocentrotus</i> sp.	5.4 \pm 0.57 (n=5)	-16.1 \pm 1.30 (n=5)	5.5	-15.7	8.5 \pm 2.05 (n=3)	-17.5 \pm 0.61 (n=3)				
Mollusca										
<i>Admete viridula</i> (Fabricius, 1780)							13.9 \pm 2.05 (n=3)	-15.2 \pm 0.86 (n=3)		
<i>Bathyrca glacialis</i> (Grey, 1824)							10.0 \pm 0.20 (n=4)	-18.7 \pm 0.04 (n=4)		
<i>Buccinum hydrophanum</i> (Hancock, 1846)	11.5 \pm 0.02 (n=3)	-17.3 \pm 0.25 (n=3)			11.7	-16.4			11.7 \pm 0.43 (n=7)	-15.9 \pm 2.43 (n=7)
<i>Buccinum</i> sp.										
<i>Chlamys islandica</i> (O. F. Müller, 1776)	8.0 \pm 0.58 (n=5)	-18.1 \pm 0.51 (n=5)	8.1	-14.0						
<i>Ciliocardium ciliatum</i> (Fabricius, 1780)	6.1 \pm 0.22 (n=5)	-17.8 \pm 0.15 (n=5)			8.5	-17.1	8.8 \pm 0.71 (n=3)	-18.4 \pm 0.42 (n=3)	6.9 \pm 0.27 (n=9)	-17.1 \pm 0.42 (n=9)
<i>Nuculana pernula</i> (O. F. Müller, 1779)							7.2 \pm 0.21 (n=3)	-18.2 \pm 0.05 (n=3)		
<i>Simulipecten greenlandicus</i> (G. B. Sowerby II, 1842)							10.1 \pm 0.21 (n=3)	-17.6 \pm 1.41 (n=3)	7.6	-18.6
<i>Testudinula testudinalis</i> (O. F. Müller, 1776)	6.2 \pm 0.42 (n=4)	-16.6 \pm 0.62 (n=4)								
<i>Tonacella marmorata</i> (O. Fabricius, 1780)	10.5 \pm 1.41 (n=2)	-10.6 \pm 9.82 (n=2)								
Polychaeta										
Lumbricinae									10.4	-18.0
<i>Maldane sarsi</i> (Malmgren, 1865)							11.3 \pm 0.23 (n=4)	-17.8 \pm 0.17 (n=4)	10.3 \pm 0.47 (n=4)	-18.3 \pm 0.28 (n=4)
<i>Maldane</i> sp.									10.6 \pm 0.56 (n=4)	-17.9 \pm 0.41 (n=4)
Maldanidae							11.9 \pm 0.23 (n=4)	-17.9 \pm 0.14 (n=4)		
Nephtyidae							10.5 \pm 0.27 (n=5)	-17.4 \pm 0.29 (n=5)		
<i>Pectinaria</i> sp.									7.8 \pm 0.82 (n=4)	-16.9 \pm 1.38 (n=4)
<i>Pherusa plumosa</i> (Müller, 1776)	7.2 \pm 0.22 (n=2)	-18.0 \pm 0.05 (n=2)								
Phyllodoceidae									12.0	-17.5
Polychaeta indet.							12.2 \pm 0.34 (n=5)	-16.6 \pm 1.04 (n=5)		
Polynoidae	10.8 \pm 0.55 (n=3)	-17.9 \pm 0.26 (n=3)					10.5 \pm 0.24 (n=5)	-18.0 \pm 0.90 (n=5)	10.6	-18.42
<i>Spiochaetopterus</i> sp.							4.9 \pm 1.32 (n=5)	-16.9 \pm 0.83 (n=5)		
Porifera										
Porifera indet.							11.5 \pm 0.08 (n=3)	-18.1 \pm 0.13 (n=3)		
Cabon sources										
Particulate Organic Matter (POM)										
Sediment	4.3	-21.5	5.9	-23.2	4.7	-24.3	6.5	-24.0	4.8	-23.6

Appendix 2

The *weighted average* ($\delta^{15}\text{N}_{\text{WA}}$) for each station was calculated by multiplying the $\mu\text{M N}$ with $\delta^{15}\text{N}$ for each depth, and the sum of this was divided by the total mass of nitrogen ($\mu\text{M N}$ of all depths). All measured $\delta^{15}\text{N}$, $\mu\text{M N}$, depth and the calculated $\delta^{15}\text{N}_{\text{WA}}$ values are given in the table underneath. Only $\delta^{15}\text{N}$ values from samples where $\mu\text{M N}$ were higher than 0.9 has been used.

Table A.2. $\delta^{15}\text{N}$, $\mu\text{M N}$, depths and the calculated $\delta^{15}\text{N}_{\text{WA}}$ for all POM samples collected in August (stations P11 – P24).

Station	Depth (m)	Mass N ($\mu\text{M N}$)	$\delta^{15}\text{N}$ measured	$\mu\text{M N} \cdot \delta^{15}\text{N}$
P11	150	0.73	Insufficient N	
	125	0.89	Insufficient N	
	100	1.15	10.14	11.71
	70	0.70	Insufficient N	
	50	0.76	Insufficient N	
	30	0.74	Insufficient N	
	20	0.94	3.04	2.85
	10	0.64	Insufficient N	
	5	1.13	6.76	7.67
Weighted average ($d^{15}\text{N}_{\text{WA}}$):				6.89 ‰
P12	400	0.67	Insufficient N	
	300	1.09	8.41	9.16
	200	0.81	Insufficient N	
	150	0.44	Insufficient N	
	100	0.76	Insufficient N	
	50	0.67	Insufficient N	
	30	0.91	10.00	9.11
	20	0.82	Insufficient N	
	10	3.12	8.75	27.28
5	1.09	8.56	9.31	
Weighted average ($d^{15}\text{N}_{\text{WA}}$):				8.84 ‰
P13	200	0.68	Insufficient N	
	150	0.24	Insufficient N	
	125	0.71	Insufficient N	
	100	0.54	Insufficient N	
	70	0.66	Insufficient N	
	50	0.48	Insufficient N	
	30	0.53	Insufficient N	
	20	0.55	Insufficient N	
	10	0.77	Insufficient N	
5	0.61	Insufficient N		
No $\mu\text{M N}$ high enough				

P21	250	1.04	0.27	0.28
	200	0.73	Insufficient N	
	150	0.80	Insufficient N	
	125	0.94	2.15	2.03
	100	0.66	Insufficient N	
	70	0.81	Insufficient N	
	50	0.81	Insufficient N	
	30	1.20	3.62	4.35
	20	0.85	Insufficient N	
	10	1.31	1.90	2.48
	5	0.97	1.64	1.59
Weighted average ($d^{15}N_{WA}$):				1.96 ‰
P22	250	0.58	Insufficient N	
	200	0.75	Insufficient N	
	150	0.72	Insufficient N	
	125	0.80	Insufficient N	
	100	0.46	Insufficient N	
	70	0.53	Insufficient N	
	50	0.63	Insufficient N	
	30	0.78	Insufficient N	
	20	1.05	1.15	1.20
	10	1.06	0.80	0.85
	5	0.78	Insufficient N	
Weighted average ($d^{15}N_{WA}$):				0.97 ‰
P23	125	0.60	Insufficient N	
	100	0.74	Insufficient N	
	70	0.48	Insufficient N	
	50	0.62	Insufficient N	
	30	0.67	Insufficient N	
	20	0.73	Insufficient N	
	10	0.91	0.38	
Weighted average ($d^{15}N_{WA}$):				0.38 ‰
P24	200	0.69	Insufficient N	
	150	0.61	Insufficient N	
	125	0.86	Insufficient N	
	100	0.61	Insufficient N	
	70	0.53	Insufficient N	
	50	0.64	Insufficient N	
	30	0.79	Insufficient N	
	20	1.59	-0.96	-1.54
	10	1.38	-0.36	-0.49
	5	1.69	0.94	1.59
Weighted average ($d^{15}N_{WA}$):				-0.44 ‰

Appendix 3

Table A.3 shows the species used in the individual feeding groups at the different depths used in Figures 7a – d and Appendix 5.

Table A.3. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger.

Depth	Feeding category	Taxa	Replicates	Reference
All stations	Copepoda	Copepoda	9	Søreide et al. 2006a
0 – 25 m (HH)	<i>Strongylocentrotus</i> sp.	<i>Strongylocentrotus</i> sp.	5	Nadon & Himmelman 2010
	SF Polychaeta	Sabellidae	1	Macdonald et al. 2011
	Bivaliva	<i>Hiatella arctica</i>	5	Kedra et al. 2012
		<i>Musculus</i> sp.	2	Macdonald et al. 2011
	Porifera	<i>Grantia</i> sp.	5	Macdonald et al. 2011
	SF Crustacea	<i>Balanus balanus</i>	5	Macdonald et al. 2011
		<i>Semibalanus balanoides</i>	5	Macdonald et al. 2011
	Grazing Mollusca	<i>Margarites</i> sp.	7	Macdonald et al. 2011
	Tunicata	<i>Halocynthia pyriformis</i>	5	Macdonald et al. 2011
		<i>Dendrodoa aggregata</i>	6	Macdonald et al. 2011
		<i>Synoicum turgens</i>	5	Macdonald et al. 2011
	DF Polychaeata	<i>Thelepus cincinatus</i>	6	Macdonald et al. 2011
	Ophiuroidea	<i>Ophiopholis acuelata</i>	5	Renaud et al. 2011
	Small PS Crustacea	<i>Hyas araneus</i>	4	Renaud et al. 2011
		<i>Lebbeus polaris</i>	3	Macdonald et al. 2011
		<i>Spirontocaris spinus</i>	3	Renaud et al. 2011
	PS Mollusca	<i>Buccinum</i> sp.	2	Renaud et al. 2011
		<i>Velutina</i> sp.	5	Macdonald et al. 2011
	PS Polychaeta	Polynoida	5	Renaud et al. 2011
		<i>Phyllodoce groenlandicus</i>	1	Kedra et al. 2012
		<i>Nereis zonata</i>	4	
	Large PS Crustacea	<i>Hyas araneus</i> (large)	3	
	Actinaria	<i>Hormathia nodosa</i>	5	Macdonald et al. 2011
<i>Sagartia troglodytes</i>		2	Macdonald et al. 2011	
<i>Actinia equina</i>		1	Macdonald et al. 2011	
<i>Urticina eques</i>		2	Macdonald et al. 2011	
140 – 200 m (P11, P13, P23 and P24)	<i>Strongylocentrotus</i> sp.	<i>Strongylocentrotus</i> sp.	6	
	SF Crustacea	<i>Balanus balanus</i>	2	
	DF Polychaeata	<i>Pherusa plumosa</i>	2	Renaud et al. 2011
	Bivaliva	<i>Ciliatocardium ciliatum</i>	10	Renaud et al. 2011
		<i>Chlamys islandica</i>	5	Renaud et al. 2011
	Grazing Mollusca	<i>Testudinalia testudinalis</i>	4	Nadon & Himmelman 2010
		<i>Tonicella marmorea</i>	2	Nadon & Himmelman 2010

PS Polychaeta	Polynoida	3
	Nereididae	3
DF Echinodermata	<i>Ctenodiscus crispatus</i>	1 Renaud et al. 2011
Ophiuroidea	<i>Ophiacantha bidentata</i>	8 Renaud et al. 2011
	<i>Ophiopholis aculeata</i>	8 Renaud et al. 2011
PS Crustacea	<i>Sabinea septemcarinata</i>	1 Renaud et al. 2011
	<i>Eualus gaimardi</i>	5 Renaud et al. 2011
	<i>Spirontocaris</i> sp.	7
Pelagic fish	<i>Gadhus morhua</i>	1
	<i>Sebastes mentella</i> (small)	1
PS Mollusca	<i>Buccinum</i> sp.	3
PS Echinodermata	<i>Crossaster papposus</i>	1
Benthic fish	<i>Lycodes</i> sp.	1
	<i>Hippoglossoides</i>	
	<i>platessoides</i>	2
210 – 270 m		
(P21 and P22)		
SF Polychaeta	<i>Spirochaetopterus</i> sp.	5 Macdonald et al. 2011
	<i>Strongylocentrotus</i> sp.	3
Bivaliva	<i>Ciliatocardium ciliatum</i>	4
	<i>Nuculana pernula</i>	3 Renaud et al. 2011
	<i>Bathyarca glacialis</i>	3 Renaud et al. 2011
PS Polychaeta	Nephtyidae	5 Macdonald et al. 2011
Ophiuroidea	<i>Ophioscolex glacialis</i>	4
	<i>Ophiacantha bidentata</i>	5
	<i>Ophiura sarsii</i>	3
	<i>Ophiocten sericeum</i>	3 Renaud et al. 2011
Porifera	Porifera indet.	3
DF Polychaeta	<i>Maldane sarsi</i>	4 Renaud et al. 2011
	Maldanidae	4
	<i>Melanogrammus</i>	
Pelagic fish	<i>aeglefinus</i>	3
	<i>Gadhus morhua</i>	3
	<i>Mallotus villosus</i>	3
	<i>Reinhardtius</i>	
	<i>hippoglossoides</i>	3
	<i>Boreogadus saida</i>	3
	<i>Sebastes mentella</i>	3
PS Crustacea	<i>Hyas araneus</i>	5
	<i>Sabinea septemcarinata</i>	14
	<i>Pandalus borealis</i>	9
	<i>Rhachotropis inflata</i>	3 Macdonald et al. 2011
Benthic fish	Rajidae	3
	<i>Leptoclinus maculatus</i>	3
	<i>Artediellus atlanticus</i>	3
	<i>Lumpenus</i>	
	<i>lampretaeformis</i>	3
PS Mollusca	<i>Admete viridula</i>	3 Macdonald et al. 2011

**400 – 410 m
(P12)**

Bivaliva	<i>Ciliatocardium ciliatum</i>	10
SF Polychaeta	<i>Pectinaria</i> sp.	4 Macdonald et al. 2011
	<i>Maldane sarsi</i>	4
Actinaria	Actinaria	1 Macdonald et al. 2011
PS Polychaeta	Polynoida	1
	Phyllodocidae	1 Macdonald et al. 2011
PS Mollusca	<i>Buccinum hydrophanum</i>	7
PS Crustacea	<i>Sabinea septemcarinata</i>	5

Appendix 4

The table shows measured $\delta^{15}\text{N}$, measured and lipid corrected $\delta^{13}\text{C}$ and C:N ratio for all *Strongylocentrotus* sp. collected. The figure shows the correlation between measured and lipid corrected $\delta^{13}\text{C}$ and C:N ratio.

Table A.4. Measured $\delta^{15}\text{N}$, measured and lipid corrected $\delta^{13}\text{C}$ and C:N ratio for all *Strongylocentrotus* sp. collected. The lipid corrected $\delta^{13}\text{C}$ are calculated based on Equation 2.

Station	Measured $\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N ratio	Lipid corrected $\delta^{13}\text{C}$ (‰)
HH	-24,32	3,74	12,09	-15,67
HH	-24,21	4,55	14,81	-12,87
HH	-23,43	4,72	8,67	-18,16
HH	-23,68	4,85	10,43	-16,67
HH	-23,13	4,77	11,38	-15,18
P11	-22,32	6,07	9,17	-16,57
P11	-24,01	4,59	13,20	-14,26
P11	-21,68	6,07	7,45	-17,62
P11	-22,59	5,14	9,42	-16,58
P11	-21,52	5,30	9,63	-15,30
P13	-22,25	5,55	10,00	-15,67
P22	-22,65	7,02	9,16	-16,90
P22	-21,60	11,43	7,64	-17,35
P22	-21,40	7,15	6,67	-18,12

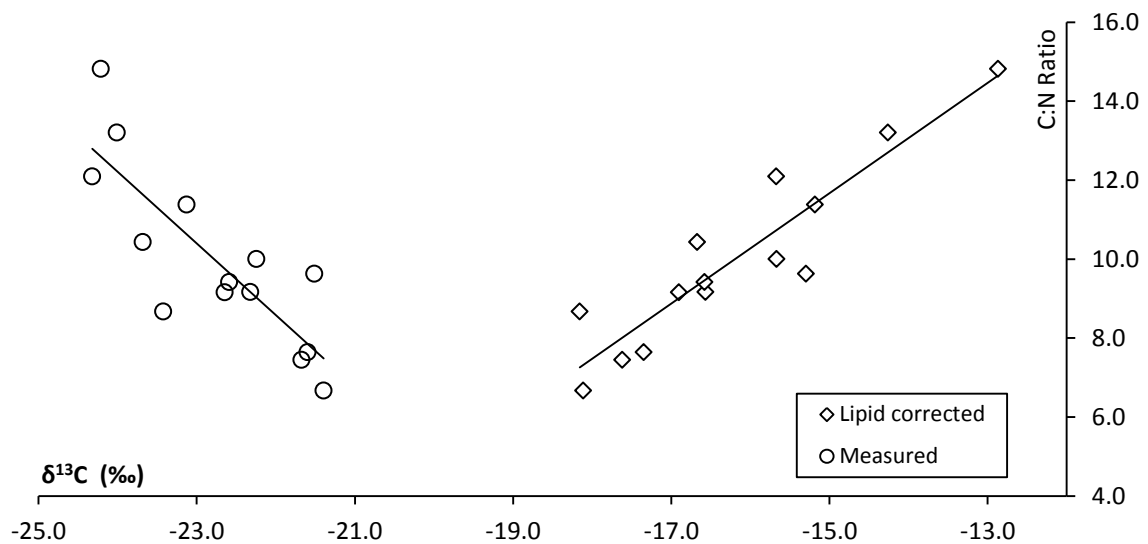


Figure A.4. Correlation between measured and lipid corrected $\delta^{13}\text{C}$ and C:N ratio for all *Strongylocentrotus* sp. samples.

Appendix 5

Tables A.5.a – d shows the $\delta^{13}\text{C}$ values for carbon sources and consumers pooled into feeding groups at the depths 0 – 25 m, 120 – 200 m, 210 – 270 m and 410 m. A description of the content of each feeding category at each depth is given in Appendix 3.

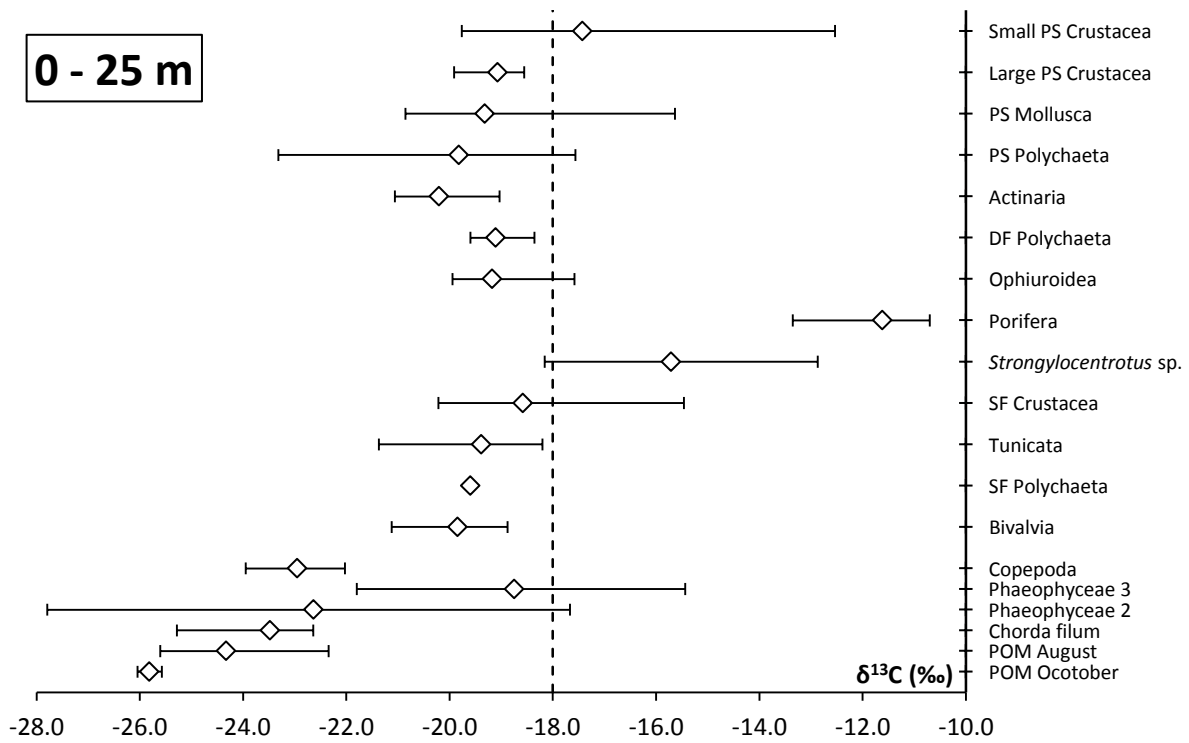


Figure A.5.a. $\delta^{13}\text{C}$ values for feeding groups at 0 – 25 m depth (station HH Dive). The error bars show the full range. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger. The dotted line (- 18.0 ‰) is included to better compare the figures.

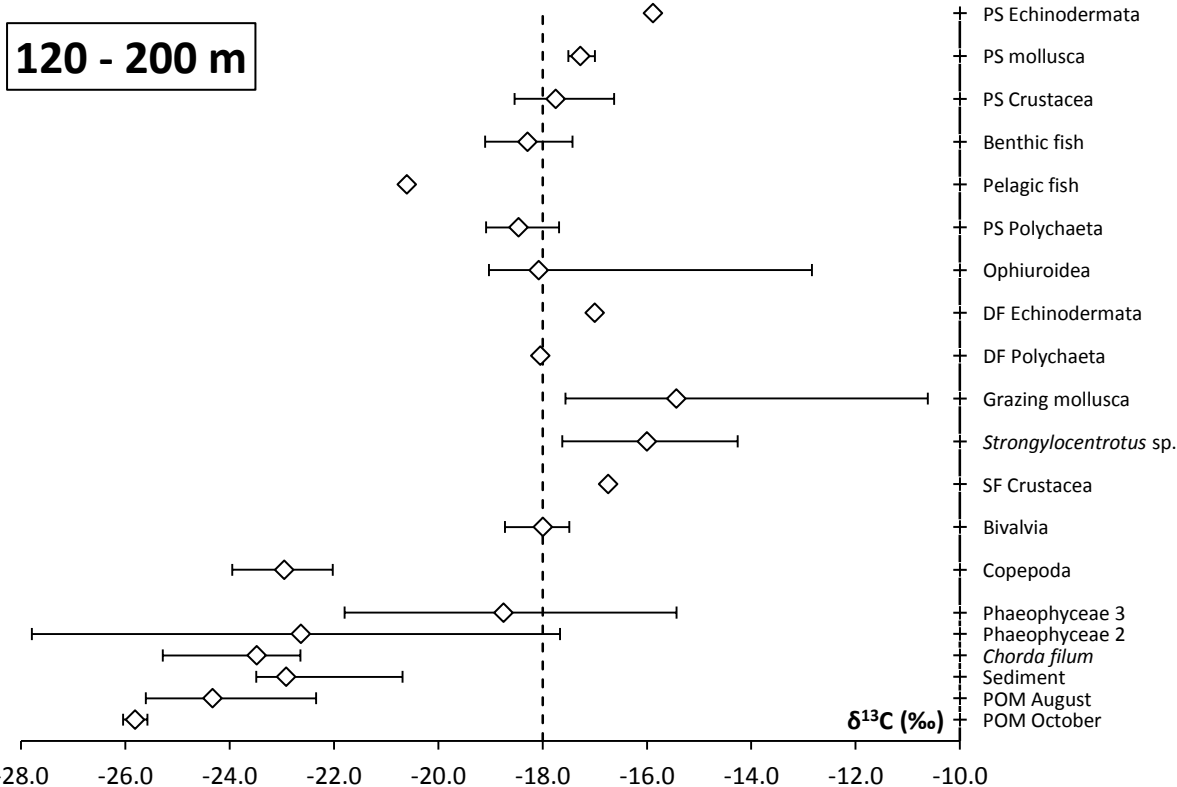


Figure A.5.b. $\delta^{13}\text{C}$ values for feeding groups at 120 - 200 m depth (stations P11, P13, P23 and P24). The error bars show the full range. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger. The dotted line (- 18.0 ‰) is included to better compare the figures.

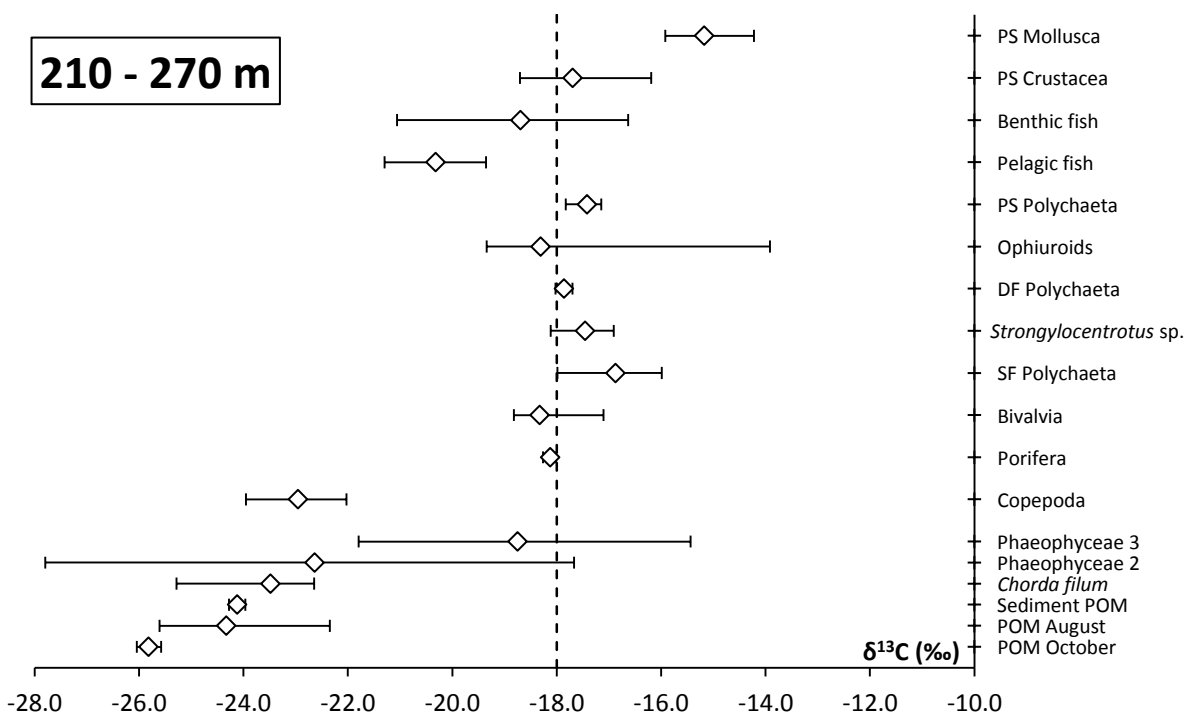


Figure A.5.c. $\delta^{13}\text{C}$ values for feeding groups at 210 - 270 m depth (stations P21 and P22). The error bars show the full range. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger. The dotted line (- 18.0 ‰) is included to better compare the figures.

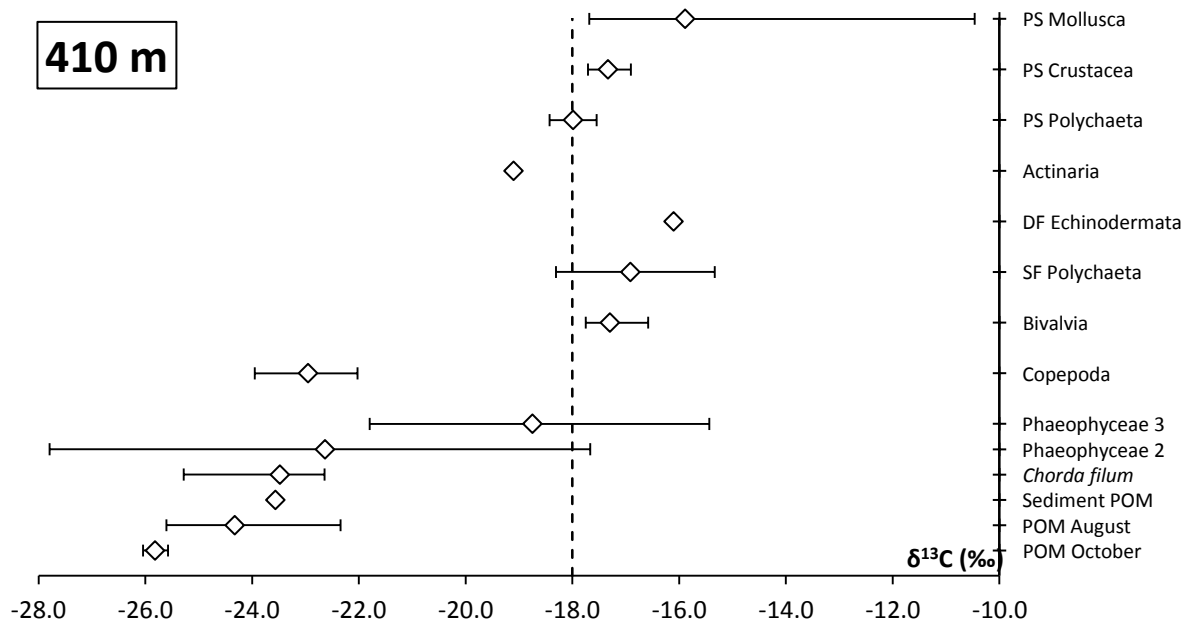


Figure A.5.c. $\delta^{13}\text{C}$ values for feeding groups at 410 m depth (station P12). The error bars show the full range. Abbreviations are as follows; DF: deposit feeding, SF: filter/surface deposit feeder, PS: Predator/Scavenger. The dotted line (- 18.0 ‰) is included to better compare the figures.