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Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient

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Tight coupling between pelagic and benthic communities is accepted as a general principle on Arctic shelves. Whereas this paradigm has been useful for guiding ecological research, it has perhaps led to a disproportionate focus on POM and ice algae as the most likely sources of carbon for the benthic food web. Arctic shelves are complex systems, including banks, fjords, and trough systems up to 350 m or more in depth. In this stable-isotope study, 13 different potential carbon sources were analyzed for their contribution to the food-webs of Isfjorden, Svalbard. A mixing model with herbivorous copepods and grazing sea urchins as end-members was applied to determine the relative contributions of the most likely carbon sources to pelagic and benthic taxa. Most taxa from the benthos feed on a broad mixture of POM and macroalgal detritus, even at depths down to 410 m. Most suspension-feeding bivalves had isotopic signals consistent with more than a 50% contribution from kelps and rockweeds. In contrast, nearly all pelagic species had diets consistent with an overwhelming contribution of pelagic POM. These results indicate that macroalgal detritus can contribute significantly to near-shore Arctic food-webs, a trophic link that may increase if macroalgae increase in the Arctic as predicted. These weaker quantitative links between pelagic and benthic components of coastal systems highlight the need for thorough sampling of potential carbon-baselines in food-web studies. A large detrital-carbon component in diets of Arctic benthos may dampen the impacts of strong seasonality in polar primary producers, leading to higher ecosystem resilience, but may also result in lower secondary productivity.

Keywords: mixing model, particulate organic carbon, pelagic-benthic coupling, stable isotope, suspension feeder, Svalbard

Introduction

Food-web structure is a key ecosystem characteristic, describing energy flow, ecological interactions, and strength of linkages within the community (Peterson and Fry, 1987; Michener et al., 2007; Böecklen et al., 2011). This information can be used to assess ecosystem stability over seasonal and multi-annual time scales (McMeans et al., 2013; Krumhansl et al., 2014), and the potential response to extrinsic changes in the system due to climatic change, distributional shifts in key taxa, and other natural or human-induced changes. The relative
importance of different potential food sources and the pathways of energy flow across whole communities, however, remain poorly understood in Arctic coastal environments (but see Kędra et al., 2012; McMeans et al., 2013). Coastal areas of the Arctic are likely to be the first to be impacted by predicted system change (Weslawski et al., 2010; Krause-Jensen et al., 2012; Renaud et al., in press), and understanding current food-web properties provides the necessary baseline for predicting ecosystem functioning in a future Arctic.

The prevailing paradigm concerning most shelf ecosystems throughout the Arctic is that pelagic and benthic components are tightly coupled in terms of structure and function (Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Hobson et al., 2002; Piepenburg, 2005). Much of the evidence for this concept comes from studies conducted away from the coast. The results have been quite consistent when comparisons are made at appropriate temporal and spatial scales (Renaud et al., 2008), and they have provided a mechanistic understanding of the links between planktonic production, zooplankton grazing, dynamics of vertical flux processes, and consequences for benthic community structure and function (Dunton et al., 2005; Grebmeier et al., 2006; Morata et al., 2008; Reigstad et al., 2008; Wexels Riser et al., 2008).

The strength of the paradigm and the dramatic seasonality and magnitude of the Arctic spring bloom, however, may have led to insufficient attention to the diverse array of other potential carbon sources. Despite the strong relevance of these other sources for coastal systems, many of the stable isotope studies of coastal food webs in the Arctic have still focused on suspended particulate organic matter (POM) as the primary food source for benthic organisms (Iken et al., 2010; Feder et al., 2011; Renaud et al., 2011; Kędra et al., 2012). Stable-isotope-based studies that have investigated sources other than POM have shown that these may contribute significantly, or even primarily, to benthic food-webs in the Arctic. These include terrestrial carbon, either from rivers or erosion of coastal sediments (Dunton et al., 2005, 2012; Iken et al., 2010; Feder et al., 2011), and ice algae (Hobson et al., 1995; Sereide et al., 2006a; Tamelander et al., 2006). Microphytobenthos is common on both soft sediments and rocky bottoms in euphotic areas of the Arctic. In these shallow (>30 m) waters, it has primary production rates comparable to that of pelagic phytoplankton (Glud et al., 2009; Woelfel et al., 2010; McIntigue et al., 2015), but its role in benthic food-webs has not been investigated.

Surprisingly little attention has been given to the role of macroalgae in coastal food webs of the Arctic, especially considering their importance in sub-Arctic food webs (e.g., Fredriksen, 2003), and the role organic detritus may play in promoting stability in benthic communities (Moore et al., 2004; McMeans et al., 2013). Where it has been investigated, however, kelp detritus has been shown to contribute significantly to shallow-water benthic food-webs in the Arctic (Dunton and Schell, 1987; McMeans et al., 2013) and Antarctic (Dunton, 2001; Norkko et al., 2007), and it is presumed to comprise a significant component of sedimentary organic matter found in some systems (Sokolowski et al., 2012). In temperate systems, canyons facilitate transport of dislodged kelp to the deep-sea, where it may enter the food web (Vetter and Dayton, 1998; De Leo et al., 2010). No studies have investigated the role of macroalgal detritus in deeper waters in the Arctic.

In recent years, the analysis of naturally occurring stable isotopes of carbon (δ13C) and nitrogen (δ15N) has been a useful tool for describing food-web structure (Fry, 2007). The stable isotopes of carbon and nitrogen can help identify the relative contribution of different potential carbon sources to a consumer and establish the relative trophic position of the food-web members, respectively (Peterson and Fry, 1987). This technique has been used to support the pelagic-benthic coupling paradigm as it relates to primary carbon sources for benthic food-web components in Arctic ecosystems (Hobson et al., 1995, 2002; Iken et al., 2005; Tamelander et al., 2006; Morata and Renaud, 2008).

Fjord ecosystems in the high Arctic are useful model systems in which to study ecological processes as they include both shallow and deep-water habitats, and the oceanographic and advective regimes are often more tractable than in open shelf systems. The objectives of our study were to: (1) identify the main carbon source(s) in the Isfjorden food-web in the Svalbard Archipelago, (2) investigate how the carbon sources and trophic position of benthic organisms in Isfjorden food-webs may vary with depth, (3) investigate potential consequences of these results for variability in food web structure, and for the paradigm of Arctic pelagic-benthic coupling in general.

Materials and Methods

Study Site and Sampling

Isfjorden is the largest fjord in the Svalbard archipelago. It is 170 km long, 24 km at its widest and up to 455 m deep (Figure 1). It is located on the west side of the Spitsbergen island and oriented in a South-West (78°7′N)—North-East (78°27′N) direction. The fjord is linked directly to the shelf and slope area along West Spitsbergen as it has no shallow sill at its mouth, thus permitting inflow of Atlantic Water from the West Spitsbergen Current (Nilsen et al., 2008; Forwick and Vorren, 2009). However, the inflow of Atlantic Water varies among years, with along-shore wind fields 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, and deeper waters influenced by ice formation (Nilsen et al., 2008; Forwick and Vorren, 2009).

All samples were collected during the summer and autumn of 2012 (Figure 1, Table 1) during research cruises, mostly in the outer 30–40 km of the fjord, with the ships RV “Viking Explorer” (August 4–7th), RV “Johan Hjort” (August 17–23rd), and RV “Helmer Hansen” (September 22nd–October 5th). Pelagic particulate organic matter (Pelagic POM) was sampled using a rosette water sampler and filtered on pre-combusted MG/F (0.7 μm pore size, 250 mL sea water filtered per sample; Stations P11–P24) or pre-combusted GF/F (0.7 μm pore size, 800–1500 mL sea water filtered per sample; Station H1 PHOM) filters. 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.
Although the marine benthic algal vegetation around Spitsbergen is not well known, Fredriksen and Kile (2012) have recently documented 83 algal taxa in Isfjorden, and a dense kelp community (Alaria esculenta, Laminaria digitata, and Saccharina latissima) on the south side of the fjord. Ten species/groups of macroalgae were collected by hand, or by using a triangular dredge or an algal rake (Station ISF12-1 and ISF12-2). One additional macroalgal sample (an additional sample of Desmarestia aculeata) was collected from an untethered buoy deployed at Sagaskjæret in early June (Station CB) and retrieved 22 September. 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 and frozen until analysis. Benthos and fish were collected using a variety of gears, depending on bottom type and functional groups targeted. 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 (8 mm mesh size) were used for most other sample collections (stations P11–P24). Other organisms were hand-picked from the Sagaskjæret buoy (station CB), or collected by SCUBA divers (Station HH Dive). The animals were sorted, identified, allowed to depurate (for 24–48 h at ambient temperatures in the dark, when appropriate), and frozen until analysis.

Whole organisms were frozen after depuration for 24–48 h (small organisms), and only muscle tissue was collected from fish, mollusks (except for Sepiola sp. where whole tentacles were used), and large crustaceans (e.g., decapods). One or several whole organisms constituted a single replicate sample for small crustaceans (e.g., cumaceans, amphipods, isopods) and polychaetes. For ophiuroids and asteroids, one or several arms were analyzed for each replicate. Internal viscera and gonads were analyzed for Strongylocentrotus sp. For sponges, tunicates and cnidarians, whole organisms or pieces approximately 1 cm³ were used. In the lab, 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 and stored frozen. Pelagic POM was collected from a single bottle cast at each station in August and from 3 casts (n = 3) in October. Five depths were sampled in the uppermost 50 m and then samples were taken every 50–100 m below this level. One sediment sample was taken from each station, and five replicates of each macroalgal source were analyzed. Replication ranged from 1 to 10 (usually 3–5) for each invertebrate and fish taxon per station, although every taxon was not collected from all stations.

**Stable Isotope Analysis**

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. Internal standards (acetanilide, caffeine, and fish muscle) were run every 8–10 samples. The reproducibility, as determined by the standard deviation of the internal standards, was ± 0.2‰ for both δ¹³C and δ¹⁵N. Because carbonates are isotopically enriched in ¹³C relative to organic matter and are not necessarily...
TABLE 1 | Sampling sites and collection information.

| Station | Date (2012) | Substrate | Latitude (N) | Longitude (E) | Depth (m) | Gear |
|---------|-------------|-----------|--------------|--------------|-----------|------|
| ISF12-1 | 04 August   | Rocky     | 78° 33.7     | 16° 32.3     | 10–14     | Δ-dredge |
| ISF12-2 | 05 August   | Rocky     | 78° 15.0     | 15° 25.0     | 1–2       | Algal rake, Hand, Littoral |
| ISF12-2 | 06 August   | Rocky     |              |              |           |      |
| ISF12-2 | 18 August   | Rocky     |              |              |           |      |
| P11     | 17 August   | Soft      | 78° 11.0     | 13° 42.3     |           | Beam trawl, CTD/rosette, Grab, WP2 |
| P12     | 18 August   | Soft      | 78° 8.7      | 13° 46.5     | 414       | Beam trawl, Campelin trawl, CTD/rosette, Grab, Harstad trawl |
| P13     | 17 August   | Soft      | 78° 6.8      | 13° 47.4     | 198       | Beam trawl, CTD/rosette, Grab, WP2 |
| P21     | 20 August   | Soft      | 78° 16.0     | 14° 33.3     | 273       | Beam trawl, Campelin trawl, CTD/rosette, Grab, Harstad trawl |
| P22     | 17 August   | Soft      | 78° 11.1°    | 14° 43.2     | 214       | Beam trawl, Campelin trawl, CTD/rosette, Grab, Harstad trawl |
| P23     | 17 August   | Soft      | 78° 8.9      | 14° 46.8     | 198       | Beam trawl, CTD/rosette, Grab, WP2 |
| P24     | 17 August   | Mud       | 78° 17.5     | 14° 30.7     | 120       | Beam trawl, CTD/rosette, Grab, WP2 |
| HH POM  | 22 Sept     | –         | 78° 10.0     | 14° 10.0     | 15        | CTD/rosette |
| HH dive | 04 October  | Rocky     | 78° 5.9      | 13° 56.0     | 0–25      | Diving |
| HH Cope | 05 October  | –         | 78° 29.0     | 16° 06.0     | 100-0     | WP2 |
| CB      | June        | –         | 78° 12.5     | 13° 57.1     | 1         | Buoy |

The longitude and latitude for the CB station refers to when and where the buoy was deployed. The buoy was retrieved 22 August near the HH POM station. Depths for the CTD, Harstad trawl, and plankton net (WP2) represent the depth range of data collection.

Representative of assimilated carbon from potential food sources, these were removed from all echinoderm specimens, and from sediments, by reacting the samples in 0.2 M H$_3$PO$_4$ for 4 h 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 δ$^{15}$N values were obtained from non-acidified samples, whereas δ$^{13}$C data came from acidified echinoderm and sediment samples (Søreide et al., 2006b; Mateo...
et al., 2008). Lipids are depleted in $^{13}\text{C}$ relative to other major biochemical compounds (proteins and carbohydrates), and a difference in lipid content in different organisms or tissues may lead to considerable bias in comparison of stable isotope values if this is not taken into account. A lipid correction was therefore performed after sample analysis using the lipid-normalization equation (Equation 1, Post et al., 2007) and the measured carbon-to-nitrogen ratio (C:N), for all samples containing more than pure muscle tissue (i.e., non-corrected values were used for decapods and post-larval fish).

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} + ((0.99) \times (\text{C:N}) - 3.32) \quad (1)$$

**Data Analyses**

To reduce the potential number of carbon sources in later analyses, a Tukey’s test (Tukey’s honest significance difference test at alpha = 0.05) was run on $\delta^{13}\text{C}$ values for all macroalgal carbon sources following an analysis of variance (ANOVA). Also, to simplify analyses and interpretation, fauna from stations with similar depths were pooled, resulting in 4 depth zones (0–25 m; station HH, 120–200 m; stations P11, P13, P23, and P24, 210–270 m; stations P21 and P22, 410 m; station P12). Previous stable-isotope studies in a nearby fjord (Kongsfjorden) indicated minimal spatial variation in food-web structure on the scale of 10 s of km (Renaud et al., 2011; Kędra et al., 2012), so we expect little bias from combining data from several stations into the depth intervals. Isotopic values for pelagic POM were calculated as weighted station means to account for different amounts of C or N filtered from bottles at different depths.

In order to compare trophic levels and carbon flow among organisms living at different water depths, the isotopic values for nitrogen and carbon at the base of the food-web are needed. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of primary producers, however, can vary significantly both among species and on spatial/temporal scales. Primary consumers have generally less variable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than primary producers and can represent a temporally and spatially integrated signal of the primary producers in the system (Post, 2002; Ikem et al., 2010; McMeans et al., 2013).

Trophic levels (TL) for each consumer were calculated from their $\delta^{15}\text{N}$ value using Equation (2):

$$\text{TL}_{\text{consumer}} = \left[ \left( \delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}} \right) / \Delta \delta^{15}\text{N} \right] + \text{TL}_{\text{base}} \quad (2)$$

where the copepod mean $\delta^{15}\text{N}$ was used as the baseline (avg ± stdev = 7.2 ± 0.6, n = 9) and represented a TLbase of 2 (as in McMeans et al., 2013). A value of 3.4‰ was used for the trophic-level fractionation constant, $\Delta \delta^{15}\text{N}$ (Post, 2002; Søreide et al., 2006a).

Values of $\delta^{13}\text{C}$ are generally heavier in macroalgae relative to phytoplankton, and these have been baselines in two end-member stable-isotope mixing-models (Fredriksen, 2003; McMeans et al., 2013). Two primary consumers were therefore chosen as baselines for calculations of the reliance on phytoplankton relative to macroalgae ($\alpha$) in Equation (3). Copepods were chosen as a baseline for a phytoplankton grazer (−22.3‰; see Results for Figure 3), and the sea urchin Strongylocentrotus sp. from station HH (0–25 m, where it is likely to exhibit a grazing strategy) was chosen as baseline for the macroalgal grazer (−15.7‰; see Results for Figure 3).

$$\alpha = \left( \delta^{13}\text{C}_{\text{consumer}} - \left[ \Delta^{13}\text{C} \times (\text{TL}_{\text{consumer}} - \text{TL}_{\text{base}}) \right] - \delta^{13}\text{C}_{\text{Strongylocentrotus}} \right) / \left( \delta^{13}\text{C}_{\text{Copepoda}} - \delta^{13}\text{C}_{\text{Strongylocentrotus}} \right) \quad (3)$$

where $\Delta^{13}\text{C}$ was set to 4‰ for the first trophic step (Hobson et al., 1995) and 1‰ thereafter (Renaud et al., 2011; Kędra et al., 2013). TLbase is 2 and TLconsumer is the result of the calculated trophic level from Equation (2). The percentage contribution of phytoplankton/POM integrated into the $^{13}\text{C}$ isotopic signature in a consumer, therefore, is 100 × $\alpha$.

**Results**

**Carbon Sources in the Isfjorden System**

Thirteen different potential carbon sources were sampled and analyzed for their contribution to the benthic and pelagic food-webs of Isfjorden. These included sampling of POM on two dates, sediment POM, and 10 algal taxa, groups, or regions of the algal thallus. On an individual replicate level, values for all potential carbon sources varied considerably (Figure 2). August POM was highly variable in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, with station means between −27.0 and −23.0‰ (δ13C) and −0.4−8.8‰ (δ15N). The single POM sampling in October fell in the middle of this range. Station means for sediment POM ranged from −24.3 to −19.0‰ (δ13C) and 3.6 to 6.5‰ (δ15N). Red algae were highly depleted in $^{13}\text{C}$, with values less than −28.0‰ (Figure 2). Brown algae as a group were highly variable in $\delta^{13}\text{C}$, but less so in $\delta^{15}\text{N}$ (Supplementary Material Table S1).

The Tukey’s HSD test following the ANOVA on macroalgal $\delta^{13}\text{C}$ values identified two distinct groups of brown algae: *Chorda filum*, *Desmarestia aculeata*, and *Saccharina latissima* (Phaeophyceae 1); and *Devaleraea ramentacea*, *Fucus sp.*, *Laminaria digitata* stipe, *L. digitata* lamina, and *Pylaiella littoralis*/*Ectocarpus fasciculatus* (Phaeophyceae 2), and identified two red algal groups (*Phycodrys* and *Polysiphonia*/*Rhodomela*, and *Odontonthalia*) (Rhodophyta) groups as distinct (Figure 2). These carbon-source classes formed the basis for a graphical assessment (Figure 3) of which carbon sources contributed most to benthic and pelagic food-webs. Source classes were plotted along with their predicted fractionation trajectories, and with presumed (from literature information) primary consumers. For simplicity, the Rhodophyta were pooled in this figure, although they were identified as separate groups by the Tukey’s test. A fractionation of 4‰ for $\delta^{13}\text{C}$ between the first two trophic levels, and then 1‰ between trophic level 2 and trophic level 3 was used to construct trajectories based on the mean values for each source/source group (Hobson et al., 1995; Nadon and Himmelman, 2006). The trophic level fractionation used for $\delta^{15}\text{N}$ was 3.4‰.

The pelagic grazer groups Copepoda and *Calanus* spp. had identical $\delta^{15}\text{N}$ values and dual isotope values that fell near the hypothetical fractionation trajectory for pelagic POM in the respective collection seasons, suggesting POM is the primary
carbon source for these taxa. All benthic primary consumers were more enriched in δ13C than trajectories predicted for Rhodophyta, pelagic POM, and sediment POM. They did, however, have carbon signatures consistent with significant contributions of the brown algal groups Phaeophyceae 1 and Phaeophyceae 2 (Figure 3). The range in δ15N for the presumed trophic level 2 (TL 2). Abbreviations are as follows: Bala, Balanus sp.; Bath, Bathyarca glacialis; Chla, Chlamys islandica; Cili, Ciliocardium ocellatum; Hiat, Hiartella arctica; Nucu, Nuculana pemula; Stro, Stronglylocentrotus sp.; and Test, Testudinaria testudinalis. Phaeophyceae 1 consists of the algal species Chorda filum, Desmarestia aculeata, and Saccharina latissima, and Phaeophyceae 2 consists of Devaleraea ramentacea, Fucus sp., Pylaiella littoralis/Ectocarpus fasciculatus, and Laminaria digitata (stipe and lamina). Horizontal lines indicate the δ15N position of TL 2 and 3 based on Calanus values.

FIGURE 2 | Isotopic distribution of all collected carbon sources. The boxes represent the full range of data from all replicates of the respective carbon sources (maximum and minimum δ13C and δ15N). Abbreviations are as follows: Chor, Chorda filum; Desm, Desmarestia aculeata; Deva, Devaleraea ramentacea; Lami blade, lamina of Laminaria digitata; Lami stipe, stipe of Laminaria digitata; PyEc, Pylaiella littoralis/Ectocarpus fasciculatus; and Sacc, Saccharina latissima.

FIGURE 3 | Isotopic composition of carbon sources (average values of all stations) and primary consumers (average values per depth interval). Dashed lines represent fractionation lines between potential carbon sources and primary consumers assuming an initial fractionation of 4‰ between TL 1 and 2 and then 1‰ between TL 2 and 3 for δ13C, and 3.4‰ for δ15N between each TL. Copepoda and POM August are the averages of all Copepoda and POM samples, respectively from stations P11–P24 (collected in August). Calanus spp. is the average of the Calanus from station HH Cope (collected in October). Both Calanus and Copepoda are assigned trophic level 2 (TL 2). Abbreviations are as follows: Bala, Balanus sp.; Bath, Bathyarca glacialis; Chla, Chlamys islandica; Cili, Ciliocardium ocellatum; Hiat, Hiartella arctica; Nucu, Nuculana pemula; Stro, Stronglylocentrotus sp.; and Test, Testudinaria testudinalis. Phaeophyceae 1 consists of the algal species Chorda filum, Desmarestia aculeata, and Saccharina latissima, and Phaeophyceae 2 consists of Devaleraea ramentacea, Fucus sp., Pylaiella littoralis/Ectocarpus fasciculatus, and Laminaria digitata (stipe and lamina). Horizontal lines indicate the δ15N position of TL 2 and 3 based on Calanus values.
primary consumers is relatively high, ranging over more than 5.6‰; the lowest value was found in *Strongylocentrotus* sp. at 0–25 m ($\delta^{15}N = 4.5\%o$) and the highest value was found for *Similipseten greenlandicus* at 210–270 m ($\delta^{15}N = 10\%o$). The $\delta^{15}N$ values for primary consumers were generally higher from deeper stations (210–270 and 410 m) than from the shallower stations (0–25 and 120–200 m), but replication levels were not sufficient for statistical testing (Figure 3).

**Variation in Carbon Source with Depth: A Mixing-model Study**

Carbon and nitrogen stable isotope values were determined for a total of 526 samples from 105 taxa (plus sediment and POM), and faunal values ranged from $-24.1$ to $-16.2\%o$ for $\delta^{13}C$ and 5.0–15.0‰ for $\delta^{15}N$, with calculated mean trophic-levels ranging from 1.4 (*Musculus* sp. at 0–25 m) to 4.4 (*Icasteiras panopla* at 410 m). Taxon means for each station are provided in the Supplementary Material (Table S1).

The relative contribution of POM vs. Phaeophyceae 2 in the $\delta^{13}C$ signatures of benthic organisms varied considerably, from 0% (*Socarnes* sp. from 0 to 25 m depth) to over 92% (*Hormathia nodosa*, 0–25 m), whereas all pelagic organisms derived over 80% of their carbon signature from POM, except for the hyperbenthic boctail squid *Sepiola* sp. (58% from 120 to 200 m) and the krill *Thysanoessa inermis* (68%, 410 m) (Figure 4). Larval/post-larval fish of a variety of species had a POM dietary-component of 90 to >100% (values >100% indicate inaccuracies in fitting mixing models to all taxa at all locations). At the shallowest station (0–25 m, Figure 4A), the reliance on phytoplankton as a carbon source varied from under 20% to over 70% for benthic organisms at or below trophic level 2. Barnacles and filter feeding polychaetes and bivalves (Sabellidae and *Hiatella arctica*) had a signature consistent with assimilating more than 48% macroalgal material. At the highest trophic levels, benthic predators and scavengers like the spider crab *Hyas araneus* and the decapod *Lebbeus polaris* received 60–75% of their carbon from POM, while the large predatory/scavenging gastropod *Buccinum* sp. derived only 23% of its carbon from POM. Four actinarians (*Hormathia nodosa*, *Urticina eques*, *Sagartia troglodytes*, and *Actinia equina*) were also among the taxa at the highest trophic levels and had POM shares of between 65 and 92%.

A large share (55–69%) of macroalgal carbon was also observed in suspension feeding bivalves (*Chlamys islandica*, *Nuculana pernula*, *Ciliocardiun ciliatum*) between 120 and 200 m (Figure 4B), whereas predatory fish, decapods, and

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**FIGURE 4** | Plots of trophic level vs. % reliance of the organism’s diet on phytoplankton for benthic (circles) and pelagic (triangles) taxa. Results are from mixing models with endpoints assuming Copepods feeding on 100% phytoplankton and *Strongylocentrotus* from 0 to 25 m depth feeding on 100% Phaeophyceae 2 material (these are marked in black symbols on each plot). (A): 0–25 m, (B): 120–200 m, (C): 210–270 m, (D): 410 m. Symbol-label abbreviations clarified in Appendix.
echinoderms exhibited diets of mixed carbon source (30–80% POM). A similar pattern was observed at the 210–270 m depth range (Figure 4C), where benthic suspension feeders generally had a reliance on POM of <50%. Pelagic crustaceans (Thysanoessa sp., Themisto spp.) and jellies (ctenophores, Cyanea capillata) were found to have a carbon signature consistent with a 5–25% contribution from Phaeo 3. Most larval fish species had a reliance on POM between 100 and 110%, whereas other pelagic fish were over 80% consistent with a phytoplankton carbon source (Figure 4C). Top benthic predators in this depth range had variable contribution from POM: predatory/scavenging gastropods and sea stars (Admete sp., Bucinum sp., Henricia sp.) had low values consistent with an over 70% contribution of Phaeo 3 material, while benthic-feeding fish, decapods, and ophiuroids (Rajidae, Lumpenus lampraetiformis, Artediella atlantica, Sabinea septemcarinata, Ophioantha bidentata, and Ophiocoleus glacialis) had 50–75% reliance on phytoplankton (Figure 4C). Finally, a similar trend toward relatively low POM contribution to benthic suspension feeders and some top predators, and consistently high reliance on POM for most pelagic taxa, was observed at the 410 m station (Figure 4D). One notable exception was the krill Thysanoessa inermis having over 30% contribution of Phaeo 3 material in its δ¹³C signature. In general, deposit and scavenging polychaetes of trophic level 2.5–3.5 (maldanids, polynoids, lumbrinerids, nephrys) had a POM contribution of 40–60% at all depth intervals (Figure 4).

Discussion

Carbon Sources in the Isfjorden System

Arguably, the most important knowledge gap in Arctic marine food-web studies is the identification of spatial and temporal variability in primary carbon sources. The 12 different potential carbon sources (plus one sampled in two seasons) sampled in this study represent the largest such investigation performed in the Arctic. The range in δ¹³C signatures of over 20% suggests isotopic analysis is a valuable tool for identifying carbon source. As in other studies (Hobson et al., 1995; Dunton, 2001; Nadon and Himmelman, 2006), red algae were severely depleted in δ¹³C. Brown algal groups, POM, and sediment organic matter had ratios varying by more than 10‰. Sediment POM in our study had a δ¹³C signature similar to that of POM, unlike in the study of Sokolowski et al. (2012) from Hornsund, a fjord south of Isfjorden on Svalbard. They found the signature to fall between POM and macroalgae, and suggested this was the main carbon source for the benthos.

Our study did not sample three sources that may contribute to Arctic food-webs: terrestrial carbon, ice algae, and microphytobenthos. In addition, ¹³C-enrichment of POM during sinking may provide the heavy carbon signal seen in the benthos. Minimal sea-ice has been observed in Isfjorden for well over 5 years, and there is little terrestrial vegetation around the fjord, suggesting these two sources may contribute very little to food webs here. Microphytobenthos, however, may exhibit photosynthetic rates equaling or exceeding that of phytoplankton in shallow water (<30 m) Arctic systems (Glud et al., 2002, 2009; Woelfel et al., 2010). This source would likely provide a heavy δ¹³C signal analogous to that from brown macroalgae (Nadon and Himmelman, 2006), but this source was not sampled in this study. It is, however, questionable as to whether microphytobenthos could be relevant at the deep stations in Isfjorden. Estimates of production in shallow waters in Arctic systems are comparable to pelagic productivity (Woelfel et al., 2010), but both pelagic and macroalgal productivity will exceed these values in deeper waters. A final possibility is that isotopic enrichment of pelagic POM during sinking may have a similar signal to that of brown macroalgae. The enrichment necessary over a maximum depth of 400 m would be ≥6‰, and the literature shows mixed findings as the change in carbon isotope values of POM with depth: from an enrichment of 4% to strong depletion of over 5% (Nakatsuka et al., 1997; Tamelander et al., 2006; Nerot et al., 2012). So while this remains a possibility, it is not clear how likely it is.

To identify candidate carbon sources for our mixing model, we investigated fractionation trajectories using an initial fractionation between primary producer and primary consumer of 4‰. This is recommended in such analyses by Nadon and Himmelman (2006), as such a fractionation between POM and benthic suspension feeders has been observed in numerous studies (Hobson et al., 1995; McMahon et al., 2006; Tamelander et al., 2006; Renaud et al., 2011). Using a 1‰ fractionation for this first step would suggest a higher contribution of macroalgal material (or other source with a heavy signature), than POC even for pelagic grazers (Calanus). From the fractionation trajectories we used, however, the most likely carbon source for grazing zooplankton was identified to be POM. The other end-member chosen was Phaeo 3, including a group of abundant nearshore taxa including kelp (Laminaria digitata) and rockweeds (Fucus spp.). The sea urchin Strongylocentrotus sp. had carbon isotopic values consistent with this group of algae making up a large portion of its diet, although its δ¹⁵N values were strangely depleted for what would be expected from an organism at TL2. Perhaps internal fractionation pathways, or even relative contributions of somatic vs. reproductive tissue, may be responsible, but we have no information to identify the cause. Regardless, this does not affect the a values calculated from the mixing model as those are based only on the δ¹³C value and the assumption that sea urchins should be at around TL2 in shallow waters.

There is some suggestion that ¹³C-enriched sources may contribute to the food web in our study since some primary consumers are more enriched than suggested by the trajectory for kelp. Recent studies indicate that aging of kelp thalli for 1–2 weeks can enrich the δ¹³C signature by approximately 1 ‰ (C. Buchholz, Alfred-Wegener-Institute, pers. comm.), suggesting aged macroalgal detritus as one pathway to a heavier food source. As discussed above, microphytobenthos may be another. But most primary consumers, including a known grazer of these macroalgae in shallow waters (Strongylocentrotus sp.), have signatures consistent with a significant contribution of Phaeo 3, even at deeper stations. A similar pattern was found for benthic suspension-feeders in Hornsund at depths less than 100 m (Sokolowski et al., 2012). It is important to keep in mind...
that a two-member mixing model is still a simplification of actual diet mixtures from which benthic fauna will derive their $\delta^{13}$C signatures.

**Variation in Carbon Source and Trophic Position with Depth**

Carbon-isotope signatures of many benthic organisms were consistent with significant contributions of brown macroalgal material at all depths investigated. This was particularly evident for lower trophic level organisms, both grazers and suspension feeders, but at least one predator and scavengers at a trophic level of between 3 and 4 exhibited a $>70\%$ share of Phaeo 3 organic matter at each depth interval. Previous benthic food-web studies in a nearby fjord did not find much difference in $\delta^{13}$C from primary consumers up through the food chain (Renaud et al., 2011; Kędra et al., 2013), and carbon sources were interpreted to be wither pelagic POM or terrestrial carbon. In this study, however, we sampled from a greater range of water depths, and this may partly explain the contrast in results. The relative abundance of macroalgae in the two fjords is not known.

Ours is the first study indicating that macroalgal detritus can contribute significantly to both shallow-water and deep-water food-webs in the Arctic. In temperate systems, kelp detritus has been found to have a significant impact on benthic food-webs where submarine canyons serve as a conduit for export to the deep sea (Vetter and Dayton, 1998; De Leo et al., 2010). The proximity of deep waters ($>400$ m) to macroalgal habitat in steep-sided fjords may be responsible for the strong macroalgal signal in deep-fjord benthos since the fjord geomorphology can facilitate rapid resuspension of both detrital macroalgal material and deposition onto the fjord bottom of whole thalli dislodged by storms.

Carbon from the kelp *Laminaria hyperborea* plays an important role in near-shore systems in sub-Arctic Norway, where it was found to constitute the ultimate carbon source for benthic organisms exhibiting several different types of feeding strategies (Fredriksen, 2003). A wide range ($0$–$100\%$) in the proportion of kelp carbon in the diets of benthic organisms was found from Arctic (Dunton and Schell, 1987) and Antarctic (Dunton, 2001) benthos. In contrast to their results, we found few benthic taxa with under $30\%$ macroalgal-derived carbon, but we collected few samples from the groups that they documented as having high POM contributions (bryozoans, soft corals, sponges). McMeans et al. (2013) investigated the food-webs at a shallow-water site near Baffin Island, Canadian Archipelago, and found that benthic grazers (limpets, snails) nearly exclusively fed on macroalgae, and a polychaete of trophic level 2.4 had an isotopic signal indicating a reliance on macroalgae of over $85\%$. Other benthic taxa, from suspension-feeding bivalves to predatory gastropods, had only $30$–$60\%$ reliance on macroalgal carbon in their diet. We replicated their mixing-model approach in our study and found comparable results, but a stronger reliance on macroalgae throughout the food web, including a $50$–$80\%$ share of macroalgae in suspension feeding bivalves and a $65$–$80\%$ share in predatory gastropods, regardless of depth. Our findings of very high reliance on POM for pelagic taxa were also similar to those of McMeans et al. (2013).

Based on their mixing-model results, McMeans et al. (2013) proposed a conceptual model of food-web structure, whereby a few lower trophic-level taxa from pelagic and benthic food-webs feed nearly exclusively on POM and macroalgae, respectively, and other taxa derive their nutrition from a broad mixture of the two (or more) carbon sources. This, they suggested, leads to a unimodal curve in the relationship between trophic level and percent reliance on POM, with sharp slopes between $0$ and $20\%$ POM and $80$ and $100\%$ POM. Our data are consistent with this concept of multiple energy channels in coastal marine food-webs and the high reliance of pelagic organisms on POM, but also suggest that in coastal systems favoring down-slope transport of macroalgal material, the pattern can extend to deep waters. Further, we found little support for a strong unimodal signal at most depths (see Figure 4). Some benthic taxa at the highest trophic levels were found with more than $80\%$ reliance on macroalgae, while others had $30$% or less. In addition, suspension-feeding bivalves in our study had variable, but often larger, shares of macroalgal material than found by McMeans et al. (2013). Our results are similar, however, in that many benthic taxa with trophic levels above $2.5$ had a broad mixture of carbon sources in their diets. The few pelagic taxa that did not strictly follow this pattern, *Sepiola* sp. and *Thysanoessa inermis* (from $410$ m), probably feed to some degree near the sea floor. The small squid is hyperbenthic and likely preys on epibenthic organisms and thus has a signal consistent with benthic carbon sources. Genetic analyses of gut contents from another species of krill (*Meganyctophanes norvegica*) identified significant amounts of sediment-associated prey, indicating a previously unknown carbon pathway linking the benthos to the pelagic food web (Cleary et al., 2012) that may be relevant in Isfjorden as well.

Studies from only two locations (Baffin Island, Isfjorden) are not sufficient to adequately test this conceptual model, however. The unimodal shape of this distribution is dependent upon the taxa sampled in the study, and the degree of opportunism/specialization (at the individual, location, or species level) in the taxa chosen. Local variability in transport and depositional processes will also affect the carbon-source signal in these taxa. Tissue turnover-time is another issue that may affect the shape of this distribution. Differential motility and/or highly omnivorous diets may also play some role in determining the ultimate carbon sources for benthic feeders at higher trophic levels: fish, decapods, and large echinoderms generally have a higher proportion of POM in their diets. Relatively sessile actinarians also exhibit a high proportion ($50$–$85\%$) of POM, but this is most likely due to the large proportion of zooplankton, and even picoplankton, in their diets (Sokolowski et al., 2012).

**Consequences and Implications for Arctic Food-webs**

The paradigm of tight pelagic-benthic coupling on Arctic shelves has been a valuable tool and null model guiding studies over the past several decades. When pelagic and benthic parameters (stocks and processes) varying on similar scales are compared, it has shown remarkable consistency (Renaud et al., 2008), and may be useful in management-related questions by helping to identify hotspots of system productivity (Link et al., 2011;...
Darnis et al., 2012; Kędra et al., 2012; Conlan et al., 2013; Roy et al., 2014). The importance of this link, however, may affect sampling design and hinder objective interpretation of data. Bivalve growth patterns have been suggested to be of high value as a proxy of climate in the Arctic due to the ability to link growth of filter feeders (Ambrose et al., 2005; Carroll et al., 2011) to presumed variability in pelagic productivity. At all depths in coastal Isfjorden, however, filter-feeding bivalves (Ciliatocardium, Hiattella, Chlamys, Similipecten) have a signature consistent with over 50% assimilation of macroalgal carbon. These results do not invalidate the climate proxy studies, but the understanding of multiple nutritional channels in the coastal benthos may improve data interpretation.

A second example of where the pelagic-benthic coupling paradigm may improperly influence ecological studies on Arctic shelves is where food-web studies have focused on POM (and perhaps ice algae) as the most likely sources of carbon for the food web. Particularly in coastal systems, macroalgae (and other sources) may contribute equally or even more. POM and sediments are often sampled in benthic food-web studies, and where faunal signatures are not consistent with a POM source, terrestrial carbon input is suggested to be the next most likely candidate source (Iken et al., 2010; Feder et al., 2011; Renaud et al., 2011; Kędra et al., 2012). This argument is usually invoked to explain lighter δ13C signatures than those from POM, whereas heavier signatures have invoked the potential role of ice algae (Søreide et al., 2006a; Tamelander et al., 2006), a source not tested but also not likely present in largely ice-free Isfjorden. Our study indicates quantitatively how benthic macroalgae can reduce the relative contributions of pelagic food sources to benthic components of coastal systems, even down to 400 m. This information highlights the need for thorough sampling of potential carbon-baselines in food-web studies, and use of mixing models to determine relative contributions of different carbon sources. Further, studies lacking good resolution of potential sources should take care when using a single second trophic-level organism as a proxy for the baseline since our results indicate that use of copepods vs. suspension-feeding bivalves would lead to quite different interpretations of food-web structure.

Detrital carbon in sediments has been suggested to promote stability in food-webs (Moore et al., 2004; McMeans et al., 2013), and may dampen the impacts of seasonal fluctuations in deposition of fresh phytodetritus (Norkko et al., 2007). This is likely to be particularly relevant in high-latitude systems where productivity occurs in discrete pulses. Taxa exhibiting omnivory and seasonal switching in nutritional channels will be able to best take advantage of such a sedimentary carbon pool. We show that much of the benthic community sampled contains a mixture of carbon sources, regardless of functional group, even during late summer. Even suspension feeders, usually presumed to feed primarily on phytodetritus, are clearly incorporating significant amounts of resuspended macroalgal detritus. A system where pulses of higher-quality food sources are buffered by abundant detrital sources may enhance biodiversity if it leads to reduced competition and well-developed recycling processes.

Macroalgae in both Arctic and Antarctic systems are predicted to increase with warming temperatures and reduced sea-ice cover (Krause-Jensen et al., 2012; Clark et al., 2013) and this may already be occurring in some areas (Wełaslawski et al., 2011; Kortsch et al., 2012). If recent results (McMeans et al., 2013; this study) are applicable to wider area of the Arctic, greater macroalgal production could set off a series of complex changes in coastal benthos, whereby sessile invertebrates can be replaced by habitat-engineering macroalgae and associated invertebrates, and fresh macroalgal and detrital food-webs are enhanced (Kortsch et al., 2012; Krause-Jensen et al., 2012; Clark et al., 2013). Reliance on recycling-based pathways, however, may reduce secondary production and negatively impact the value of coastal benthic communities as feeding resources for fish, seabirds, and mammals.

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Supplementary Material

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## Appendix

### TABLE A1 | List of abbreviations used for taxa in Figure 4 and the taxon and larger taxonomic group referred to.

| Abbreviation | Taxon | Taxonomic group | Habitat | Feeding strategy |
|--------------|-------|-----------------|---------|------------------|
| Acti         | Actinia equina | Actinaria | Benthic | Pred/Scav |
| Adme         | Admete viridula | Gastropoda | Benthic | Pred/Scav |
| Anaj         | Anarhichas lupus—juv | Vertebrata | Pelagic |       |
| Anij         | Anarhichas medus—juv | Vertebrata | Pelagic |       |
| Anh          | Anthis phyllonyx | Amphipoda | Benthic | Pred/Scav |
| Arte         | Artedielius atlanticus | Vertebrata | Benthic | Predator |
| Bala         | Balanus sp. | Cirripedia | Benthic | Suspension |
| Bath         | Bathya caricea | Bivalvia | Benthic | Suspension |
| Bero         | Beroe cucumis | Ctenophora | Pelagic | Pred/Scav |
| Bosa         | Boreogadus saida | Vertebrata | Pelagic | Predator |
| Bosj         | Boreogadus saida—juv. | Vertebrata | Pelagic |       |
| Bucc         | Buccinum sp. | Gastropoda | Benthic | Pred/Scav |
| Buch         | Buccinum hydromanum | Gastropoda | Benthic | Pred/Scav |
| Capr         | Caprella sp. | Amphipoda | Benthic | Omni |
| Chae         | Chaetognatha | Chaetognatha | Pelagic | Predator |
| Chla         | Chlamys islandica | Bivalvia | Benthic | Suspension |
| Clio         | Ciliocardioma cilium | Bivalvia | Benthic | Suspension |
| Clio         | Clione limacina | Opisthobranchia | Pelagic | Predator |
| Cluj         | Clupea harengus—juv. | Vertebrata | Pelagic |       |
| Cope         | Copepodida | Copepodida | Pelagic |       |
| Cope         | Calanus spp. | Copepodida | Pelagic | Herb |
| Cros         | Crossaster papposus | Asteroidea | Benthic | Pred/Scav |
| Cten         | Ctenodiscus crispatus | Asteroidea | Benthic | Omni |
| Ctop         | Ctenophora | Ctenophora | Pelagic | Predator |
| Cyan         | Cyanea capillata | Scyphozoa | Pelagic | Predator |
| Dena         | Dendroidea aggregata | Ascidiaeae | Benthic |       |
| Dend         | Dendronotus frondosus | Opisthobranchia | Benthic | Omni |
| Eual         | Euilus gaimardii | Decapoda | Benthic | Pred/Scav |
| Gadj         | Gadus morhua—juv. | Vertebrata | Pelagic |       |
| Gadu         | Gadus morhua | Vertebrata | Pelagic | Predator |
| Gamm         | Gammaricollis hani | Amphipoda | Benthic | Omni |
| Halo         | Halocynthia pyriformis | Ascidiaeae | Benthic | Suspension |
| Heli         | Helleotrema sp. | Ophiuroidea | Benthic | Pred/Scav |
| Henr         | Henricia sp. | Asteroidea | Benthic | Pred/Scav |
| Hiat         | Histella arctica | Bivalvia | Benthic | Suspension |
| Hipp         | Hippoglossoides platessoides | Vertebrata | Pelagic | Pred/Scav |
| Horn         | Hymata nuda | Actinaria | Benthic | Pred/Scav |
| HyaL         | Hyas araneus, large | Decapoda | Benthic | Pred/Scav |
| Hyas         | Hyas araneus | Decapoda | Benthic | Pred/Scav |
| HyaS         | Hyas araneus, small | Decapoda | Benthic | Pred/Scav |
| Icas         | Icasterias panopla | Asteroidea | Benthic | Pred/Scav |
| Isch         | Ischyrocerus anguipes | Amphipoda | Benthic | Herb/Suspension |
| Lebb         | Lebbeus polaris | Decapoda | Benthic | Pred/Scav |
| Lepj         | Leptoclinus maculatus—juv | Vertebrata | Pelagic |       |
| Lepj         | Leptagonus decagonus—juv | Vertebrata | Pelagic |       |
| Lept         | Leptoclinus maculatus | Vertebrata | Benthic | Predator |
| Lifj         | Liparis faluci—juv. | Vertebrata | Pelagic |       |
| Ligj         | Liparis gibbus—juv | Vertebrata | Pelagic |       |
| Lumb         | Lumbrinae | Polychaeta | Benthic | Pred/Scav |

(Continued)
| Abbreviation | Taxon | Taxonomic group | Habitat | Feeding strategy |
|--------------|-------|----------------|---------|-----------------|
| Lumpj        | Lumpenus lampretaeformis—juv. | Vertebrata | Pelagic |                   |
| Lump         | Lumpenus lampretaeformis       | Vertebrata | Benthic | Predator         |
| Lyco         | Lycodes sp.                    | Vertebrata | Benthic | Pred/Scav        |
| Madi         | Maldanidae                     | Polychaeta | Benthic | Omni             |
| Maid         | Maldane sarsii                 | Polychaeta | Benthic | Omni             |
| Malj         | Mallotus villosus—juv.         | Vertebrata | Pelagic | Predator         |
| Mall         | Mallotus villosus              | Vertebrata | Pelagic | Predator         |
| Mals         | Maldane sp.                    | Polychaeta | Benthic | Omni             |
| Mega         | Megalopis                      | Decapoda   | Pelagic |                  |
| Meia         | Melanogrammus aeglefinus       | Vertebrata | Pelagic | Predator         |
| Mert         | Mertensia ovum                 | Ctenophora | Pelagic | Pred/Scav        |
| Musc         | Musculus sp.                   | Bivalvia   | Benthic | Suspenion        |
| Myoj         | Myxocephalus scorpius—juv.     | Vertebrata | Pelagic |                  |
| Neph         | Nephtididae                    | Polychaeta | Benthic | Pred/Scav        |
| Nere         | Nereididae                     | Polychaeta | Benthic | Pred/Scav        |
| Nere         | Nereis zonata                  | Polychaeta | Benthic | Omni             |
| Noth         | Nothia sp.                     | Polychaeta | Benthic | Pred/Scav        |
| Nucu         | Nuculana pemula                | Bivalvia   | Benthic | Suspenion        |
| Nymph        | Nymphon sp.                    | Pycnogonida| Benthic | Pred/Scav        |
| Opac         | Ophiopholis aculeata           | Ophiuroidea| Benthic | Omni             |
| Opti         | Ophiacantha bidentata          | Ophiuroidea| Benthic | Omni             |
| Opgl         | Ophiocolex glacialis           | Ophiuroidea| Benthic | Omni             |
| Opsa         | Ophura sarsii                  | Ophiuroidea| Benthic | Omni             |
| Opse         | Ophiocerion sericeum           | Ophiuroidea| Benthic | Omni             |
| Pagu         | Pagurus pubescens              | Decapoda   | Benthic | Pred/Scav        |
| Pand         | Pandalus borealis              | Decapoda   | Benthic | Pred/Scav        |
| Pect         | Pectinaria sp.                 | Polychaeta | Benthic | Suspension/     |
| Pher         | Pherusa plumosa                | Polychaeta | Benthic | Surf. deposit feeder |
| Phyl         | Phylodocidae                   | Polychaeta | Benthic | Pred/Scav        |
| Poch         | Polychaeta                     | Polychaeta | Benthic | Pred/Scav        |
| Poly         | Polynoidae                     | Polychaeta | Benthic | Pred/Scav        |
| Raji         | Rajidae                        | Vertebrata | Benthic | Predator         |
| Relj         | Reinhardtus                    | Vertebrata | Pelagic |                  |
| Rein         | Reinhardtus hippoglossoides    | Vertebrata | Pelagic | Predator         |
| Rhac         | Rhachochitos inflata           | Amphipoda  | Benthic | Pred/Scav        |
| Sabe         | Sabellidae                     | Polychaeta | Benthic | Suspenion        |
| Sabi         | Sabinea septemcarinata         | Decapoda   | Benthic | Pred/Scav        |
| Saga         | Sagartia troglodytes           | Actinaria  | Benthic | Pred/Scav        |
| Sagi         | Sagitta elegans                | Chaetognatha| Pelagic | Pred/Scav        |
| Sars         | Sarsia sp.                     | Hydrozoa   | Pelagic | Predator         |
| Seba         | Sebastes mentella              | Vertebrata | Pelagic | Predator         |
| Seba         | Sebastes mentella—small        | Vertebrata | Pelagic | Predator         |
| Semi         | Semibalanus balanoides         | Cirripedia | Benthic | Suspenion        |
| Sepi         | Sepiota sp.                    | Cephalopoda| Benthic-pelagic | Predator |
| Simi         | Similpecten greenlandicus      | Bivalvia   | Benthic | Suspenion        |
| Soce         | Socarnes sp.                   | Amphipoda  | Benthic | Pred/Scav        |
| Spir         | Spirontocaris sp.              | Decapoda   | Benthic | Predator         |
| Spon         | Sponge P21                     | Porifera   | Benthic | Suspenion        |
TABLE A1 | Continued

| Abbreviation | Taxon | Taxonomic group | Habitat | Feeding strategy |
|--------------|-------|-----------------|---------|-----------------|
| Stro         | Strongylocentrotus sp. | Echinoidea | Benthic | Grazer/Omni |
| Syno         | Synoicum turgens | Asciidiaceae | Benthic | Suspension |
| Test         | Testudinaria testudinalis | Gastropoda | Benthic | Grazer |
| Thea         | Themisto abyssorum | Amphipoda | Pelagic | Predator |
| Thec         | Thelepus cincinnatus | Polychaeta | Benthic | Suspension |
| Thel         | Themisto libellulida | Amphipoda | Pelagic | Predator |
| Them         | Themisto sp. | Amphipoda | Pelagic | Pred/Scav |
| Thin         | Thysanoessa inermis | Euphausiacea | Pelagic | Pred/Scav |
| Thys         | Thysanoessa sp. | Euphausiacea | Pelagic | Pred/Scav |
| Urti         | Urticina eques | Actinaria | Benthic | Pred/Scav |
| Velu         | Velutina sp. | Gastropoda | Benthic | Predator |

Primary habitat is also shown, along with presumed general feeding strategy. Pred/Sav, Predator/Scavenger; Omni, Omnivore; Herb, Herbivore.