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Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-produced carbon: Evidence from stomach content, fatty acid and stable isotope analyses

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ABSTRACT

The polar cod (*Boreogadus saida*) is considered an ecological key species, because it reaches high stock biomasses and constitutes an important carbon source for seabirds and marine mammals in high-Arctic ecosystems. Young polar cod (1–2 years) are often associated with the underside of sea ice. To evaluate the impact of changing Arctic sea ice habitats on polar cod, we examined the diet composition and quantified the contribution of ice algae-produced carbon (α_{Ice}) to the carbon budget of polar cod. Young polar cod were sampled in the ice-water interface layer in the central Arctic Ocean during late summer 2012. Diets and carbon sources of these fish were examined using 4 approaches: (1) stomach content analysis, (2) fatty acid (FA) analysis, (3) bulk nitrogen and carbon stable isotope analysis (BSIA) and (4) compound-specific stable isotope analysis (CSIA) of FAs.

The ice-associated (sympagic) amphipod *Apherusa glacialis* dominated the stomach contents by mass, indicating a high importance of sympagic fauna in young polar cod diets. The biomass of food measured in stomachs implied constant feeding at daily rates of ~1.2% body mass per fish, indicating the potential for positive growth. FA profiles of polar cod indicated that diatoms were the primary carbon source, indirectly obtained via amphipods and copepods. The α_{Ice} using bulk isotope data from muscle was estimated to be >90%. In comparison, α_{Ice} based on CSIA ranged from 34 to 65%, with the highest estimates from muscle and the lowest from liver tissue. Overall, our results indicate a strong dependency of polar cod on ice-algae produced carbon. This suggests that young polar cod may be particularly vulnerable to changes in the distribution and structure of sea ice habitats. Due to the ecological key role of polar cod, changes at the base of the sea ice-associated food web are likely to affect the higher trophic levels of high-Arctic ecosystems.

1. Introduction

The impact of climate change on Arctic sea ice properties, most evidently characterized by decreased sea ice coverage and thickness, has been well documented over the past decades (e.g. Johannessen et al., 1995, 2004; Rothrock et al., 1999; Kwok et al., 2009; Maslanik et al., 2011; Harada, 2016). As a result, dramatic changes are expected in terms of timing, magnitude, and the spatial distribution of both ice-associated and pelagic primary production, with subsequent impacts on higher vertebrates (Wassmann et al., 2006; Søreide et al., 2013).

Polar cod, *Boreogadus saida* (Lepechin, 1774), are highly abundant in the Arctic Ocean (Falk-Petersen et al., 1986; Harter et al., 2013; Hop and Gjøsæter, 2013) and play a key role in Arctic ecosystems, accounting for up to 75% of the energy transfer from the pelagic food web to endotherm predators (Bradstreet and Cross, 1982; Jensen et al., 1991; Benoit et al., 2010; Rand et al.,

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2013). The diet of polar cod has been frequently found to be variable and associated with pelagic and benthic food webs, dominated by copepods and amphipods (Hop et al., 1997b; Christiansen et al., 2012; Renaud et al., 2012; Majewski et al., 2016; McNicholl et al., 2016). However, polar cod are assumed to rely on sea ice for foraging, spawning and shelter using cavities, gaps and rafted ice during at least a part of the larval and juvenile phase (Lønne and Gulliksen, 1989; Scott et al., 1999; Gradinger and Bluhm, 2004; David et al., 2016). This indicates that polar cod might show an indirect dependency on the sea ice primary production when feeding on ice-associated (sympagic) fauna (Lowry and Frost, 1981; Bradstreet and Cross, 1982; Budge et al., 2008).

Studies on the carbon source and diet composition of young polar cod caught directly from underneath the ice in the high Arctic are very limited (Lønne and Gulliksen, 1989; Søreide et al., 2006). Moreover, the relative contribution of carbon originating from ice algae compared to pelagic phytoplankton to the carbon budget of polar cod has been scarcely quantified (Søreide et al., 2006). While the stomach content provides information on the very recent food compositions, fatty acid (FA) and stable isotope compositions give information on diet and carbon sources over a longer time span. Certain FAs are assumed to be transferred conservatively along the marine food web and are therefore called trophic markers (Graeve et al., 1994a; Falk-Petersen et al., 1998; Dalsgaard et al., 2003; Bergé and Barnathan, 2005; Iverson, 2009). Hence, the composition of these trophic markers in a consumer reflects the composition of FAs biosynthesized by primary producers. This qualitative investigation of predator-prey relationships based on FAs is substantially improved by its combination with stable isotope analyses of the bulk organic carbon content (BSIA - Bulk Stable Isotope Analysis) (Dehn et al., 2007; Feder et al., 2011) and/or specific FAs (CSIA - Compound-specific Stable Isotope Analysis) (Budge et al., 2008; Graham et al., 2014; Wang et al., 2015; Kohlbach et al., 2016). Algal communities differ not only in their proportions of certain FAs (Dalsgaard et al., 2003), but are also often characterized by relatively higher carbon stable isotope values (expressed as $\delta^{13}C$) in sea ice algae compared to pelagic phytoplankton (Hobson et al., 2002; Søreide et al., 2006; Budge et al., 2008). Capitalizing on this isotopic difference, the isotopic composition enables the quantification of sea ice algae-produced carbon versus phytoplankton-produced carbon to the carbon budget of a consumer. The results of the few existing CSIA-based analyses on polar cod are controversial. A recent study based on fatty acid-specific stable isotope analyses suggested a negligible ice algal contribution ($\leq$2%) to the diet of age class 0 polar cod in the ice-free Beaufort Sea at the end of summer (Graham et al., 2014). In contrast, results from an Alaskan study suggested a remarkable proportional ice algal contribution in shelf-bound adult polar cod, with values between 8 and 77%, depending on the sampling location and analytical approach taken (Budge et al., 2008). In addition, the trophic level of a consumer can be defined based on its nitrogen isotopic composition (expressed as $\delta^{15}N$) due to the stepwise enrichment in ^{15}N between each trophic level related to isotopic fractionation (Minagawa and Wada, 1984; Post, 2002).

Different tissue types integrate dietary information over different time spans due to varying turnover rates (Vander Zanden et al., 2015; Mohan et al., 2016). For example, the liver is described as a metabolically active tissue, characterized by a faster turnover rate compared to the muscle tissue (Tieszen et al., 1983; Buchheister and Latour, 2010). The half-life of carbon stable isotopes is only few days in liver tissue compared to multiple weeks in muscle tissue of bony fish (Suzuki et al., 2005). As a result, the combination of stomach content analysis and determination of FA and isotopic compositions on several types of tissues enables a more comprehensive investigation of the food resources used by consumers, giving information at several temporal scales and about the origin of carbon as well as ingested prey items.

A first basin-wide survey of polar cod in the under-ice habitat indicated that the fish were widely distributed throughout the Eurasian Basin in 2012, and potentially followed the sea ice drift from the Siberian shelf across the Arctic Ocean (David et al., 2016). In the light of their good nutritional condition and potential month-long association with drifting sea ice, it was hypothesized that the Arctic under-ice habitat constitutes a favorable environment for the fish in terms of high-energetic food supply, until they reach maturity and leave the under-ice environment (David et al., 2016). We aimed to investigate this hypothesis by assessing whether the close relationship of young polar cod from the central Arctic Ocean with the sea ice is accompanied by a diet relying on food resources provided by sea ice. We combined stomach content analysis, lipid fingerprinting and the investigation of the stable isotope composition of different polar cod tissues (muscle, liver, gonads) to reveal diet composition and carbon sources of polar cod under sea ice. Furthermore, we quantified the proportional contribution of ice algae-produced carbon to the carbon budget of polar cod, based on stomach content analyses and the isotopic compositions of polar cod tissues, respectively.

2. Materials and methods

2.1. Study area and sampling methods

Sample collection was conducted during the RV '*Polarstern*' expedition 'IceArc' (PS80; 2 August to 7 October 2012) in the Eurasian Basin of the Arctic Ocean (Table 1, Fig. 1). Detailed information on the sampling during PS80 can be found in David et al. (2015, 2016), and Kohlbach et al. (2016).

Ice-associated particulate organic matter (I-POM), representing the ice algae community, was sampled by taking ice cores with a 9 cm interior diameter ice corer (Kovacs Enterprises). Ice cores were melted in the dark at 4 °C on board and from 0.7 to 10.5 L water were filtered using a vacuum pump through pre-combusted 0.7 μm GF/F filters (Whatmann, 3 h, 550 °C). Either the whole core or the bottom part of the ice core was used. Chlorophyll *a* (Chl *a*) concentrations of the ice cores ranged from 0.4 to 6.5 mg m^{-3} (0.3–8 mg m^{-2}) (Fernández-Méndez et al., 2015). Pelagic particulate organic matter (P-POM), representing the phytoplankton community, was sampled using a carousel water sampler connected to a CTD probe (Seabird SBE9+). Water collection was performed at the surface layer and at the depth of the Chl *a* maximum (between 20 and 50 m). Depending on the biomass, from 2.0 to 11.0 L water were filtered using pre-combusted GF/F filters. Chl *a* concentrations of the water column at the Chl *a* maximum ranged from 0.2 to 1.2 mg m^{-3}. All filters were stored at −80 °C until further processing.

Polar cod were caught with a Surface and Under-Ice Trawl (SUIT) (van Franeker et al., 2009) within the uppermost 2 m surface layer. Detailed information on the description and use of the SUIT can be found in David et al. (2015). After measurements of the total lengths (TL), and the determination of the sex, fish for the lipid and stable isotope analyses were subsampled for muscle, liver and gonad tissues. The subsamples were immediately frozen at −80 °C in pre-combusted and pre-weighed sample vials (Wheaton, 6 h, 500 °C). Whole fish were frozen at −20 °C for stomach content analysis.

The condition index *CI* per individual fish in % was calculated as

$$CI = 100 * W_{ev}/WW \quad (1)$$

where W_{ev} is the eviscerated wet weight (g) and *WW* is the wet weight (g) of the individual fish.