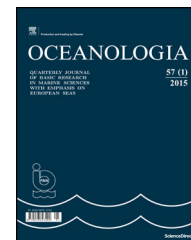




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ORIGINAL RESEARCH ARTICLE

Spatial distribution and diet of larval snailfishes (*Liparis fabricii*, *Liparis gibbus*, *Liparis tunicatus*) in the Canadian Beaufort Sea[☆]

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Summary This paper presents information on diet and distribution of larval snailfishes from the genus *Liparis* on the Canadian Beaufort Sea Shelf. In this study, 153 larval snailfishes of three species, *Liparis fabricii*, *L. gibbus* and *L. tunicatus*, were collected during 4 summer cruises (2003–2005, 2007). The majority of the larvae were either in flexion or post-flexion stage, and some were in pre-flexion stage. *Liparis* larvae appeared to be generalists in terms of diet and fed on a wide range of planktonic organisms. Pre-flexion larvae fed on small copepods (mainly adult stages of *Triconia borealis*). As larvae grew their diet shifted towards larger copepods (copepodids III/IV of *Calanus hyperboreus*, copepodids II–IV of *Calanus glacialis* and females of *Metridia longa*) and amphipods (*Themisto libellula*). Remarkably, larvaceans *Oikopleura* spp. and pelagic snails *Limacina helicina* made up a substantial part of the larval diet. This paper contributes to the knowledge on arctic larval fishes and to the ongoing efforts regarding Canadian Beaufort Sea ecosystem modeling.

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1. Introduction

Of the more than 400 snailfish species known worldwide (www.fishbase.org), eight *Liparis* species are listed as present in the Arctic (Mecklenburg et al., 2013) but only four from this genus are regularly found on the shelves and upper slopes in the Arctic seas: *Liparis fabricii* (commonly known as Gelatinous Snailfish), *L. gibbus* (known as either Variegated or Dusky Snailfish), *L. tunicatus* (known as Kelp Snailfish) and *L. bathyartcticus* (known as Nebulous Snailfish) (Able, 1990; Evseenko et al., 2006; Chernova, 2008; Mecklenburg et al., 2011). These are distributed circumpolarly and all but one (*L. bathyartcticus*) were recorded previously in the Beaufort Sea (Chiperzak et al., 2003; Jarvela and Thorsteinson, 1999; Paulic and Papst, 2013; Wong et al., 2013). All four *Liparis* species were also found in the Chukchi Sea and Bering Strait (Mecklenburg et al., 2011; Mecklenburg et al., 2007; Norcross et al., 2010), while the former three species were also collected in Hudson Bay (Morin and Dodson, 1986; Ponton et al., 1993). Snailfishes, particularly adults during the spawning period, are found in the nearshore areas that have hard substrate and often kelp beds to which the fishes show an affinity (Byers and Prach, 1988; Dunton et al., 1982).

Little is known about the ecology of snailfishes, their significance in food webs and their importance in the Arctic ecosystems, though studies so far show that they are important food source for marine birds (Gaston, 1985) and seals (Falk-Petersen et al., 2004). Adult snailfishes feed mainly on bottom-associated amphipods, polychaetes and cumaceans (Atkinson and Percy, 1992; Byers and Prach, 1988), which suggests they occupy and thus feed in the benthic habitats. Apart from a few records of larval snailfish occurrence (e.g. Paulic and Papst, 2013; Suzuki et al., 2015; Wong et al., 2013) there is virtually no published information on their ecology in the Arctic.

When compared to the neighboring locations, e.g. the Canadian Arctic Archipelago (Stern and Gaden, 2015), the Canadian Beaufort Sea Shelf (<100 m depth) holds a relatively rich fish community. In the ice-free season it consists of approximately 25 species in both bottom and pelagic habitats (Lowdon et al., 2011; Majewski et al., 2009; Paulic and Papst, 2013; Wong et al., 2013). The spatial distribution of these fishes varies in relation to the oceanographic conditions that are mainly shaped by the Mackenzie River plume and sea currents (Paulic and Papst, 2013; Wong et al., 2013). Both the larval/juvenile and adult snailfishes rank relatively high in terms of their abundance (approx. 10% of total fish abundance; Lowdon et al., 2011; Paulic and Papst, 2013; Wong et al., 2013). Snailfishes, however, remain less abundant than Arctic Cod (*Boreogadus saida*; up to 60% of total fish abundance; Paulic and Papst, 2013) and Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*, up to 13% of total fish abundance: Lowdon et al., 2011). Considering the role of fish as food for higher predators (e.g. whales), snailfishes and Arctic Cod are energetically similar prey due to their comparable weight at given length and high calorific content, which is greater than in Arctic Staghorn Sculpin, for example (Walkusz et al., 2012).

There is virtually no information existing on the feeding and growth of snailfishes in the Arctic. Although sometimes numerous in catches, snailfishes generally are an understudied component of the Arctic nearshore marine ecosystems. This motivated our research, results of which are summarized in this paper, the aim of which is to provide

new information on spatial distribution and diet of the larval snailfishes in the Canadian Beaufort Sea.

2. Material and methods

Larval fishes were collected during 4 summer expeditions (August 9–20, 2003; August 6–20, 2004; August 3–26, 2005; July 24–August 18, 2007) to the Canadian Beaufort Sea (Fig. 1), aboard the Canadian Coast Guard Ship (CCGS) *Nahidik*. For the purpose of this paper all fish larvae collected during the 4 years were pooled together, however none of the stations was sampled twice over that time. Larval fishes were collected with a 500 µm Bongo net (60 cm diameter, 300 cm total length) towed obliquely for 15–20 min from the near-bottom to the sub-surface with the speed of 2 knots. All larvae were sorted from a sample and immediately preserved in a 4% solution of formaldehyde in seawater. After approximately one month from collection all fishes were identified to species (using primarily meristic characteristics from Fahay, 2007), weighed (0.0001 g accuracy; wet mass) and measured (0.01 mm accuracy; standard length) in the lab. Larvae that were found problematic for routine identification were re-examined in the Atlantic Reference Centre (Huntsman Marine Science Centre, St. Andrews, NB, Canada). The developmental stage of each larva was determined (based on Moser et al., 1984) and its digestive tract removed. All recognizable items from the stomach/intestines were identified to the lowest possible taxonomic level. Developmental stages of larger copepod species were determined for further biomass calculations. Lengths of all remaining food items were recorded. Since the majority of the material found in the guts was damaged due to swallowing/digestion, the wet weight of the food items was calculated based on the published information for particular species and developmental stage when applicable (Hansen, 1997; Hay et al., 1991; Karnovsky et al., 2003; Mumm, 1991). ANOVA and Tukey HSD test were performed for statistical analysis of differences among species for larval stage sizes, weights and food mass.

Breadth of diet of each developmental stage of the three species was assessed with a Levin's standardized index (Hurlbert, 1978):

$$B_i = \frac{1}{n-1} \left(\frac{1}{\sum_j p_{ij}^2} - 1 \right),$$

where B_i is the Levin's standardized index for predator i , p_{ij} is the proportion of diet of predator i that is made up of prey j , and n is the number of prey categories.

This index ranges from 0 to 1 with low values indicating diets dominated by few prey items and higher values indicating broader diets.

Diet overlap between the three *Liparis* species and their developmental stages was calculated (based on the average biomass percentage of food items) using Schoener's index (α) (Schoener, 1970):

$$\alpha = 1 - 0.5 \times \left(\sum |p_{xi} - p_{yi}| \right),$$

where α is the Schoener's index, p_{xi} the proportion of food category i in the diet of species x , and p_{yi} is the proportion of food category i in the diet of species y .

The Schoener's index ranges from 0 (no dietary overlap) to 1 (complete dietary overlap).

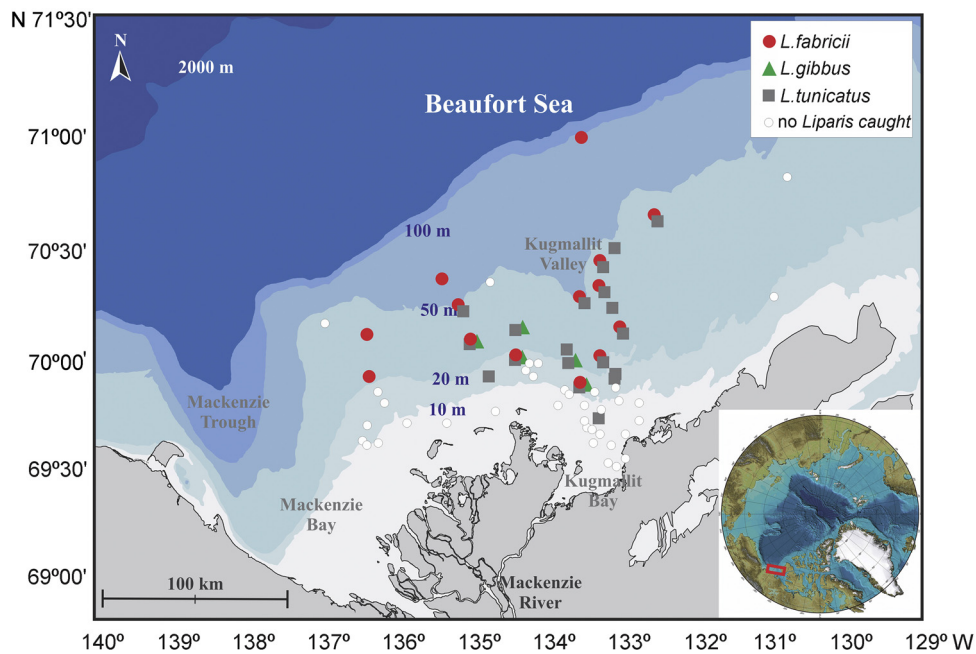


Figure 1 Map of the study area with occurrences of larval *Liparis* indicated. The general location of the study area (red rectangle) in the Arctic is presented in the insert (Arctic map source: www.ngdc.noaa.gov). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Distribution of larvae

Over the 4 years of sampling we visited 60 stations (Fig. 1). Overall, 1039 larval fishes were captured representing 12 taxa. *Liparis* larvae comprised 15% of the total with 153 individuals collected, including 83 individuals of *L. tunicatus*,

35 individuals of *L. fabricii* and 35 individuals of *L. gibbus* (Table 1). *Liparis* larvae were caught at 23 stations (Fig. 1; Table 2). With the exception of one station where *L. tunicatus* was captured, all *Liparis* larvae occurred in areas deeper than 10 m. Most stations where *Liparis* larvae were captured were between 20 and 50 m of depth. The three species were caught concurrently only at three stations. *Liparis fabricii* were captured over the greatest depth range (20–100 m) and

Table 1 Summary of weight and standard length (\pm SD) of the three *Liparis* larval species in different developmental stages. Average count of prey items and average food load mass for each developmental stage are presented. Numbers of larvae collected in each developmental stage are provided in parentheses.

Stage		Species		
		<i>L. fabricii</i>	<i>L. gibbus</i>	<i>L. tunicatus</i>
Pre-flexion	Weight [g]	0.016 \pm 0.005 (3)	0.029 (1)	0.024 \pm 0.006 (2)
	Standard length [mm]	12.7 \pm 1.3 (3)	10.2 (1)	10.5 \pm 4.4 (2)
	Av. food load abundance [ind. larvae ⁻¹]	4 \pm 4	5	1 \pm 1
	Av. food load mass [mg dw larvae ⁻¹]	0.02 \pm 0.03	0.01	<0.001
Flexion	Weight [g]	0.063 \pm 0.037 (10)	0.075 \pm 0.034 (32)	0.130 \pm 0.072 (30)
	Standard length [mm]	16.9 \pm 4.1 (10)	16.3 \pm 3.1 (32)	19.9 \pm 2.7 (30)
	Av. food load abundance [ind. larvae ⁻¹]	3 \pm 3	8 \pm 8	8 \pm 9
	Av. food load mass [mg dw larvae ⁻¹]	0.267 \pm 0.548	0.880 \pm 1.739	1.723 \pm 2.805
Post-flexion	Weight [g]	0.154 \pm 0.093 (22)	0.303 \pm 0.191 (2)	0.266 \pm 0.141 (48)
	Standard length [mm]	22.6 \pm 4.9 (22)	22.7 \pm 2.7 (2)	24.3 \pm 3.7 (48)
	Av. food load abundance [ind. larvae ⁻¹]	5 \pm 6	13 \pm 15	13 \pm 16
	Av. food load mass [mg dw larvae ⁻¹]	1.156 \pm 2.227	3.899 \pm 4.702	3.069 \pm 3.521
Juvenile	Weight [g]	—	—	0.375 \pm 0.095 (3)
	Standard length [mm]	—	—	28.4 \pm 0.9 (3)
	Av. food load abundance [ind. larvae ⁻¹]	—	—	21 \pm 18
	Av. food load mass [mg dw larvae ⁻¹]	—	—	6.636 \pm 6.171

Table 2 Occurrences of larval *Liparis* species in relation to station depth.

Depth zone [m]	No. of stations in zone	No. of stations with		
		<i>L. fabricii</i>	<i>L. gibbus</i>	<i>L. tunicatus</i>
0–10	25	—	—	1
10–20	16	2	2	5
20–50	17	8	3	12
50–100	2	2	—	—

widest geographical area, with *L. tunicatus* being over the next greatest range (10–50 m) and area. *Liparis gibbus* were captured over the narrowest depth range (20–50 m) and geographical area.

3.2. Developmental characteristics of larvae

We found more larvae in post-flexion stage for *L. fabricii* and *L. tunicatus* than for *L. gibbus* – virtually all individuals of the latter species occurred in the flexion stage. Due to the low number of pre-flexion and juvenile larvae a statistical comparison of sizes and weights for these stages could not be performed. Larvae of *L. tunicatus* in the flexion stage were longer and heavier than larvae of the two other species (ANOVA, Tukey HSD test, $p < 0.01$). There were no differences between the length and weight of flexion larvae of *L. fabricii* and *L. gibbus*. There was no difference between *L. fabricii* and *L. tunicatus* post-flexion larvae in regards to

their length (Table 1), however, *L. tunicatus* larvae were heavier (ANOVA, Tukey HSD test, $p < 0.01$). Both the sum of individual prey items and the food mass in an individual stomach increased with fish length in all species.

3.3. Diet of larvae

Overall, the diet of larval snailfishes contained 28 taxa/food categories (Fig. 2). There was no significant interspecific difference in total weight of gut contents at each developmental stage (ANOVA, Tukey HSD test, $p > 0.01$). The pre-flexion stage of all three species relied heavily on small cyclopoid copepods *Triconia borealis* and polychaete larvae. At the flexion stage, all three fish species fed on diverse food items, including the larvacean *Oikopleura* spp., the large-sized copepods *Metridia longa* and *Calanus glacialis* and the pelagic snail *Limacina helicina*. Once the larvae reached the post-flexion stage, their diet, apart from *Oikopleura* spp. and

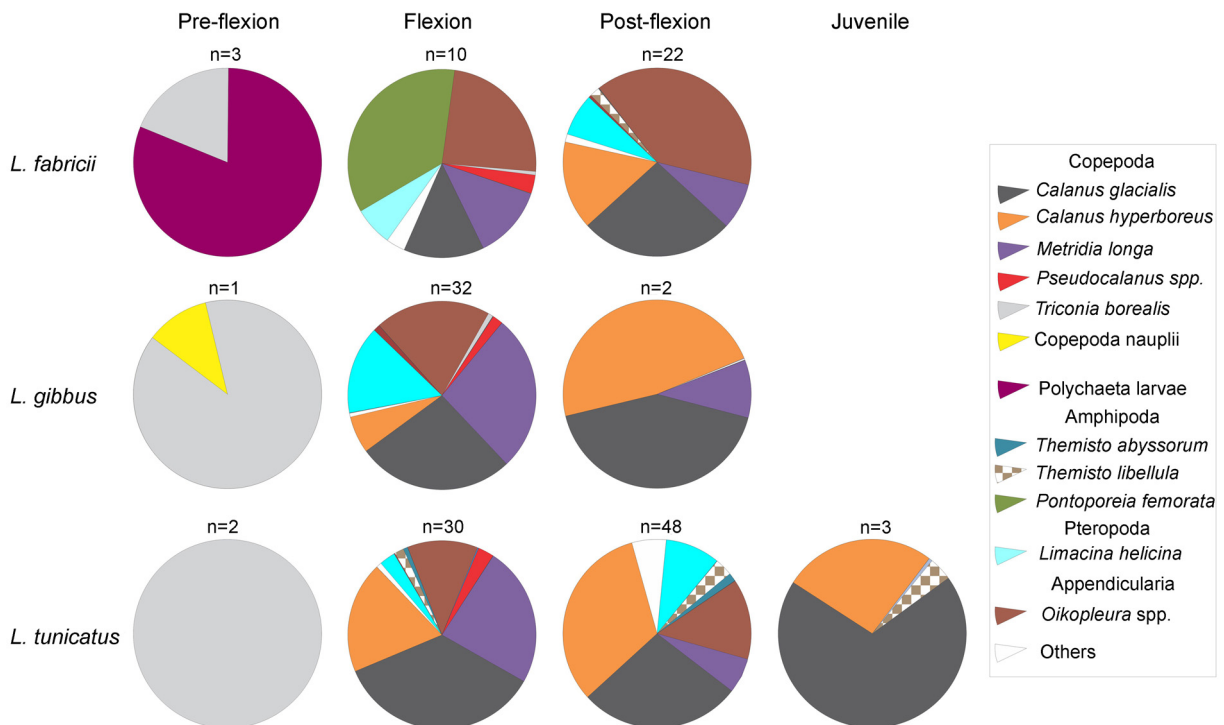


Figure 2 Weight composition of gut contents of the three larval *Liparis* species. The category “Others” includes the following taxa found in trace quantities: diatoms, *Podon leuckartii* (Cladocera), *Acartia* spp. (Copepoda), *Eurytemora herdmanii* (Copepoda), *Oithona similis* (Copepoda), *Microcalanus* spp. (Copepoda), *Jashnovia tolli* (Copepoda), *Paraeuchaeta glacialis* (Copepoda), *Scolecithricella minor* (Copepoda), Harpacticoida (Copepoda), *Onisimus glacialis* (Amphipoda), *Apherusa glacialis* (Amphipoda), *Sabinea septemcarinata* (Decapoda), Echinodermata larvae, Cirripedia nauplii/cypris and insects.

Table 3 Values of the Levin's index obtained from the diets of the particular developmental stages of the three *Liparis* species.

	<i>L. fabricii</i>	<i>L. gibbus</i>	<i>L. tunicatus</i>
Pre-flexion	0.018	0.010	0.000
Flexion	0.160	0.110	0.167
Post-flexion	0.250	0.070	0.147
Juvenile	—	—	0.076

Table 4 The Schoener overlap index calculated for the diets of the three *Liparis* species and their developmental stages. *Note:* sample sizes for pre-flexion larvae were too small for meaningful comparisons.

	Pair of species compared		
	<i>L. fabricii</i> / <i>L. gibbus</i>	<i>L. fabricii</i> / <i>L. tunicatus</i>	<i>L. gibbus</i> / <i>L. tunicatus</i>
Pre-flexion	—	—	—
Flexion	0.51	0.41	0.68
Post-flexion	0.46	0.68	0.52

L. helicina, contained late copepodid stages of *C. glacialis* and *Calanus hyperboreus*. At post-flexion, larvae of *L. fabricii* and *L. tunicatus* fed also on the amphipod *Themisto libellula*. The juvenile *L. tunicatus* diet consisted almost exclusively of *Calanus* copepods and *T. libellula* while *L. helicina* and *Oikopleura* spp. were absent.

The diversity of diet items for all species, calculated here as a Levin's index, increased as the fish grew (Table 3). Also, overall *L. gibbus* had the least diverse diet while *L. fabricii* had the greatest diet breadth.

A low number of pre-flexion larvae collected precluded us from the diet overlap analysis for this stage. There was a moderate diet overlap amongst flexion and post-flexion stages of the three *Liparis* species investigated (Schoener index between 0.41 and 0.68; Table 4).

4. Discussion

Adult *Liparis* seem to depend, particularly during spawning, on the presence of a hard substrate and often kelp beds for successful reproduction (Byers and Prach, 1988; Dunton et al., 1982). There are, however, no reported kelp beds or rocky bottoms in the Mackenzie Shelf area of the Canadian Beaufort Sea. Therefore, the *Liparis* larvae found in this study are most likely expatriates from other areas, advected to this region. In the neighboring waters kelp beds were observed to the west in the Alaskan Beaufort Shelf (Dunton et al., 1982) and to the east in the Amundsen Gulf and Darnley Bay (Andrew Majewski, Fisheries and Oceans Canada, pers. comm.), and this is from where the larvae were most likely carried into the study area by currents (Pickart, 2004; Shadwick et al., 2011).

The larval distributions presented herein demonstrate occurrence of the three *Liparis* species in the study area. It appears that the *L. fabricii* larvae were more frequently

present in the off-shore stations, while *L. tunicatus* were observed in areas that are more heavily influenced by the Mackenzie plume (Walkusz et al., 2010). Jarvela and Thorsteinson (1999) observed in large numbers only two larval snailfish species, *L. fabricii* and *L. gibbus*, in coastal waters of the Alaskan Beaufort Sea. On the other hand, Moulton and Tarbox (1987) did not find any of the aforementioned species but only collected adults of *L. tunicatus* in this area. Rand and Logerwell (2010) collected adults of only two species (*L. fabricii* and *L. gibbus*) further offshore in the Alaskan Beaufort Sea, which agrees with the more offshore presence of the *L. fabricii* in this study. This is likely due to the lower influence of the riverine plume in offshore waters. These observations suggest either a geographical separation of these species along an on- to off-shore gradient, differences in spawning timing that result in the larvae being present differentially at certain times of the year, or differences in sampling efficiency by different gear for adults (e.g. purse seine vs. otter-trawl, in Jarvela and Thorsteinson (1999) and Moulton and Tarbox (1987), respectively).

An increase in the prey diversity and prey size was observed for all three *Liparis* species as the larvae grew, demonstrated by the shift from the small copepod *T. borealis* (max. size of adults 0.7 mm), through younger stages of larger copepod species (2–3 mm) towards the adults of larger copepods and amphipods (4–6 mm). This transition has been already noted for Arctic Cod in the studied area and can be related to a larger gape size and increasing ability to catch more mobile prey as the larvae grow (Walkusz et al., 2011). Changing feeding focus from smaller to larger prey implies higher amounts of lipids are consumed to sustain rapid growth of larvae (10-fold weight increase between pre- and post-flexion). For example, the lipid content per individual copepodid increases approximately 50 times between the early and late life stages in *C. glacialis* (Falk-Petersen et al., 2009). Remarkably, the larvae of all three species fed heavily on larvacean *Oikopleura* spp. and pelagic snail *L. helicina* of which both may be an easy target due to their relatively slow motion. *Oikopleura* has been observed to be a key diet item of other larval fishes (e.g. Pacific herring (Foy and Norcross, 1999) or plaice (Shelbourne, 1962)). Madin et al. (1981) reported that tunicates, to which larvaceans belong, have high protein content (approx. 80% of organic content). Consuming this food, along with lipid-rich copepods, may help the *Liparis* larvae obtain the required energy supply and have a better balanced diet. Similarly, high lipid content found in *L. helicina*, particularly in the juvenile individuals (approx. 30% of dry mass; Gannefors et al., 2005), can explain notable frequency and biomass contribution of this food item to the larval snailfishes diet found in our study.

Diet overlap, particularly amongst the youngest larvae of *L. gibbus* and *L. tunicatus*, could suggest a shared dietary niche in early life history of these fishes. However, small sample size limits confidence in any conclusions. Nevertheless, Walkusz et al. (2013) showed the opposite habitat preferences for Polychaeta larvae and the copepod *T. borealis*, the potential planktonic food items of the larval fish, with the latter being affiliated with more saline (near bottom) water masses on the shelf. Thus, one could suggest that in the studied locations, pre-flexion *L. gibbus* and *L. tunicatus* are more associated with saline waters found deeper in

the water column as opposed to pre-flexion *L. fabricii*, which dietary preferences suggest feeding in the near-surface, fresher plume waters.

In summary, the *Liparis* larvae in the coastal Canadian Beaufort Sea were found to be generalists in terms of their feeding approach and relied on a broad spectrum of planktonic organisms (relatively high diversity of taxa as prey). A switch was observed in the diet, from small diet items in pre-flexion larvae (small copepods) towards larger items in flexion and post-flexion larvae (larger copepods and amphipods). This presumably results in the fish consuming food items having higher amounts of lipids, that provides the necessary amounts of energy required by larger snailfishes for proper development. The larval snailfishes in the study area fed also on larvaceans (*Oikopleura*) and pelagic snails (*L. helicina*) that can contribute significantly to the fish diet due to their high protein and lipid content, respectively. This study, along with many others, contributes to the current and future attempts of quantifying biomass/energy transfers in the Canadian Beaufort Sea. It can also be applied as baseline information in environmental assessments of the region.

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