



Dense ampeliscid bed on the Canadian Beaufort Shelf: an explanation for species patterns

Kathleen E. Conlan¹ · Ed A. Hendrycks¹ · Alec E. Aitken²

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Abstract

The first known ampeliscid (Amphipoda: Ampeliscidae) bed for the Canadian Arctic was reported in 2013 from the Canadian Beaufort Shelf (CBS), but species patterns were not examined. This study examines their distributions relative to differences in life strategies and environmental variables. The intent is to build a better understanding of this highly productive system in comparison with ampeliscid beds in the neighboring Bering and Chukchi Seas which are important resources for higher trophic level consumers. Data from 412 samples collected to 1000 m depth over 2002–2009 indicate that there are at least eight ampeliscid species on the CBS. Five occur elsewhere in polar and temperate latitudes and three may be new to science or are species complexes. All are limited to bottom temperatures <0.41 °C. Congeners do not distribute coherently (Similarity Profiles analysis, $p < 0.05$). Resource-demanding *Ampelisca macrocephala* (max. 8467 ind. m^{-2}) dominates *Byblis* spp. and *Haploops laevis* on the shelf enriched by wind-driven upwelling but dominance switches with depth to *Haploops tubicola*, *Haploops sibirica* and *Haploops* sp. Obligate suspension feeding with adaptations for fine particle capture enables deep living while abundance dominants supplement their diets with deposit feeding and predation. The ampeliscids may facilitate other amphipods by providing attachment sites on their tubes. Polychaetes may facilitate the ampeliscids by bringing buried resources to the surface. Given that the CBS is undergoing substantial environmental change, we recommend the CBS ampeliscids for monitoring its environmental regime to complement ongoing monitoring in other polar and temperate ampeliscid beds.

Keywords Ampeliscid amphipods · Arctic · Beaufort · Cape Bathurst

Introduction

Ampeliscid amphipods in the eastern Russian and western North American Arctic are a key resource for Pacific gray whales (*Eschrichtius robustus*), which travel from as far as Baja California, Mexico to the Bering and Chukchi Seas to forage there during the summer ice-free season (Highsmith et al. 2007; Fadeev 2011; Budnikova and Blokhin 2012;

Heide-Jørgensen et al. 2012; Schonberg et al. 2014; Demchenko et al. 2016; Brower et al. 2017). Ampeliscids are one of the most abundant prey species, because they form dense beds of self-made tubes, with a biomass up to 300 g wet wt m^{-2} (Heide-Jørgensen et al. 2012). These Arctic ampeliscids have high caloric value for gray whale predators (Highsmith and Coyle 1990; Tu et al. 2015; Demchenko et al. 2016) and along with ~ 150 other prey species provide ~ 220,800 kg of food per gray whale during the gray whales' ~ 184 day residence in the Arctic (Jones and Swartz 2009). Ampeliscids are also a resource for demersal fish, nemerteans, polychaetes and sea stars, and also their associated parasites (Mills 1967; Franz and Worley 1982; McDermott and Snyder 1988; Franz and Tanacredi 1992; Sheader 1998; Cui et al. 2012). Surface feeding seabirds consume ampeliscids when they are brought to the surface by benthic feeding gray whales (Grebmeier and Harrison 1992) and pelagic fish prey on ampeliscids migrating into the water column to disperse or mate (Borowsky and Aitken-Ander 1991; Sudo and Azeta

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✉ Kathleen E. Conlan
kconlan@nature.ca

¹ Canadian Museum of Nature, Station D, P. O. Box 3443, Station D, Ottawa, ON K1P 6P4, Canada

² Department of Geography and Planning, University of Saskatchewan, 117 Kirk Hall, 117 Science Place, Saskatoon, SK S7N 5C8, Canada

1992; Dauvin and Zouhiri 1996). Migrating ampeliscids are also available to Arctic phocid seals, which eat amphipods along with many other invertebrates and fish (Dehn et al. 2007; Giraldo et al. 2016). Benthic feeding seabirds either consume ampeliscids directly or benefit indirectly when the ampeliscid tube mats enhance growing conditions for their bivalve prey (MacKenzie et al. 2006; Loring et al. 2013). Because of their reliance on dense prey assemblages, top predators are sentinels of change in the Arctic and essential food resources for indigenous cultures (Moore et al. 2014).

Ampeliscid beds occur in more temperate parts of the Atlantic and Pacific where they may have been a resource for Atlantic gray whales before the whales were exterminated by whalers about 300 years ago (Jones and Swartz 2009). Conlan et al. (2013) located the first ampeliscid bed known for the Canadian Arctic, situated on the Canadian Beaufort Shelf (CBS) (=Mackenzie Shelf, Fig. 1). Biomass of the ampeliscids was comparable to that in the Bering and Chukchi feeding area (up to 307.3 ± 51.2 g wet wt m^{-2}) and there was evidence that gray whales also visited the CBS ampeliscid bed, in spite of its being ~1600 km to the east of the prime gray whale feeding grounds (Conlan et al. 2013). Wind-driven upwelling of plankton onto the CBS was thought to sustain the ampeliscid bed, which covered an estimated 2550 km^2 of the CBS (Conlan et al. 2013). As in the Bering and Chukchi beds, the CBS ampeliscid bed was multi-specific, comprising species of *Ampelisca*, *Byblis* and *Haploops*.

There are 238 species of *Ampelisca*, 85 species of *Byblis* and 29 species of *Haploops* described world-wide (Horton et al. 2018). Most are little known beyond their morphology and collection data. Only a few are known to form dense beds (Rigolet et al. 2012; Conlan et al. 2013), but knowledge of how the ampeliscids distribute and interact within these beds can provide an important understanding of how their sensitivities and resilience may affect top predators (Highsmith and Coyle 1991; Coyle and Highsmith 1994). The CBS ampeliscid bed has not been previously analyzed for its species content, although it is known to be compositionally similar (but not identical) to the well-studied Bering and Chukchi beds to the west (Conlan et al. 2013). The purpose of this paper is to gain a better understanding of the CBS ampeliscid bed and its surrounding populations. We ask whether all species are coherently distributed there, suggesting that they all respond similarly to environmental conditions. If this is the case, we ask whether their distributions can be related to differences in individual or groups of abiotic variables as well as to biotic variables such as life history, feeding behavior and morphology. Furthermore, we ask whether other benthic community members are coherently distributed with one or more ampeliscid species and if so, how they may interact. The overall goal is to gain an understanding of the drivers for the ampeliscids as well

as their interactions with other community members on the CBS. This is important as the proportion of ampeliscid species may change in the future to a different species complex depending on individual vulnerabilities and this may affect the size of the ampeliscid bed and the species that interact with them. Recent record warm winters have occurred in the Arctic with record low sea ice and high sea surface temperatures that have changed atmospheric circulation and a reversal in sea ice drift through the Beaufort Sea (Moore et al. 2018; Petty 2018). Summer sea-ice extent in 2018 is 1.59 million square kilometers below the 1981–2010 long-term average sea ice extent, the seventh lowest August extent in the satellite record (National Snow & Ice Data Center 2018). Much of the Arctic's multi-year ice is being lost in the Beaufort Sea, and atmosphere and ocean are substantially changing (Carmack and Macdonald 2002; Barber et al. 2008; Carmack et al. 2016; Tooth and Tschudi 2018). Increased primary and secondary productivity from increasing light availability are not necessarily a consequence of sea ice loss due to increased stratification, but increased freshwater inflow, turbidity, acidification, precipitation, storms and shelf-edge upwelling also are being recorded or predicted in the Arctic (Carmack et al. 2016). Increased penetration and residence time of warm Pacific and Atlantic water masses in the Arctic Ocean are also being observed (Wassmann et al. 2011). Taxonomic and functional shifts are a logical consequence of such changes with poleward shifts of generalists and changing characteristics of residents (Wassmann et al. 2011; Kortsch et al. 2015; Renaud et al. 2015). A shift of ampeliscid content on the CBS to smaller species could have repercussions for the ampeliscids and their associates and predators (Coyle and Highsmith 1994) but a longer growing season could enhance ampeliscid growth and dominance by large species in nutrient-enriched passages and channels of shelf archipelagos (Carmack et al. 2016), thus favouring their vertebrate predators.

Materials and methods

Sampling locations

Sampling covered the area 69.32–72.38°N, 121.28–139.05°W and depth 4.8–1000 m. There were 412 samples analyzed from 194 sites over 2002–2009 in a longitudinal range of 670 km from Amundsen Gulf in the east to the Mackenzie Trough in the west. Sample number differs from Conlan et al. (2013) who based a biomass analysis on the full sample collection (540 samples) which did not require full faunal identification. Conlan et al. (2008) based their macrofaunal analysis on a smaller subset (134 samples) that had been fully identified at the time. Conlan et al. (2008) found that macrofaunal patterns were related

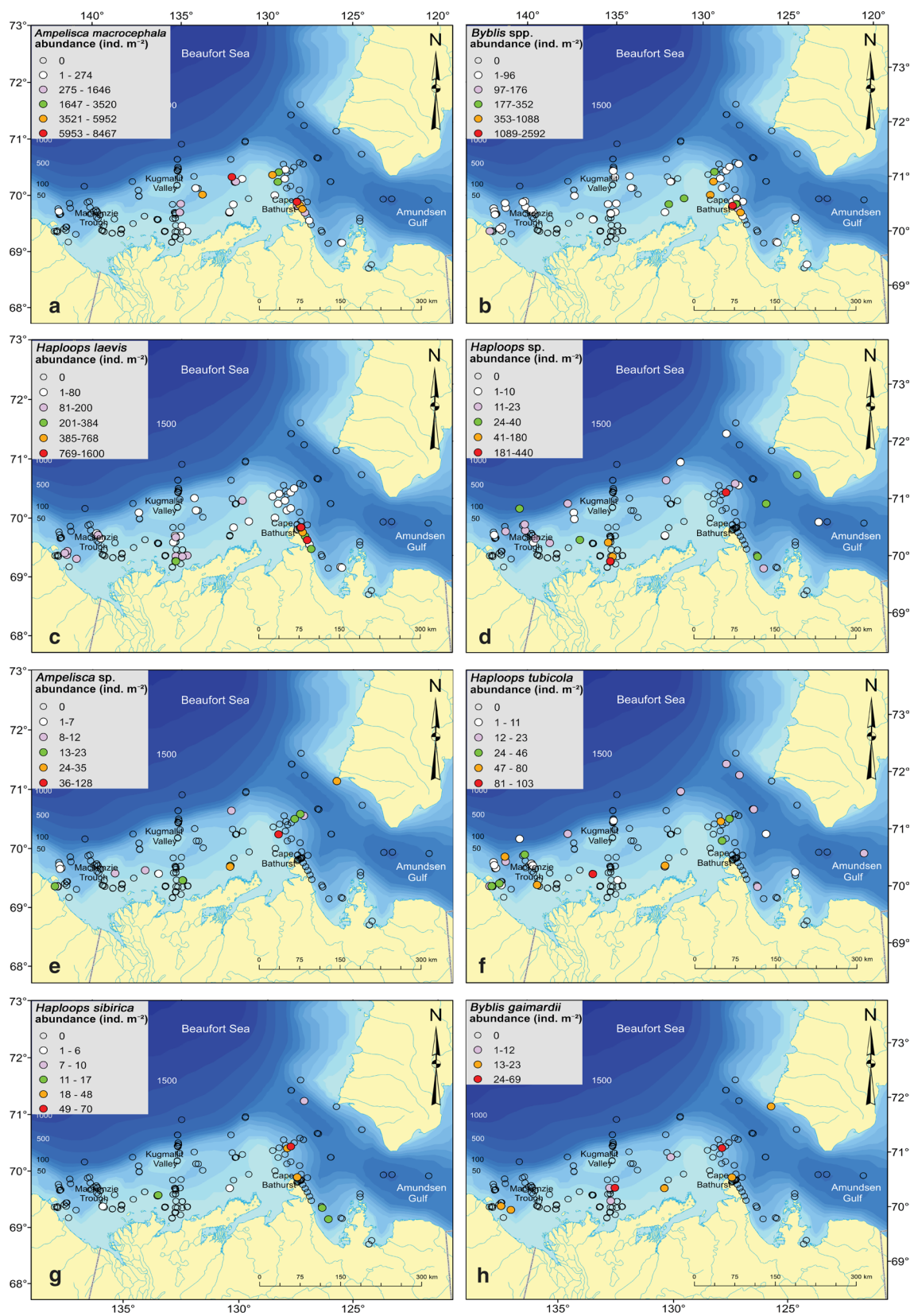


Fig. 1 Distribution of ampeliscid amphipods on the Canadian Beaufort Shelf, with abundance partitioned by the Jenks criterion (Jenks and Caspall 1971) and color coded (left inset of each map). **a** *Ampe-*

lisca macrocephala; **b** *Byblis* spp.; **c** *Haploops laevis*; **d** *Haploops* sp.; **e** *Ampelisca* sp.; **f** *Haploops tubicola*; **g** *Haploops sibirica*; **h** *Byblis gaimardii*

to depth and depth-related variables more than to sampling date. Therefore, for this analysis, the 7-year data set is considered to be a single sampling campaign rather than 7 independent campaigns. Species distributions were mapped with ArcGIS 10.2 using color bins for abundance defined by the Jenks iterative method which minimizes within-class differences and maximizes between-class differences (Jenks and Caspall 1971). The projection is North Pole Azimuthal Equidistant. When two or more locations were so close together that they overlapped, the symbol with the greatest value was superimposed on the other(s).

Sampling methods and environmental analyses

The methods for sampling and identifying biota, bottom water composition and sediment grain size and C and N levels are as described in Conlan et al. (2008, 2013). Briefly, the samples were collected by 0.25 m² box core ($n = 349$) or by 0.1 m² van Veen grab ($n = 63$). At the time of sampling, each box core sample was partitioned into biotic and sediment sample areas. The biotic area was 0.14 ± 0.04 m² ($n = 349$) (mean \pm SD) with extraction to 15 cm depth. The van Veen grab samples were taken separately for biota and sediment. The biota were elutriated and the supernatant washed through 0.5 mm mesh. Heavy biota that remained in the sediment (only large mollusks and polychaetes) were removed by hand. All biota were fixed in 5% buffered formalin-seawater and preserved in 70% ethanol, and then identified to the lowest possible level. The ampeliscids were fully identified by one of us (EH), who is an authority on the taxonomy of amphipods. A high powered microscope (Nikon SMZ-U) and current taxonomic literature were used. Taxonomic experts for other taxa are noted in Conlan et al. (2008).

Sediment samples were taken from the surface 2 cm, frozen and analyzed as described in Conlan et al. (2008, 2013). The sediment samples were analyzed for grain size, %N, %organic C and $\delta^{13}\text{C}$ at the University of Calgary or the Geological Survey of Canada. For grain size, subsamples (0.15–0.20 g if siltier, 0.80–0.90 g if sandier) were treated with a 30% solution of H₂O₂ to remove the organic matter and then analyzed by a Malvern Instruments Mastersizer 2000 with Hydro G sample dispersion unit. Total carbon was determined by the loss on ignition method in McKeague (1976). $\delta^{13}\text{C}$ was determined by Continuous Flow-Elemental Analysis-Isotope Ratio Mass Spectrometry technology. Total nitrogen was determined by the Kjeldahl digestion procedure in Schuman et al. (1973). Bottom water data were collected from a temperature-conductivity recorder (Sea Bird Instruments SBE37) about 2 m above the seabed, which is comparable to at-seabed conditions (Conlan et al. 2013).

Species distributions relative to environmental variables

The BEST procedure in Primer v.7 (Clarke et al. 2014) was applied to address the question of whether the ampeliscid abundance patterns correlated with environmental patterns. Environmental values were plotted and transformed by square root if right skewed or by the value's inverse if left skewed and then normalized. Correlated variables (Pearson correlation > 0.8) were reduced to a single variable acting as proxy for the other(s). Combinations of variables to a maximum of 5 were examined. Date of sampling, sampler type and sample area were included to determine whether sampling method influenced the results. Ampeliscid abundances m⁻² were calculated from numbers sample⁻¹/sample area and averaged across replicate samples ($n = 73$, 19 and 102 for 1, 2 and 3 replicates, respectively). Subsequently, they were square root transformed to reduce the overwhelming effect of abundant species.

Coherent species distributions

The Similarity Profiles (SIMPROF) test in Primer v.7 was applied to determine whether all ampeliscid species on the CBS were distributed similarly or whether there were subgroups that were significantly coherent in distribution. Somerfield and Clarke (2013) developed this non-parametric permutation method to address the inherent difficulties of analyzing species distributions over samples (inverse analysis): non-independence of species distributions, non-monotonic abundance response to gradients, more species than samples, large variations in abundance, and large variations in species frequency. The method compares species distributions against the null hypothesis of no multivariate structure in the data and detects species subsets that have the same degree of association (i.e., that form a coherent group).

While the ampeliscids were found in 129 sites, 7 sites lacked a full suite of data for all the macrofauna. Therefore, these sites were removed to maintain consistency among SIMPROF tests but included in the BEST analyses which required only the ampeliscid data set. Similarities in distribution were determined by the Index of Association (IA), a Bray–Curtis measure based on standardization by percentage abundance (Bray and Curtis 1957). When two species have exactly the same distribution of percentage abundance across the samples, IA = 100 (full positive association). If IA = 0, the species have a fully negative association. A similarity profile was constructed for all species associations with each other (the real similarity profile). Subsequently, a simulated profile of non-association was generated by randomising species' relative proportions separately across the samples (Type 2 SIMPROF; Somerfield and Clarke 2013). The test statistic, π , is the

sum of absolute departures of the real similarity profile from a mean profile of non-association, permuted 999 times. The null hypothesis was rejected if the observed π was greater than all except $p = 5\%$ of π values for a new set of simulated profiles.

If significant species associations existed, Type 3 SIMPROF was applied to explore which species were associated. A dendrogram of species associations was generated by group average sorting. At each node of the tree, a SIMPROF test was run to assess whether the subset of species at that node had a significantly similar association (they formed a coherent group). In this case, the profile of non-association was generated by randomly exchanging the proportional abundance across the species subset independently for each sample and determining π . After repeating this 999 times, if this exchange altered the similarity profile among the species more than $p = 5\%$ of the time, then the null hypothesis that the species were coherently associated was rejected.

Repeat Type 2 and 3 SIMPROF analyses were run on (1) all eight ampeliscid taxa; (2) incompletely identified ampeliscids merged with their congener; and (3) potentially coherently distributed non-ampeliscids. The purpose of the first SIMPROF analysis was to address the question of whether congeners had significantly similar or dissimilar distributions. The purpose of the second SIMPROF analysis was to examine the effects of mis-identifying specimens. Identification to genus was with 100% confidence and it was assumed in the first SIMPROF analysis that *Byblis* spp., *Ampelisca* sp. and *Haploops* sp. were different from their named congeners. However, it was possible that these un-named species were actually their named congener but the individuals were too small or damaged to identify conclusively. Accordingly, six combinations of species merges were run by summing the abundances of congeners: (i) *Ampelisca* sp. + *A. macrocephala*; (ii) *Byblis* spp. + *B. gaimardii*; (iii) *Haploops* sp. + *H. laevis*; (iv) *Haploops* sp. + *H. sibirica*; (v) *Haploops* sp. + *H. tubicola*; and (vi) 1/3 *Haploops* sp. apportioned to each of *H. laevis*, *H. sibirica* and *H. tubicola*. If the named species maintained their relationships with other species despite being merged with an un-named congener, this gave confidence in the results of the SIMPROF analysis when all taxa were assumed to be separate species. The purpose of the third SIMPROF analysis was to address the question of biological interactions between ampeliscids and non-ampeliscids. This analysis targeted the abundance dominants and common macrofauna that occurred in > 10 sites on the CBS and co-occurred with at least one of the dominants. Biological characteristics of coherently distributed macrofauna such as taxonomic relatedness, substrate use, feeding mode and known associations with ampeliscids were determined from the literature.

Distribution patterns at Cape Bathurst

Along a 140 km stretch to the north and south of Cape Bathurst, 31 samples were taken on the shelf (12–50 m), shelf-break (59–74 m) and slope (80–119 m) (depth categories defined by Williams and Carmack 2008), with the intent of examining dominant species distribution patterns where previous study had found the ampeliscids to be particularly abundant (Conlan et al. 2008, 2013). Cross-shelf distribution patterns were examined in four transects. Two were run at 66–73 km and 51–52 km north of the tip of Cape Bathurst where the shelf was wide (respectively, running 59–17 and 58–44 km west of an Acoustic Doppler Current Profiler (ADCP) moored at station CA-5 in Williams and Carmack 2008). Termed Wide N and Wide S, these were 42 and 14 km long and covered a depth range of 42.4–85.1 m and 39.6–48.2 m, respectively. The two other transects were run at 13–18 km south of the tip of Cape Bathurst where the shelf was narrow (respectively, running 17–14 km and 19–13 km south of an ADCP moored at station CA6 in Williams and Carmack 2008). Termed Narrow N and Narrow S, these were 7 and 10 km long and covered a depth range of 20.9–74.2 m and 12.1–119.2 m, respectively. The Narrow S transect was run in 2007 while the other three were run in 2008.

Results

There were 10,304 specimens of *Ampelisca*, 1332 specimens of *Byblis* and 2051 specimens of *Haploops* found in 231 of the 412 samples (129 of the 194 sites). These were identified as *Ampelisca macrocephala*, *Ampelisca* sp., *Byblis gaimardii*, *Byblis* spp., *Haploops laevis*, *H. sibirica*, *H. tubicola* and *Haploops* sp. (Table 1). *Ampelisca macrocephala* is the largest species (max. 33 mm body length) and *H. sibirica* is the smallest (max. 7 mm). The others are intermediate, ordered *B. gaimardii* > *H. laevis* > *H. tubicola* > *Haploops* sp. = *Ampelisca* sp. = *Byblis* spp. The five nominal species range outside the Arctic, with *H. sibirica* and *H. tubicola* also occurring in the North Pacific and *A. macrocephala*, *H. laevis*, *H. tubicola* and *B. gaimardii* in the North Atlantic. *Haploops tubicola* is the most wide ranging and also spans a greater depth range than the others.

The three un-named species were considered to be distinct from the named species, with *Byblis* spp. possibly comprising more than one species. *Ampelisca* sp. could have been *A. eschrichtii* as one sample on the NE shelf of Amundsen Gulf was confirmed to be this species. However, identifications for other samples could not be unequivocally attributed to this species. In addition, 37 *Haploops* hatchlings were found in 4% of the samples. These could not be identified confidently to any of the four *Haploops* species

Table 1 Variables measured for the eight species of *Ampelisca*, *Byblis* and *Haploops*, ordered by maximum abundance on the CBS

	No. sites measured	No. ampeliscid sites measured	<i>Ampelisca macrocephala</i>	<i>Byblis</i> spp.	<i>Haploops laevis</i>	<i>Haploops sp.</i>	<i>Ampelisca sp.</i>	<i>Haploops tubicola</i>	<i>Haploops sibirica</i>	<i>Byblis gainardii</i>	Range over all samples
Maximum abundance m ⁻²	194	129	8467	2592	1600	440	128	103	70	69	
Maximum body length (mm)			33	10	20	10	10	15	7	25	
Biogeography			A, NEA, NWA		A, NEA			NEP, A, NEA, NWA	NWP, A	A, NEA, NWA	
Frequency (in samples)			65	76	72	34	27	41	13	12	
Frequency (in sites)	194	129	39	59	52	30	21	33	10	10	
Latitude (° N)	194	129	Min 69.83 Max 71.17	69.45	69.49	69.75	69.46	69.46	69.65	69.49	69.32
Longitude (° W)	194	129	Min 125.51 Max 138.99	124.13	125.51	123.50	125.87	121.28	126.16	125.87	121.28
Depth range (world-wide) (m)			Min 10 Max 890		10			10		5	
Depth range (CBS) (m)	194	129	Min 13 Max 119	12	7	8	13	12	19	18	5
Fluorescence (µg L ⁻¹)	66	44	Min 0.08 Max 1.48	0.02	0.10	0	0.04	0	0.01	0.08	0
Temperature (° C)	66	44	Min -1.38 Max -0.95	-1.50	-1.50	-1.47	-1.35	-1.52	-1.46	-1.40	-1.61
Salinity (psu)	66	44	Min 29.25 Max 32.33	29.25	22.50	22.50	31.75	31.00	31.93	-0.50	7.75
Oxygen (mL L ⁻¹)	63	43	Min 7.01 Max 7.74	5.10	6.66	5.14	5.40	5.18	5.50	6.66	5.10
Nitrogen (%)	136	93	Min 0.02 Max 0.38	0.02	0.02	0.04	0.04	0	0	0	0
Organic carbon (%)	152	100	Min 0.12 Max 8.24	0.46	0.54	0.54	0.09	0.61	0.59	0.68	0.06
δ ¹³ C (‰)	57	39	Min -26.91 Max -22.23	-27.47	-27.47	-26.45	-26.54	-27.47	-26.94	-26.20	-28.83
Clay + silt (%)	161	106	Min 0 Max 99.90	5.81	46.26	46.26	0	0	37.19	43.72	0
				99.85	99.63	99.83	99.76	99.68	99.81	99.63	100.00

Table 1 (continued)

	No. sites measured	No. ampeliscid sites measured	<i>Ampelisca macrocephala</i>	<i>Byblis</i> spp.	<i>Haploops laevis</i>	<i>Haploops tubicola</i>	<i>Ampelisca</i> sp.	<i>Haploops sibirica</i>	<i>Byblis gaimardii</i>	Range over all samples
Sand (%)	161	106	Min 0.10 Max 100.00	0 94.19	0 53.74	0 53.74	0 100.00	0 62.81	0 56.28	0 100.00
Mean grain size (φ)	94	59	Min 1.16 Max 8.45	3.16 9.28	4.07 9.38	4.07 9.38	1.16 8.85	3.86 8.64	4.38 8.96	1.13 9.40
Grain sorting (φ)	94	59	Min 0.47 Max 4.34	1.46 3.74	1.25 3.52	1.33 2.83	0.41 3.62	1.40 3.62	1.79 3.07	0.37 4.34
Skewness (φ)	94	59	Min -0.12 Max 0.79	-0.22 0.79	-0.10 0.61	-0.08 0.61	-0.30 0.35	-0.15 0.61	0.13 0.38	-0.44 0.79
Kurtosis (φ)	94	59	Min 0.63 Max 1.56	0.67 2.64	0.63 1.88	0.67 1.78	0.73 1.95	0.67 1.55	0.78 1.51	0.31 3.14

Fluorescence, temperature, salinity and oxygen were measured on the bottom water. Nitrogen, organic carbon, δ¹³C and particle characteristics were measured on the surface sediment. Maximum body length, biogeography and depth range world-wide are given for context from literature sources and observation. Biogeographic abbreviations: NEP (NE Pacific), NWP (NW Pacific), A (Arctic), NEA (NE Atlantic), NWA (NW Atlantic). The Bering Sea is considered to be in the Arctic as it is more Arctic than Pacific in temperature (Melling et al. 2012). Sources: Gurjanova (1951), Buchanan (1963), Kamneworff (1965, 1966), Mills (1965, 1967, 1971), Dickinson (1982, 1983), Dauvin and Bellan-Santini (1990), Highsmith and Coyle (1991), Brandt (1996, 1997), Bellan-Santini and Dauvin (1997), Jørgensen et al. (1999), Dauvin et al. (2012, 2017), Peart (2018)

because of their small size and so were excluded from this study.

Distribution patterns over the CBS

Ampelisca macrocephala (Fig. 1a) was by far the most abundant, with up to 8467 ind. m⁻² found on the eastern shelf-edge at Cape Bathurst and 5953 ind. m⁻² on the shelf-edge to the northwest. *Byblis* spp. (Fig. 1b) and *H. laevis* (Fig. 1c) were also found at maximal abundance on the eastern shelf-edge of Cape Bathurst but at lower densities (up to 2592 and 1600 ind. m⁻², respectively). To the north of Cape Bathurst, the shelf-edge was more gradual. All three were present there but their abundance was at least half their abundance on the steeper slope to the south. All three species ranged to the west of Cape Bathurst but mostly in low numbers relative to the shelf-edge at Cape Bathurst. Of the three, *A. macrocephala* had the most abbreviated distribution (found in 39 sites), being nearly absent from the samples taken west of Kugmallit Valley, with the exception of one site on the western edge of Mackenzie Trough. *Byblis* spp. and *H. laevis* were more widespread than *A. macrocephala*. *Byblis* spp. were the most frequently found (59 sites), followed by *H. laevis* (52 sites) but their distributions were nearly opposite. *Byblis* spp. were more abundant offshore than inshore while *H. laevis* showed abundance peaks inshore. Neither was present close to the inflow of the large Mackenzie River.

Collectively, the ampeliscids spanned nearly the full latitudinal and longitudinal range of sampling. Even the five other ampeliscid species (Figs. 1d–h), which were less abundant than the previous three species by close to an order of magnitude, were distributed widely on the CBS. Most showed an abundance peak on the shelf near Kugmallit Valley or on the shelf-edge or slope to the north of Cape Bathurst. *Haploops* sp., *Ampelisca* sp. and *H. tubicola* were moderately frequent (21–33 sites). The two rarest species, *H. sibirica* and *B. gaimardii*, were found at only 10 sites. Few specimens of *H. sibirica* were found away from Cape Bathurst, while *B. gaimardii* also occurred in proportionally larger numbers on the shelf to the east and west, across Amundsen Gulf, in Kugmallit Valley and on the edge of Mackenzie Trough.

While samples were taken from 5 to 1000 m depth, the ampeliscids were found between 7 and 580 m. Maximal depths on the CBS were 7–23% of maximal depths known elsewhere in the world. All species were found close to their minimal depths, though. For all species, the highest abundances occurred on the shelf or shelf-edge. *Haploops laevis* and the species of *Ampelisca* and *Byblis* were restricted to the shelf while *Haploops* sp., *H. tubicola* and *H. sibirica* ranged into the deeper waters of the Beaufort Sea and Amundsen Gulf.

Environmental summary

Bottom water fluorescence, temperature, salinity and oxygen were measured at 63–66 of the 194 sites (43–44 of the 129 sites where ampeliscids were present) (Table 1). Most species were found where bottom water fluorescence was low (0–1.91 $\mu\text{g L}^{-1}$). Only *Ampelisca* sp. and *B. gaimardii* occurred in the full range sampled (0–10.33 $\mu\text{g L}^{-1}$). Despite sampling at sites with bottom temperatures as high as 7.75 °C, the ampeliscids were found only in the colder bottom water (–1.52 to 0.41 °C). All species of *Haploops* occurred in slightly warmer water (max. 0.20–0.41 °C) than species of *Ampelisca* (max. –0.95 to –0.35 °C). *Byblis* was more variable (max. –0.51 to 0.41 °C). While samples were taken from a bottom salinity range of 16.00–34.89 psu, most of the ampeliscids occurred in the more saline areas (22.50–34.84 psu). *Byblis gaimardii* was found in the widest salinity range (16.00–32.61 psu). Bottom water oxygen levels ranged from 5.10 to 9.05 mL L^{-1} . The ampeliscids collectively spanned this range, with *Byblis* spp., *H. tubicola* and *Haploops* sp. in the lower part of the range and *Ampelisca* sp. and *B. gaimardii* at the upper part of the range.

Surface sediment samples were analyzed at 57–161 of the 194 sites, with most sites being measured for grain size, N and organic C. Ampeliscids were present in mostly the full range of N and org. C sampled (0–0.42% N, 0.09–8.24% org. C for ampeliscids vs. 0–0.49% N, 0.06–10.22% org. C for all samples). *Haploops sibirica* occurred in a narrower

range than the other species (0–0.1% N, 0.59–2.89% org. C). Surface sediment $\delta^{13}\text{C}$ content became more enriched with increasing depth. The ampeliscids occurred across nearly the full range of $\delta^{13}\text{C}$ (–28.83 to –22.23‰). Most parts of the CBS had a high clay/silt fraction but isolated areas were up to 100% sand. *Ampelisca macrocephala*, *Ampelisca* sp., *Byblis* spp. and *H. tubicola* occurred in both clay/silt and sand while the other species were restricted to a clay/silt fraction > 37%.

Species distributions relative to environmental variables

Sediment % clay/silt, % sand and median grain size were highly correlated (Pearson correlation, $r \geq 0.8$) (n given in Table 1). These were reduced to a single variable (% clay/silt) acting as proxy for the others. The BEST analysis identified that depth was the single variable that produced the highest correlation of rank similarity matrices generated by the environmental and ampeliscid distributions over the 129 sites (Spearman rank correlation, $r_s = 0.110$, $n = 129$). The top 10 correlations produced by various combinations of 5 variables ranged from $r_s = 0.139$ –0.141. The best combination of 5 environmental variables was depth, bottom water fluorescence and salinity and sediment org. C and sorting. Replacing salinity with oxygen gave the same correlation ($r_s = 0.141$). The lower correlations ($r_s = 0.139$ –0.40) were with various combinations of these variables with

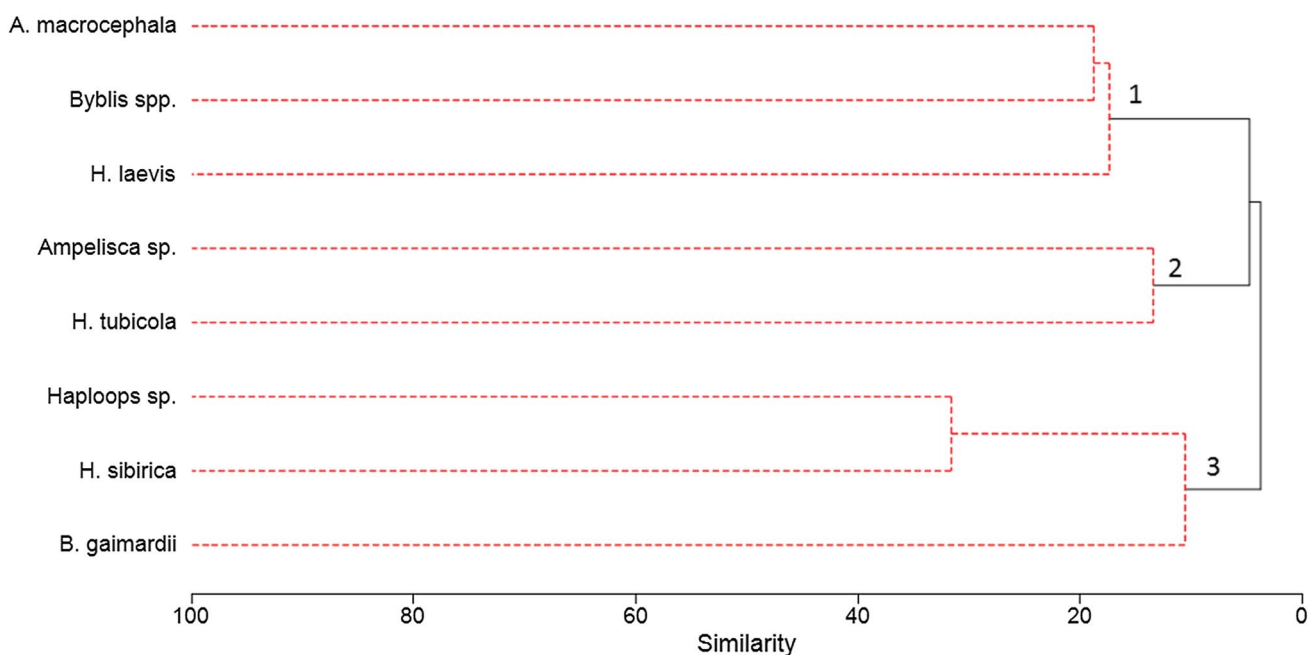


Fig. 2 Dendrogram of % similarity of the eight ampeliscid species associations. Within each of the three groups linked by a dashed line, the null hypothesis that all pairs of species have the same association

cannot be rejected (Type 3 SIMPROF test, $p = 0.05$). Conversely, subgroupings linked by a solid line have statistical support. π values at each of the numbered nodes are given in the text

temperature added to the 5-variable mix but at no time were sampling methods part of the combinations that gave the highest correlations.

Depth was most correlated with increasing bottom water salinity (Pearson correlation, $r=0.50$), followed by increasing surface sediment $\delta^{13}\text{C}$ ($r=0.47$) and declining bottom water oxygen ($r=0.37$) (n given in Table 1). Other variables were less correlated ($r<0.30$). BEST analysis after removal of depth and sampling variables reduced the correlations of the abiotic with the biotic rank similarity matrices. The single variable that produced the highest correlation ($rs=0.074$) was surface sediment sorting. Slightly higher correlations ($rs=0.080$) were produced by various 4- and 5-variable combinations of surface sediment sorting with bottom water fluorescence, temperature, salinity and oxygen.

Coherent distributions among the ampeliscids

The Type 2 SIMPROF test at $p=0.05$ rejected the null hypothesis that the eight species were not associated with each other ($\pi=2.847$, $p=0.014$, $n=999$). Three ampeliscid groups had coherent distributions (Type 3 SIMPROF test; Fig. 2): (1) *A. macrocephala*—*Byblis* spp.—*H. laevis* ($\pi=3.36$, $p=0.148$, $n=999$); (2) *Ampelisca* sp.—*H.*

tubicola ($\pi=0.49$, $p=0.481$, $n=999$); and (3) *Haploops* sp.—*H. sibirica*—*B. gaimardii* ($\pi=3.19$, $p=0.744$, $n=999$). Within Group 1, the Index of Association (IA) was: 18.7 between *A. macrocephala* and *Byblis* spp., 17.5 between *Byblis* spp. and *H. laevis* and 17.2 between *A. macrocephala* and *H. laevis*. Within Group 2, IA = 13.4 between *Ampelisca* sp. and *H. tubicola*. Within Group 3, IA = 31.6 between *Haploops* sp. and *H. sibirica*, 21.1 between *H. sibirica* and *B. gaimardii* and 0 between *Haploops* sp. and *B. gaimardii*. Despite the dis-association of *B. gaimardii* with *Haploops* sp., *B. gaimardii* was more similar to Group 3 than to the other two groups.

Identification effects

The re-runs of SIMPROF on merged congeners (Online Resource 1) consistently produced a cohesive Group 1, consisting of *A. macrocephala*, *Byblis* spp. and *H. laevis*. Addition of the un-named congener to the named congener did not change this grouping. Conversely, Groups 2 and 3, which comprised the less frequently occurring species (Table 1), were more labile. *Haploops tubicola* and *H. sibirica*, which were indicated to be significantly different in distribution (Fig. 2) when all un-named species were considered to be

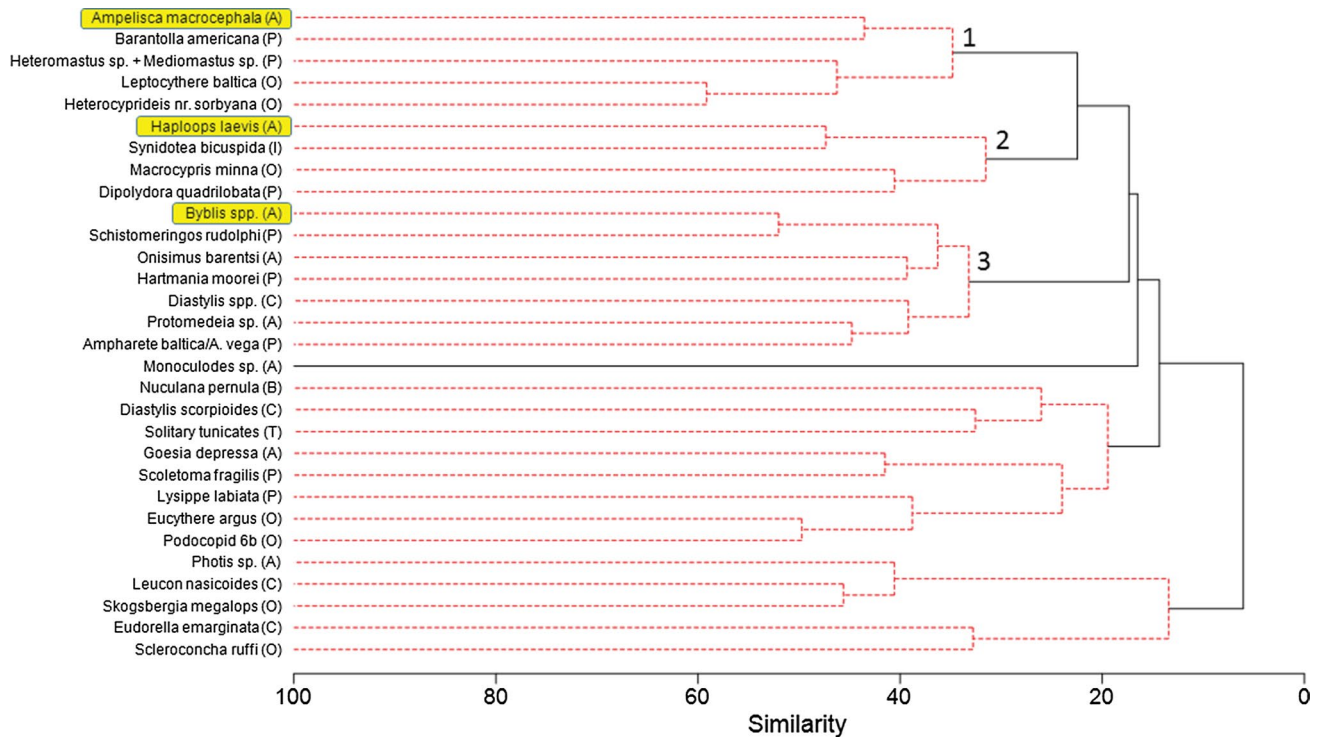


Fig. 3 Dendrogram of % similarity of associations of 27 non-ampeliscid taxa with the three dominant ampeliscid species, *A. macrocephala*, *H. laevis* and *Byblis* spp. (highlighted). Within each of the groups linked by a dashed line, the null hypothesis that all pairs of species have the same association cannot be rejected (Type 3 SIM-

PROF test, $p=0.05$). Conversely, subgroupings linked by a solid line have statistical support. π values at each of the numbered nodes are given in the text. Taxon codes: A Amphipoda, C Cumacea, I Isopoda, O Ostracoda, P Polychaeta, T Tunicata

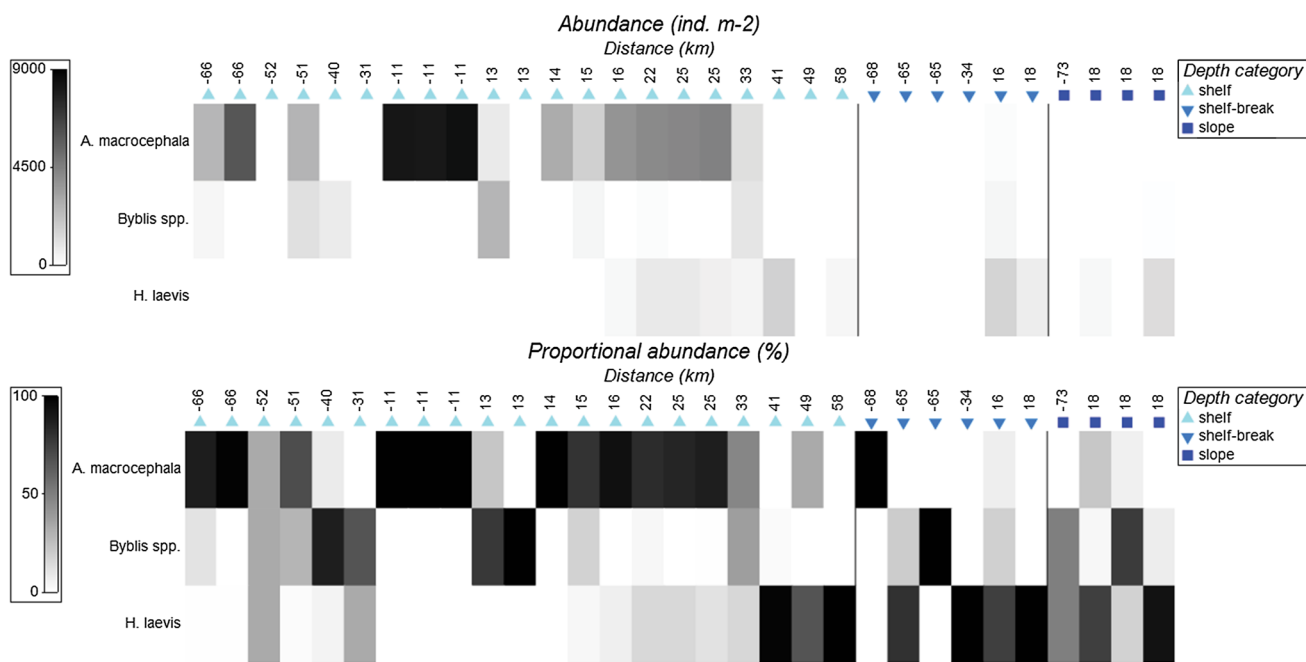


Fig. 4 Shade plots of abundance (no. ind. m⁻²) and proportional abundance (%) of *A. macrocephala*, *Byblis* spp. and *H. laevis* along the shelf (12–50 m depth), shelf-break (59–74 m) and slope (80–

119 m) of eastern Cape Bathurst. Distances are km north (negative sign) and south (positive sign) of the tip of Cape Bathurst at 70.57°N, –128.02°W

distinct, consistently grouped cohesively when *Haploops* sp. was merged with them, either fully or partially. The less frequently found *B. gaimardii* was affected by the merging of *Haploops* sp. with *H. sibirica* and *H. tubicola* by distancing its relationship with the others. Because of the potential for mis-identification to affect the congruence among the Group 2 and 3 species more than those in Group 1, further study was restricted to Group 1 species, which are the abundance dominants on the CBS.

Coherent distributions of non-ampeliscids with the dominant ampeliscids

Thirteen of the 27 non-ampeliscids were coherently distributed with the three dominant ampeliscids (Fig. 3). Congruent with *A. macrocephala* (Group 1; $\pi = 2.47$, $p = 0.188$, $n = 999$) were the polychaetes *Barantolla americana* and *Heteromastus/Mediomastus* as well as the ostracods *Leptocythere baltica* and *Heterocyprideis* nr. *sorbyana*. Congruent with *H. laevis* (Group 2; $\pi = 1.00$, $p = 0.962$, $n = 999$) were the isopod *Synidotea bicuspidata*, the ostracod *Macrocypris minna* and the polychaete *Dipolydora quadrilobata*. Congruent with *Byblis* spp. (Group 3; $\pi = 1.18$, $p = 0.751$, $n = 999$) were the polychaetes *Schistomeringos rudolphi*, *Hartmania moorei* and *Ampharete baltica*. *A. vega*, the amphipods *Onisimus barentsi* and *Protomedeia* sp. and the cumacean *Diastylis* spp. Characteristics of these associates are given in Online Resource 2. The other 14 non-ampeliscids showed

closer association with each other than with the dominant ampeliscids.

Distribution patterns at Cape Bathurst

Ampelisca macrocephala was the most frequent dominant at Cape Bathurst, occurring in 17 of the 21 shelf samples and ranging over 115 of the 124 km sampled (from 66 km north of the cape to 49 km south) (Fig. 4). *Byblis* spp. and *H. laevis* were found in 13 and 15 shelf samples, respectively (sometimes in small numbers) and co-occurred in 10 of these. They co-occurred with *A. macrocephala* in 10 and 12 of the 21 shelf samples, respectively, though in different locations from each other. All three species co-occurred in only 8 samples. Where *A. macrocephala* co-occurred with either of the other two species, it usually was proportionally more abundant. Its greatest abundance was at 11 km north of the cape (8467 ind. m⁻²) but it dominated the other two species from 66 km north to 33 km south. *Byblis* spp. was proportionally more abundant than *A. macrocephala* only in 3 samples. Its greatest abundance was from 51 km north to 33 km south of the cape with a peak (2592 ind. m⁻²) at 13 km south of the cape. *Haploops laevis* was absent or in low numbers close to the cape where *A. macrocephala* or *Byblis* spp. dominated but was proportionally more abundant further away when the other species dwindled out. Its abundance on the shelf peaked at 41 km south of the cape (1600 ind. m⁻²).

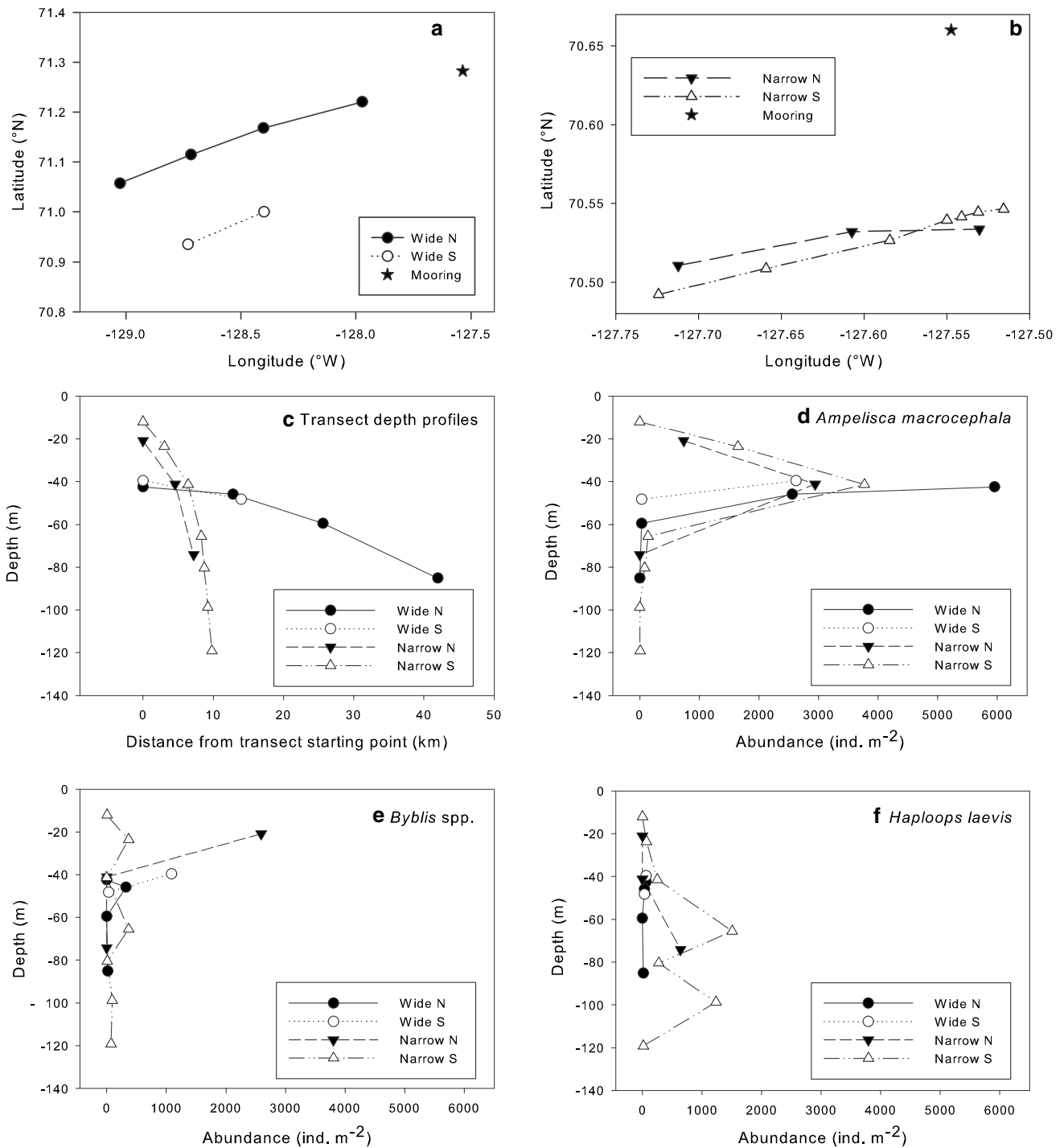


Fig. 5 Cross-shelf transects to the north and south of the tip of Cape Bathurst. **a**, **b** location of the transects relative to each other and to moorings set by Williams and Carmack (2008); **c** depth profiles of

the four transects; **d–f** abundance profiles of *A. macrocephala*, *Byblis* spp. and *H. laevis* on the four transects

In the limited number of samples taken at the shelf-break (6 samples from 59 to 74 m depth) and slope (4 samples from 80 to 119 m depth), *H. laevis* dominated in abundance more than either of the other two species. It was consistently present, even if in low numbers, from

73 km north to 18 km south of the cape. Relative to the shelf, its peak abundances were comparably high on the shelf-break (1509 ind. m⁻²) and slope (1234 ind. m⁻²). The peaks were where the other two species were rare or absent, at 16 and 18 km south of the cape, respectively.

Cross-shelf distribution patterns of the three dominant species are shown in Fig. 5. *Ampelisca macrocephala* was the dominant ampeliscid on the shelf in all four transects, with abundance peaks at ~40 m (Fig. 5d). Abundance was highest on the Wide N transect (5952 ind. m⁻²) while on the other three transects, the maximum recorded abundance was 2624–3771 ind. m⁻². Inshore, abundance was zero at 12 m but at ~20 m it was well above zero (736 ind. m⁻² at Narrow N and 1646 ind. m⁻² at Narrow S; this depth not sampled on the Wide transects). Offshore, at ~50 m and deeper, *A. macrocephala* was absent or in small numbers (32–137 ind. m⁻²). The pattern of abundance was strongly consistent among the four transects.

Byblis spp. co-occurred with *A. macrocephala* and showed similar peaks inshore, though it was not as strongly depth related as was *A. macrocephala* (Fig. 5e). Highest abundances were at 21–46 m (320–2592 ind. m⁻²) but on the Narrow S transect, abundance peaked again to 366 ind. m⁻² at 66 m. On the other transects, abundance was 0–91 ind. m⁻² at >50 m.

Haploops laevis was rare on the two wide shelf transects (0–64 ind. m⁻²) but was found at higher densities on the narrow shelf transects (0–1509 ind. m⁻²) (Fig. 5f). The highest abundance was at 66 m on the Narrow S transect and 74 m on the Narrow N transect (66 m not sampled). A second abundance peak was found on the Narrow S transect at 91 m (1234 ind. m⁻²). Small numbers (17 ind. m⁻²) were found deeper at the Narrow S transect end-point at 119 m. These deeper depths were not sampled on the other transects.

Discussion

Ampeliscid biogeography and species composition

The presence of *A. macrocephala*, *B. gaimardii*, *H. laevis*, *H. tubicola* and *H. sibirica* on the CBS can be explained by its oceanography, which includes three main water layers: the shallow Polar Mixed Layer which is dominated by the large Mackenzie River, underlain by the warmer, nutrient rich, and saltier (but freshened) Pacific water beginning at 60–100 m and below that, at >200 m, the warm and salty Atlantic water (Carmack et al. 1989; Carmack and Macdonald 2002; Carmack et al. 2004; Melling et al. 2012). All the CBS species ranged into the riverine coastal domain (<20 m; Carmack et al. 2016), suggesting that they could tolerate periodic influence of the Mackenzie River (Fig. 1). All species also occurred on the shelf and showed abundance peaks around Cape Bathurst, indicating that they were influenced by the nutrient-rich Pacific water. *Ampelisca macrocephala*, *B. gaimardii* and *H. laevis* dominate in Pacific waters of the adjacent Bering and/or Chukchi Seas which flow into the CBS (Coyle and Highsmith 1989; Highsmith

and Coyle 1990, 1991; Feder et al. 1994; Carmack and Macdonald 2002). *Haploops tubicola* and *H. sibirica* were found well into the Atlantic layer in Amundsen Gulf (396–514 m) (Table 1). *Haploops tubicola* has the most wide-ranging biogeography of the CBS ampeliscids, both latitudinally and longitudinally. It is known as far south as California on the NE Pacific coast and to the Iberian Peninsula in the NW Atlantic (Dickinson 1983; Dauvin et al. 2012). *Haploops* is considered to be a deeper living genus than *Ampelisca* (Bellan-Santini and Dauvin 1997), although bathymetric overlap is considerable (Dauvin et al. 2012). The rarest species on the CBS, *H. sibirica*, occurs widely in the Russian Arctic and NW Pacific south to the Sea of Japan (Gurjanova 1951). All the ampeliscids were collected shallower than the maximum depth known for the species. This may reflect the Beaufort environment, where productivity is highly seasonal and interannually variable (Carmack and Macdonald 2002; Arrigo and van Dijken 2004). Given these wide distributions, these species will likely be found in other parts of the Canadian Arctic and under the right conditions may form dense beds.

The three un-named species, *Ampelisca* sp., *Byblis* spp. and *Haploops* sp., may be new to science or unrecognized species complexes. Five species of *Ampelisca*, six species of *Byblis* and four species of *Haploops* are known in the Bering, Chukchi and/or Beaufort Seas (Dickinson 1982, 1983; Coyle and Highsmith 1989). Only the most abundant have been previously distinguished for ecological studies there, because species are inseparable if they are damaged or young (Highsmith and Coyle 1991; Coyle and Highsmith 1994). In this study, great care was given to species identification but preservation prevented the use of additional distinguishing characters such as living color, behavior and genetic material. Small individuals of the five nominal species lacking the diagnostic characters of adults could have also fallen within these un-named categories, although misidentification of the genus was unlikely as generic characteristics were recognizable at any size.

Environmental relationships

The BEST analysis showed that site similarities based on environmental versus individual species distributions had very low correlation and that different combinations of water and sediment variables produced nearly the same correlations. Sampling variables (date, sampler and sample size) were never part of the 5-variable combinations that produced the highest correlations. This indicates that sampling bias was low. Many of the environmental variables transition with distance from land, but this is not entirely related to depth because of offshore rises and the inshore effect of the Mackenzie River on the western part of the CBS. Thus, fluorescence is highest close to the delta and sediment $\delta^{13}\text{C}$

transitions from land-derived organic matter near the delta to planktonic offshore (Conlan et al. 2008, 2013). However, depth may embrace a variety of spatially and temporally varying variables that collectively influence the benthos. Depth was also found to be the best correlate for benthic invertebrate distributions in the Chukchi Sea (Schonberg et al. 2014) and demersal fish distributions on the CBS because of the layered water masses (Majewski et al. 2017).

All three ampeliscid genera were mostly concentrated in cold, high salinity water, although *H. laevis*, *Haploops* sp. and *B. gaimardii* were also found close to the Mackenzie Delta where the bottom water was brackish (Fig. 1 and Table 1). Warm, low salinity surface water from the Mackenzie River can spread eastwards along the coast as far as the base of Cape Bathurst (Carmack et al. 1989). The deeper living species of *Haploops* spanned a greater temperature range than the species of *Ampelisca* because they penetrated into the slightly warmer (>0 °C) Atlantic water at >200 m depth. All species did not occur in bottom water any warmer than 0.41 °C, however.

Besides fresh water and heat, the Mackenzie River brings in massive amounts of sediment (127 Mt a^{-1} ; Macdonald et al. 1998), far exceeding that of other Arctic rivers (Carmack and Macdonald 2002). This produces a dynamically moving plume of predominantly clay and silt settling close to the Mackenzie Delta that moves with the winds and currents and also re-suspends (Carmack and Macdonald 2002). Coastal erosion contributes an added $\sim 5\%$ of sediment (Carmack and Macdonald 2002). All ampeliscid species were found in sediments with high clay–silt content. Sediment characteristics are important to ampeliscids as they supply substrate for tube building. The ampeliscids spend most of their lives in self-built tubes, where they position themselves ventral side up at the tube mouth for feeding (Enequist 1949). They glue the sediment particles with “amphipod silk” secreted from glands in pereopods 3 and 4. *Ampelisca macrocephala* and *H. tubicola* build tubes most readily in clay or clay mixed with fine sand. Clay increases the tube’s firmness but pure clay prevents the threads from taking hold while threads constructed in pure sand cannot be stretched (Enequist 1949). Sediment maps for the CBS show the prevalence of silt close to the Mackenzie River inflow and in the Mackenzie Trough with a higher proportion of sand on the western half of the CBS, especially around Cape Bathurst where currents are high (Jerosch 2013). High sand proportions also occur where former beaches and old drilling islands are now submerged (Croasdale and Marcellus 1978). The coarser sediment, along with greater distance from the influence of the Mackenzie River, may influence ampeliscid settlement. At least some ampeliscids also settle preferentially where occupied or empty ampeliscid tubes are present (Dauvin and Bellan-Santini 1990).

The low correlations of environmental variables with the ampeliscid distributions could have been due to several factors: that the environmental variables measured were not those that were highly influential; the environmental measurements were only single snapshots at the time of sampling and did not supply sufficient information on conditions encountered throughout the species’ lives; that missing environmental data lowered the correlations; and that congeners broadly overlapped in environmental requirements. Carmack and Macdonald (2002) suggest that the timing of the seasonal cycle on the CBS (e.g., Mackenzie River freshet, sea ice breakup and freeze-up) is more important to biota than individual quantifiable measures. Other seasonal factors that may influence ampeliscid distributions are the effects of ice scour over the shelf, the winter-spring flaw lead-polynya system, spring ice algal production, late spring and autumn phytoplankton blooms and upwelling during the summer-autumn open water season.

Seafloor disturbance by ice scour will impact ampeliscids to 50 m depth and most intensively where the land-fast ice meets the moving pack ice at 10–20 m (Gilbert and Pedersen 1987; Lewis and Blasco 1990; Héquette et al. 1995; Myers et al. 1996; Carmack and Macdonald 2002). This may explain why the abundance of *A. macrocephala* peaks at 40–50 m and declines inshore, as observed in the four transects near Cape Bathurst (although *Byblis* spp. peaked at shallower depths in some transects). Ice scour can have a positive influence on biodiversity, though, by creating a mosaic of recolonizing benthos (Conlan and Kvitek 2005).

The winter flaw lead develops over the CBS between the land-fast ice and the moving pack ice mid-shelf, approximately seaward of the 20 m isobath and runs from Mackenzie Trough to Amundsen Gulf (Carmack and Macdonald 2002; Barber and Hanesiak 2004). It opens and closes over the winter, with a maximum width of about 70 km to the 30 m isobath (Williams et al. 2008). An extension of the flaw lead at the mouth of Amundsen Gulf is a polynya, a consequence of wind-driven upwelling near the shelf-break (Lukovich and Barber 2005; Williams and Carmack 2008). This flaw lead-polynya system enables a spring phytoplankton bloom, although the timing and persistence of this system are variable (Arrigo and van Dijken 2004; Simpson et al. 2013a, b). Early phytoplankton production should benefit ampeliscids that were found in relatively high numbers on the shelf between Kugmallit Valley and Cape Bathurst (*H. tubicola*, *B. gaimardii* and *Ampelisca* sp.) and also on the shelf-edge to the north and east of Cape Bathurst (all species). A carbon flow model in the polynya indicated that 60% of the benthic carbon demand was supplied by sinking carbon in the flaw lead-polynya system in spring–summer 2008 (Forest et al. 2011). Ice algae can also be an important spring carbon source for the benthos in Amundsen Gulf (Renaud et al.

2007b). Polynyas can also influence the benthos as a result of brine injection at the flaw lead and polynya edge, either by brine flow over the benthos or by baroclinic currents mixing the surface layer to as deep as 40–50 m (Grebmeier and Cooper 1995; Carmack and Macdonald 2002).

Late-spring pelagic production offshore after sea ice retreat is also a carbon source to the benthos on the CBS. Later in autumn, a second but smaller phytoplankton bloom induced by nutrient mixing spreads widely over the CBS and should benefit the ampeliscids (Arrigo and van Dijken 2004). While winter primary production is low (Simpson et al. 2013a), some species in the Arctic may grow and reproduce primarily in winter (Demchenko et al. 2016).

The elevated abundances of each ampeliscid species around Cape Bathurst point to upwelling as an important influence. Wind-driven upwelling draws up larger and older copepod stages which have descended into Amundsen Gulf to overwinter (Walkusz et al. 2012, 2013), and these copepods may be preyed upon by the larger *A. macrocephala*. Whole zooplankton abundance and biomass at Cape Bathurst can be 2–3 × that on the shelf to the west. Sampling zooplankton close to the Wide and Narrow shelf transects after 7 weeks of upwelling favorable winds, Walkusz et al. (2012) found 279 ± 307 ind. m^{-3} (dry mass 0.068 ± 0.043 g m^{-3}) close to the Wide Shelf transect and 368 ± 520 ind. m^{-3} (0.066 ± 0.049 g m^{-3}) close to the Narrow Shelf transect at Cape Bathurst. By comparison, in Kugmallit Bay (~160 km west of Cape Bathurst), density and biomass were 130 ± 114 ind. m^{-3} (0.026 ± 0.012 g m^{-3}). During summer open water on the CBS (May–October), upwelling favorable winds dominate (Ben Mustapha et al. 2010), which should lead to a reliable and frequent suspended food supply at, and to the west of Cape Bathurst.

Along with a draw-up of zooplankton, wind-driven upwelling also brings nutrient-rich water to the surface which spreads northwards and westwards over the shelf of the CBS, following the divergence of the isobaths (Arrigo and van Dijken 2004; Williams and Carmack 2008). This fuels phytoplankton production, an essential food resource for all the ampeliscids (Online Resource 3). This is primarily in the form of diatoms, which are considerably more productive off Cape Bathurst than elsewhere on the CBS (128.7 g C m^{-2} year $^{-1}$ at mooring CA6 in 2003–2004 compared to 14.5 g C m^{-2} year $^{-1}$ in Mackenzie Trough and 2.8 g C m^{-2} year $^{-1}$ mid-slope; Sampei et al. 2011). This elevated diatom production reaches the benthos, as evidenced by increased fucoxanthin in the sediment, a diatom marker, and benthic carbon demand is substantially higher at Cape Bathurst than elsewhere on the CBS (Renaud et al. 2007a; Morata et al. 2008).

Upwelling (and downwelling) can create high currents, especially on steep slopes. Water flow of up to 70 cm s^{-1} was recorded by the ADCP moored at 13 m depth at CA6

over Sep. 2002–Sep. 2003 (Williams and Carmack 2008) (Fig. 5). By comparison, at mooring CA5, where the shelf is wider and the slope is more gradual, flows did not exceed 30 cm s^{-1} over the same period and at comparative depth. The matching pattern of ampeliscid abundance (highest at the eastern edge of Cape Bathurst and spreading westward) suggests a strong effect of upwelling events with *A. macrocephala* tolerating high currents and concentrating where upwelling effects are greatest. Along the Cape Bathurst eastern shore, the dominance was *A. macrocephala* > *Byblis* spp. > *H. laevis* at < 50 m depth. Feder et al. (1994) found a similar depth relationship in the adjacent Chukchi Sea. At > 50 m, the dominance reversed, with the smaller *H. laevis* dominating, indicating a greater capacity to live in a less food-rich environment with potentially smaller particle size. The other five species also peaked in abundance at Cape Bathurst but were less abundant or less frequently found there.

Mackenzie Trough and Kugmallit Valley likely also influence ampeliscid distributions as they are conduits for upwelling, caused by wind in summer and ice motion in winter and also for downwelling of near-freezing salty water from the flaw-lead (Carmack and Kulikov 1998; Williams et al. 2006, 2008). In Mackenzie Trough, upwelling can draw water from the nutrient maximum 100–200 m deep, affecting the eastern side of the trough (Williams et al. 2006). *Haploops laevis*, *Haploops* sp. and *H. tubicola* showed some abundance increases there, but the absence of the larger *Ampelisca macrocephala* shows that upwelling there is not as influential on the benthos as at Cape Bathurst. In Kugmallit Valley, upwelling draws water cross-shelf and to the east (Williams et al. 2008). Upwelling from Mackenzie Trough and Cape Bathurst can also reach this area (Williams and Carmack 2008; Williams et al. 2008; Walkusz et al. 2012). The presence of *A. macrocephala* along the eastern edge of the valley, but near absence to the west, and sustained high numbers on the shelf further east of the valley suggests that adequate resources are reaching this large ampeliscid there. These resources may not have to be consistently high. Temperate *A. macrocephala* can withstand starvation for at least 5 months in aquaria (Kannevorff 1965) and its Arctic congener, *A. eschrichtii*, can starve through the summer when phytoplankton are largely out of reach, growing and reproducing in winter when storms mix phytoplankton to within reach (Durkina et al. 2018).

Biological differences among the ampeliscids

The ampeliscid distributions can also be explained by differences in feeding morphology and behavior. Ampeliscids consume suspended and deposited particles (diatoms, detritus and small organisms) filtered and combed through the setae and spines on their antennae and legs (Online Resource

Table 2 Comparison of the life history and stable isotope composition of *Ampelisca macrocephala* and *Byblis gaimardii* in the Bering and Chukchi Seas

Comparator	<i>Ampelisca macrocephala</i>	<i>Byblis gaimardii</i>
Annual growth (mm)	4–5	6
Max. body length (mm)	33	~23 to 25
Age at female maturation (years)	4–5	2.5
Number of possible broods	2–3	3–4
Max. brood size	58	30
Hatchling length (mm)	5	4
Carbon requirement to reach 20–24 mm length ($\text{g m}^{-2} \text{ year}^{-1}$)	221	110
Stable isotope composition (under the relatively unproductive Alaska Coastal Water in the southern Chukchi Sea) (<i>mean</i> \pm <i>SD</i> , <i>n</i> = 3)	$\delta^{15}\text{N}$ 13.99 \pm 0.41	$\delta^{15}\text{N}$ 10.93 \pm 0.97
	$\delta^{13}\text{C}$ – 18.92 \pm 0.39	$\delta^{13}\text{C}$ – 22.69 \pm 0.67
Stable isotope composition (under the highly productive Anadyr Water) (<i>mean</i> \pm <i>SD</i> , <i>n</i> = 6)	$\delta^{15}\text{N}$ 8.10 \pm 0.58	$\delta^{15}\text{N}$ 8.08 \pm 0.48
	$\delta^{13}\text{C}$ – 20.00 \pm 0.35	$\delta^{13}\text{C}$ – 20.68 \pm 0.42

Sources Highsmith and Coyle (1991) for life history and Iken et al. (2010) for stable isotope composition. Data were based on specimens that were dominated by these species but could have had congeners mixed with them

3). Studies on three species common to the CBS (European *H. tubicola* and *A. macrocephala* and Chukchi Sea *B. gaimardii* and *A. macrocephala*) indicate behavioral differences. *Haploops tubicola* is an obligate suspension feeder on diatoms, detritus and microorganisms; it does not capture zooplankton, at least in laboratory experiments (Enequist 1949; Rigolet et al. 2011). Its antennal net is fine meshed and sticky and it can feed in turbid conditions (Rigolet et al. 2011). Its morphology reflects this with dense setation along the body, mouthparts and legs. Its tube is elevated above the sediment to aid suspended particle capture and it rarely leaves its tube (Enequist 1949; Dauvin and Zouhiri 1996).

By comparison, in *B. gaimardii* and *A. macrocephala*, the antennal mesh is coarser than in *H. tubicola* and non-sticky. Their tubes are flush with the sediment where they can sweep the surface of deposited material to supplement suspension feeding. They also prey on small crustaceans and they easily leave their tubes and swim into the water column (Enequist 1949; Kannevorff 1965; Mills 1967; Highsmith and Coyle 1990, 1991; Dauvin and Zouhiri 1996; Rigolet et al. 2011). They have four eyes instead of two and the pereopod 7 basis is posteriorly winged, features that may assist in swimming, prey location and current funnelling.

Comparing *B. gaimardii* to *A. macrocephala* in the Bering Sea (Table 2), *B. gaimardii* is able to dominate over the larger *A. macrocephala* when carbon flux is lower because it has about half the carbon demand and a shorter generation time (Highsmith and Coyle 1991; Coyle and Highsmith 1994). While both genera consume phytoplankton and ice algae when available, *A. macrocephala* can shift to a greater animal diet when particulate matter is sparse. *Byblis gaimardii* is able to sustain itself in both high and low particulate waters (Iken et al. 2010; Tu et al. 2015; McTigue and Duntun 2017). A comparison of the sediment $\delta^{13}\text{C}$ range for *A. macrocephala* and *B. gaimardii* on the CBS (Table 1) with

the tissue and sediment levels in the Chukchi Sea (Table 2; Grebmeier et al. 2006a) indicates that these species may have different carbon sources in the two areas, with the CBS being more land based due to the high sediment load supplied by the Mackenzie River.

These biological differences are reflected in the broad distribution patterns found on the CBS (Fig. 1): concentration of the high resource-demanding *A. macrocephala* in the most intense upwelling areas but declining abundance further away, compared to broader distributions of the less demanding *B. gaimardii*, and the presence of the fine particulate-feeding *H. tubicola* in the deep parts of Amundsen Gulf. For the other two nominal species, *H. laevis* and *H. sibirica*, there is much less biological information. *Haploops laevis* has a shorter tube than *H. tubicola* because its antennae are shorter (Kannevorff 1966). It is also larger than *H. tubicola*, suggesting greater resource requirements which are met in upwelling areas but not on the slope. *Haploops tubicola* has been found in dense aggregations on European coasts, suggesting that on the CBS it may be out-competed by *H. laevis*. *Haploops sibirica* is morphologically similar to *H. laevis* (Kannevorff 1966), which suggests a similar biology. The two species overlap on the shelf of the CBS but *H. sibirica* was found in Amundsen Gulf while *H. laevis* was never found so deep.

Coherent distributions among the ampeliscids

The SIMPROF analysis demonstrated that species in the same genus did not generally have similar distributions. Differing morphologies, feeding and swimming behaviors and differences in size, carbon demand, reproductive potential, space competition and predation rates will all enable cohabitation (Coyle and Highsmith 1994). The low similarities of

the Index of Association may be due to their relatively low frequency of occurrence (5–30% of the sites, depending on the species). While some species were widespread on the CBS (*Haploops* sp. and *H. tubicola*), others were primarily in the Cape Bathurst area (*A. macrocephala*, *Byblis* spp. and *H. laevis*). Although effort was made to cover the shelf and slope adequately over the 2002–2009 sampling period, ship operations were directed by differing scientific aims, resulting in an under-sampling of the Cape Bathurst area and more intensive sampling of the central and western part of the shelf, which was not an ampeliscid-rich area. The shelf also received more sampling effort than the slope. A more intensive sampling of the eastern part of the shelf would have more clearly delineated the extent of upwelling effects on the ampeliscids, as noted in Conlan et al. (2013). More intensive sampling of the slope may have targeted the deeper living species of *Haploops*, although these also occurred on the shelf.

Identification effects

The investigation of how potential mis-identifications might affect the results showed that the Group 1 species *A. macrocephala*, *Byblis* spp. and *H. laevis* formed a strongly cohesive group that held when mis-identifications were introduced (Online Resource 1). These species were the most frequently found and their distributions overlapped, with the greatest proportion of their abundance concentrating at Cape Bathurst. Introduction of mis-identifications to Group 2 (*Ampelisca* sp. and *H. tubicola*) and Group 3 (*Haploops* sp., *H. sibirica* and *B. gaimardii*) caused *H. tubicola* and *H. sibirica* to appear more cohesive in distribution and *B. gaimardii* to be more distinctive. These were the less frequent species and consequently, merging of congeners added additional sites to their distributions rather than simply reinforcing their already known distributions. For example, *Haploops* sp. occurred in nearly 3x as many sites as *H. sibirica* (Fig. 1, Table 1) and so, when merged, effectively boosted the frequency of *H. sibirica* to occurring in as many sites as *H. tubicola*.

Coherent distributions of non-ampeliscids with the dominant ampeliscids

Many of the 13 species coherently distributed with the dominant three ampeliscids (Fig. 3, Online Resource 2) were small crustaceans (amphipods, podocopid ostracods, cumaceans or isopods) or polychaetes (five families) that could have been responding independently to similar environmental conditions as the ampeliscids or were interacting with them. Many of these associates were surface mobile, tube dwelling or burrowing deposit feeders, suggesting that high deposition of labile, phytoplankton-derived organic

matter at Cape Bathurst (rather than refractory, land-derived carbon) was the prime driver. Biological interactions may also be occurring, though. Those organisms identified as predators or deposit feeders may affect ampeliscid distributions by preying on or disturbing the adults or small juveniles. They may also re-work the sediment, bringing resources to the surface for the ampeliscids. In turn, they may be positively influenced by changes effected by the ampeliscids to the surface sediment grain size, C and N content, benthic primary production, flow mechanics, sediment stability and availability of refuges from predation (Mills 1967; Rigolet et al. 2014a, b). The ampeliscid tubes also provide attachment sites to elevate into the water column. Various tube-living amphipods associate with ampeliscid beds in this way (Wildish 1984; Rigolet et al. 2011, 2012; Myers et al. 2012; Mironov 2013; Brower et al. 2017).

There are documented examples of apparent facilitation and exclusion in ampeliscid beds. *Ampelisca abdita* in Raritan Bay (New Jersey) is thought to facilitate the bivalve *Mercenaria mercenaria* by providing a low-current, low-silt and solid settlement site on its tubes for the bivalve larvae as well as deterring the crab and oyster drill predators of the bivalves (Mackenzie et al. 2006). *Haploops niraie* off the coast of Brittany is thought to facilitate diatom attachment and growth on its tubes which then provides opportunities for grazers and deposit feeders (Rigolet et al. 2014a, b; Dubois et al. 2015). *Ampelisca macrocephala* in the Bering Sea consumes juveniles of the northern sand dollar, *Echinarrachnius parma*, thereby excluding a potential space competitor (Highsmith and Coyle 1991). In these tube mats, species composition is significantly different from that outside the mat, indicating both facilitation and exclusion.

Ampeliscids and gray whales

Ampelisca macrocephala reached a maximal abundance of 8467 ind. m⁻² at Cape Bathurst, a value that is slightly greater than as reported in Conlan et al. (2013) which was based on fewer samples. This value exceeds by 3x the maximum abundance attained by the more frequently occurring *Byblis* spp. and by 5x that by *H. laevis*. *Ampelisca macrocephala* is the most abundant ampeliscid in the Bering and Chukchi Seas as well, where it also dominates in biomass and production (Highsmith and Coyle 1992; Coyle and Highsmith 1994). This species is a better space competitor than other Arctic species but requires a low predation rate and high fluxes of organic matter (Coyle and Highsmith 1994). It is the prime prey of eastern Pacific gray whales here (Coyle and Highsmith 1994); *A. eschrichti* supports a smaller population of western Pacific gray whales (Demchenko et al. 2016). Seafloor disturbance by feeding gray whales leaves *A. macrocephala* vulnerable to attack by scavenging benthic amphipods (Oliver and Slattery 1985) as

well as surface and diving seabirds (Grebmeier and Harrison 1992). However, gray whale feeding also creates a mosaic of seafloor depressions which are colonized by different species, resulting in an overall higher biodiversity (Oliver et al. 1984; Oliver and Slattery 1985). Such an effect of natural disturbance on macrofauna is paralleled by the effects of seafloor excavations created by ice scour (Conlan and Kvittek 2005) and gas venting (Dubois et al. 2015).

In the Chukchi Sea, gray whales target areas where amphipod densities are $> 85 \text{ m}^{-2}$ (Brower et al. 2017). Most parts of the CBS meet this density criterion for ampeliscids alone (Fig. 1). The widespread soft sediment on the CBS (Jerosch 2013) would be suitable for benthic feeding gray whales which suck the sediment and strain the contents through their baleen (Highsmith et al. 2007). Since gray whales also consume a wide variety of other benthic, epibenthic and pelagic organisms (Highsmith et al. 2007; Budnikova and Blokhin 2012), other areas of the CBS that are less ampeliscid rich but have high densities of other taxa (Conlan et al. 2008) may also be suitable. Elevated macrofaunal biomass is estimated to cover 4550 km^2 of the CBS at and to the west of Cape Bathurst (Conlan et al. 2013). Elevated pelagic resources occur at times of wind-driven upwelling which attract bowhead whales (Walkusz et al. 2012) but gray whales have also been seen there (Conlan et al. 2013).

Dense ampeliscid beds exist in other parts of the world also and the Atlantic beds may have been foraged previously by gray whales before the whale's Atlantic population was driven to extinction by whaling (Jones and Swartz 2009). Some ampeliscid densities in the Atlantic surpass $150,000 \text{ ind. m}^{-2}$ (Rigolet et al. 2012; Conlan et al. 2013). There have been recent sightings of two different Pacific gray whales in the Atlantic, one seen off Israel and then off Spain in 2010 and another off Namibia in 2013 (Zimmer 2015; Schiffman 2016). These were presumed to have accessed the Atlantic through the Arctic. If regime shifts occur in the Bering and Chukchi Seas, as has been documented previously (Grebmeier et al. 2006b; Bluhm and Gradinger 2008), and ice-free periods on the CBS are extensive, the CBS may be more frequently visited than previously documented. Whether this is happening is not known, however, as offshore whale monitoring and industrial activity in the CBS, which would have increased the chance of sighting gray whales, were discontinued after 2010 (Lois Harwood, pers. comm., 13 July 2018). Changes to gray whale movements will depend on how climate forcing and disturbance influence the gray whales as well as the productivity of the ampeliscids and other prey (Moore et al. 2003; Grebmeier et al. 2006; Tremblay et al. 2011; Kędra et al. 2015; Burnham and Duffus 2016; Villegas-Amtmann et al. 2017).

Future monitoring

With the many physical and chemical changes to the CBS that can be initiated by climate forcing will come biotic changes in every habitat at every trophic level (Carmack and Macdonald 2002; Barber et al. 2008; Wassmann et al. 2011; Kędra et al. 2015). Arctic ampeliscids, especially the large *A. macrocephala*, have slow growth rates and long generation times and they may be unable to recover quickly from biological or physical changes (Coyle et al. 2007). Arctic *A. macrocephala* appear to be specially adapted to a high latitude environment by having a larger genome than any other Arctic amphipod that has been investigated so far (Rees et al. 2007). Although most of the species in this study, including *A. macrocephala*, have populations at lower latitudes, suggesting potential environmental resilience, there are no data on how similar they are genetically or physiologically. This study showed that none of the CBS species occurred in water warmer than $0.41 \text{ }^\circ\text{C}$, suggesting that the CBS species may be intolerant of warming.

Ampeliscids support a variety of upper trophic level predators because of their tendency to live in aggregations, be highly productive, and be available to both benthic and pelagic consumers because they swarm to mate. The composition, distribution and seasonality of these ampeliscid populations will be worth monitoring as their environmental sensitivities, ecological interactions, physiological tolerances, life histories and linkages to large predators are becoming better understood (Moore et al. 2003; Renaud et al. 2015). Impetus toward pan-Arctic biodiversity monitoring is growing and Cape Bathurst has been designated as a desired benthic monitoring area for benthic changes in the CBS (Gill et al. 2011). The Inuvialuit and the Canadian government co-manage the natural resources of the CBS. There are six permanent communities on the shores of the CBS which make use of the local marine mammals, birds and fish for sustenance (Ayles et al. 2016).

This study has demonstrated that at least eight species of ampeliscids span the CBS yet each is distributed differently. They are clearly dependent on events in the water column (upwelling) and also benthic availability of resources and sediment particulates for tube building. Changes to any one species could signal underlying environmental changes that may not be evident through physico-chemical monitoring. Of particular focus should be *A. macrocephala* because of its dependence on high productivity and *H. sibirica* because it is primarily Arctic in distribution. Long-term changes to *H. tubicola* and *B. gaimardii*, with temperate ranges, high generation times and ability to capture small particulates may indicate environmental change also. All the nominal species are known from other parts of the Arctic and range

shifts have been reported from the warming Barents Sea (Lyubina et al. 2014). Other polar and temperate ampeliscid beds have been or are beginning to be monitored long term (Poggiale and Dauvin 2001; Ehrhold et al. 2006; Coyle et al. 2007; Burnham and Duffus 2016; Demchenko et al. 2016), giving trend data that may predict changes on the CBS. The information that is now available on the CBS and neighboring Bering and Chukchi ampeliscids, their importance to upper trophic level predators, and their biological differences and environmental sensitivities outlined in this and other studies all point to these amphipods as being valuable environmental monitors.

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