Polar Biol (2017) 40:2027–2033
DOI 10.1007/s00300-017-2122-3

ORIGINAL PAPER

Interdecadal changes in the marine food web along the west Spitsbergen coast detected in the stable isotope composition of ringed seal (*Pusa hispida*) whiskers

Andrew D. Lowther[1] · Aaron Fisk[2] · Kit M. Kovacs[1] · Christian Lydersen[1]

Received: 18 November 2016 / Revised: 3 April 2017 / Accepted: 6 April 2017 / Published online: 7 June 2017

Abstract Recent influxes of warm Atlantic water into the fjords of west Spitsbergen have led to concomitant influx of more temperate and boreal fish species. The changes in the water masses within the fjords naturally affect all trophic levels of the sympagic, benthic, and pelagic food chains in the area. The most abundant marine mammal species in the fjords of west Spitsbergen is the ringed seal (*Pusa hispida*), which feeds, breeds, and moults in this area. In this study, we used isotopic data from whiskers of two cohorts of adult ringed seals (sampled in 1990 and 2013) to determine whether signals of ecosystem changes were detectable in this top marine predator. Acknowledging the limitations to our understanding of whisker growth in phocid seals, we interpreted the isotopic data from whiskers under two alternate hypotheses of whisker replacement dynamics and the dietary periods that might be represented. Even under the most conservative hypothesis, it is clear from our data that changes in the marine food web of the west Spitsbergen coast have occurred over the last 20 years, and that these are detectable in the isotopes incorporated into higher trophic predators. Concluding which aspect of the food web has been modified is complicated by a lack of recent ringed seal dietary studies, a knowledge gap that should be prioritised as the climate continues to change.

Keywords Climate change · Diet · Foraging ecology · Prey shifting · Trophic levels · Vibrissae

✉ Andrew D. Lowther
andrew.lowther@npolar.no

1 Norwegian Polar Institute, Fram Centre, 9692 Tromsø, Norway

2 Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Canada

Introduction

Over recent decades, the predictions of climate change-driven modifications to polar habitats are being replaced by quantitative observations. Evidence of changes occurring within marine environments of the High Arctic is increasing, with dramatic reductions in ice cover, altered ocean circulation patterns, and rises in sea temperatures (Comiso et al. 2008; Wassmann et al. 2011; Marshall et al. 2014). Alteration of the shelf and shelf-break hydrography along the west Spitsbergen coast is one such environment that has received considerable scientific attention. Atlantic water originating from the North Atlantic Current flows northward into the Fram Strait as the West Spitsbergen Current (WSC). The WSC is responsible for most of the oceanic heat transported into the Arctic Ocean, and is also a very important determinant of the regional oceanography and thus has a major influence on marine ecosystems in Svalbard. Less saline and colder Arctic water also flows northwards over the continental shelf of western Spitsbergen, east of the WSC, and forms a barrier for the fjords on western Spitsbergen from direct impact of the warmer Atlantic water. Exchange across this barrier, mainly wind driven, results in influxes of Atlantic water into these fjord systems (Tverberg et al. 2014; Blanchet et al. 2015). Thus, the variation in influx of the warm saline Atlantic water and colder less saline Arctic water, in addition to river run-off and glacial melt, dominates the physical conditions within the fjords in this area including the processes connected to sea-ice formation and melting (Cottier et al. 2005).

The temperatures of the Atlantic water in the WSC have never been higher than those from the start of the twenty-first century (Spielhagen et al. 2011). Recently, several episodes of flooding of this warm Atlantic water into the fjords of west Spitsbergen have occurred (especially during winter

2005/06) with reduced sea-ice formation as one of the consequences (Cottier et al. 2005; Spielhagen et al. 2011). These changes in water masses also have serious implication for the marine ecosystems in these fjord systems. As an example, the local fish communities have experienced an influx of more temperate and boreal fish species; recently, Atlantic mackerel (*Scomber scombrus*) was recorded in Isfjorden, a large fjord in the region, for the first time (Berge et al. 2015). Other Atlantic fish species, including Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and herring (*Clupea harengus*), have recently replaced the native Arctic fish fauna to a large degree, in particular polar cod (*Borogadus saida*), which has declined in the region (Fossheim et al. 2015). The change in this fish community is attributed to continued warming of the ocean in this region, consistent with a predicted trend of southern species extending their ranges northwards into the Arctic with warming oceans (Gilg et al. 2012). The changes in these water masses naturally affect other trophic levels of the sympagic, benthic, and pelagic food chain in the area (Søreide et al. 2013).

The most abundant marine mammal species in the fjords of west Spitsbergen is the ringed seal (*Pusa hispida*), which feeds, breeds, and moults in this area (Lydersen 1998). Several studies of the feeding habits of ringed seals collected from Svalbard show that this seal species has a diet that included various fish and invertebrate species, but which is generally dominated by polar cod (Gjertz and Lydersen 1986; Weslawski et al. 1994; Labansen et al. 2007). However, there have been no ringed seal dietary studies with material collected after 2002 around Svalbard, making the impact of the hydrographic changes that have taken place in recent years challenging to assess for this species.

Recently, the use of biogeochemical markers such as the relative abundance of isotopically-stable variants of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$, respectively) have been used to characterise the feeding ecology of diving marine predators (Crawford et al. 2008). The timeframe over which $\delta^{13}C$ and $\delta^{15}N$ reflect the diet is tissue dependent; for example, the isotopic composition of blood plasma reflects foraging over a short period (~last few days), whereas isotopic incorporation into muscle or bone reflects a longer period (on average months to years) (Newsome et al. 2010). Inert tissues such as whiskers (vibrissae) have the potential to provide a timeline of feeding behaviour; isotopes are incorporated into a tissue that is then inert, preserving the dietary information over time.

There are several challenges to using stable isotopes in the whiskers of ringed seals to provide dietary information. Unlike the linear growth of otariid whiskers, which provides the opportunity to recover a timeline of feeding behaviour (Cherel et al. 2009), the growth and replacement patterns of phocid whiskers are still largely unknown. Five studies have characterised the growth of phocid whiskers; these studies have suggested that grey seals (*Halichoerus grypus)* (Greaves et al. 2004), harbour seals (*Phoca vitulina)* (Hirons et al. 2001), leopard seals (*Hydrurga leptonyx*) (Hall-Aspland et al. 2005), spotted seal (*Phoca largha*) (McHuron et al. 2016), and captive northern elephant seals (*Miroungia angustirostris*) (Beltran et al. 2015) display whisker growth that is characterised as exponential, and often best fitted by a Von Bertalanffy growth function. Furthermore, using both biogeochemical techniques and visual observation, there are ambiguous reports of whether whisker shedding occurs annually during the moult (e.g., McHuron et al. 2016) or in a random fashion, with some whiskers being retained for multiple years (Hirons et al. 2001; Beltran et al. 2015). However, all studies of phocid whisker growth suggest that there is no catastrophic seasonal shedding of whiskers and individuals have a fully functional whisker bed year-round.

The purpose of our study was to determine whether recently observed changes in the hydrography and the marine food web around the west coast of Spitsbergen could be detected in the $\delta^{13}C$ and $\delta^{15}N$ values present in the whiskers of two cohorts of ringed seals collected in 1990 and 2013. Acknowledging the limitations for whisker growth discussed above, the data from our study are interpreted under two alternate hypotheses relating to whisker replacement and the dietary periods that might be represented for ringed seals: H_1: When individual whisker replacement occurs, it does so in the same season on each occasion (Hirons et al. 2001; McHuron et al. 2016). Thus, early stage whisker growth will be comparable between individuals in terms of which season the dietary information reflects. H_2: Individual whisker replacement is completely random; thus, no part of an individual's whisker is directly comparable with whiskers from any other individual, either within or between cohorts. We make the conservative assumption that whisker growth asymptotes at approximately 200 days as reported for other phocid species (see above). Consequently, the data from whiskers within a cohort can be used only to characterise the complete niche breadth of the cohort during a random 200 day period at some stage during the 2 years prior to sampling.

Considering this, we hypothesise that the increased intrusion of temperate North Atlantic water onto the western shelf of Spitsbergen between 1990 and 2013 has modified the food web to such an extent that such changes will be detectable using stable isotope values present in whiskers (vibrissae) of the local adult ringed seals, which inhabit the region year-round (Hamilton et al. 2016).

Materials and methods

Whisker sampling and preparation

Entire whisker beds from juvenile and adult male ringed seals were collected in 1990 ($n=23$) and 2013 ($n=27$) from animals harvested for other purposes at several locations along the west coast of Svalbard (Fig. 1). Given that ringed seals can travel considerable distances while foraging at sea (Hamilton et al. 2016), in the context of our overall goal, any differences in the distribution of samples sites between the 2 years are irrelevant. Whisker beds were placed in aluminium foil and stored at −20 °C until prepared for analyses. The longest whisker from each bed was snipped at the base flush with the muzzle. Each whisker was then placed into a glass vial with 2:1 chloroform:methanol for removal of lipids (expected to be very low), and agitated in an ultrasonic bath at 40 °C for 15 min. Vials were then drained, and each whisker was cleaned by hand using a wet lint-free cloth (Kimwipe™). Vials were then refilled with distilled water and placed back into the ultrasonic bath for an additional 10–15 min. After this stage, excess water was drained and each whisker was oven-dried for 24 h at 40 °C. Before sectioning, each whisker was checked for debris visually under a stereomicroscope and any further cleaning was performed using a scalpel blade. Each whisker was then measured to the nearest millimeter and sectioned into quarters. The middle 1 mm from each quarter and the first 1 mm proximal to the muzzle were sampled, resulting in five distinct samples from each whisker. Each 1 mm segment was then weighed, to ensure the target weight of >180 µg, necessary for $\delta^{13}C$ and $\delta^{15}N$ analysis. Note that, in some cases, it was necessary to take slightly more than 1 mm, particularly towards the distal end of the whisker. However, no segment was greater than 1.5 mm in length. Each segment was then labelled from 'A' to 'E' starting at the proximal end.

Stable isotope analysis

Clean and cut whiskers from each segment were weighed into tin cups, and $\delta^{13}C$ and $\delta^{15}N$ of each sample were determined using a Delta V Advantage Thermoscientific continuous flow mass spectrometer (Thermo Electron Corporation, Bremen, Germany) coupled to a 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA). Stable isotope values are reported as per mil (δ) and were calculated using the equation:

$$\delta X = \left(\left[\frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}} \right] - 1 \right) \times 1000 \,,$$

where X represents ^{13}C or ^{15}N and R is represented by ^{13}C:^{12}C and ^{15}N:^{14}N. By convention, Vienna Pee Dee

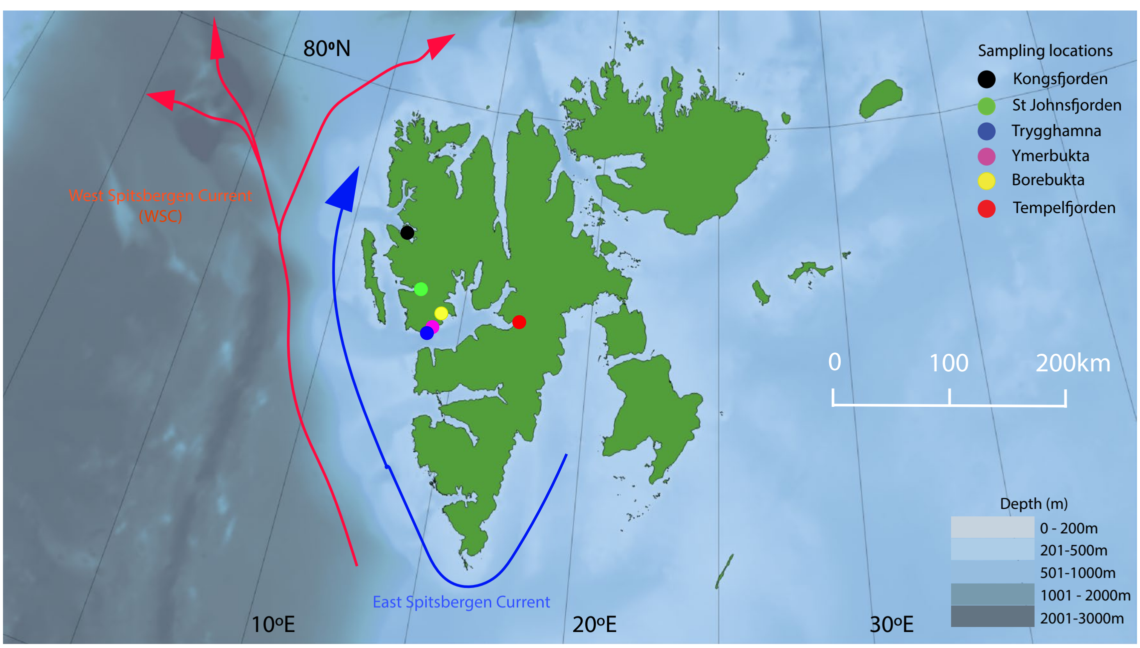

Fig. 1 Locations of ringed seal (*Pusa hispida)* whisker sampling events in 1990 ($n=23$) and 2013 ($n=27$). The West Spitsbergen Current (WSC) is a northward-flowing, warm, saline current of Atlantic water that flows along the western shelf of Svalbard. A cooler, Arctic water current runs parallel to the WSC but along the shelf. During the last decade, seasonal intrusions of the WSC onto the shelf and more recently into the fjords along the western coastline of Spitsbergen have been recorded, leading to a gradual "borealisation" of the marine ecosystem in the region

Belemnite (VPDB) and atmospheric nitrogen (AIR) were used as standard reference materials for carbon (δ^{13}C) and nitrogen (δ^{15}N), respectively. Analysis precision met standards acceptable in published literature based on standard deviation values of <0.2‰ for δ^{13}C and δ^{15}N for internal laboratory standards run after every 12 samples (NIST 1577c and internal lab standard tilapia (*Oreochromus* spp.) muscle [both $n=221$)], which were <0.2‰ for δ^{13}C and <0.2‰ for δ^{15}N. Accuracy was deemed acceptable based on achieving δ^{13}C and δ^{15}N values within 0.2‰ of certified NIST standards analysed during the same time as sample; δ^{15}N values were within 0.1‰ (NIST 8573) and (NIST 8549), and for δ^{13}C within 0.2‰ (NIST 8542) and −0.1‰ (NIST 8573) of certified values.

Data analyses

To determine whether inter-individual variability existed, we ran a series of linear mixed models for each time period, with isotope value (δ^{13}C and δ^{15}N) as the dependent variable, whisker segment as the fixed effect, and individual as a random effect. Based on model outputs, whisker segments that exhibited non-significant levels of individual-level variability were pooled for each time period. Further analyses were then conducted in line with the hypotheses outlined above.

Hypothesis #1: whiskers are shed at a predictable time of year

Under this hypothesis, and considering the presumed exponential growth of phocid whiskers, sections D and E represent the most rapid period of growth during the initial eruption of the new whisker, incorporating isotopes from dietary intake over a period of weeks (Beltran et al. 2015). As such, the isotope values from these distal segments should be comparable across time periods. Consequently, given the results from the modelling process outlined above, we employed a model-based clustering approach with two input parameters (δ^{13}C and δ^{15}N) from each time period, using the R package 'Mclust' (Fraley and Raftery 2007). Model selection was made using Bayesian Information Criteria (BIC), because this approach typically penalises overly complicated models. A posteriori classification was made using leave-one-out quadratic discriminant analysis (LOOCV-QDA). Assessments of different clustered means of δ^{13}C and δ^{15}N within and between time periods were made using a Bayesian approach with non-informative priors and a normally distributed likelihood model. The degree of support for mean differences was assessed by resampling the posterior distribution with a Gibbs resampler, applied using JAGS v.3.4.0 and the R package 'rjags' (Plummer 2003) with 10,000 Markov Chain Monte Carlo iterations after a burn-in of 1000 iterations. Discrete groupings were given to clusters with strong support (posterior probability >95%) for differences in isotopic values.

Hypothesis #2: whiskers are shed randomly throughout the year

Given the implications of random shedding of whiskers, the analytical scope for characterising differences between time periods is limited. Consequently, we relied on biplots of all whisker segment δ^{13}C and δ^{15}N values and qualitatively compared trends between time periods.

Results

In total, 250 whisker segment samples were analysed, representing 23 individuals from 1990 to 27 individuals from 2013. Linear mixed effects modelling resulted in whisker segments D and E displaying no differences in isotopic values across individuals within time periods (linear mixed effects $F_{22}=0.03$, $p=0.7$). Consequently, segments D and E were used for further clustering analysis under Hypothesis #1. On the basis of δ^{13}C and δ^{15}N values of whisker segments D and E, model-based clustering and subsequent BIC model selection identified two distinct clusters based on the different time periods, for which LOOCV-QDA correctly assigned isotopic samples with relatively high certainty to their time period of origin (1990: 89.4%; 2013: 78.7%; Fig. 2). Based on the δ^{13}C values in these clusters, there was strong support for a mean decrease of δ^{13}C in segments D and E of 1.1‰ (posterior probability >99%, 95% CI 0.88–1.4‰ and 0.87–1.4‰, respectively). Similarly, there was strong support for a slight decrease in δ^{15}N between 1990 and 2013 of approximately 0.6‰ (posterior probability >95%, 95% CI 0.08–1.1‰) in segment D samples, with weaker support for differences between the time periods in segment E (mean difference 0.3‰, posterior probability = 80%, 95% CI −0.28 to 0.8‰).

Under Hypothesis #2, isotope biplots of δ^{13}C and δ^{15}N showed a broadening of the range of δ^{13}C values from 1990 (−16.97 to −19.23‰) to 2013 (−17.4 to −20.25‰), though this coarse-scale interpretation failed to show any major changes in δ^{15}N between decades (Fig. 3).

Discussion

For diving predators such as the ringed seal, explanations of isotopic variability must reflect changes in the food web at a scale relevant to the predators' movement patterns. Considering this, irrespective of the assumptions made behind growth rates and shedding patterns of ringed seal

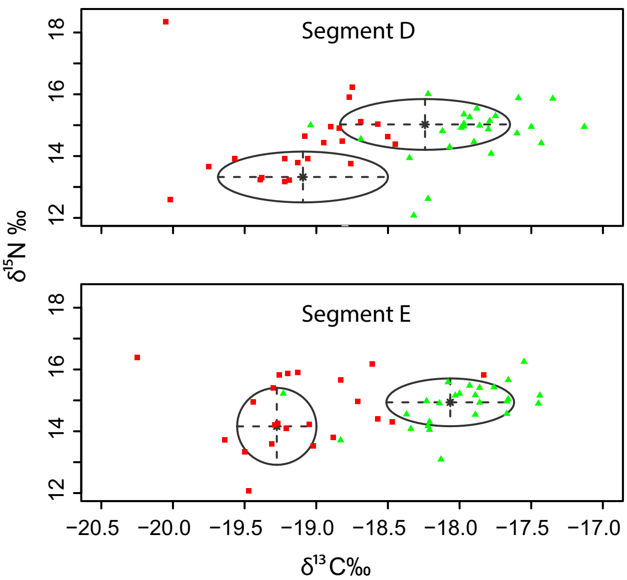

Fig. 2 Clustered isotopic data of whisker segments D and E from male ringed seals (*Pusa hispida)* harvested in 1990 (*green triangles*) and 2013 (*red squares*). Segments represented the early stages of whisker growth that captured foraging activity over a period of weeks. Samples from the respective time periods were correctly assigned to their respective cluster with high certainty (>78% in all cases). Under the assumption that whisker replacement occurs during the same season, a shift to a more depleted $\delta^{13}C$ signal from 1990 was strongly supported (minimum mean difference 1.4‰, 95% CI 1.23–1.59‰)

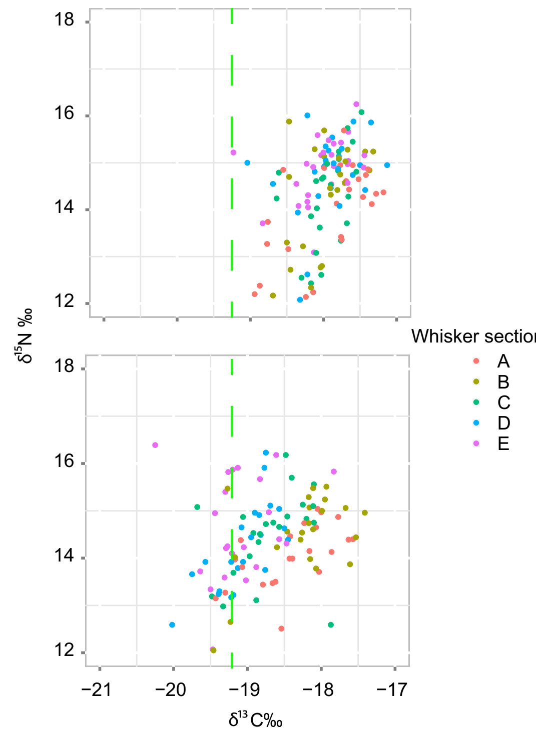

Fig. 3 Isotopic biplot of $\delta^{13}C$ and $\delta^{15}N$ values recovered from whisker segments of ringed seals (*Pusa hispida)* harvested in 1990 (*top*) and 2013 (*bottom*). The green vertical dotted line highlights the extent of the most depleted $\delta^{13}C$ value detected in 1990, and the corresponding number of values falling below this level in 2013. Under the hypothesis that individual whiskers represent a random sample of foraging behaviour over the 2 years preceding sampling, there was a broadening of $\delta^{13}C$ compared to 1990, with whisker segments representing early whisker growth (and consequently, a foraging record spanning weeks) appearing to dominate the depleted $\delta^{13}C$ in the 2013 cohort

whiskers, the results of our study suggest that the carbon base of the West Spitsbergen marine food web exploited by ringed seals has broadened, with a decrease in the lower limit of $\delta^{13}C$ of at least 1‰. Similarly, given the emerging evidence of diminished diet tissue discrimination factors with increased $\delta^{15}N$ (Hussey et al. 2014), a decrease in $\delta^{15}N$ of ~0.6‰ for an apex predator such as the ringed seal may reflect a relatively large trophic position shift between the sampling periods.

A predator's $\delta^{13}C$ and $\delta^{15}N$ reflects its diet and these ratios vary in relation to the ecology of predators and their prey. When $\delta^{13}C$ variability is detected, it can be interpreted as a shift in the geographic location of foraging by the predator or a change in the carbon cycle supporting the food web that supports their prey field (Crawford et al. 2008). In the High Arctic, changes in dietary $\delta^{13}C$ reflect changes in the source of carbon between isotopically distinct pelagic, sympagic, and benthic-dominated food webs (Tamelander et al. 2006). Consequently, our results must be related to some combination of (1) shifting between the different food webs by the ringed seals, and (2) a change in the biogeochemical composition of the food web underpinning the preferred prey items of the seals.

Recent studies have recorded an influx of temperate, Atlantic water-associated fish species along western Svalbard. Atlantic mackerel, Atlantic cod, haddock, capelin (*Mallotus villosus*), and snake pipefish (*Entelurus aequoreus*) (Fleischer et al. 2007; Renaud et al. 2012; Berge et al. 2015; Fossheim et al. 2015; Dalpadado et al. 2016) have all been recorded moving into the fjords along the western coastline of the Svalbard Archipelago, in line with the increased influx of warm north Atlantic water into the region. Since 2006, Atlantic cod and haddock have been in sufficient densities in the coastal waters of Svalbard as to be regularly caught in the same trawls with polar cod, resulting in concerns regarding competitive exclusion of polar cod by boreal fishes (Renaud et al. 2012). Interestingly, the $\delta^{15}N$ ratios of Atlantic cod and haddock sampled near the ice edge in 2006 by Renaud et al. (2012) were approximately 2‰ lower than polar cod caught in the same trawl (Atlantic cod 9.6‰; haddock 10.3‰; polar cod 12.0‰). Under the assumption that polar cod still comprise the largest proportion of ringed seal diet and accounting for a typical trophic level of $\delta^{15}N$ increase of approximately 3‰ (Newsome et al. 2010), then ringed seals should express a $\delta^{15}N$ approaching 15‰. This value matches closely with those seen in the whiskers of seals from the 1990s cohort in the current study, and the small though significant decrease described between these earlier samples and that from 2013 may reflect the incorporation of lower $\delta^{15}N$ boreal fish species into their diet. If ringed seals shed their whiskers during the annual early summer moult (sensu Hypothesis #1 above), then the change in isotope signals we describe may represent a response to the increased seasonal intrusion of Atlantic water and a corresponding change in the availability of boreal fish species as potential prey during the summer period. Telemetry studies of adult ringed seal movements along the western Spitsbergen coast show that the vast majority of at-sea time of adult ringed seals is spent in close proximity to glacier fronts deep inside fjords (Hamilton et al. 2016). In addition, other recent studies in the region show the traditional Arctic zooplankton prey of polar cod such as *Themisto libellula* are becoming confined to the inner areas of fjord systems along western Spitsbergen during the summer as a result of the seasonal intrusion of Atlantic water (Dalpadado et al. 2016). Ringed seals may be seeking out their preferred prey in vestiges of Arctic water close to glacier fronts, but opportunistically consuming Atlantic water-associated prey during movements between glacier fronts.

Alternatively, ringed seals may still maintain a diet heavily dominated by polar cod, but the "prey of their prey" may have changed, with our data reflecting a change in the underlying zooplankton composition driven by the recent "borealisation" of the marine environment along west Spitsbergen (Fossheim et al. 2015). For example, although polar cod normally feed on *T. libellula*, Dalpadado et al. (2016) have shown an overlap in prey of polar cod and capelin in the Svalbard region of up to 47%, with both species feeding on copepods (*Calanus* spp). The increased "borealisation" Atlantic water into the western fjords has likely led to the replacement of true Arctic copepods such as *C. glacialis* with more Atlantic water-associated species such as *C. finmarchicus* (Slagstad et al. 2011; Gluchowska et al. 2016). In addition, *T. libellula* also preys on copepods (Dalpadado et al. 2016), providing an additional pathway for changes in the zooplankton community along western Spitsbergen to be reflected in the changes in the isotopic signal of ringed seal whiskers over time, without the seals switching prey. Krill are also much more common in the fjords, since the intrusions of warm water started to occur (Dalpadado et al. 2016) and thus represent a food source for fishes in the fjords, including polar cod.

Conclusions

Our results clearly show that there have been changes in the marine food web of the west Spitsbergen coast over the last 20 years, which are detectable in the isotopes incorporated into higher trophic predators. However, given that there have been no studies of Svalbard ringed seal diet after 2004, we are unable to conclusively determine whether the cause of the isotopic shifts we observed is due to changes in the prey consumed by the seals or that the diets of their prey have changed. Given the ecosystem modification that has occurred along the western coast of Spitsbergen and considering that ringed seals are a key Arctic endemic species, a major consumer within Svalbard fjords, and a hunted species throughout much of their range, addressing that this crucial knowledge gap should be a priority.

Acknowledgements This study was supported by the Norwegian Polar Institute. We thank Ms. Anna Hussey for her assistance in processing and analysing the whisker samples.

References

Beltran RS, Sadou MC, Condit R et al (2015) Fine-scale whisker growth measurements can reveal temporal foraging patterns from stable isotope signatures. Mar Ecol Prog Ser 523:243–253. doi:10.3354/meps11176

Berge J, Heggland K, Lønne OJ et al (2015) First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard archipelago, Norway, with possible explanations for the extension of its distribution. Arctic 68:54–61. doi:10.14430/arctic4455

Blanchet MA, Lydersen C, Ims RA, Kovacs KM (2015) Seasonal, oceanographic and atmospheric drivers of diving behaviour in a temperate seal species living in the high arctic. PLoS ONE 10:e0132686. doi:10.1371/journal.pone.0132686

Cherel Y, Kernaleguen L, Richard P, Guinet C (2009) Whisker isotopic signature depicts migration patterns and multi-year intra- and inter-individual foraging strategies in fur seals. Biol Lett 5:830–832. doi:10.1098/rsbl.2009.0552

Comiso JC, Parkinson CL, Gersten R, Stock L (2008) Accelerated decline in the Arctic sea ice cover. Geophys Res Lett 35:1–6. doi:10.1029/2007GL031972

Cottier F, Tverberg V, Inall M et al (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. J Geophys Res 110:1–18. doi:10.1029/2004JC002757

Crawford K, McDonald RA, Bearhop S (2008) Application of stable isotope techniques to the ecology of mammals. Mamm Rev 38:87–107. doi:10.1111/j.1365-2907.2008.00120.x

Dalpadado P, Hop H, Rønning J et al (2016) Distribution and abundance of euphausiids and pelagic amphipods in Kongsfjorden, Isfjorden and Rijpfjorden (Svalbard) and changes in their relative importance as key prey in a warming marine ecosystem. Polar Biol 39:1765–1784. doi:10.1007/s00300-015-1874-x

Fleischer D, Schaber M, Piepenburg D (2007) Atlantic snake pipefish (*Entelurus aequoreus*) extends its northward distribution range to Svalbard (Arctic Ocean). Polar Biol 30:1359–1362. doi:10.1007/s00300-007-0322-y

Fossheim M, Primicerio R, Johannesen E et al (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Change 5:1–6. doi:10.1038/nclimate2647

Fraley C, Raftery AE (2007) Bayesian regularization for normal mixture estimation and model-based clustering. J Classif 24:155–181. doi:10.1007/s00357-007-0004-5

Gilg O, Kovacs KM, Aars J et al (2012) Climate change and the ecology and evolution of Arctic. Ann N Y Acad Sci 1249:166–190. doi:10.1111/j.1749-6632.2011.06412.x

Gjertz I, Lydersen C (1986) The Ringed Seal (*Phoca hispida*) spring diet in nortwestern Spitsbergen, Svalbard. Polar Res 4:53–56. doi:10.3402/polar.v4i1.6919

Gluchowska M, Kwasniewski S, Prominska A et al (2016) Zooplankton in Svalbard fjords on the Atlantic–Arctic boundary. Polar Biol 39:1785–1802

Greaves DK, Hammill MO, Eddington JD, et al (2004) Growth rate and shedding of vibrissae in the gray seal, *Halichoerus grypus*: a cautionary note for stable isotope diet analysis. Mar Mamm Sci 20:296–304. doi:10.1111/J.1748-7692.2004.Tb01158.X

Hall-Aspland SA, Rogers TL, Canfield RB (2005) Stable carbon and nitrogen isotope analysis reveals seasonal variation in the diet of leopard seals. Mar Ecol Prog Ser 305:249–259. doi:10.3354/meps305249

Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2016) Coastal habitat use by ringed seals *Pusa hispida* following a regional sea-ice collapse: importance of glacial refugia in a changing Arctic. Mar Ecol Prog Ser 545:261–277. doi:10.3354/meps11598

Hirons AC, Schell DM, St. Aubin DJ (2001) Growth rates of vibrissae of harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*). Can J Zool 79:1053–1061. doi:10.1139/cjz-79-6-1053

Hussey NE, Macneil MA, Mcmeans BC et al (2014) Rescaling the trophic structure of marine food webs. Ecol Lett 17:239–250. doi:10.1111/ele.12226

Labansen AL, Lydersen C, Haug T, Kovacs KM (2007) Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway. ICES J Mar Sci 64(6):1246–1256. doi:10.1093/icesjms/fsm090

Lydersen C (1998) Status and biology of ringed seals (Phoca hispida) in Svalbard. NAMMCO Sci Publ 1:46–62. doi:10.7557/3.2980

Marshall J, Armour KC, Scott JR et al (2014) The ocean's role in polar climate change: asymmetric Arctic and Antarctic responses to greenhouse gas and ozone forcing. Philos Trans R Soc Lond A 372:20130040. doi:10.1098/rsta.2013.0040

McHuron E, Walcott S, Zeligs J, Skrovan S (2016) Whisker growth dynamics in two North Pacific pinnipeds: implications for determining foraging ecology from stable isotope analysis. Mar Ecol Prog Ser 554:213–244. doi:10.3354/meps11793

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mamm Sci 26:509–572.

Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd international workshop on distributed statistical computing, 20–22 March 2013, Vienna, pp 1–10

Renaud PE, Berge J, Varpe O et al (2012) Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*. Polar Biol 35:401–412

Slagstad D, Ellingsen IH, Wassmann P (2011) Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: an experimental simulation approach. Prog Oceanogr 90:117–131. doi:10.1016/j.pocean.2011.02.009

Søreide JE, Carroll ML, Hop H et al (2013) Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. Mar Biol Res 9:831–850. doi:10.1080/17451000.2013.775457

Spielhagen RF, Werner K, Sørensen SA et al (2011) Enhanced modern heat transfer to the Arctic by warm Atlantic water. Science 331:450–453. doi:10.1126/science.1197397

Tamelander T, Renaud PE, Hop H et al (2006) Trophic relationships and pelagic—benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. Mar Ecol Prog Ser 310:33–46. doi:10.3354/meps310033

Tverberg V, Nøst OA, Lydersen C, Kovacs KM (2014) Winter sea ice melting in the Atlantic Water subduction area, Svalbard Norway. J Geophys Res C Oceans 119:5945–5967. doi:10.1002/2014JC010013

Wassmann P, Duarte CM, Agusti S, Sejr MK (2011) Footprints of climate change in the Arctic marine ecosystem. Glob Chang Biol 17:1235–1249. doi:10.1111/j.1365-2486.2010.02311.x

Weslawski JM, Ryg M, Smith TG, Oritsland NA (1994) Diet of ringed seals (*Phoca hispida*) in a fjord of west Svalbard. Arctic 47:109–114