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Implications of trophic discrimination factor selection for stable isotope food web models of low trophic levels in the Arctic nearshore

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ABSTRACT: Stable isotope analysis (SIA) has become a useful tool to investigate food web structures in Arctic marine ecosystems. This method requires assumptions about how isotopes are assimilated from food into tissues. Few controlled lab experiments have determined the appropriate trophic discrimination factors (TDFs) for Arctic marine species, thus many studies have resorted to using global averages or values determined from species in different habitats or taxa. We examined the trophic niche space for prey resources predicted from the isotopic ratios of fish collected in the coastal Beaufort and Chukchi Seas using several published Arctic marine TDFs. The different predictions were compared to highlight the implications of selecting appropriate TDFs in Arctic marine food web models. Predicted trophic niche space of prey resources differed greatly depending on the TDFs used, and the most appropriate TDFs from those that are currently available were identified for modeling Arctic nearshore lower trophic levels.

KEY WORDS: Trophic · Enrichment · Fractionation · Carbon · Nitrogen · Fish · Plankton

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1. INTRODUCTION

As climate change and anthropogenic activities continue to increase in Arctic marine ecosystems, species' ranges will likely expand, contract, or shift in response to new conditions, and as a result species assemblages in the Arctic are expected to change (Poloczanska et al. 2008, Grebmeier 2012, Barton et al. 2017). These changes in community composition are expected to shift food web structure and available resources (Dunton et al. 2012, McTigue & Dunton 2014). In response, there has been great effort to better understand the current structure of Arctic food webs and basal resource dependence to gain insight into how they will be affected in the future as lower-latitude species compete for resources (Dunton et al. 2012, McTigue & Dunton 2014, Barton et al. 2017).

Past work has suggested that the use of stable isotope analysis (SIA) would allow for food web-wide comparisons of different trophic structures, and that the difference in these structures offers insight to the resilience and functionality of an ecosystem (Post 2002). SIA of animal and plant tissues has become a useful method to investigate trophic structures in food webs at many spatial and temporal scales (Hobson & Welch 1992, Dunton et al. 2012), since SI ratios in consumers should resemble those in their prey.

Gannes et al. (1997) called for more experimental SI studies after recognizing the rapid increase in the use of SI ecology and a paucity of experimental studies to support and further develop these methods.

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These experiments aim to understand how the assimilation of isotopes into tissues is affected by the physiochemical processes that break down and rebuild macromolecules after ingestion. Through the processes of digestion and synthesis of new tissues, metabolic processes preferentially use lighter isotopes, leaving behind heavier isotopes to be assimilated into new tissues, resulting in isotopically heavier or more enriched tissues than the material that was consumed (Gannes et al. 1997). This process, known as trophic fractionation, causes a difference between prey and consumer (trophic discrimination factor, TDF), which is used to predict the trophic niche space of an individual's prey or predator, and plays a crucial role in reconstructing food webs using SIA.

For practical reasons, most isotope studies assume that TDFs are constant through a food web. Commonly cited averages derived from early work have shown that fish muscle tissues often have TDFs of 3.4‰ for ^{15}N and 1‰ for ^{13}C (Post 2002), but other studies have shown that TDFs are more variable than was once believed (Gannes et al. 1997, McCutchan et al. 2003). TDFs not only vary among taxa, tissue types, and trophic levels (TLs), but are also affected by nutrition and dietary quality (Mohan et al. 2016, Barton et al. 2019), excretion (Tamelander et al. 2006, Barton et al. 2019), temperature (Barnes et al. 2007), and metabolic rate (Gaye-Siessegger et al. 2004). It is possible that these factors affect the isotopic fractionation in Arctic fish species, and it is important to gain a more comprehensive database of TDFs.

The call for more isotope experiments (Gannes et al. 1997) has largely been answered with lower-latitude species (Logan et al. 2006, Madigan et al. 2012, Rosenblatt & Heithaus 2013, Mohan et al. 2016), but experiments focused on Arctic species are still lacking, and until recently there were no published isotopic lab-based experiments for Arctic marine fish species (Barton et al. 2019). Consequently, studies focused on fish have relied on TDFs derived from experiments on species from vastly different ecosystems or taxonomic groups (Hobson & Welch 1992, Hobson et al. 1996, Dunton et al. 2012, McTigue & Dunton 2014). Given the important role of fish in the transfer of energy from lower to higher TLs in Arctic food webs, it is imperative to use appropriate TDFs when modeling trophodynamics in these systems.

If TDFs of Arctic fish are different from those that have been used in past studies, there could be important implications for interpreting SIA data in the context of food web structure; this is especially important to consider when studying resource use between different species, the same species from different habitats, or when applying a single TDF to all species in a food web. We tested the hypothesis that the use of different TDFs in food web reconstructions affects estimates of prey resource dependence. Our objectives were to compare TDFs that are cited for studies on Arctic marine fish and apply them to SIA data of fish collected in the Arctic nearshore to determine the possible implications of variable TDF values on estimating trophic niche space of the resources on which these fish depend.

2. MATERIALS AND METHODS

2.1. Study area and sample collection

To understand the potential impact of TDFs on predicted food web structure, we applied the published values to a nearshore food web near Point Barrow, Alaska, USA. This is a unique area where multiple Arctic nearshore habitat types are found near each other in 3 waterbodies: Chukchi Sea (CHS), Beaufort Sea (BFS), and Elson Lagoon (ESL; Fig. 1). These waterbodies have distinct conditions that support different species assemblages, and the sampled fish community here is representative of a variety of Arctic nearshore habitats (Vollenweider et al. 2016).

Fish communities were sampled using a beach seine at 12 stations (5 CHS, 3 BFS, and 4 ESL) at weekly intervals from 14 July to 25 August (Weeks 1–6) for 2 consecutive years (2013–2014; Barton et al. 2017). Fish were sorted by species and enumerated, and a maximum of 5 individuals of each species per haul were stored in a −80°C freezer for SIA.

Zooplankton samples were collected weekly from CHS, BFS, and ESL during the 2014 beach seine surveys. A 50 cm diameter, 333 µm plankton net was towed behind a 3 m rigid hull inflatable at 3 knots for approximately 3 min. Larger taxa (krill, amphipods, ichthyoplankton, etc.) were sorted first, and then smaller taxa (small larvae) were sorted under a dissecting microscope. Samples of calanoid copepods were not available for analysis, but given their importance in lower-TL food webs; their isotope values were taken from the literature, as were values for basal resources (McTigue & Dunton 2014).

2.2. SIA

For all fish specimens larger than 25 mm total length (TL), a muscle sample was collected on the left dorsal side, and all skin and bones were removed.

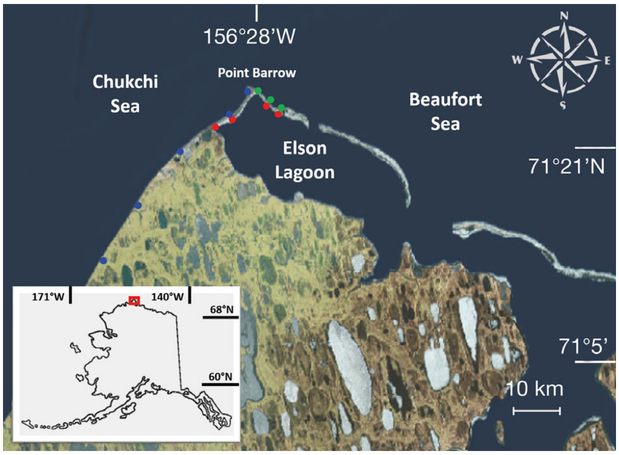

Fig. 1. Study area, showing relevant geographic features surrounding Point Barrow, Alaska, USA. Sampling stations are depicted by colored points (blue = Chukchi Sea, green = Beaufort Sea, red = Elson Lagoon). Source: Google Maps

Fish that were <25 mm TL and zooplankton samples were processed whole, in composite samples of at least 5 individuals. Tissues were dried to a consistent weight at 50°C for at least 7 d and homogenized to a uniform consistency using a mortar and pestle. Subsamples of dried fish homogenate were sent to the Southeast Environmental Research Center's SIA Lab at Florida International University and analyzed using elemental analysis — isotope ratio mass spectrometry (Barton et al. 2019). Error based on standard deviations of internal glycine standards ranged from 0.09–0.21‰ for δ^{15}N and 0.07–0.10‰ for δ^{13}C. Isotope ratios are expressed in delta-notation (δ) as per mil (‰) relative to the standard Vienna Peedee Belemnite (VPDB) for ^{13}C and atmospheric nitrogen (AN) for ^{15}N:

$$\delta^q X = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000 \quad (1)$$

where q is the atomic mass in the isotope, X is the element of the isotope, and R represents the ratio of heavy to light isotopes within the sample or the standards VPDB and AN (^{13}C/^{12}C for C; ^{15}N/^{14}N for N). C isotope ratios were corrected for the effects of lipid content in sample tissues using C/N ratios as a proxy for lipid content (McConnaughey & McRoy 1979).

2.3. Data analysis

Published TDFs for muscle tissues of Arctic marine species were compiled from literature searches in Google Scholar© and Research Gate©. Five commonly cited TDFs were selected and used in subsequent analyses.

First, the trophic niche space of the sampled Arctic nearshore fish community was determined as the 2-dimensional area taken up by the isotope signatures of species in bivariate space (δ^{13}C-δ^{15}N). This trophic niche space was represented as the 90% confidence ellipse of the C and N isotope ratios of all fish, centered at the average δ^{13}C–δ^{15}N values (CRAN-R v3.4.4, library 'car').

Next, we generated the predicted trophic niche spaces of prey and basal resources on which those fish depend by displacing the center of the ellipse by whole trophic steps by subtracting literatur-derived TDF values (Δ^{13}C and Δ^{15}N) from the average δ^{13}C and δ^{15}N values for the fish community. This displacement of the ellipse occurs along a straight line with a slope of Δ^{15}N/Δ^{13}C, and models the trophic fractionation between each TL based on the N and C TDFs that are used and will be referred to as the trophic discrimination slope (TDS). The TDS was used to generate the predicted trophic niche space 1, 2, and 3 TLs below that of the fish community using the published TDFs of 4 Arctic marine species and recently published TDFs for Arctic Sculpin *Myoxocephalus scorpioides* (Barton et al. 2019). In general, it may be more appropriate to apply a non-linear model with different TDFs at different levels, but this is not possible in Arctic marine systems due to the lack of known TDFs.

Finally, the predicted trophic niche spaces of lower TLs generated using the 5 different sets of TDFs were compared to the actual isotope values of lower-TL species from the Arctic nearshore to assess the accuracy of predictions and the differences between predicted niche space.

3. RESULTS

3.1. Trophic niche space of samples

The average isotope signatures of all fish species collected from the Arctic nearshore ranged from −22.08 to −17.58‰ for δ^{13}C (mean ± SD = −19.89 ± 1.59‰), and 13.41 to 15.27‰ for δ^{15}N (14.46 ± 0.58‰). Isotope values for near-surface sediment particulate organic matter (SPOM), near-bottom SPOM, phytoplankton, and sediment bulk OM from McTigue & Dunton (2014) were used to represent basal resources in Arctic nearshore habitats, and averages ranged from −24.70 to −21.60‰ for δ^{13}C (−23.95 ± 0.50 ‰), and 4.6 to 7.7‰ for δ^{15}N (6.48 ± 1.22). Isotope values for calanoid copepods (McTigue & Dunton 2014), pteropods, and krill were used to

Table 1. Results from literature searches on Google Scholar© and Research Gate©. Lab based: controlled experiments where the isotopic ratio of food was known and controlled. Field isotopes: deduction of trophic discrimination factors (TDFs) from isotope ratios of species collected in a field study (requiring the assumption that the consumer species is a specialist, feeding only on the prey species). $\Delta^{15}N$ and $\Delta^{13}C$: differences in $\delta^{15}N$ and $\delta^{13}C$ between prey and consumer. TDS: trophic discrimination slope, calculated from the TDFs from each study ($\Delta^{15}N/\Delta^{13}C$). n: sample size used to determine each TDF

Common name	Species	Experiment type	n	$\Delta^{15}N$ (‰)	$\Delta^{13}C$ (‰)	TDS	Source
Arctic Sculpin	*Myoxocephalus scorpioides*	Lab based	78	3.2	1.8	1.7	Barton et al. (2019)
Harp seal	*Pagophilus groenlandicus*	Lab based	2	2.4	1.3	1.8	Hobson et al. (1996)
Polar bear	*Ursus maritimus*	Field isotopes	3	3.8	0.7	5.4	Hobson & Welch (1992)
Amphipod	*Ampelisca macrocephala*	Field isotopes	8	3.4	0.4	8.5	McTigue & Dunton (2014)
Chaetognaths	*Parasagitta elegans*	Field isotopes	36	2.5	1.3	1.9	Dunton et al. (2012)

represent direct prey for the community of zooplanktotrophic fish, and ranged from −21.91 to −19.97‰ for $\delta^{13}C$ (−21.16 ± 0.85‰), and 11.10 to 12.03‰ for $\delta^{15}N$ (11.51 ± 0.39‰).

3.2. TDFs

TDFs for N ranged from 2.4‰ for harp seals *Pagophilus groenlandicus* (Hobson et al. 1996) to 3.8‰ for polar bears *Ursus maritimus* (3.8 ± 0.5‰; Hobson & Welch 1992), and for C they ranged from 0.4‰ for an Arctic amphipod (*Ampelisca macrocephala*; McTigue & Dunton 2014) to 1.8‰ for Arctic Sculpin (1.8 ± 0.5‰; Barton et al. 2019). The TDSs ranged from 1.7 for Arctic Sculpin to 8.5 for *A. macrocephala* (Table 1).

3.3. Predictions of trophic niche space

For the TDSs derived from TDFs for all 5 Arctic species, estimated trophic niche space of zooplankton was 1 TL below that of fishes; however, the estimated trophic niche space of basal resources differed greatly depending on the set of TDFs used. Using TDFs from harp seals (Fig. 2A) and chaetognaths (Fig. 2B), the predicted trophic niche space of basal resources was 3 TLs below that of the fish. TDFs from polar bears (Fig. 2C) and *A. macrocephala* (Fig. 2D) estimated the trophic niche space of basal resources at 2 and 3 TLs below fish, but C ranges of the predicted space were too enriched compared to actual values of basal resources from McTigue & Dunton (2014). Only the TDFs from Arctic Sculpin (Fig. 3) both estimated the trophic niche space of basal resources at 2 and 3 TLs below fish and predicted the correct range of $\delta^{13}C$ values.

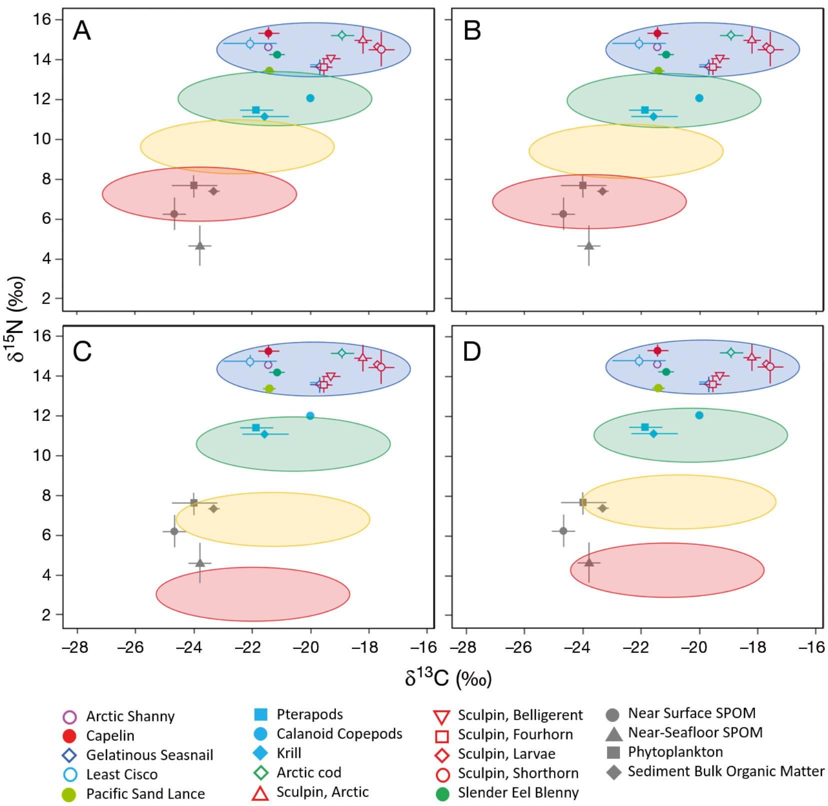

Fig. 2. Trophic level (TL) niche spaces estimated from published trophic discrimination factors (TDFs) of 4 Arctic species: (A) harp seals, (B) chaetognaths, (C) polar bears, and (D) amphipods. Data points: mean (+2 SE) measured C and N isotope values of fish and zooplankton collected from the Arctic nearshore in 2013–2014. Blue ellipses: measured trophic niche space of all fish. Green, yellow, and red ellipses: estimated trophic niche space of their prey resources at 1, 2, and 3 TLs below the fish, respectively. SPOM: sediment particulate organic matter

4. DISCUSSION

The appropriate set of TDFs for N and C should not only estimate the appropriate $\delta^{15}N$ ranges for known TLs, but also estimate the position of trophic niche spaces of the organisms within the habitat in question. The Arctic fish that were collected in the nearshore habitats around Point Barrow were mostly juvenile fishes with relatively small gape sizes that are expected to be zooplanktivores feeding at the third or sometimes fourth TL (Hussey et al. 2014, Barton et al. 2017).

All 5 of the food web models represented in Figs. 2 & 3 suggest that these Arctic nearshore fish are dependent on the trophic niche space occupied by calanoid copepods, krill (*Thysanoessa* spp.), pteropods, and similar plankton. However, the difference between these models is amplified and becomes evident as they are extrapolated to further TLs, leading to contrasting predictions about the basal resource dependence of Arctic nearshore fish and zooplankton. The calculated $\Delta^{15}N$ values for harp seals or chaetognaths are relatively low (2.4 and 2.5, respectively), and their TDSs predict that there is a TL in between the basal resources and zooplankton, and that these zooplankton are feeding on the third TL. Although it is possible that these zooplankton are feeding on microzooplankton and would have more enriched $\delta^{15}N$ values, this seems unlikely, as copepods, krill, and pteropods are more commonly known as primary consumers at the second TL (Hobson & Schell 1998, Eisner et al. 2013), and suggests that these TDFs may be inappropriate to model the structure of lower TLs in Arctic nearshore food webs. Alternatively, it is possible that the represented basal resources (McTigue & Dunton 2014) have different isotopic ratios than those that the collected zooplankton and fish were actually dependent on. However, this is unlikely because the values for basal resources presented in this analysis are similar in a variety of Arctic isotope studies (Hobson & Welch 1992, Iken et al. 2010, Dunton et al. 2012).

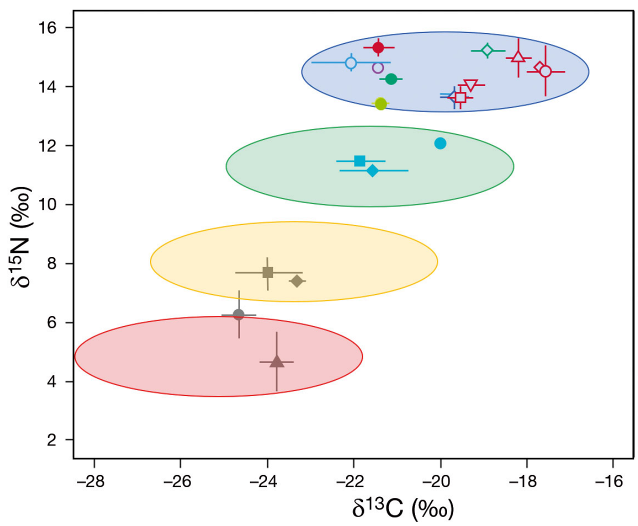

Fig. 3. Trophic level niche spaces estimated from the published trophic discrimination factor (TDF) of Arctic Sculpin (Barton et al. 2019). Other details and symbols as in Fig. 2

The remaining 3 models (TDFs from polar bears, *Ampelisca macrocephala*, and Arctic Sculpin) are derived of $\Delta^{15}N$ values between 3 and 3.8, and thus the predicted TLs of fish and plankton fit known values; however, there is much variation in the $\Delta^{13}C$ values, causing the TDSs to differ greatly. Due to the low $\Delta^{13}C$ derived from the polar bear and *A. macrocephala* studies, models using their TDFs suggest that fish and zooplankton are mostly dependent on basal resources that have less depleted C isotope ratios than the basal resources found in this region of the Arctic nearshore (Dunton et al. 2012, McTigue & Dunton 2014). However, when the TDFs for Arctic Sculpin are used, the model predicts that these juvenile Arctic nearshore fish are feeding at the third or fourth TLs as expected and demonstrates the appropriate isotopic niche space for the lower TL resources in this food web.

In this example, the use of inappropriate TDFs could lead to erroneous food web models. Inappropriate $\Delta^{15}N$ (TDFs from harp seals and chaetognaths) would have led to the conclusion that an entire TL was missing from our community samples, whereas incorrect $\Delta^{13}C$ (TDFs from polar bears and *A. macrocephala*) would have led to the conclusion that the community is dependent on an unknown or unsampled basal resource or primary producer. As rapid climate change occurs in the Arctic, it is important that the baseline SI food web models are accurate so that changes in food web structure can be quantified in the future.

5. CONCLUSION

Our results exemplify that the use of inappropriate TDFs can lead to erroneous conclusions regarding food web structure from SI food web models, and therefore it is important to select the most appropriate TDFs. Using this example, the TDFs for Arctic Sculpin are different from the TDFs of the other 4 Arctic species previously examined, and the same is probably true for other species of Arctic fish. Due to this apparent variability in TDFs in Arctic marine species, it is imperative that a more comprehensive database of TDFs is created so that SI food web models can be used accurately to investigate the trophodynamics of Arctic fish and other key Arctic species in the future.

Although the TDFs for Arctic Sculpin may be the best values currently available to represent trophodynamics between Arctic fish and their prey, they should not be regarded as the correct values for all isotope models of lower TLs in the Arctic. On the contrary, this analysis should function as a call for more experimental determination of TDFs for Arctic marine species at all TLs, as the current database of TDFs is greatly lacking.

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