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BIOLOGISK PROJEKTARBEJDE

Latitudinal Differences in the Diet of Northern Sand Lance, *Ammodytes dubius*

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Abstract

The schooling pelagic forage fish Northern sand lance, *Ammodytes dubius*, is an important species in the northern atlantic, due to its role in linking the lower and higher trophic levels, allowing the energy produced by the planktonic species to reach seabirds and higher mammals. Knowledge of sand lance diet composition in the arctic is, however, lacking. This study examines differences in sand lance diet at 2 latitudes off the western coast of Greenland, by analyzing their stomach content. Results indicate that amphipods and copepods were the main food subjects, contributing roughly 98% of total carbon consumed. Amphipods contribute up towards 40% of carbon consumed at the southern location, whilst being neglectible in the northern station, where copepods make up virtually all food consumed. The copepod species, *Calanus finmarchicus, C. glacialis* and *C. hyperboreus* were the primary food items, with *C. hyperboreus* being more important at the northern station, and *C. finmarchicus* and *C. glacialis* dominating the southern station diet composition. This information may improve modelling of sand lance response to climate change, by allowing models to account for the spatial variability in importance of prey species.

Introduction

Northern Sand Lance, *Ammodytes dubius*, is a common forage fish, native to the northern Atlantic. Along the western coast of Greenland, *A. dubius* acts as a 'wasp-waist species' (Bakun, 2006). A wasp-waist species is a species whose trophic position acts as a bridge between the lower trophic levels, e.g. primary production, and the higher trophic levels, e.g. piscivores. This intermediate trophic position may be filled by few, or even one, species forming a trophic wasp-waist within the ecosystem; hence the name. While this might be confused with the term 'keystone species', there are some differences. Power et al (1996) defines a keystone species as "A species whose impact on its community is large, and disproportionately large relative to its abundance". Sand lances are important in linking these trophic levels in the ecosystem, but they are abundant, and as such, do not meet the requirements for being considered a keystone species; indeed, they are important to the ecosystem because of their high biomass, which enables them to supply several groups of higher trophic levels, such as marine mammals and seabirds (Furness, 2007).

An example of the importance of these wasp-waist species are found in Frederiksen et al (2013). They found a strong correlation between habitat suitability for the copepod, *Calanus finmarchicus*, and the breeding success of 3 piscivorous seabird species in the northeast boreal Atlantic. This was due to the dependance on *C. finmarchicus* by the birds main food source, schooling pelagic fishes, such as sand lance and herring. Since there are no obvious species able to fill the niche left by these wasp-waist species, any decline in their populations could spawn further declines of the higher trophic levels that depend on them.

Since wasp-waist species provide this important linkage, knowledge about their ecology could prove invaluable in the coming years, where climate changes might alter the boreal ecosystems at several different levels, such as altering the food availability or composition, which the sand lances depend on (Hays et al, 2005; Brander, 2010). Therefore, not only do we need knowledge of the zooplankton species, but also on their importance to the wasp-waist species.

While Frederiksen et al (2013) showed that *C. finmarchicus* was vital to the success of sand lances in the northeastern boreal Atlantic, this cannot be assumed for all sand lance populations. The diet composition of sand lances may vary both spatially and temporally, and other populations may be reliant on entirely different zooplankton. Hedeholm et al (2012) showed such seasonal and spatial variation for the capelin, another important arctic zooplanktivorous fish, along a latitudinal gradient. This latitudinal change is presumed to reflect changes in the zooplankton composition, which was supported by data on zooplankton distribution and abundance (Pedersen & Smidt, 2000).

This paper aims to assess the difference in diet of *A. dubius* at 2 different latitudes off the western coast of Greenland. This knowledge could potentially improve modelling of this ecosystem, providing valuable insight in the possible consequences of the upcoming climate changes.

Methods

Stomachs were collected from *A. dubius* at 2 stations off the southwestern coast of Greenland. Sampling was conducted during daytime, on the 4. June 16:06 UTC (PA01011) and the 8. june 17:20 UTC (PA01045) 2016, on a trawl survey with the RV Paamiut. Trawls were performed with a 2cm mesh size, and were carried out for 30 minutes at each station. The sourthern station, PA01011, was located northwest of Nuuk, at 64,6 ^{O}N, at Sukkertop Bank (Figure 1). The fishing depth was 84m, and the bottom temperature was 1.06 ^{O}C. The northern station, PA01045, was located west of Sarfánguaq, at 66,4 ^{O}N, at Lille Hellefisk Bank. The fishing depth was 64m, and the bottom temperature was 0.25 ^{O}C.

Fork length was measured on the caught *A. dubius*, rounded to the nearest cm. Individuals for stomach analysis were chosen randomly, and assigned to 2cm intervals prior to gutting. The extracted stomachs were then preserved in a 6% formaldehyde-saltwater solution, and analyzed at Aarhus University in Denmark.

Only individuals from the 3 size groups: 14-16cm, 16-18cm and 18-20cm was analyzed. These size categories were chosen because they contained sufficient replicates, and because the smaller stomachs were more likely to be empty.

In the lab, the stomachs were rinsed thoroughly with freshwater, before being emptied. The stomach content was examined under a stereomicroscope, allowing determination of prey items to lowest taxonomic level (categories can be seen in table 1). The order in which the stomachs were analyzed were chosen haphazardly in regards to size category, to minimize influence from observer education and fatigue.

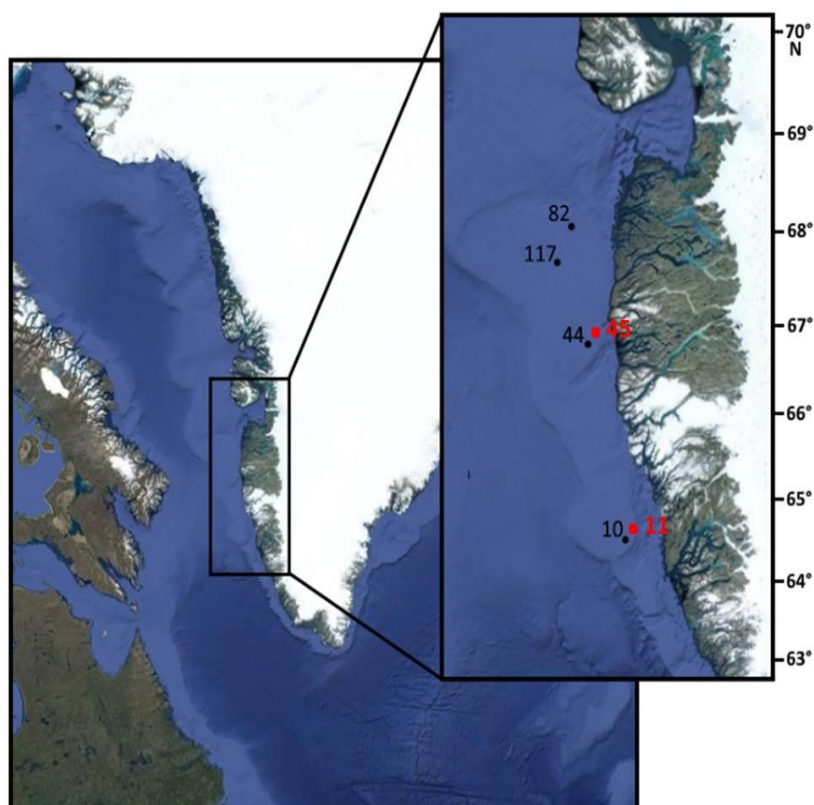After determining the lowest taxonomic level of all the individuals in a stomach, and sorting

Figure 1: Map of the survey area along the western coast of greenland. Stations covered in this study (11 and 45) marked in red.

accordingly, pictures were taken to allow for measurement of protosome length for the copepods, and total length for all other prey items using the ImageJ (v. 1.50i) software. Using these lengths, carbon biomass was calculated using the formulas provided by Pearre et al 1982 (chaetognaths), Agersted & Nielsen 2014 (euphasiids), and Danielsen et al 2016 (remaining taxa). Carbon contribution from copepods and amphipods that could not be fully identified were left out of statistical analysis (except the total carbon analysis, and the total copepod carbon analysis), and carbon contribution percentage numbers from the identified individuals were scaled to compensate. Additionally, empty stomachs were excluded.

ANOVAs, general linear models (GLMs), cluster analysis and simper analysis were all carried out in R (v. 3.3.2).

Results

A total of 4853 fish were caught at station 11, while 166 were caught at station 45. From these catches 36 fish stomachs were analysed, 18 for each station. Seven stomachs were empty, all of these from station 45. A complete summary of percentage contributions by the various food items, as well as the number of stomachs analysed from each size group, can be found in table 1. The major differences between the stations appear to be that the sand lances at station 45 got nearly all of their carbon from copepods, whereas the larger size groups from station 11 also got a significant amount from amphipods. Furthermore, the fishes at station 45 appeared to have eaten less total carbon. A two-way ANOVA describing total carbon content as a function of size category and station confirmed this (2-way ANOVA, $F_{1,23}$=20.418, P<0.001). This also means that, despite copepods making up more of the total carbon consumed at station 45, the fish at station 11 had more copepod carbon in their stomachs on average, 6.7mg and 10.4mg respectively, even when accounting for the larger number of fish in the 18-20cm size category at station 11 (2-way ANOVA, $F_{1,23}$=5.4, P=0.03)

There did not appear to be any relation between total amphipod consumption and total copepod consumption at station 11 (GLM, $F_{1,16}$=1.5, P=0.24).

A cluster analysis (Figure 2) shows that station accounted for more dissimilarity in the carbon contributions, than did the size categories of the fish.
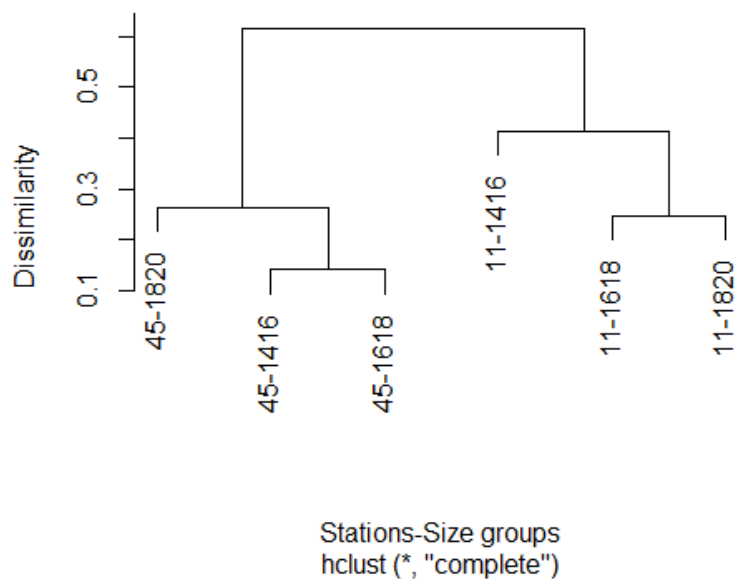

Figure 2: Cluster analysis of Station-Size group dissimilarity, based on percentage carbon contribution, excluding unknown copepods and amphipods (45-1416 indicates station PA01045, size group 14-16 cm).

A simper test (Table 2) revealed the main contributor to dissimilarity between the stations to be *C. hyperboreus.* For the larger size categories, amphipods, namely *T. libellula*, also contributed significantly. *Calanus glacialis* also appear to make a relevant contribution to the dissimilarity in the 18-20cm size group as well as the pooled data, but this may be a result of the underestimation of *C. glacialis* at station 11 in this size group (see table 1). Percentage carbon contributed by *C. hyperboreus* was found to be significantly different between stations (1-way ANOVA, $F_{1,27}$=6.9, P=0.014).

Table 1: Percentage number of carbon contribution by prey species found in the stomach of A. dubius, size 14-20 cm, at both stations along the coast of Western Greenland. Average carbon contributions were calculated only using non-empty stomachs.
* C. finmarchius is likely overestimated, while C. glacialis is likely underestimated for the 18-20cm sice group at station PA01011, due to observer education.

Prey group species	----14-16 cm----		----16-18 cm----		----18-20 cm----	
	11	45	11	45	11	45
Amphipoda						
Themisto abyssorum	3.6	–	8.3	–	13.5	–
Themisto libellula	6.2	–	25.5	1.1	26.1	2.2
Unknown.	3.7	–	3.4	–	2.4	–
Copepoda						
Calanus finmarchicus	22.9	9.9	18.9	8.4	17.3*	3.8
Calanus glacialis	21.1	9.4	12.9	9.0	2.7*	12.9
Calanus hyperboreus	9.9	24.1	8.7	13.7	26.6	30.7
Metridia longa	–	2.8	–	1.1	–	1.2
Unknown	23.5	53.8	20.4	66.7	9.7	49.2
Euphausiacea						
Euphausiid	0.6	–	–	0.1	–	–
Young crustacean stages						
Nauplii	1.7	–	0.3	–	0.1	–
Cypris	6.8	–	1.3	–	1.3	–
Other						
Chaetognath	–	–	0.3	–	0.3	–
Number of prey	776	59	1198	159	2077	116
Total Carbon weight (mg)	32.58	16.79	86.37	37.67	193.95	19.66
Number of non-empty stomachs	3	3	6	4	9	4
Average no. of prey in stomachs	259	20	200	40	231	30
Number of empty stomachs	0	3	0	2	0	2

Table 2: Cumulative contribution (%) to dissimilarity (Simper test) between stations by the most important species, ranked in order of importance.

14-16 cm		16-18 cm		18-20 cm		Pooled	
Species	Cum. Contribution	Species	Cum. Contribution	Species	Cum. Contribution	Species	Cum. Contribution
C. hyperboreus	0.43	*T. libellula*	0.35	*C. hyperboreus*	0.28	*C. hyperboreus*	0.29
C. finmarchicus	0.54	*C. Hyperboreus*	0.69	*T. libellula*	0.51	*T. libellula*	0.57
cypris	0.65	*T. abyssorum*	0.81	*C. glacialis*	0.71	*C. glacialis*	0.74
C. glacialis	0.74						

Discussion

When considering all sand lances, regardless of station, it appears that copepods and amphipods make up the vast majority of consumed carbon. While nauplii and cypris larvae may contribute meaningfully to the smaller fishes, overall their contribution appear to be negligible, making up only 1.8% of the total consumed carbon. Chaetognaths and euphasiids account for 0.3% of total carbon contribution, which means that the remaining ~98% are supplied by copepods and amphipods. Hence, they will be the focus of this dicussion.

The scaling of data when excluding unidentified individuals implies the assumption that the composition of the identified idividuals are representative of the composition of unidentified stomach content, which was judged to be reasonable. Additionally, whether the unknowns were amphipods or copepods were not taken into account. This causes a slight overestimation of the relative contribution of amphipods in the data from station 11, due to their lower overall contribution, but it was judged that this was not enough to impact the analysis in any major way.

While copepods make up a the majority of the contributed carbon at both stations, there is a striking difference in the consumption of amphipods. The amphipods, particularly *T. libellula*, contribute approximately 40% of total carbon in the 18-20cm size group at station 11, whilst they are negligible in all size categories at station 45. This likely reflects the availability of amphipods at the different latitudes, because the sand lances would be expected to have an optimal feeding strategy; that is, if eating amphipods is an advantage, we would expect sand lances to do so whenever they are available. An alternative explanation would be that sand lances are relegated to feeding on amphipods at station 11 due to competition with other conspecifics (or other zooplanktivores), in accordance with Optimal Foraging Theory (Pyke et al, 1977). This explanation, however, is not supported by these data. Besides eating amphipods, the sand lances at station 11 also consumed significantly more copepod carbon on average, and as such, it is unlikely that there was more competition for copepods at station 11 than at station 45. Furthermore, this theory would imply a relation between amphipod consumption and copepod consumption at station 11, because high amphipod consumption would be the result of being out-competed in regards to the copepods. As this relation in not found, it seems more likely that the lack of amphipods in sand lance stomachs from station 45 reflect their absence at the sampling site. This is not supported by the findings of Pedersen & Smidt (2000), who found hyperiids all the way up to Disko Bay. This discrepancy may be caused by a shift in community structure between their sampling period (1956-83) and the present, but it may also be caused by factors not accounted for in this study, such as temporal variation. Further research into the distribution of amphipods off the western coast of Greenland would be required to accurately explain this disparity.

The lower contribution of amphipods at the 14-16cm size group likely reflects an ontogenetic diet shift of the sand lances, causing them to start feeding on amphipods as they increase in size. This could be caused by the amphipods', particularly *T. libellula*, large size relative to other food items coupled with their tougher carapace compared with the softer copepods (Personal observation), but these data does not account for potentiel confounding variables, and further studies would be needed to determine if this is the case.

Calanus hyperboreus was the primary cause of difference between the stations. This difference is presumably due to *C. hyperboreus* being more dominant in the north, as was confirmed by Pedersen & Smidt (2000), as well as Hedeholm et al (2012), who used capelin as an indicator for zooplankton abundance.

The disparity between the stations regarding total consumption, suggests a difference in prey availability at the two latitudes, which may be caused by a number of reasons. One such reason, is a delayed onset primary and secondary production at station 45, induced by the later warming or prolonged icecover of this more northern location (Pedersen & Smidt, 2000). Sampling may then have been conducted too early to capture the full potential for secondary production, and any comparisons with station 11 would then be prejudiced. Another possibility is that station 45 is simply less productive, implying a bottom-up control of available zooplankton. This is not supported by Pedersen & Smidt (2000), but may have changed since their sampling period (1950-84). More recent data of zooplankton distribution would be required to rule out this possibility. Lastly, it is possible that, although they were caught at approximately the same time of day, the sand lances caught at station 45 had gone longer without ample feeding opportunities. The lower food content in their stomach would then reflect them having digested more of their food prior to preservation, than did the sand lances from station 11. This theory is supported by the data, as the content of the stomachs were much harder to determine in the station 45 stomachs (Personal observation). This difficulty is also reflected in the ratio of determined vs. undetermined amphipods and copepods, when comparing the stations (83% determined at station 11 vs. 41% determined at station 45).

In conclusion, copepods are the main food item for *A. dubius*, and any projections regarding future fish stocks will need to take the copepod abundance and composition into account. Amphipods are important in the south, but this paper cannot rule out potentiel influence in the north. Specifically, it appears that as one moves north along the southwestern coast of Greenland, the *A. dubius* diet shifts from relying primarily on *C. finmarchicus* and *C. glacialis*, as well as amphipods, to a reliance on *C. hyperboreus*. Knowledge on how all of these groups respond to variations in their ecosystem, particularly those associated with climate change, will be necessary if we are to predict the consequences for *A. dubius*.

References

Agersted MD, Nielsen TG (2014) Krill diversity and population structure along the sub-Arctic Godthabsfjord, SW Greenland. Journal of Plankton Research 36(3): 800-815

Bakun A (2006) Wasp-waist populations and marine ecosystem dynamics: navigating the ''predator pit'' topographies. Prog Oceanogr 68:271–288.

Brander K (2010) Impacts of climate change on fisheries. Journal of Marine Systems 79: 389-402.

Danielsen N, Hedeholm R, Grønkjær P (2016) Seasonal changes in diet and lipid content of northern sand lance *Ammodytes dubius* on Fyllas Bank, West Greenland. Mar Ecol Prog Ser 558:97-113

Frederiksen M, Anker-Nilssen T, Beaugrand G, Wanless S (2013) Climate, copepods and seabirds in the boreal Northeast Atlantic – current state and future outlook. Global Change Biology 19: 364-372.

Furness RW (2007) Responses of seabirds to depletion of food fish stocks. J Ornithol 148(2): 247-252.

Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. Trends in Ecology and Evolution 20(6): 337-344.

Hedeholm R, Grønkjær P, Rysgaard S (2012) Feeding ecology of capelin (*Mallotus villosus* Müller) in West Greenland waters. Polar Biol (2012) 35: 1533

Pearre S Jr. (1982) Feeding by Chaetognatha: Aspects of Inter- and Intra-Specific Predation. Mar Ecol Prog 7: 33-45

Pedersen SA, Smidt ELB (2000) Zooplankton distribution and abundance in West Greenland waters, 1950–1984. J Northwest Atl Fish Sci 26:45–102

Power M, Tilman D, Estes J, Menge B, Bond W, Mills L, Paine, R. (1996). Challenges in the Quest for Keystones. *BioScience, 46*(8), 609-620.

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal Foraging: A Selective Review of Theory and Tests. The quarterly review of Biology 52(2): 137-154.