



FEATURE ARTICLE

Blue whiting *Micromesistius poutassou* diel feeding behaviour in the Irminger Sea

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ABSTRACT: With warming ocean temperatures, the abundance of blue whiting *Micromesistius poutassou* is increasing in the waters around Greenland. However, in this region, knowledge about the species' trophic role in the ecosystem is scarce. Consequently, we investigated the diet composition and diel feeding behaviour of blue whiting in the north-eastern part of the Irminger Sea in Greenland waters by analysing their stomach contents and the vertical position/movements of their prey from zooplankton samples and hydroacoustic measurements. We collected the data during a designated experimental survey in July 2016 with repeated sampling at the same location. Results from the stomachs of 624 blue whiting individuals ranging from 22–39 cm long (total length) showed that the highest food intake took place from noon until late evening, with minimum feeding occurring in the morning. The most essential prey groups consisted of euphausiids, copepods, amphipods and fish, in that respective order. Regarding copepod prey, blue whiting had a strong affinity for *Calanus hyperboreus* and *Paraeuchaeta* spp. and showed potential for local depletion of these large copepods. On the other hand, the more abundant but smaller *C. finmarchicus* was almost absent in the fish stomachs, in contrast to findings in other regions. This new understanding provides an early indication of some of the emerging trophodynamics in the Irminger Sea and similar subarctic zooplankton communities with increasing numbers of blue whiting. Our results confirm the importance of accounting for diel and size-specific differences in blue whiting feeding when studying various aspects of its food intake.

KEY WORDS: *Calanus* copepods · Diel migration · Food selectivity · Greenland waters · mesopelagic fish · Stomach content analysis



Blue whiting caught with a pelagic trawl in the Irminger Sea.

Photo: Søren Post

1. INTRODUCTION

Climate change scenarios predict an increase in the abundance of boreal fish species in Arctic and Subarctic areas, such as Greenland waters (Fossheim et al. 2015, Andrews et al. 2019, Hastings et al. 2020). To understand how an increase of these species will impact the state of the marine ecosystem, one of many issues to clarify is how the species impact the marine food web. The Irminger Sea is located in Southeast Greenland in a transition zone where cold fresh Polar water meets warmer saline Atlantic water (see Fig. 1) (Våge et al. 2011, Sutherland et al. 2013). As a result of the varying oceanographic conditions, both Arctic and boreal species can be found in the region, including small planktonic organisms and fish (Mecklenburg et al. 2018, Strand et al. 2020).

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The physical environment of the Irminger Sea undergoes substantial intra- and interannual variations which affect the entire ecosystem (Hátún et al. 2016, 2017). Since the mid-1990s, the summer surface temperature has generally increased, and several long-term climate projections forecast a continuation of this trend (Jansen et al. 2016). However, some parts of the Irminger Sea are projected to experience future cooling, likely due to the possible slowing of the Atlantic Meridional Overturning Circulation (AMOC) (Caesar et al. 2018). Nevertheless, during periods of warm ocean temperatures, the Greenland shelf and shelf-ridge have shown higher numbers of boreal fish species (Post et al. 2021). The off-shelf areas in the central part of the Irminger Sea have also recently, concurrently with warmer temperatures, experienced colonisation of certain boreal species, e.g. the highly mobile Atlantic mackerel *Scomber scombrus* and bluefin tuna *Thunnus thynnus*, which otherwise traditionally prefer warmer waters than usually prevailing in the Irminger Sea (Jansen et al. 2016, 2021).

Blue whiting *Micromesistius poutassou* (Risso, 1827) is one of the boreal fish species that is currently scarce in Greenland waters but expected to increase in abundance with warming temperatures (Post et al. 2019, 2021). The blue whiting is a small gadoid fish distributed in most of the Northeast Atlantic but also occurs in less abundance in the Mediterranean Sea and Northwest Atlantic (i.e. Greenland waters and along the East American shelf) (Bailey 1982, Trenkel et al. 2014). In the last 2 decades, the annual average global catches have exceeded 1 million tons and constitute one of the largest fisheries in the world (FAO 2018, ICES 2018b). The species is commonly found on banks and along shelf edges in the mesopelagic zone at depths between 200 and 500 m (Pawson et al. 1975, Monstad 1990, 1995). The principal spawning grounds are located west of the British Isles, but spawning also occurs off Portugal, the Biscay, the Faroe Islands, Norway and Iceland (Raitt 1968, Zilanov 1968). Spawning occurs during winter and spring, with an earlier onset at southern latitudes (Bailey 1982). After spawning, the majority of blue whiting conduct annual summer feeding migrations towards northern latitudes before returning to the spawning grounds during late autumn and winter (Bailey 1982).

The diet of blue whiting has been studied throughout most of its geographic distribution (e.g. Timokhina 1974, Zilanov 1982, Prokopchuk & Sentyabov 2006, Bachiller et al. 2016). Diet and feeding behaviour varies and depends on life stage, time of year

and geographical location (Cabral & Murta 2002, Dolgov et al. 2010). The highest food intake occurs during spring (after spawning), summer and autumn (Bachiller et al. 2018). While larval stages primarily consume smaller zooplankton such as tintinnids and naupliar stages of cyclopoid and calanoid copepods, juvenile and adult blue whiting prey on larger zooplankton such as larger copepods, euphausiids, amphipods and fish (Bailey 1982, Hillgruber et al. 1997, Dolgov et al. 2010).

However, the diet of blue whiting in Greenland waters has only been superficially investigated and reported by Zilanov (1982). These few observations are approximately 40 yr old, when environmental and biological conditions were different from what they are today (IPCC 2019). To shed more light on this knowledge gap and to assess possible predatory impacts on the zooplankton community by blue whiting, we examined its diet and feeding behaviour. Our study took place in a shelf area at the northern boundary of the Irminger Sea, as it is one of the regions with the highest blue whiting density in Greenland waters (Post et al. 2019). Various boreal fish species pass through this region during summer feeding migration to Greenland waters from areas further south and east (Post et al. 2019, 2021, Jansen et al. 2021). Therefore, the current situation in the Irminger Sea likely reflects conditions in other Greenland shelf areas when ocean temperatures get warmer.

As blue whiting perform diel migrations from deeper layers during daytime to shallower depths at night (Bailey 1982, Johnsen & Godø 2007), diel differences in diet consumption must be considered when analysing its food intake. Hence, we examined possible differences in feeding throughout the day from blue whiting stomach contents and zooplankton samples collected in the morning, day, evening and night. Our repeated sampling in a relatively small sampling area was done to attain a fine temporal resolution of the species' daily feeding and to lower the risk of introducing a bias caused by spatial variations.

2. MATERIALS AND METHODS

Fieldwork was conducted from 27 (05:11 h) to 30 (10:07 h) July 2016 on the Icelandic research vessel Árni Friðriksson (Marine and Freshwater Research Institute, Iceland). After locating blue whiting with acoustics and trawl catches, a location was chosen in the Irminger Sea along the shelf edge with the presence of warm Atlantic surface waters (Fig. 1). At the site, sampling was carried out repeatedly within

5 × 5 km (with 2 exceptions: sampling occurred 35 km to the east of the others) (Table 1 & Table S1 in the Supplement at www.int-res.com/articles/suppl/m678p001_supp/). Sampling was done using a pelagic trawl for collecting fish, a MultiNet for sampling zooplankton, vertical acoustics for observing the vertical distribution of fish and zooplankton and a CTD for temperature profiling of the water column.

2.1. Fish sampling and diet data

Blue whiting sampled for stomach content analysis were caught during the International Ecosystem Summer Survey in the Nordic Seas (IESSNS) cruise, which has targeted blue whiting since 2016 (ICES 2013b, 2016, Nøttestad et al. 2016). Pelagic trawling was done with a Mulpelt 832 trawl; trawling speed was ~2.5 knots during the mesopelagic hauls and 4.5 knots at the surface, with a vertical opening of the trawl between 30 and 40 m. The mesopelagic trawling time was 34 min on average (range: 30–54 min) (for trawl-specific information, see Table S1). Acoustic observations were used as guidance for setting the trawling depth for every deep-trawl haul. We did this to collect fish from the layers with the highest density and, thereby, the most representative depth layer for each time period. The blue whiting were handled immediately after the trawl was on deck. For every station, up to 50 individuals were haphazardly chosen and processed as follows. Length (total length rounded down to nearest whole cm) and weight

(nearest 0.1 g) were measured, and sagittal otoliths were removed for age determination. Otolith reading was carried out at the Marine and Freshwater Research Institute in Iceland. All fish were aged, except 4 individuals whose age was estimated based on the age–length relationship generated by the actual measurements. Stomachs were removed and stored separately in zip-lock bags at –18°C. This procedure resulted in a typical handling time of approximately 1–1:30 h from catch to freezing. Based on visual inspection of stomach contents after thawing, this was fast enough to exclude digestion after sampling from having a significant impact on the results.

Blue whiting specimens that showed signs of gut evacuation, either by visual inspection of the fish mouthparts or the stomachs (turned outside out), were excluded from this study. In total, 627 blue whiting stomachs were collected from 17 mesopelagic trawl hauls. Three of these individuals showed signs of evacuation and were therefore excluded, which resulted in 624 stomachs analysed. Lengths of the sampled individuals ranged from 22–39 cm, weight from 85–416 g and ages ranging from 1–9 yr. No blue whiting were caught in the 17 surface hauls conducted at the same locality.

In the laboratory, each stomach was thawed for a few minutes and weighed to give total stomach wet weight. The contents were then transferred to a Petri dish, and the empty stomach was weighed to determine wet weight of the total stomach contents. The contents were sorted into 11 taxonomic groups (see Fig. 2). Each taxonomic group was divided into 2 di-

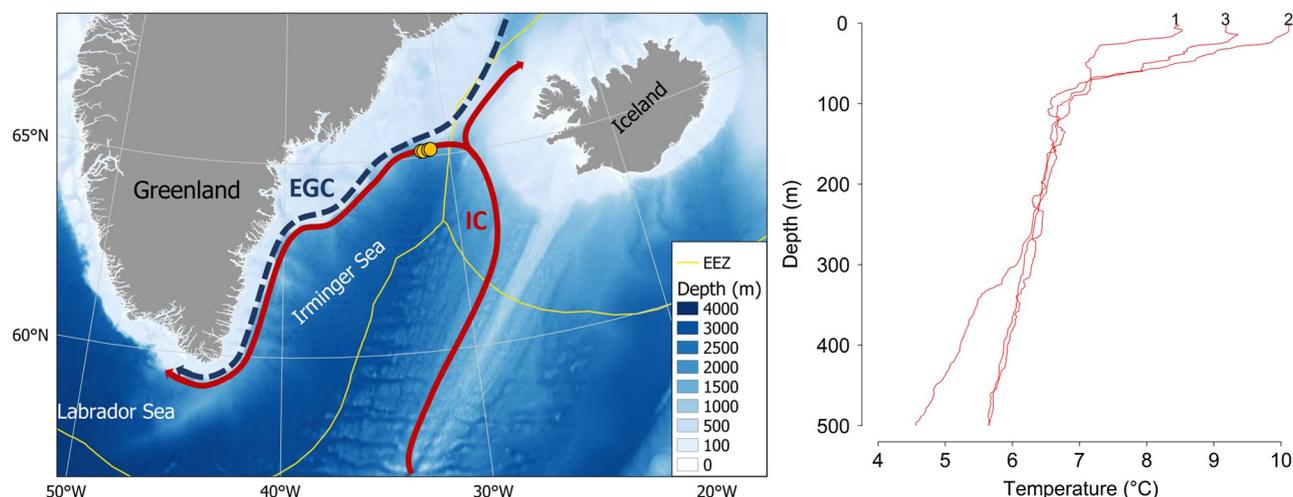


Fig. 1. (Left) Irminger Sea region with important surface currents. Red arrow line: typical route of the Irminger Current (IC) carrying warm, salty Atlantic water; blue dashed arrow line: colder East Greenland Current (EGC) carrying cold, fresh polar-origin water; yellow circles: mesopelagic trawling positions. Borders of exclusive economic zones are outlined in yellow. (Right) Temperature profiles from 0–500 m depth. Numbers above profiles indicate CTD casts (see Table S1)

Table 1. Sampling overview by gear and depth

Gear	Depth (m)	No. of samples
Trawl	0–30/40	17 stations, 0 stomachs
Trawl	225–405	17 stations, 624 stomachs
MultiNet	0–50	4 casts with 5 nets
MultiNet	50–500	4 casts with 5 nets
Acoustics	0–750	1 frequency ⁻¹ s ⁻¹ (4 frequencies)
CTD	0–500	3 casts

gestion stages: 'not fresh' and 'fresh'; the latter was defined when digestion had started, but the prey could still be identified to genus level. Each taxonomic group was subsequently weighed (wet weight) to the nearest 0.001 g. A total of 39 stomachs (6%) were randomly chosen to analyse the size composition of the 3 most important prey items: amphipods, copepods and euphausiids. As *Paraeuchaeta* spp. were easily identified, the group 'copepods' was further split into *Paraeuchaeta* spp. and 'other copepods'. Lengths of individual prey items in the stomachs were measured by scanning individuals with an Epson Perfection V8000 photo scanner using the VueScan 9x64 (9.6.35) software (Hamrick Software) and subsequently measuring them using ImageJ (Schneider et al. 2012). For amphipods and euphausiids, the length was measured from the tip of the head to the tail along the back; prosome length was measured for copepods. All measurements were rounded to the nearest 0.1 mm. To calculate the relative weight of different copepod groups/species in the diet, we applied a length (L , mm) to wet weight (WW , mg) relationship of $WW = 0.0632 \times L^{3.248}$ for *Paraeuchaeta* spp. (Yamaguchi & Ikeda 2002) and $WW = 0.006458 \times L^{3.9}$ for other copepods (Robertson 1968).

2.2. Zooplankton data

Depth-stratified samples of mesozooplankton were sampled using a MultiNet Mini (Hydro-Bios; www.hydrobios.de). The MultiNet was equipped with 5 nets. Each net had an opening area of 0.125 m², a mesh size of 50 µm and was programmed to open and close at fixed depths. The MultiNet was hauled vertically at approximately 0.5 m s⁻¹, and samples were collected in distinct layers from shallow (0–10, 10–20, 20–30, 30–40 and 40–50 m) and deep (50–100, 100–200, 200–300, 300–400 and 400–500 m) casts. The mesozooplankton sample was immediately fixed in buffered 4% formaldehyde. Mesozooplankton were identified to either species or genus level, and

developmental stage was recorded. For each copepod species and development stage, prosome lengths were measured on a minimum of 10 individuals. Identifications and length measurements of mesozooplankton were carried out by Arctic Agency (Gdańsk, Poland).

The preference of blue whiting for different copepod size groups was investigated using the Strauss index, a linear food selection index (L):

$$L_i = r_i - p_i$$

which provides the difference in proportions (in numbers) between prey items in the stomach (r) and habitat (p) (Strauss 1979, Kohler & Ney 1982). The index ranges from -1 to $+1$, where negative values indicate avoidance or inaccessibility, and positive values indicate preference. The expected index value for random feeding is 0. To calculate the index, we used MultiNet samples from 200–400 m, which was approximately the same depth as that at which sampling for blue whiting occurred. Euphausiids and amphipods were not representatively sampled with the MultiNet, and hence we only investigated their length distributions from the stomach contents.

2.3. Acoustic sampling, oceanography and light

Zooplankton and mesopelagic fish were observed using Simrad EK60 split-beam echo sounders. The acoustic data were sampled using 4 calibrated frequencies: 18, 38, 120 and 200 kHz (Table 2). The relative frequency response was used to categorise the backscattering organisms with the use of the software LSSS (Korneliussen & Ona 2002, Korneliussen et al. 2006) with an integration threshold set to -90 dB. The echoes seen in the upper 150 m with the strongest backscattering at 200 kHz were primarily classified as copepods based on the MultiNet samples. Larger zooplankton were categorised as 'euphausiids' and had a similar strong reflection at 200 and 120 kHz

Table 2. Main parameters of the transducers and transceivers of the EK60 echosounders

Parameter	Echosounder frequency (kHz)			
	18	38	120	200
Transducer type	ES38-12	ES70-7C	ES120-7	ES200-7C
Power output (W)	2000	2000	250	120
Pulse length (ms)	1.024	1.024	1.024	1.024
Two-way beam angle (dB)	-17.3	-20.8	-20.5	-20.5

and relative low at 38 and 18 kHz (Korneliussen & Ona 2002, Korneliussen et al. 2006). The signal-to-noise ratio decreases with depth, and therefore the 200 and 120 kHz frequencies were not used below a depth of 150 and 350 m, respectively. Mesopelagic fish with swim bladders resonate at 18 kHz, although some species resonate closer to 38 kHz (Godø et al. 2009). The most abundant acoustic category, mainly at 300–600 m depth, resonated at 18 kHz and was assumed to be ‘mesopelagic fish’.

Vertical temperature profile data were collected 3 times at the sampling location (at the beginning, during and after trawling). Temperature data was measured with a CTD (Seabird SBE 911 plus) from the surface down to 500 m depth. The accuracies of the temperature and pressure measurements were 0.001°C and 0.3 dbar, respectively. Light intensity was not measured during sampling. Still, as a proxy, we used the theoretical photosynthetically active radiation (PAR) value calculated at the surface using the ‘maptools’ and ‘fishmethods’ packages (Bivand & Lewin-Koh 2018, Nelson 2017) in R (R Core Team 2018).

2.4. Data analysis

Data were analysed using R v.3.5.1 (R Core Team 2018). To investigate possible non-linear differences in dietary intake between time of day and blue whiting size, we applied generalized additive models (GAMs) (Hastie & Tibshirani 1986). For constructing the models, we used an information–theoretic approach (Burnham & Anderson 2002) by defining candidate models (based on biological knowledge) and fitted them to the observations. To deal with zero inflation and overdispersion in the observations, we chose a Tweedie distribution for the observations (Tweedie 1984). A logarithmic link function between the predictors and response variable was chosen to handle the large heteroscedasticity typical of stomach content data. Model fitting was done using the ‘mgcv’ package (Wood 2017). In the full model, before model selection, both for total stomach content and every prey type separately (amphipods, copepods, euphausiids and fish), we assumed the following relationship between the weight of stomach content of fresh prey (μ) in stomach ‘ i ’ and the external factors:

$$\log(\mu_i) = f(\text{length}_i) + f(\text{solar time}_i) + f(\text{trawl depth}_i) + f(\text{bottom depth}_i) + \varepsilon_i$$

where $\varepsilon_i \sim N(0, \sigma^2)$, length is the total blue whiting length and solar time is sundial time used for explor-

ing differences between time of day, calculated using the ‘fishmethods’ package (Nelson 2017) (hereafter, time of day is referred to as solar time). Trawl depth and bottom depth (in m) at the trawled station were included to account for differences in sampling depth and position along the shelf. For modelling the non-linear effects, smoothing functions $f()$ were used; for constructing these functions we mainly followed Wood (2017). Thin plate regression splines were applied for $f(\text{length})$, $f(\text{bottom depth})$ and $f(\text{trawl depth})$; a cyclic cubic regression spline was used for $f(\text{solar time})$. A small value ($k = 3$) was chosen for the basis dimension, k (related to the number of knots), for length, trawl depth and bottom depth, while a slightly larger value ($k = 5$) was used for solar time. This setting allowed for only a few optima, which is a realistic representation of the dependence of prey intake with these variables. The final models for every species were selected using Akaike’s Information criteria (AIC) (Akaike 1974) through a backward selection procedure, beginning with all covariates included and stepwise reduction. We also tested possible 2-dimensional interaction effects between all variables using a tensor product smoother (Wood 2017). An example of the model selection procedure is given in the Supplement (R-code.txt). Initial data exploration followed guidance from Zuur et al. (2010) and showed no collinearity problems between predictor variables used (variance inflation factor < 2).

3. RESULTS

Of the 624 blue whiting stomachs analysed, 15 (2.4%) were empty. Total stomach content ranged from <0.01–14.0 g (mean \pm SD: 3.4 ± 2.5 g) and for fresh content, <0.01–12.2 g (1.3 ± 1.7 g). In terms of weight, euphausiids (44.7%), copepods (23.7%), amphipods (17%) and fish (12.8%) were the most important (Fig. 2). Stomach content (both all digestion stages and only fresh) was generally higher for the largest blue whiting specimens (Fig. 3).

3.1. Model results

Models that included interactions fitted very poorly to the observations near the parameter limits (‘edge effects’) and were therefore disregarded in further analyses. The final GAMs differed between the different prey groups (Table 3; AIC score and summaries of the model output in R can be found in Tables S2 & S3, respectively). The models explained

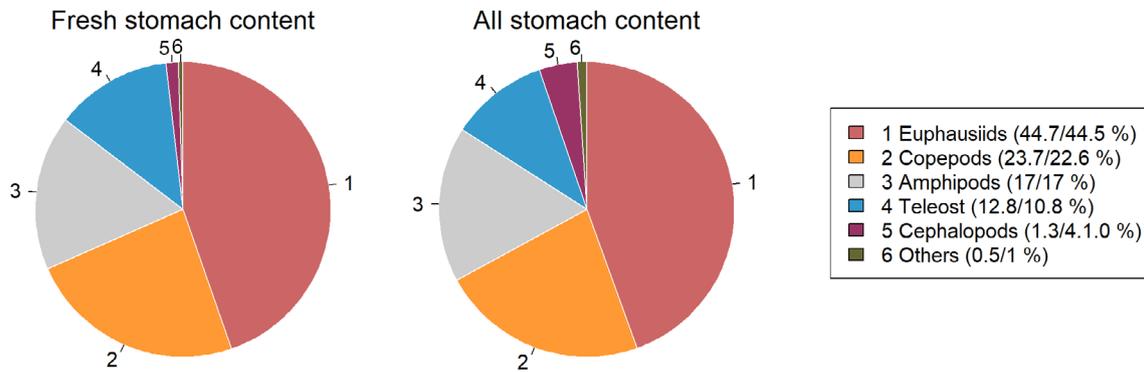


Fig. 2. Proportion of stomach contents (in weight) from all blue whiting stomachs sampled. Prey category ‘others’ includes chaetognaths, decapods, gastropods and isopods. Two prey groups (other crustaceans and unidentified) were only found as stomach contents that were not fresh and are included in ‘others’. Numbers in parentheses denote percentages for fresh and all stomach contents, respectively

2.0–21.6% (avg.: 10.8%) of the variation in the observations (except for fish prey, where none of the fitted models could be accepted). Solar time was statisti-

cally significant ($p < 0.05$) for the content of all prey grouped, euphausiids and copepods, but not for amphipods (Table 3). Length of blue whiting was significant for the content of copepods and amphipods, while it was not significant for all prey grouped and euphausiids (Table 3). Trawl depth of the mesopelagic hauls ranged from 225–405 m and was significantly related to total prey and copepod weight. Bottom depth (570–1070 m) significantly affected the content weight of copepods, amphipods and all prey grouped.

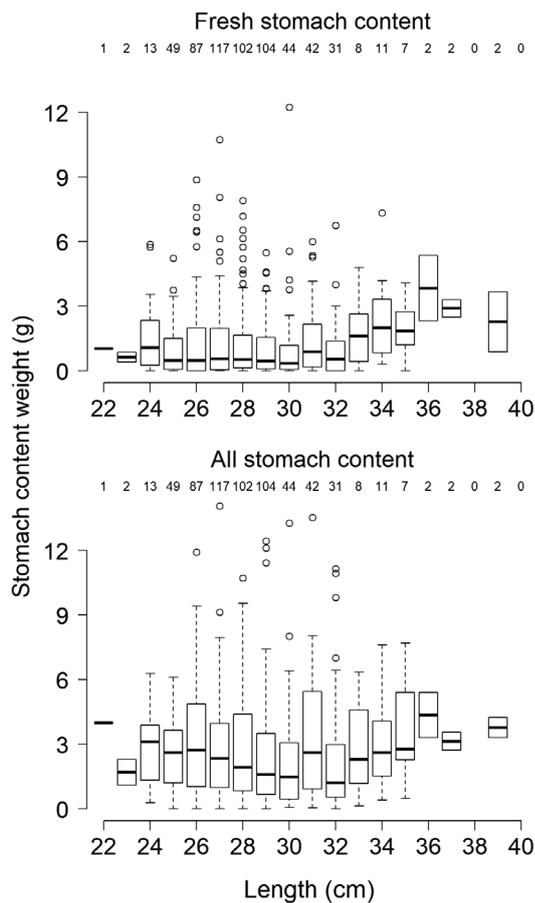


Fig. 3. Stomach content weight by blue whiting length. Bars: 25, 75 and 50% (median) quartiles; whiskers: 1.5 times the interquartile range above the upper quartile and below the lower quartile; dots plotted outside whiskers: single observations; numbers above bars: sample numbers by length group

3.2 Diel patterns and differences between blue whiting size groups

Stomach content weight varied with time of day (Table 3, Fig. 4a,b). Models for specific prey groups predicted that copepod weight in stomachs peaked at a solar time around 13:30 h, followed by all taxa and euphausiids at approximately 15:00 and 17:00 h, respectively (Fig. 5a). Total stomach content was

Table 3. Overview of significant terms and their p-values in the generalized additive models by prey groups. A p-value indicates that the term was significant and present in the final model

Response variable	Explanatory variable			
	Solar time	Length	Trawl depth	Bottom depth
All prey	<0.001		0.001	<0.001
Euphausiids	0.001			
Copepods	<0.001	<0.001	<0.001	<0.001
Amphipods		<0.001		0.002

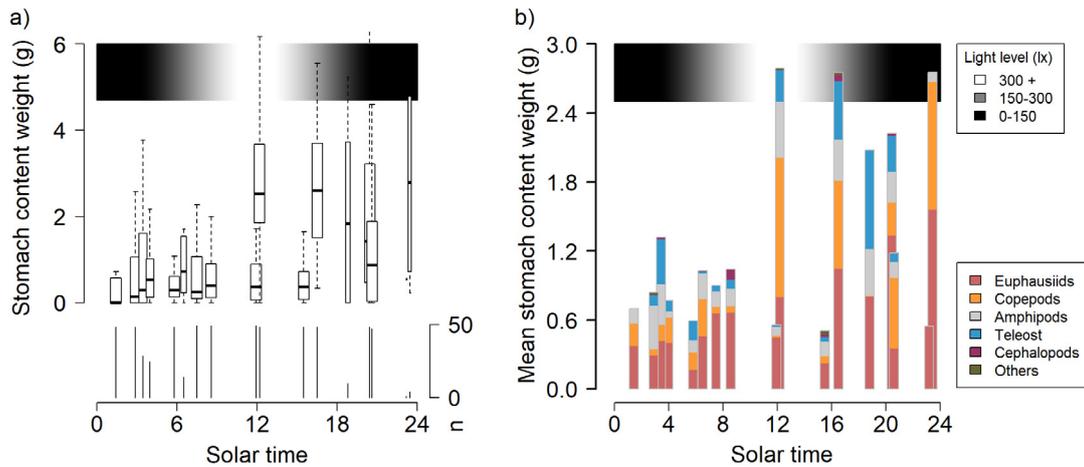


Fig. 4. (a) Blue whiting fresh prey weight by solar time. Bars: 25, 75 and 50% (median) quartiles; whiskers: most extreme observations. The lower part of the figure shows the number of stomachs per station. (b) Mean weight of fresh prey by solar time

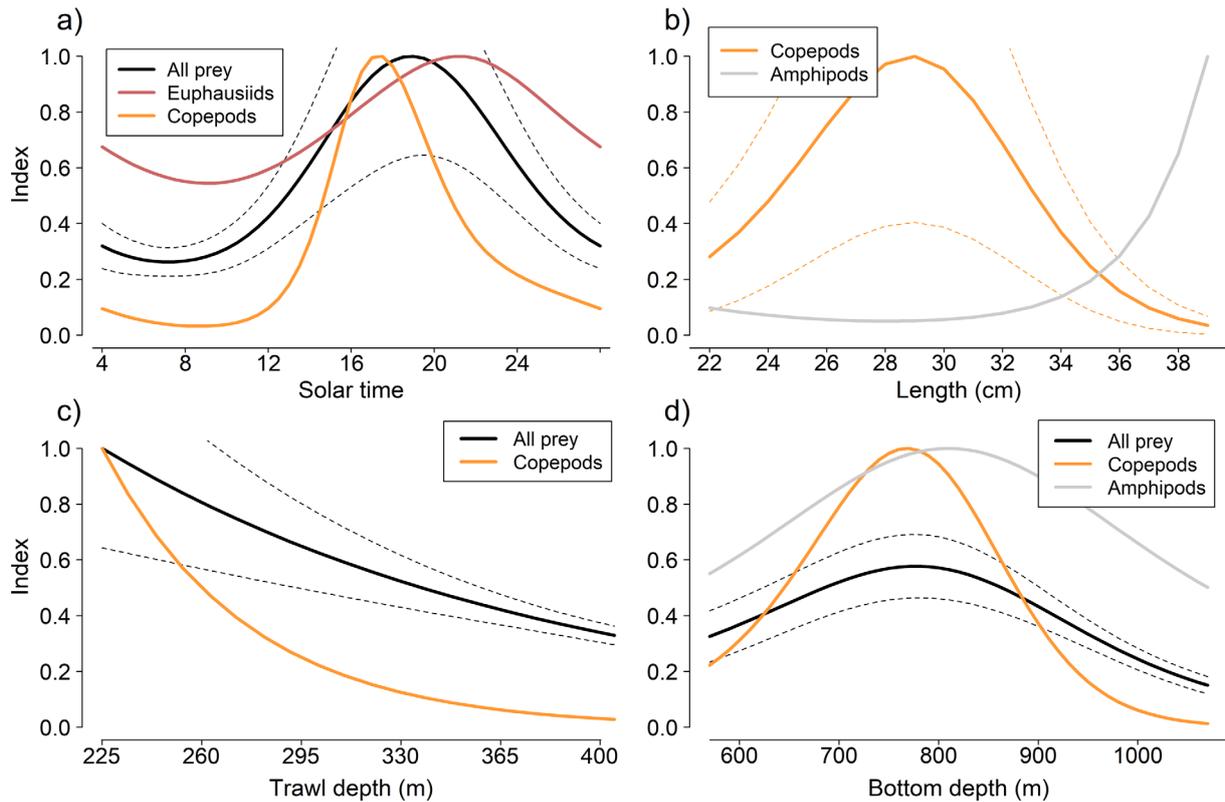


Fig. 5. Modelled fresh content of prey weight (all prey aggregated, euphausiids, copepods and amphipods) in blue whiting stomachs according to (a) solar time, (b) blue whiting length, (c) trawl depth and (d) bottom depth. Values are standardised to the maximum predicted values. Only values for parameters included in the final models after model selection are shown (i.e. significant parameters). Dashed lines: 95% confidence limits for the top prey group in the legend. For information on confidence limits for all prey types, see Fig. S1

lowest during the night (~00:00–05:00 h), while the contribution of euphausiids and copepods was lowest at around 04:00–08:00 h. Blue whiting length significantly influenced the weight of total stomach content

and contribution of copepods (Table 3, Fig. 5b). The weight of copepods in the stomachs was highest for fish with a length of 29 cm and lowest for the largest fish (39 cm) (Figs. 5b, S2 & S3).

3.3. Prey species, length and selection

Amphipods in the stomachs consisted almost exclusively of hyperiids with lengths from 5.4–37.2 mm (12.7 ± 4.9 mm), whereas euphausiids were generally larger at 7.8–42.4 mm (23.8 ± 9.4 mm) (Fig. 6b,c). The copepod size distribution in the stomachs ranged from 2.4–8.3 mm (5.6 ± 0.9 mm) (Fig. 6) and were considerably larger than observed in the water column from the MultiNet samples (Figs. 6 & S4). Based on the length distribution of copepods species in the MultiNet samples (Fig. S5), we can presume that all copepods (except *Paraeuchaeta* spp.) above 4 mm in

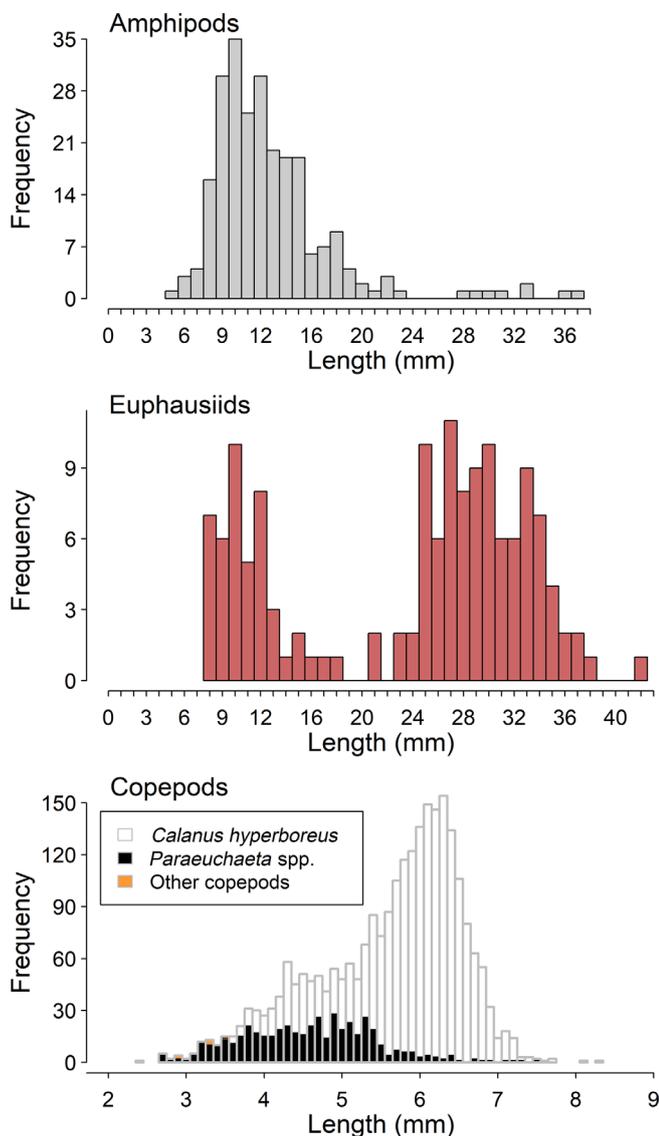


Fig. 6. Length distribution of fresh amphipods, euphausiids and copepods (*Calanus hyperboreus*, *Paraeuchaeta* spp. and other copepod species) in 39 randomly selected blue whiting stomachs

the stomachs were the large copepod species *Calanus hyperboreus*. The copepod fraction of *C. hyperboreus* and *Paraeuchaeta* spp. below 4 mm was calculated from numbers of the length groups relative to the other copepods in the MultiNet samples from the same depth range as the fish were caught, between 200–400 m. Based on these assumptions, 74.2% of the copepods in the stomachs (in terms of wet weight) consisted of *C. hyperboreus*, 25.8% were *Paraeuchaeta* spp. and <0.01% were other copepod species.

Blue whiting showed a high affinity for larger copepods (Fig. 7). The highest affinity was for copepods between 6–7 mm, which corresponded to a Strauss index of 0.42 and were present ~250 times more than expected if the copepods were randomly eaten. All copepods smaller than 3.5 mm had a negative Strauss index value, indicating that they were avoided by blue whiting. Smaller copepods (*Oithona*

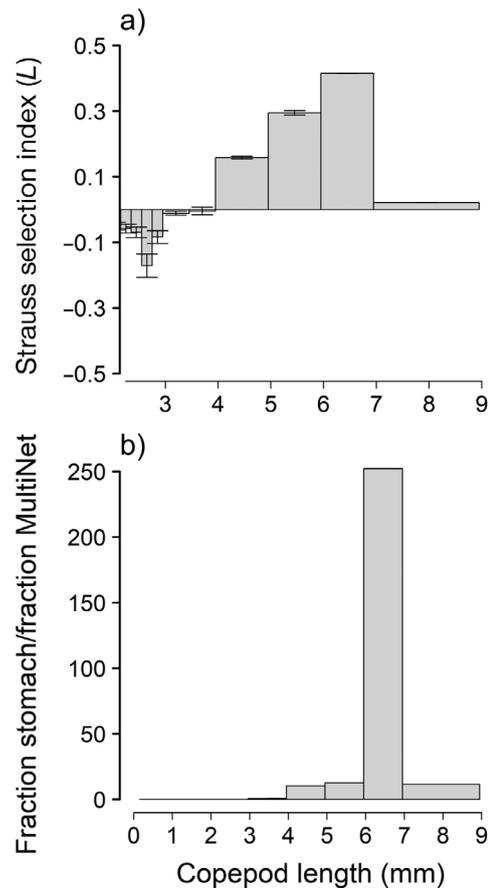


Fig. 7. (a) Strauss selection index for blue whiting selection of different copepod length groups. Error bars indicate the sampling variance, S^2 (Strauss 1979). (b) Relative proportion of different copepod length groups (in numbers) in the blue whiting stomachs versus relative proportions in the MultiNet samples from 200–400 m

similis, *C. finmarchicus* and *Pseudocalanus* spp.) dominated MultiNet samples from above 200 m (Fig. S4). All identified species in the MultiNet samples are listed in Table S4.

3.4. Vertical migration of prey and its presence in the stomachs

The acoustic observations showed that organisms in the ‘euphausiid’ category primarily occurred from 200–350 m depths during the light hours and migrated closer to the surface near sunset (Fig. 8). In the morning when the light increased, they returned to greater depths. However, some tended to remain either close to the surface or at greater depths throughout the whole daily cycle. Euphausiid weight in the stomachs of blue whiting peaked right before or when the majority of the euphausiids initially ascended to shallower depths at 17:00 h (Fig. 8). Mesopelagic fish generally stayed below the layer of euphausiids, but low densities also occurred right above and within the layer of euphausiids (Fig. 8). The bulk of copepods remained in the upper 100 m (verified with MultiNet; Table S5) but also performed diel migration, being primarily at the surface during the dark hours. These copepods mainly consisted of sizes less than 3.0 mm and were not selected by the blue whiting (Figs. S4 & S5). As blue whiting only occurred in low densities, they could not be identi-

fied with certainty in the acoustic recordings and could not be separated from other ‘fish’ signals.

4. DISCUSSION

The present study is the first in many decades to focus on the feeding of blue whiting in the Irminger Sea. While the Irminger Sea still has a relatively small and variable blue whiting population that migrates there for feeding, its presence is expected to increase in the future with changing climate conditions (Post et al. 2019, 2021).

4.1. Diet

Our observations indicate that the Irminger Sea, at least during the period of study, is a fruitful feeding area for blue whiting. The blue whiting analysed in our study had an average stomach content (1.7% of the total body weight) higher than individuals in other summer feeding areas such as the Barents Sea (1.5%) and Norwegian Sea (<1%) (Timokhina 1974, Dolgov et al. 2010). We also found fewer empty stomachs (2.4%) than reported in most other studies. For instance, in the Norwegian Sea, Bjelland & Monstad (1997) found 12% of the stomachs to be empty during spring and summer. Prokopchuk & Sentyabov (2006) reported up to 25% in July, while Dolgov et al. (2010)

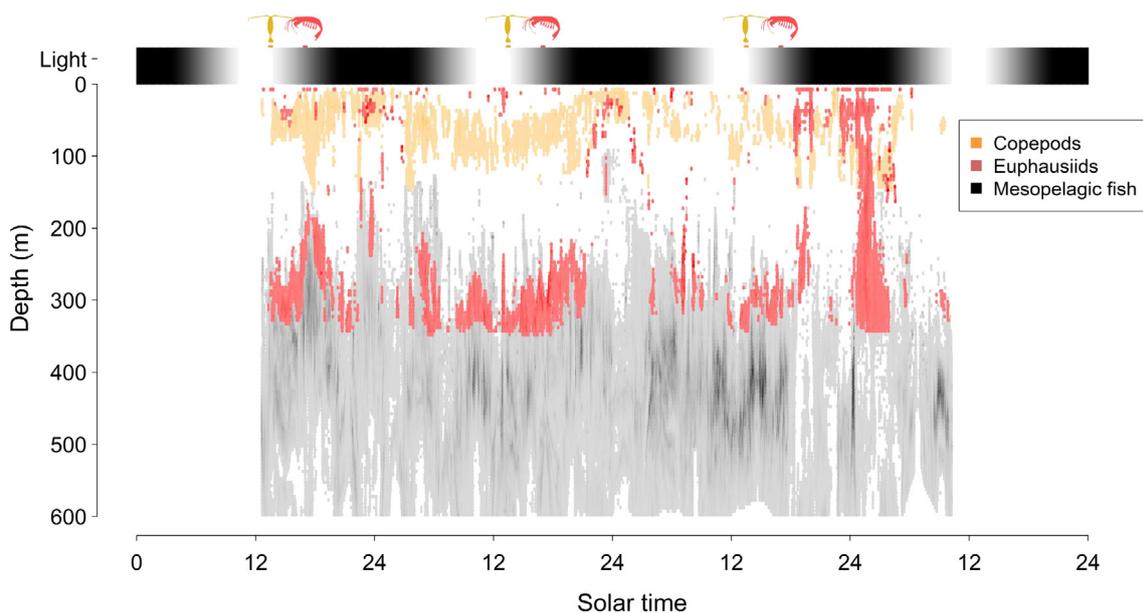


Fig. 8. Echogram display of vertical dynamics of the acoustic categories copepods, euphausiids and mesopelagic fish with a swim bladder. Silhouettes above the light bar represent the time the stomach contents of copepods (13:30 h) and euphausiids (17:00 h) peaked (modelled)

found 26% during summer in the Barents Sea, another northern fringe distribution area of blue whiting.

The general composition of stomach contents in the present study was in agreement with most studies on post-larval blue whiting, showing that euphausiids, amphipods, copepods and fish are the most important prey types (Zilanov 1968, Dolgov et al. 2010, Bachiller et al. 2016). However, in contrast to other studies, the specific composition of copepods in the stomachs primarily consisted of *Calanus hyperboreus* and *Paraeuchaeta* spp. (>99% wet weight), with few *C. finmarchicus* (<0.01%)—a species that was abundant in the planktonic community. In the Norwegian and Barents seas, *C. finmarchicus* is by far the most important of the copepod species in the blue whiting diet, with *C. hyperboreus* and *Paraeuchaeta* spp. less frequently found (Timokhina 1974, Prokopchuk & Sentyabov 2006, Dolgov et al. 2010, Langøy et al. 2012, Utne et al. 2012). This pattern appears to reflect their availability in the ambient zooplankton communities in each of the studied areas. The large polar copepod *C. hyperboreus* contributed to 7% of the copepod numbers in the plankton samples from 200–400 m (Table S5), while it comprised 70% of the copepods in the blue whiting stomachs. *C. hyperboreus* is abundant in the Iceland and Greenland seas (Gislason & Silva 2012, Visser et al. 2017) and is transported by the East Greenland Current into the Irminger Sea. Therefore, *C. hyperboreus* could be expected to be more abundant in the northern Irminger Sea and on the East Greenland shelf than in most other blue whiting feeding areas. In the central part of the Irminger Sea, further away from the East Greenland Current, *C. hyperboreus* abundance was much lower in samples from June 1997 and 2013 (Gislason 2003, Strand et al. 2020) compared to what we found in the present study (>1000 ind. m⁻²; Table S5). Therefore, the importance of *C. hyperboreus* in the diet of blue whiting appears to depend on the geographical location. *Paraeuchaeta* spp. comprised 3% of copepod numbers in the plankton samples from 200–400 m (Table S5), whereas it made up 19% in the stomachs. *Paraeuchaeta* spp. is generally more abundant in the Irminger Sea than most other areas where blue whiting are found (Gislason 2003, Strand et al. 2020). Thus, it might not be surprising that they appeared more frequently in the stomachs and water column compared to other described blue whiting feeding areas.

Another notable observation is that almost none of the examined blue whiting stomachs contained *C. finmarchicus*, despite the species being more abun-

dant in the water column than *C. hyperboreus* and *Paraeuchaeta* spp. together (Fig. S5). The largest *C. finmarchicus* is 3 mm prosome length; *C. glacialis* is 4 mm, while larger stages of *C. hyperboreus* (CV and later) and *Paraeuchaeta* spp. (IVF and later) are over 4 mm (Unstad & Tande 1991, Madsen et al. 2001, Dvoretzky & Dvoretzky 2015). Therefore, our results strongly demonstrate that blue whiting in this region target the largest copepods and potentially exert heavy predation pressure on populations of those copepod groups. Moreover, the size groups of copepods that primarily occurred in the blue whiting stomachs (~6–7 mm; Fig. 6) were very limited in the water column (MultiNet samples; Fig. S5). This observation suggests local depletion of certain copepod size groups by blue whiting predation.

4.2. Diel vertical feeding patterns

Blue whiting were totally absent from the 17 surface hauls conducted in the present study, and this was also true for all 194 surface hauls in Greenland waters during the IESSNS from 2013–2020 (ICES 2013a, 2014, 2015, 2016, 2017, 2018a, 2019, 2020). This indicates that during summer, blue whiting in the Irminger Sea do not migrate above 35 m, in concert with observations in most other study areas (Johnsen & Godø 2007, Huse et al. 2012). However, in some areas of its distribution (e.g. the Norwegian Sea), blue whiting occasionally migrate close to the surface during feeding (Prokopchuk & Sentyabov 2006), which could be linked to the varying environmental and biological conditions among the regions.

Blue whiting are known to exhibit diel vertical migration behaviour, moving towards the surface at night when feeding (Degnbol & Munch-Petersen 1985, Huse et al. 2012). However, in the present study, the highest fresh stomach content weight was from individuals captured between noon and evening (~12:00–20:00 h) (Figs. 4 & 5), indicating that blue whiting primarily feed during daytime. Stomach content was lowest during the early morning hours (Figs. 4 & 5), which coincides with the time of peak catchability of blue whiting in bottom trawl surveys around Greenland (Post et al. 2019). This timing suggests that blue whiting tend to stay closer to the bottom and digest during the morning hours. Timokhina (1974) found that blue whiting stomach fullness in the Norwegian Sea peaked 2 times a day and was highest at around midnight and 14:00 h. Degnbol & Munch-Petersen (1985) observed a single feeding peak around midnight for blue whiting in Skagerrak

that primarily fed on euphausiids. Because of these deviations, it appears that diel feeding activity varies between regions and that prey abundance and their vertical distribution influence when blue whiting feeding occurs. The feeding patterns could also be affected by predator avoidance—the diel vertical migrations of many species are a result of the trade-off between maximising feeding and avoiding predators (Kaatvedt et al. 1996). However, the behaviour of blue whiting to predators is not known. Elucidating their diel behaviour may help better understand how the species feeds and also how they are positioned in the water column. The quality of acoustic surveys monitoring blue whiting abundance is influenced by varying spatiotemporal behaviours, reflected in varying vertical distributions (Jacobsen et al. 2002, Johnsen & Godø 2007). Therefore, a better understanding of processes influencing blue whiting behaviour can help to improve the design of acoustic surveys targeting blue whiting and thereby the final stock assessment.

We observed temporal differences in the presence of different prey groups in the blue whiting stomachs. The euphausiid content in the stomachs peaked at 17:00 h, which was around the time when the majority of euphausiids began ascending towards shallower depths (Fig. 8). In Skagerrak, where the diet consists mainly of euphausiids, feeding increases during the evening and is at a maximum around and after midnight (local time) (Degnbol & Munch-Petersen 1985). We saw the peak earlier in the evening, probably attributed to the different behaviours of the euphausiids between the 2 areas. Euphausiids make diel vertical migrations, particularly the smaller individuals and females which migrate closer to the surface at night (Degnbol & Munch-Petersen 1985, Kaatvedt 2010). Even though we did not quantitatively estimate euphausiid vertical migration patterns, the acoustic observations confirmed this pattern, which in this region appeared to span from at least 350 m to the surface (Fig. 8). There is a strong indication that the blue whiting ingested euphausiids during the day at 250–350 m depth where the euphausiids resided and peaked in the stomach contents by 17:00 h.

The copepod content in stomachs was highest in the afternoon (13:30 h), right after the dense layer of copepods near the surface was located at its greatest depth (~150 m) (Fig. 8). However, this layer primarily consisted of smaller copepod species not eaten by blue whiting (Figs. S5 & 6). Zooplankton samples from the MultiNet revealed that smaller copepod species (including *C. finmarchicus*) and the larger *C. hyperboreus* and *Paraeuchaeta* spp. were present

throughout the whole sampled depth range (0–500 m; Table S5). Therefore, theoretically, these copepod species could have been consumed at all depths. However, the highest intake of copepods was observed for blue whiting sampled at the shallowest depths (Fig. 5). This pattern is similar to observations from the Norwegian Sea, where copepods are more abundant in stomachs in blue whiting from upper layers and even constitute as much as 97% of the stomach contents of fish caught in the upper 10 m (Prokopchuk & Sentyabov 2006). The present study also showed that bottom depth significantly influenced blue whiting stomach content (Table 3, Fig. 5). There may be several reasons for this; e.g. the vertical distributions and/or compositions of the prey may differ between depths or blue whiting feeding behaviour may change with different depth conditions. We did not have enough zooplankton samples to test the causes meticulously, but the results demonstrate that blue whiting feeding behaviour can change within a relatively small geographical area depending on the topographic conditions.

We did not find any significant diel differences in the presence of amphipods in blue whiting stomachs, but their contribution increased with blue whiting length. Amphipods, like euphausiids, are known to exhibit diel vertical migrations whereby they are found at shallower depths at night than during the day (Williams & Robins 1981). As they likely also have similar multifrequency backscattering properties, some of the acoustic signals we classified as ‘euphausiid’ backscatter could also have been amphipods. Unfortunately, we did not have a suitable sampling procedure for ground-truthing the acoustic signals of these 2 groups, and we were not able to determine differences in abundance and depth distribution between the groups.

4.3. Interaction and competition with other species

Blue whiting compete for food with other planktivorous fish species, as reported in the Norwegian and Barents seas for capelin *Mallotus villosus*, herring *Clupea harengus*, mackerel and polar cod *Boreogadus saida* (Dolgov et al. 2010, Utne & Huse 2012, Bachiller et al. 2016). The extent of this competition is not fully known and likely depends on the area, season and yearly variations in abundance.

In Greenland waters, mackerel and blue whiting overlap in horizontal but not vertical distribution (ICES 2017, Jansen et al. 2019, Post et al. 2019). In the Irminger Sea, at the same location as the present

study, mackerel were found only to feed in the surface waters, above approximately 40 m, but to a large extent on the same prey groups i.e. copepods, euphausiids, amphipods and fish (Jansen et al. 2019). As several of the prey groups, such as euphausiids and amphipods, conduct diel vertical migrations between the depth zones of the 2 fish species, these species appear to compete for some parts of their diet. However, competition for copepods (the most important prey of mackerel) does not seem to be the case in this area, as it appears that mackerels select *C. finmarchicus* while blue whiting select the larger copepod species (Jansen et al. 2019). In Greenland waters, blue whiting likely compete with capelin, herring and other gadoids as apparent in the North-east Atlantic (Utne & Huse 2012, Bachiller et al. 2016). The extent of competition depends on the abundance of these species and available food in the region.

In the present study, we demonstrated that blue whiting select the largest copepod species in this region. Therefore, it could be expected that with increasing amounts of blue whiting in Subarctic and Arctic areas, predation pressure on *C. hyperboreus* would substantially increase. This pressure on the population would be in addition to the effects exerted by warmer temperatures, as smaller copepod species, like *C. finmarchicus*, have become more abundant than larger copepods (Møller & Nielsen 2020). *C. hyperboreus* contains more lipids than the smaller copepod species and their phenology differs, resulting in a dissimilar timing of lipid accumulation over the year (i.e. more energy-rich during spring and summer) (Møller & Nielsen 2020). Consequently, the mentioned shift in copepod species composition will likely have a substantial impact on species relying on *C. hyperboreus*; for instance, polar cod, capelin and the little auk *Alle alle* (Hedeholm et al. 2010, Frandsen et al. 2014, Majewski et al. 2016).

In the present study, we also demonstrated that euphausiids constitute a significant part of the diet of blue whiting in the Irminger Sea (Fig. 2). Presently, 5 species of boreal baleen whales occur in Greenland waters (blue whale *Balaenoptera musculus*, fin whale *B. physalus*, humpback whale *Megaptera novaeangliae*, minke whale *B. acutorostrata* and sei whale *B. borealis*), which form a central part of the ecosystem and have a high cultural value in Greenland society (Ugarte et al. 2020). All these whales eat euphausiids; for the fin and blue whale, it comprises their diet almost exclusively (Moore et al. 2019). These 2 whale species are currently listed as Vulnerable and Endangered, respectively, on the IUCN Red List (Cooke 2018a,b), indicating that several stressors are al-

ready negatively influencing their abundance. In the Irminger Sea region, euphausiids are also an essential prey for sea birds, such as the little auk, and commercially important fish species, such as the beaked redfish *Sebastes mentella* (Petursdottir et al. 2008, Rosing-Asvid et al. 2013). Therefore, the blue whiting competes with various species for food resources, and these species will likely experience increased feeding competition if blue whiting abundances increase. Disentangling the competition pattern of food resources in Greenland waters may be performed by analysing spatiotemporal and dietary overlap, including abundance estimates of their prey, but there is currently a lack of data to carry out such an analysis.

4.4. Experimental limitations and uncertainties

As with most field studies, our research represents a snapshot in time and space. Hence, it is difficult to evaluate whether our observations are representative of the entire region or if the observed pattern is representative of other seasons and years. Spatiotemporal descriptions of the prey groups in the area (both in-shelf and off-shelf regions) could help to reveal these patterns, but as yet no data exists. Another approach for investigating the diet could be to analyse the stable isotope composition of the blue whiting. This approach might reveal the importance of the prey groups over an extended period and whether additional prey are important outside the studied time window (Matthews & Mazumder 2004, Smyntek et al. 2007). However, such an analysis would include prey consumed in areas outside the Irminger Sea region, as they spend a large part of their lives outside this area (Post et al. 2019), and it would most likely not be at a high enough resolution to identify the different taxa being ingested to the species level. Moreover, this type of analysis would not reveal the time of day or at what depths the prey were consumed.

The geographical offset of 2 of the 17 sampling locations does not appear to have added notable bias or uncertainty to the general results. The fish from the 2 deep trawl stations (collected at 05:40 and 07:30 h), located ~35 km east of the other 15 stations, had similar stomach contents to those taken during the night and morning at the remaining stations (Fig. 4). Therefore, the data from all 17 stations can be regarded as comparable.

The present study demonstrated that sampling depth of the blue whiting influences the stomach content weight and presence of different prey (Table 3,

Fig. 5). Therefore, the depth of sampling should be taken into account in blue whiting feeding studies. In our study, acoustic observations of blue whiting were used to guide decisions on trawling depth and obtain stomachs from individuals in the densest blue whiting layer. As a result, we feel that the collected individuals provided the most representative picture of the blue whiting diet.

Using wet weight allowed us to compare our results to other regions, as most blue whiting diet studies are based on wet weight (Bailey 1982, Dolgov et al. 2010, Mir-Arguimbau et al. 2020). The drawback of using wet weight is that water content varies considerably among the studied prey groups and seasons (Postel 2000). Therefore, this measure does not provide the best indication of the energy contribution from the different prey, as the relative importance of the prey groups as an energy resource is not directly reflected by the wet weight. Nevertheless, uncertainties around this unit are likely to have only a minor influence on the results in this study, as the taxa were modelled individually.

Zooplankton sampling is always subject to errors, the main error originating from escapement, avoidance and patchiness (Skjoldal et al. 2013). In the present study, we used a MultiNet, as it can sample zooplankton from several distinct depths and covers most size groups of the mesozooplankton community (Sameoto et al. 2000). Our zooplankton estimates are based on the average of 4 multiple hauls. That approach reduces the patchiness error. However, the MultiNet is not well suited to sampling larger macrozooplankton, such as euphausiids and amphipods, as they actively avoid the gear (Sameoto et al. 2000). Therefore, we could not include the presence of these groups in the MultiNet data to estimate their abundance in our study.

Copepods, on the other hand, are reliably sampled, as they have a much smaller capacity for escaping the gear (Sameoto et al. 2000). Small copepods (<1 mm) occasionally escape MultiNets with large mesh sizes (200 μm and above) as they pass through the mesh; by using finer mesh (50 μm) we managed to avoid this problem (Sameoto et al. 2000). Thus, we believe that the samples represented the mesozooplankton community in the water column at the time of collection.

5. CONCLUSIONS

We show that blue whiting in the Irminger Sea exhibit a distinct diel feeding pattern during summer

and primarily feed from around noon until late evening (~12:00–21:00 h, solar time). Their main diet consists of euphausiids, copepods, amphipods and juvenile fish, which largely agrees with the species' diet in other areas. Blue whiting primarily eat euphausiids immediately before or just as the euphausiids start to ascent towards shallower depths. Amphipods become more dominant in the diet with larger fish sizes, while copepods become less dominant. Blue whiting in the Irminger Sea select the large copepods *Calanus hyperboreus* and *Paraeuchaeta* spp. Despite *C. finmarchicus* being much more abundant than the other larger copepods in the region and its importance as prey of blue whiting in other areas of its distribution, this species did not contribute to the stomach content of the blue whiting during the time the present study was conducted. The Irminger Sea and the East Greenland shelf is an area of increasing interest for fisheries and climate-induced ecological changes in fish stocks. Therefore, this study represents an important piece of the puzzle for understanding the ecology of the region.

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