







Spatiotemporal variability in diet composition of Greenland halibut (*Reinhardtius hippoglossoides*) from the eastern Canadian Arctic

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Abstract

Greenland halibut (*Reinhardtius hippoglossoides*) sustain one of the most lucrative fisheries in the eastern Canadian Arctic and Labrador Sea. This species also plays an important role in food web connectivity and benthic–pelagic coupling. Despite the relatively rich knowledge of this species, *R. hippoglossoides* ecology in these specific areas remains poorly understood. The main aim of this study was to characterize the diet of this deepwater fish in the Labrador Sea and Davis and Hudson Straits and characterize the predator–prey relationship with northern shrimp (*Pandalus borealis*), another commercially important species in the region. Stomach contents analyses were conducted on 1199 fish captured from 2018 to 2020. Small specimens (<20 cm) fed on invertebrates, whereas larger individuals (>60 cm) fed primarily on fish, indicative of size-related changes in diet composition. The relative abundance of *Pandalus* shrimp species in the environment was reflected in the diet. Location appeared to be the most influential variable on feeding patterns. Distinct oceanographic conditions among areas, resulting in differences in prey availability, could explain these results. Arctic cod (*Boreogadus saida*) and redfish (*Sebastes* sp.) were selected in locations where fish prey were the most abundant. These results shed light on the opportunistic nature of *R. hippoglossoides* and its preference for fish at large size. With the rapidly changing oceanographic conditions of Arctic waters, a distributional change in the biomass of shrimp is expected. Results suggest that an increase in abundance of predatory groundfish species in the system (e.g., *Sebastes* sp.) could lead to acute predation on shrimp and competition with *R. hippoglossoides*. By revealing key trophic links within the demersal ecosystem, this work provides valuable information on the development of ecosystem approaches to fisheries management for the region.

KEYWORDS

food web, Labrador Sea, northern shrimp, predator–prey relationship, stomach content, trophic ecology

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1 | INTRODUCTION

Fisheries for Greenland halibut *Reinhardtius hippoglossoides* (Walbaum 1792) are well established across the species' distribution, yielding annual global landings of c. 129,000 t in 2020 (FAO, 2022). In Canadian waters and particularly for Newfoundland and Labrador, as well as Nunavut, it represents one of the most lucrative groundfish species, with commercial landings totaling \$52 million in 2020 (DFO, 2021a). Since the late 1990s, *R. hippoglossoides* exploitation has constantly increased in the eastern Canadian Arctic along with the general expansion of Arctic commercial fisheries (Treble & Nogueira, 2020). In these regions, access to fishing grounds is heavily controlled by sea ice conditions. With the predicted reductions in the extent, duration, and thickness of sea ice resulting from climate warming, it is expected that additional opportunities to expand this fishery will emerge (Hedges et al., 2017).

R. hippoglossoides is a flatfish characterized by a circumpolar distribution (Vihtakari et al., 2021), with its highest abundance in the North Atlantic and North Pacific sectors (Hedges et al., 2017). It has a high trophic position in Arctic marine food webs (Dennard et al., 2009; Giraldo et al., 2018) and has the ability to migrate vertically and feed in the water column, making them a key species in the benthic–pelagic coupling of Arctic marine ecosystems (Giraldo et al., 2018; Vollen & Albert, 2008). *R. hippoglossoides* are often considered as opportunistic feeders (Dwyer et al., 2010). Their diet is characterized by high spatial (Chumakov & Podrazhanskaya, 1986; Dwyer et al., 2010; Hovde et al., 2002; Vollen et al., 2004) and temporal (Hovde et al., 2002; Solmundsson, 2007; Vollen & Albert, 2008) variability and is also driven by prey availability (Dawe et al., 1998; Hovde et al., 2002; Orr & Bowering, 1997) and depth (Hovde et al., 2002; Orr & Bowering, 1997; Yang & Livingston, 1988). Their diet composition also varies with size (Bowering & Lilly, 1992; Orr & Bowering, 1997; Vollen et al., 2004; Yang & Livingston, 1988). Previous studies have shown that large adult *R. hippoglossoides* mainly feed on fish (Bowering & Lilly, 1992; Chumakov & Podrazhanskaya, 1986; de Groot, 1970; Gauthier et al., 2020; Solmundsson, 2007). However, at intermediate sizes, the commercially important northern shrimp *Pandalus borealis* (Krøyer 1838) and striped shrimp *Pandalus montagui* (Leach 1814) constitute a key component of their diet (Chumakov & Podrazhanskaya, 1986; Dwyer et al., 2010; Gauthier et al., 2020).

Currently, limited information is available on the ecology of *R. hippoglossoides* in the Labrador Sea, Davis Strait, and Hudson Strait regions. The confluence area between the Hudson Strait and the Labrador Sea is a highly dynamic system subjected to strong tidal currents and located in a transition zone between mixed and stratified waters (Hudon, 1990). This area is characterized by a high level of temporal variability in species abundance, notably in *P. borealis* and *P. montagui*, causing fluctuations in trophic relations in the system (Hudon, 1990; Siferd, 2014). Given the specificity of the region, and because the diet of *R. hippoglossoides* can vary widely in relation to fluctuations in prey availability and other environmental conditions, it would not be appropriate to make simple assumptions on this species' feeding ecology based on knowledge from other regions (Pedersen & Riget, 1993).

Thus, investigating the diet composition of *R. hippoglossoides* in the Labrador Sea, Hudson Strait, and Davis Strait can provide a better understanding of the species' trophic ecology and contribution to energy flow in the regional food web, which in turn may provide valuable information for developing an ecosystem approach to fisheries management in the region.

The *P. borealis* fishery supports major economic activity in the northwest Atlantic region of Canada (DFO, 2018). *P. borealis* present in this region was documented as a genetically homogeneous population (Jorde et al., 2015) that experiences genetic mixing across the different stocks that are delimited by the North Atlantic Fisheries Organization divisions (Le Corre et al., 2020). With ocean warming, the potential for larval settlement and adult growth decreases in the south of its distribution. Consequently, ocean warming, with a variety of other factors, are inducing a decrease in stocks located on the southern Labrador and Newfoundland shelves (DFO, 2018, 2021b, 2021c). Farther north, shrimp stocks located in Davis and Hudson Straits are still considered healthy (NAFO, 2020). However, as water temperatures continue to increase, these stocks could undergo similar biomass decreases. Therefore, investigating the relationships linking *R. hippoglossoides* to its potential prey, including *P. borealis*, is crucial to inform robust conservation and management decisions in the region.

The main aim of the present study was to assess diet composition and infer on feeding behavior of *R. hippoglossoides* in the Labrador Sea, Davis Strait, and Hudson Strait regions, and to determine and interpret patterns in prey species composition in relation to the predator's spatial and temporal distribution. We also aimed to assess which biological and oceanographic parameters (year, assessment zone, water temperature, depth, and predator size) explained variability in *R. hippoglossoides* diet composition. In light of the results, the trophic relationship between *R. hippoglossoides* and *P. borealis* is discussed to provide a better understanding of the dynamics between the two most commercially important species in the region.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

Sampling was carried out over a 6-week period each summer ranging from mid-July to late August 2018–2020 covering the Davis Strait, Hudson Strait, and northern Labrador shelf regions in the Labrador Sea (Figure 1). This area covers three assessment zones for *P. borealis* and *P. montagui* fisheries as used by Fisheries and Oceans Canada (DFO) for stock assessment: the Western Assessment Zone (WAZ, analogous to Hudson Strait), the Eastern Assessment Zone (EAZ, analogous to Davis Strait), and Shrimp Fishing Area 4 (SFA 4, analogous to the northern Labrador Sea).

During each year of this study, surveys were carried out onboard the F.V. *Aqviq* (2018–2019) and the F.V. *Katsheshuk II* (2020). This sampling effort was part of the collaborative survey between the Northern Shrimp Research Foundation (NSRF) and DFO, which has

been in place since 2005. The survey was conducted using a buffered random stratified sampling design (Kingsley et al., 2004). Consequently, each zone was divided into the following depth-based strata: 100–200, 200–300, 300–400, 400–500, and 500–750 m. The number of sampling locations within a given depth stratum was proportional to the surface area of that depth stratum within the zone. Approximately 320 stations were sampled annually, with 15-min tows using a standard Campelen 1800 shrimp trawl (12.8-mm codend mesh) in SFA 4 and a modified Campelen shrimp trawl (12.8-mm codend mesh; for modification details see Siferd & Legge, 2014), in WAZ and EAZ. In addition to direct quantification of the two

commercial shrimp species *P. borealis* and *P. montagui*, one of the other aims of the survey in recent years was to collect stomach samples of *R. hippoglossoides*. Stomachs were collected at 29 stations in 2018, 51 in 2019, and 26 in 2020 (Figure 1). The selection of stations for stomach sampling aimed to cover the widest possible geographical area with considerations for limited human resources and time available on a daily basis.

2.2 | Stomach sampling

In 2018 and 2019, up to 10 *R. hippoglossoides* stomachs per 5-cm size classes based on total length (TL) and depth strata were collected from each of the three zones (Tables 1 and 2). Fish were measured (TL, ± 0.1 cm) and weighed (± 0.01 kg), and sex was determined. Stomachs were excised at sea and kept frozen at -20°C until further analysis. In 2020, sampling was conducted by the vessel crew when no biologist was allowed onboard due to COVID-19 restrictions. The protocol stated to randomly sample whole specimens of *R. hippoglossoides* at each station. Up to nine specimens were sampled per station (i.e., three small [0–30 cm], three medium [31–60 cm], and three large [≥ 61 cm]). Fish were immediately frozen (-20°C) whole onboard the vessel on capture until they were processed in the laboratory. In the laboratory, fish were thawed, measured (TL, ± 0.1 cm), and weighed (± 0.01 kg), and then the stomachs were excised.

2.3 | Stomach content analysis and taxonomic identification

Samples from the 2018 and 2019 surveys were analysed at DFO's Freshwater Institute in Winnipeg. Samples from the 2020 survey were analysed at the Institut des Sciences de la Mer de Rimouski of the Université du Québec à Rimouski. Once thawed in the laboratory, each stomach was opened to remove and weigh its contents. Stomach contents were examined, and all prey were identified to the lowest

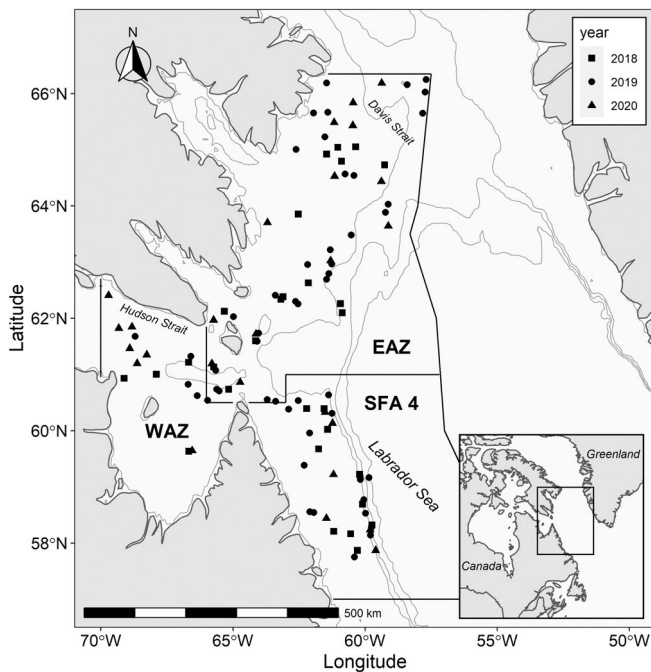


FIGURE 1 Locations of stations where Greenland halibut *Reinhardtius hippoglossoides* were collected for stomach analysis ($n = 106$), and the division of the three assessment zones (Western Assessment Zone [WAZ], Eastern Assessment Zone [EAZ], and Shrimp Fishing Area 4 [SFA 4]) considered in the study.

TABLE 1 Total number of sampled Greenland halibut *Reinhardtius hippoglossoides* stomachs by year, zone, and length group.

Length (cm)	Total	2018			2019			2020		
		EAZ	WAZ	SFA 4	EAZ	WAZ	SFA 4	EAZ	WAZ	SFA 4
<20	335 (21)	99 (15)	36 (28)	25 (40)	39 (23)	8 (13)	8 (50)	78 (9)	32 (13)	10 (40)
[20–30]	264 (27)	52 (33)	49 (29)	30 (27)	40 (43)	11 (0)	23 (39)	18 (39)	26 (12)	15 (0)
[30–40]	285 (38)	58 (34)	41 (37)	63 (40)	42 (45)	11 (9)	31 (55)	14 (50)	14 (0)	11 (0)
[40–50]	165 (44)	53 (45)	27 (37)	20 (55)	28 (39)	7 (14)	18 (61)	7 (29)	5 (20)	0
[50–60]	94 (36)	32 (31)	15 (20)	7 (57)	29 (34)	4 (25)	7 (100)	0	0	0
≥ 60	56 (37)	14 (36)	6 (0)	6 (50)	21 (43)	4 (0)	5 (60)	0	0	0
Total	1199 (31)	308 (30)	174 (30)	151 (40)	199 (38)	45 (9)	92 (55)	117 (20)	77 (10)	36 (11)

Note: Values in parentheses represent the percentage of empty stomachs; values in parentheses for the total represent the percentage of empty stomachs in the entire collection in a given year/zone.

Abbreviations: EAZ, Eastern Assessment Zone; SFA 4, Shrimp Fishing Area 4; WAZ, Western Assessment Zone.

TABLE 2 Station depths and bottom temperatures by year and zone in which Greenland halibut *Reinhardtius hippoglossoides* were collected.

Year	Zone	Depth range (m)	Depth mean \pm SE (m)	Bottom temperature range ($^{\circ}$ C)	Bottom temperature mean \pm SE ($^{\circ}$ C)	Number of stations
2018	EAZ	182–626	355 \pm 143	–0.5 to 3.9	2.5 \pm 1.2	15
	WAZ	–	335	–	–0.2	1
	SFA 4	160–614	336 \pm 157	–0.1 to 4.3	2.6 \pm 1.8	10
2019	EAZ	164–612	397 \pm 136	–1.4 to 4.2	2.2 \pm 1.4	29
	WAZ	205–419	340 \pm 92	–0.2 to 2.2	1.3 \pm 1.0	5
	SFA 4	130–701	360 \pm 163	–0.8 to 4.4	2.6 \pm 2.0	15
2020	EAZ	178–696	380 \pm 154	–1.1 to 3.8	1.5 \pm 1.4	13
	WAZ	159–412	325 \pm 89	–1.1 to 1.9	0.6 \pm 1.1	7
	SFA 4	137–501	276 \pm 142	–0.1 to 3.9	2.1 \pm 1.8	5
All	EAZ	164–696	382 \pm 140	–1.4 to 4.2	2.1 \pm 1.4	57
	WAZ	159–419	332 \pm 83	–0.8 to 2.2	0.8 \pm 1.1	13
	SFA 4	130–701	338 \pm 156	–0.8 to 4.4	2.6 \pm 1.8	30

Abbreviations: EAZ, Eastern Assessment Zone; SE, standard error; SFA 4, Shrimp Fishing Area 4; WAZ, Western Assessment Zone.

possible taxonomic level that could be achieved with a high degree of certainty using a binocular microscope (100 \times). Mucus, sand, parasites, liquids, and other nonfood items were excluded from further analyses. The number of individuals within each taxonomic category was recorded, with an “individual” defined as any specimen that had more than half of its body intact. Specimens that had less than half their body intact were described as “partial” individuals and not counted. When available, otoliths were collected from the stomach contents and/or extracted directly from fish prey. Otoliths were mainly used to confirm fish species identification or to determine the presence of unidentified fish in stomach contents. Shrimp species other than *Pandalus* spp., for which identification was impossible, were categorized as Natantia. Remaining items, after separation of the stomach contents into the different taxonomic categories, were often highly digested, unidentifiable material, which was weighed and entered as “unidentifiable material” in the database.

2.4 | Diet analysis

Size classes used to analyse the effect of predator size on the diet were 10-cm size classes, a uniform cutoff, as <20.0, 20–29.9, 30–39.9, 40–49.9, 50–59.9, and \geq 60.0 cm. *R. hippoglossoides* diet was described using two different measures. First, the relative importance of different prey taxa was assessed for percentage of occurrence (%O, Hyslop, 1980). Percentage of occurrence was used to qualitatively indicate the proportion of *R. hippoglossoides* that feed on a given prey:

$$\%O = \frac{N_i}{N} \times 100 \quad (1)$$

where N_i is the number of stomachs in the sample containing prey i and N is the total number of stomachs analysed.

Then, the percentage fullness index (%FI, Bernier & Chabot, 2013) was calculated to assess the proportion of the contribution of prey in the diet of *R. hippoglossoides*. To obtain the %FI, intermediate calculations were made.

First, the partial fullness index (PFI; Orr & Bowering, 1997; Bernier & Chabot, 2013) was calculated using the following equation:

$$PFI_{ij} = M_{ij} \times L_j^{-b} \times 10^4 \quad (2)$$

where M_{ij} is the mass of prey i in predator j , L_j is the TL (cm) of predator j , and b is the specific allometric exponent calculated for *R. hippoglossoides* ($b = 3.31$). The latter corresponds to the slope of the linear relationship of *R. hippoglossoides* $\log_{10}(\text{weight})$ and $\log_{10}(\text{TL})$ collected for this study during the 2019 and 2020 (no length measurements in 2018) surveys ($n = 566$, $r^2 = 0.99$, $p < 0.001$). The PFI adjusts the quantity of each prey taxon found in a stomach for the effect of predator size. The mean PFI of prey i in the sample (year, size class, and/or zone) was then obtained as follows:

$$PFI_i = \frac{1}{N} \times \sum_{j=1}^N PFI_{ij} \quad (3)$$

where N is the number of *R. hippoglossoides* in the sample.

Total stomach fullness index (TFI) is the sum of all PFIs:

$$TFI_j = \sum_{i=1}^I PFI_{ij} \quad (4)$$

$$TFI = \frac{1}{N} \times \sum_{j=1}^N TFI_j \quad (5)$$

where I represents the number of different prey taxa found in the sample.

Then, %FI_i (Bernier & Chabot, 2013) was calculated using the mean PFI_i and the TFI:

$$\%FI_i = \frac{PFI_i}{TFI} \times 100 \quad (6)$$

2.5 | Statistical analyses

Stomach sample sufficiency to describe the diet was assessed using cumulative prey curves (Ferry & Cailliet, 1996). Prey curves were randomly generated (100 permutations) from the original diet data (%FI) and based on the number of prey categories considered. The slope of the linear regression (*b*) through the last five subsamples was used to quantitatively determine if the curve reached an asymptote, where $b \leq 0.05$ signified an adequate leveling off of the prey curve for diet characterization (Brown et al., 2012).

Relationships between environmental variables and *R. hippoglossoides* diet were investigated using canonical correspondence analysis (CCA; Ter Braak, 1986). Initially, the linearity of the response of explained (environmental/biological) variables to explanatory (prey items) variables was tested by comparing the length of gradients from detrended correspondence analysis (DCA). The length of the longest gradient in the DCA (5.6 SD [standard deviation]) was greater than 4 SD units, which indicates a clear unimodal response in the data. Therefore, the unimodal method of CCA was employed. CCA is a direct gradient multivariate technique that directly associates the variation in one matrix with the variation in another (Legendre & Legendre, 1998; Ter Braak, 1986). In this study, *R. hippoglossoides* diet (species) was associated with location, environmental, and biological data. The variables included assessment zone, predator length, depth, temperature, year, latitude, and longitude. Only the most frequently occurring (%O >2%) and highly contributing (%FI >2%) prey taxa were included. Additionally, some of the taxa that did not meet those criteria (e.g., *Boreomysis artica*, *Boreomysis tridens*, *Boreomysis* sp.) were combined to form relevant (%O and %FI >2%) taxonomical groups (e.g., *Boreomysis* spp. [Mysids]) that were included in the analysis. Prey identified as *Pandalus* sp. were considered as either *P. borealis* or *P. montagui* based on the species present in the same content or same station. The CCA diet data subset input was selected over two criteria: biological and oceanographic parameters (year, assessment zone, water temperature, depth, and predator size) were known, and at least one targeted prey group (see Figure 5) was present in the diet. As a result, the analysis was performed with 365 samples (*R. hippoglossoides* stomach subsamples) distributed over 76 stations (Supporting Information Table S2).

To select and rank explanatory variables with significant ($p < 0.05$) contributions to the observed variation, forward stepwise selection of environmental variables was conducted. The variance inflation factors (VIF) for each explanatory variable was calculated to test collinearity and redundancy. Any variable that yielded a VIF >4 was removed from the final model (James et al., 2013). Forward-selection permutation tests (1000 permutations) were then used to test the significance ($p < 0.05$) of the model, terms, and canonical axes. Type two scaling of the triplot was used to emphasize the relationships among response variables. All analyses were performed using

the R software version 4.1.2 (R Core Team, 2021) using packages “vegan” (Oksanen et al., 2020) and “ggvegan” (Simpson, 2019).

3 | RESULTS

3.1 | Stomach sampling data set

From 106 sampling sites (Figure 1), 1199 *R. hippoglossoides* stomachs were collected from 2018 to 2020 throughout the entire study area, of which 830 contained prey (31% of stomachs were empty). A total of 633 stomachs from 29 stations were sampled in 2018, 336 stomachs from 51 stations in 2019, and 230 stomachs from 26 stations in 2020 (Table 1). All years combined, 624 stomachs were collected in the EAZ, 296 in the WAZ, and 279 in the SFA 4.

Cumulative prey curves calculated for the overall diet (all years and zones combined, Supporting Information Figure S1) showed that most size classes reached a stable asymptote, indicating an adequate number of stomachs for an accurate description of the diet. However, the asymptote was not reached for specimens ≥ 60 cm, indicating an insufficient sample size for this size class. Cumulative prey curves calculated for each separate year and assessment zones of sampling showed that about half of the subsets did not reach a sufficient number of samples to make an accurate description of the diet. This is mostly observed for larger size classes, especially in less sampled years and assessment zones.

The mean TL (\pm SE [standard error]) of *R. hippoglossoides* in 2018 and 2019 was 32.7 cm (± 14.8) and 36.0 cm (± 16.1), respectively. In 2020, the mean TL (\pm SE) was much lower at 21.9 cm (± 9.3 ; Figure 2). This low mean size does not reflect the size distribution in the catch; instead, it reflects the fish subsample that was retained in 2020 by the vessel crew when no biologist was allowed onboard due to COVID-19 restrictions. Freezer space was likely an issue in 2020 due to the freezing of whole fish rather than individual stomachs. As a result, the TL range of fish from 2020 was only 10.5–48.5 cm, when compared to 8.0–78.0 cm in 2018 and 9.9–84.9 cm in 2019.

The mean depth (\pm SE) of the 106 sampling stations, including all 3 years and zones, was 362 m (± 140) with a range of 130–701 m. Fish were captured at similar depths across all years of sampling (Table 2). In 2018 and 2019, mean water temperatures were similar at stations where *R. hippoglossoides* were caught, whereas stations in 2020 were generally colder. Over the 3 years, the WAZ stations were notably colder than those in the other two zones, with a mean of 0.8°C (± 1.1 ; range: -0.8 to 2.2°C), compared to a mean of 2.1°C (± 1.4 ; range: -1.4 to 4.2°C) in the EAZ and a mean of 2.6°C (± 1.8 ; range: -0.8 to 4.4°C) in the SFA 4. Additionally, the WAZ stations were generally shallower, with a mean depth \pm SE of 332 m (± 83), but with a narrower range of 159–419 m.

3.2 | Diet composition

A total of 69 taxa were observed in the diet of *R. hippoglossoides* (Supporting Information Table S1), pointing to an overall diverse diet.

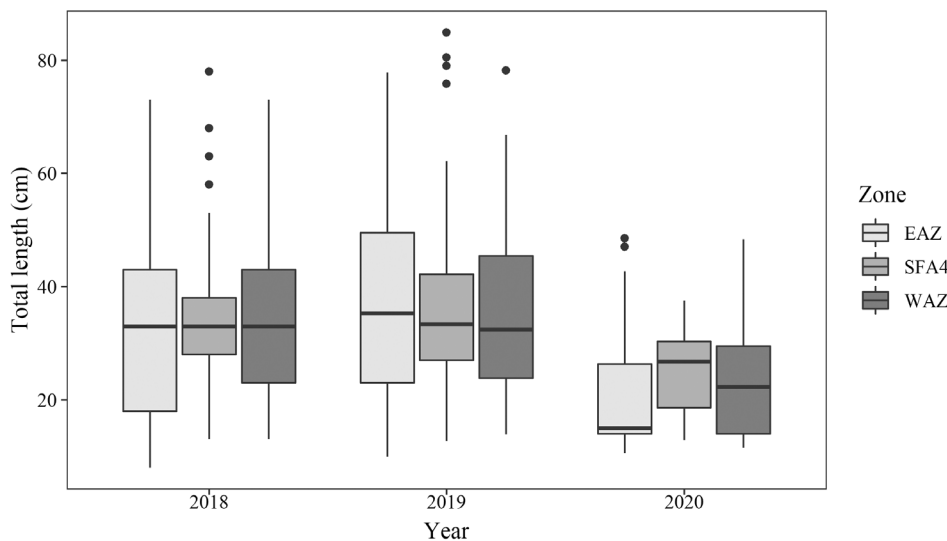


FIGURE 2 Total length (cm) distribution of Greenland halibut *Reinhardtius hippoglossoides* caught by year and zone. Boxes indicate the interquartile range (25th–75th percentiles), with adjacent values as whiskers (5th and 95th percentiles), outlying values as black dots, and medians indicated by a horizontal black line.

However, only a small portion of prey taxa identified to the genus or species level significantly contributed to the diet. Arthropods contributed the most to the overall diet (50.2). Within this group, the genus *Themisto* sp. had the highest contribution (20%). *P. borealis* and *P. montagui* were the most prevalent shrimp species in the diet with a contribution of 8.8% and 4.3%, respectively. An important part of the diet was also composed of fish, with a total contribution of 37.1%. Arctic cod *Boreogadus saida* (Lepechin 1774) was by far the most dominant fish species in the diet (9.2%), followed by gelatinous snailfish *Liparis fabricii* (Krøyer 1847; 3.9%), and small specimens of redfish *Sebastes* sp. (Cuvier 1829; 2.0%). The cephalopods completed the prey species range (Table 3).

3.3 | Effect of predator size on diet

To provide a complete description and facilitate the understanding of the *R. hippoglossoides* diet while focusing on the most common prey species, the diet was represented by 13 categories, which are single and pooled species based on the %FI results: 4 single taxa, 4 genera, 1 class, and 4 broader categories of prey. Whereas certain key taxa were singled out (*P. borealis*, *P. montagui*, *B. saida*, and *R. hippoglossoides*), other important taxa were combined under the same genus to add weight to the category. For example, *Themisto* spp. includes *Themisto* sp. and *Themisto libellula*. The broader categories included all other arthropods (unidentified/other arthropod), all other fish (unidentified/other fish), all other taxa not included in already-considered categories (other), and unidentified stomach content material (unidentified material; Figure 3).

Small (i.e., <20 cm TL) *R. hippoglossoides* mainly fed on *Themisto* spp., with a 56% contribution to the diet. Specimens ranging between 20 and 59.9 cm mainly fed on fish and shrimp, with a clear diet shift occurring between the <20 and 20–29.9 cm size classes (Figure 3). *B. saida* was a high-contributing prey for the 20–29.9 cm fish (22%), but it decreased to become null from the size of 50 cm.

P. borealis contributed the most to the diet with a 20% and 18% contribution for 30–49.9 cm size classes respectively. *P. montagui* was also a major prey, particularly in the 40–59.9 cm specimens where its contribution reached 12%. *Sebastes* sp. appeared in the diet of the 30–39.9 cm fish with a contribution of 8%. Despite the modest overall contribution of cephalopods, this taxon had a notable presence (4%) in the diet of the 20–49.9 cm *R. hippoglossoides*. The contribution of *Boreomysis* spp. to *R. hippoglossoides* diet increased with size, peaking at 4% in the 50–59.9 cm fish. Cannibalism was especially prevalent in the largest *R. hippoglossoides* specimens. Indeed, specimens ≥ 60 cm showed a clear dominance of fish in their diet with a concurrent decrease in shrimp, suggesting a second diet shift.

3.4 | Yearly variation in diet

In 2018, *Themisto* spp. was largely dominant in the diet of <20-cm *R. hippoglossoides* (67%; Figure 4). That contribution gradually decreased in 2019 and 2020, paralleled by an increase in “unidentified/other arthropod.” Cephalopods made a higher contribution to the diet in 2019 relative to 2018 and 2020. In all 3 years, *R. hippoglossoides* shifted from an arthropod-dominated diet to a shrimp-/fish-dominated diet between the <20 and 20–29.9 cm size classes. From 2018 to 2020, the contribution of shrimp, and particularly *P. borealis*, decreased, whereas fish contribution increased for the 20–39.9 cm fish. In 2020, the 20–29.9 cm size class was dominated by *B. saida* with a contribution of 47%, whereas *Sebastes* sp., which appeared only from 2020, dominated the diet of the 30–39.9 cm size class with a contribution of 38%. Specimens ≥ 40 cm showed similar feeding patterns between 2018 and 2019. Cannibalism was prevalent in larger specimens and tended to increase with size. In 2020, the absence of observed cannibalism likely resulted from the fact that no specimen longer than 48.5 cm was analysed. Compared to the two previous years, there was still a considerable contribution of *B. saida*

TABLE 3 Diet composition of Greenland halibut *Reinhardtius hippoglossoides* expressed in percentage fullness index (%FI) and percentage of occurrence (%O).

Prey taxon	%FI	%O
Fish	37.2	46.6
Unidentifiable fish	12.7	24.6
Gadidae		
Unidentifiable Gadidae	3.8	4.2
<i>Arctogadus glacialis</i>	*	*
<i>Boreogadus saida</i>	9.2	5.1
Macrouridae		
<i>Macrourus berglax</i>	*	*
Myctophidae		
Unidentifiable Myctophidae	*	*
<i>Benthoosema glaciale</i>	*	*
Stichaeidae		
<i>Leptoclinus maculatus</i>	*	*
<i>Lumpenus lampretaeformis</i>	*	*
<i>Lumpenus</i> sp.	*	*
Zoarcidae		
<i>Lycodes</i> sp.	*	*
Unidentifiable Pleuronectidae	*	*
<i>R. hippoglossoides</i>	1.1	1.0
Cottidae		
Unidentifiable Cottidae	1.6	1.1
<i>Myoxocephalus</i> sp.	*	*
<i>Triglops nybelini</i>	0.7	0.6
<i>Triglops</i> sp.	*	*
Liparidae		
Unidentifiable Liparidae	0.6	1.1
<i>Liparis fabricii</i>	3.9	4.2
Sebastidae		
<i>Sebastes</i> sp.	2.0	2.7
Shrimp	14.7	22.4
<i>Argis dentate</i>	*	*
<i>Atlantopandalus propinquus</i>	*	0.6
<i>Eualus</i> sp.	*	*
<i>Pandalus borealis</i>	8.8	10.7
<i>Pandalus montagui</i>	4.3	7.5
<i>Pandalus</i> sp.	1.2	1.9
<i>Pasiphaea multidentata</i>	*	1.2
<i>Pontophilus norvegicus</i>	*	*
Mysid	2.5	13.7
Unidentifiable Mysida	*	*
<i>Boreomysis arctica</i>	1.7	9.5
<i>Boreomysis</i> sp.	0.6	2.3
<i>Boreomysis tridens</i>	*	0.7
<i>Mysis oculata</i>	*	*

(Continues)

TABLE 3 (Continued)

Prey taxon	%FI	%O
<i>Mysis</i> sp.	*	*
<i>Pseudomma</i> sp.	*	*
Mollusca	4.2	4.0
Cephalopoda		
Unidentifiable cephalopoda	1.5	2.2
Decabrachia		
Unidentifiable Decabrachia	1.1	0.7
Octobrachia		
Unidentifiable Incirrata	*	*
Oegopsida		
<i>Gonatus fabricii</i>	*	*
<i>Gonatus</i> sp.	1.0	0.8
Amphipod	24.7	38.8
Unidentifiable Amphipoda	3.4	6.9
<i>Apherusa</i> sp.	*	*
<i>Eusirus cuspidatus</i>	*	*
<i>Eusirus holmi</i>	*	*
<i>Themisto libellula</i>	1.4	4.0
<i>Themisto</i> sp.	20.0	27.3
Other invertebrates	8.6	26.7
Unidentifiable material	8.1	26.3

* $p < 0.5$.

to the diet for 2020. Interestingly, *P. montagui* contribution increased 10-fold from 2019 (4%) to 2020 (38%) for 40–49.9 cm lengths, whereas the contribution of *P. borealis* decreased by half over the same period. However, these small subsample diet descriptions are associated with uncertainty.

3.5 | Spatial variation in diet

Although *Themisto* spp. was a key prey for halibut <20 cm in all three zones, it was the most prevalent in the diet of fish from the EAZ, with a contribution of 66% (Figure 4). Along with *Themisto* spp., *Boreomysis* spp. was a highly contributing prey taxon to diet in the WAZ, which was a unique feature of this zone. In SFA 4, *P. montagui* already significantly contributed to the <20 cm fish, so that the dietary shift from arthropods to fish and shrimp was not as clear in SFA 4 as it was in the two other zones. Major differences were observed in the diets of the 20–59.9 cm specimens among the three zones. The diet of *R. hippoglossoides* in the EAZ was characterized by a fish dominance, with an important contribution of *P. borealis*, and a notable presence of cephalopods. In WAZ, *P. borealis* was nearly absent from the diet, and *R. hippoglossoides* fed primarily on fish, especially *B. saida*. In contrast, the diet in SFA 4 was dominated by *Pandalus* spp. shrimp and arthropods with an outstanding contribution of 78% of *P. borealis* for the 50–59.9 cm specimens. *Sebastes* sp. made its most important

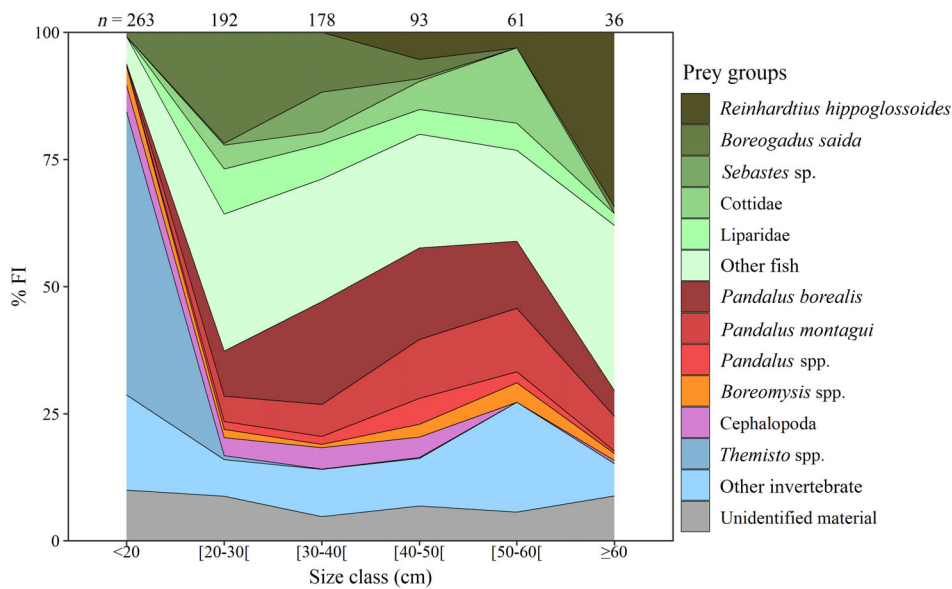


FIGURE 3 Contribution of the 13 prey categories to Greenland halibut *Reinhardtius hippoglossoides* diet, expressed as percentage fullness index (%FI) as a function of 10-cm size class. n is the number of stomachs containing prey analysed for each size class.

contribution among fish prey in SFA 4. Most of the cannibalism was observed in the WAZ at the 40–49.9 and ≥ 60 cm size classes.

3.6 | Multivariate effects on Greenland halibut diet

The data subset biological and oceanographic parameters used for the CCA analysis are described in Supporting Information Table S2. The final model included five variables and eight dietary taxa. The CCA results revealed a significant relationship between dietary data and explanatory variables ($p = 0.001$, $F = 17.05$; Figure 5). The model explained 25.1% of the total variance. The first two canonical axes explained 74.3% of the constrained inertia in the species data. Forward selection of the variables included in the CCA revealed that the “zone” variable explained most variance in diet composition (10.5%), followed by predator length (8.2%), year (2.8%), depth (1.9%), and temperature (1.7%), all of which were significant (Table 4). A permutation test confirmed that each of these variables significantly affected the variation in species data ($p < 0.001$).

CCA results revealed an ontogenetic shift in *R. hippoglossoides* diet from smaller prey items (e.g., *Themisto* sp.) to larger prey items such as fish (e.g., *B. saida*, *Sebastes* sp., and *R. hippoglossoides*) and shrimp (e.g., *P. borealis* and *P. montagui*), as indicated by the position of these taxa in relation to the vector representing predator length (Figure 5). The position of prey taxa in relation to zone centroids also revealed where the predation on a given prey was most likely. For example, *B. saida* was highly associated with the WAZ, whereas *P. montagui* was associated with the SFA 4 and cephalopods with the EAZ. Years occupied a relatively central position in the ordination space, suggesting that they are not strongly associated with any specific prey items. CCA results revealed that *R. hippoglossoides* found at different water temperatures fed on different prey. For example, *Sebastes* sp. and *B. saida* were associated with relatively higher and lower water temperatures, respectively. Prey taxa such as

Boreomysis spp., cephalopods, and *Themisto* spp. were strongly associated with depth. The depth vector also appeared to go along the predator length vector, which is expected for *R. hippoglossoides* as they migrate to deeper waters through ontogeny. Predation on smaller prey was thus generally observed at shallow depths and predation on larger prey at greater depths.

4 | DISCUSSION

Considering the important variability in stomach content data, a large number of samples are usually required to have a valid representation of the diet. Baker et al. (2014) stated in their literature review that a sample size of ≥ 100 stomachs would be generally adequate to provide a reliable description of the diet. In the present study, many of the data subsets, related to different size classes, sampling year of assessment zone, did not comprise 100 samples (Figures 3 and 4). However, prey accumulation curves showed that the asymptote was still reached for half of them (Supporting Information Figures S1 and S2). Large specimens were especially lacking in the samples, which makes the diet composition less robust for these sizes. The year 2020 and assessment zone SFA were also relatively short on samples, and asymptotes were not reached for most of their size class subset. Therefore, diet description for these subsets comes with an uncertainty.

This study revealed important information on the feeding behavior of *R. hippoglossoides* in the Labrador Sea, Davis Strait, and Hudson Strait regions. Stomach content analysis showed that this species feeds mainly on arthropods at smaller size and shifts its diet to shrimps and fish in relation to size. Dietary indices indicated that *P. borealis* was indeed a major prey for *R. hippoglossoides*. However, prey with high-energy content, as *B. saida* and *Sebastes* sp., appeared to be important contributors to the diet as well. Diet changed

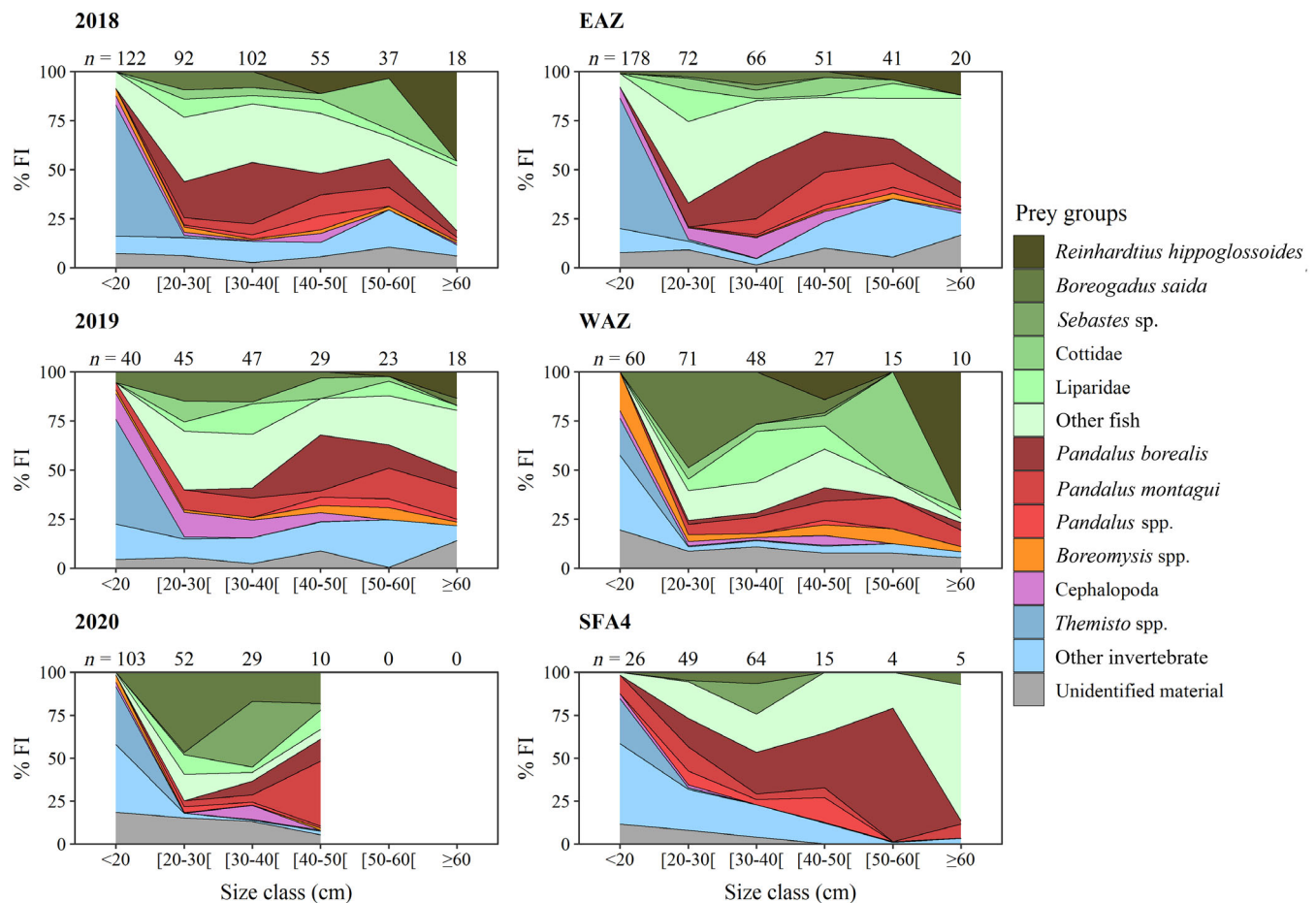


FIGURE 4 Contribution of the 13 prey categories to Greenland halibut *Reinhardtius hippoglossoides* diet, expressed as percentage fullness index (%FI) as a function of 10-cm size class, by year (left) and zone (right). *n* is the number of stomachs containing prey analysed for each size class.

significantly on the spatial and temporal scale considered, showcasing *R. hippoglossoides* to be a diverse and flexible feeder. As a result, prey availability, influenced by oceanographic conditions, appears to be the main driver of *R. hippoglossoides* diet composition.

4.1 | Effects of size on Greenland halibut diet

Analysis of *R. hippoglossoides* diet composition revealed a clear pattern of size-related dietary shifts. Generally, small *R. hippoglossoides* (<20 cm) fed on small crustaceans (i.e., amphipods) and then quickly transitioned (<20 to 20–29.9 cm) to a diet based on fish and shrimp (i.e., *B. saida*, *Sebastes* sp., and *Pandalus* shrimp), whereas larger specimens (≥60 cm) preyed mainly on fish. Size-related dietary shifts have been commonly observed and documented in fish (e.g., Brown-Vuillemin et al., 2022; Sánchez-Hernández et al., 2019; Temperoni et al., 2021), including *R. hippoglossoides* (Dwyer et al., 2010; Orr & Bowering, 1997; Vollen et al., 2004). These changes are attributed to a combination of factors, which include prey availability (Kimirei et al., 2013; Sánchez-Hernández & Cobo, 2018), predation risks (Kimirei et al., 2013; Reñones et al., 2005), habitat use (Hammar et al., 2018), morphological constraints (Sánchez-Hernández

et al., 2012), and swimming ability (Sánchez-Hernández & Cobo, 2018). Small *R. hippoglossoides* (<20 cm) have a limited mobility and relatively small mouth gape and face a high risk of predation. Thus, they typically inhabit shallower depths where they feed on smaller prey while avoiding large groundfish predators, including conspecifics (Dwyer et al., 2010; Wheeland & Morgan, 2020). As they grow in size (≥20 cm), they acquire better swimming abilities and reduced risk of predation, allowing them to reach new habitats, which are usually represented by grounds ranging from 400 to 600-m depth in the case of medium-sized *R. hippoglossoides* (Wheeland & Morgan, 2020). As results indicate, this allows them to feed on newly available prey such as small pelagic fish and shrimp, which are abundant in these environments (Bowering & Lilly, 1992; Geoffroy et al., 2016; Siferd, 2014), thus resulting in a diet shift. Many studies also observed a prevalence of large groundfish (i.e., *Sebastes* sp., *R. hippoglossoides*, *Gadus morhua*, and other Gadiforms) in the diet of specimens ≥60 cm, highlighting a second diet shift at these lengths (Bowering & Lilly, 1992; Dwyer et al., 2010; Rodriguez-Marin et al., 1995; Vollen et al., 2004; Yang & Livingston, 1988). As pointed out by Vollen et al. (2004), a fish-dominated diet for large specimens of nonspecialist fish like *R. hippoglossoides* is advantageous due to the greater energy content associated with fish compared to crustaceans.

TABLE 4 Results of the canonical correspondence analysis of Greenland halibut *Reinhardtius hippoglossoides* diet data showing χ^2 values of explanatory variables and significance levels of their effect.

Variable	χ^2	p-Values
Zone	0.6785 (10.5%)	<0.001
Length	0.5254 (8.2%)	<0.001
Year	0.1788 (2.8%)	<0.001
Depth	0.1200 (1.9%)	<0.001
Temperature	0.1117 (1.7%)	<0.001
Total inertia	6.443 (100%)	
Constrained	1.614 (25.1%)	
Unconstrained	4.828 (74.9%)	

Note: Values in parentheses represent the percentage of total inertia.

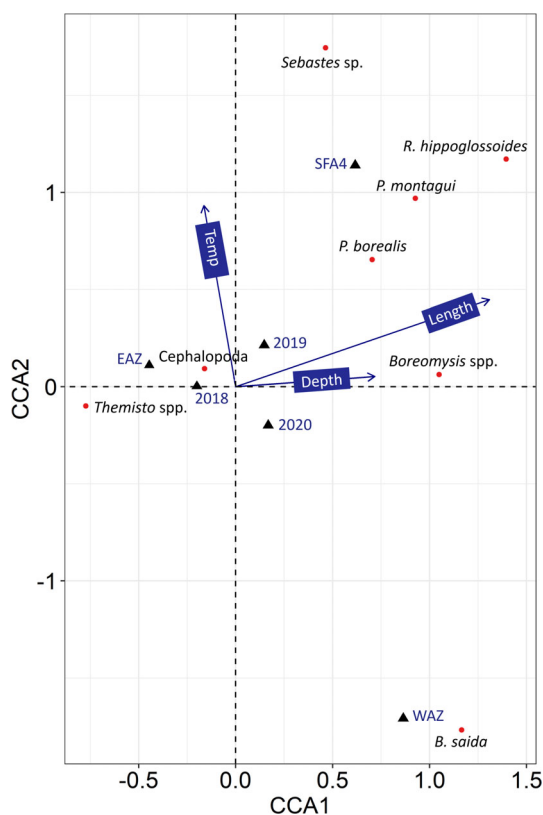


FIGURE 5 Canonical correspondence analysis ordination for diet data of Greenland halibut *Reinhardtius hippoglossoides*. Prey groups are plotted as red dots, indicating their optimal distribution in the ordination space. Continuous explanatory variables are represented by vectors (arrows), pointing toward the increase in gradient. Centroids for the categorical variable are plotted as black triangles.

Moreover, larger specimens are usually found at greater depths (≥ 800 m, Peklova et al., 2012; Wheeland & Morgan, 2020), where large groundfish are available. In this study, *R. hippoglossoides* were the main prey species for the largest (≥ 60 cm) specimens, indicating a high occurrence of cannibalism. Observations supporting an increase in cannibalism with predator size were previously made in the Flemish Pass by Rodriguez-Marin et al. (1995) and in the Davis Strait by Orr

and Bowering (1997). There is currently one documented major spawning ground that overlaps our study area, which is the Davis Strait area between West Greenland and Arctic Canada (reviewed in Bowering & Brodie, 1995). In this study, no links between the intensity of cannibalism and specimens captured near that area could be made. Spawning may also occur outside of the major spawning grounds (Albert et al., 2001; Bowering & Brodie, 1995), and although these localized spawning events produce fewer recruits, they can potentially influence the distribution of young specimens (Vihtakari et al., 2021). These spawning events could have an influence on the intensity of cannibalism for specimens in the different assessment zones. However, the lack of knowledge of potential localized spawning grounds in our study area and the small sample size for large *R. hippoglossoides* prevent us from drawing any robust conclusions on that matter.

4.2 | Spatial and temporal variations in the diet

Predatory fish are generally large-bodied organisms with great foraging capacity that require high-energy input to self-maintain and grow (Myers et al., 2019; Young et al., 2015). Therefore, they often behave as opportunistic feeders, allowing them to feed on a wide variety of prey to optimize energy acquisition. In the present study, spatial variability in diet composition reflected differences in prey availability for *R. hippoglossoides*, an opportunistic predator. *P. borealis* greatly contributed to the diet of *R. hippoglossoides* captured in the Davis Strait (EAZ) and on the northern Labrador shelf (SFA 4). Several previous studies also described it as a key prey for this predator (Bowering & Lilly, 1992; Gauthier et al., 2020; Hovde et al., 2002; Orr & Bowering, 1997; Pedersen & Riget, 1993; Vollen et al., 2004). In the Labrador Sea and Davis Strait, the influence of Atlantic currents maintains mean bottom water temperatures above 1°C during the survey period, which creates an optimal environment for *P. borealis* (Hudon, 1990). This species is mainly found in waters characterized by temperatures between 1 and 3°C and at 300–400 m depth (Siferd, 2014). Most *R. hippoglossoides* caught in the EAZ and SFA 4 were found at similar temperatures and depths (Table 2), which suggests that they shared similar habitat, making *P. borealis* a widely common and available prey.

Over a 25-year period, Dwyer et al. (2010) found a strong match between *Pandalus* spp. shrimp abundances from trawl surveys and their relative contribution to the diet of *R. hippoglossoides* in the northwest Atlantic. This relation was also apparent for *P. borealis* and *P. montagui* biomasses in the Labrador Sea. From 2018 to 2020, *P. borealis* mean fishable biomass was 5 times higher than that of *P. montagui* in the EAZ and 1.3 times higher in SFA 4 (DFO, 2021b). This trend was reflected in the *R. hippoglossoides* diet as *P. montagui* had a significantly lower contribution compared to *P. borealis* during this period. In contrast, *P. montagui* were more predominant in the diet of *R. hippoglossoides* caught in the WAZ. This phenomenon can be attributed to the segregation of the two shrimp species observed between the Labrador Sea and Hudson Strait waters (Hudon, 1990; Siferd, 2014). Arctic and subarctic waters meet at the mouth of the

Hudson Strait and spread over the Ungava Bay and western Hudson Strait. The influx of cold Arctic waters has a greater influence west of the Hudson Strait entrance (Hudon, 1990), where the WAZ is located. Therefore, it creates a more suitable environment for *P. montagui*, a species that is generally found at lower temperatures (−1 to 2°C), than *P. borealis* (DFO, 2018). These habitat preferences also match the recorded temperatures from the survey, which were lower in the WAZ compared to the EAZ and SFA 4 (Table 2). From 2018 to 2020, *P. montagui* biomass was on average 2.8 times higher than that of *P. borealis* in the WAZ, which can explain its higher contribution to the diet of *R. hippoglossoides* in this zone. Therefore, environmental conditions can influence shrimp distribution and consequently its frequency in the diet of *R. hippoglossoides*. Determining the oceanographic features associated with management units appears to be crucial as it can help explain the distribution of potential prey and the community structure on which *R. hippoglossoides* feed.

Although there is a link between the abundance of shrimp in the environment of *R. hippoglossoides* and the contribution of these prey to its diet, the predator functional response must be considered when investigating diet trends related to community structure (Dwyer et al., 2010). It implies that changes observed in predator diet composition reflect the relative changes in availability among prey groups rather than their absolute changes in abundance (Koen-Alonso, 2007). There was a stronger dominance of fish in the diet of *R. hippoglossoides* caught in the WAZ (Figure 4). In this case, the low contribution of shrimp could be attributed to the high availability of fish in the zone, which *R. hippoglossoides* could be actively targeting over shrimp, due to their presumed higher energetic content (Elliott & Gaston, 2008).

Other studies also reported the selectivity of fish prey over invertebrates in *R. hippoglossoides* feeding behavior (Pedersen & Riget, 1993; Solmundsson, 2007; Vollen et al., 2004). Vollen et al. (2004) studied specimens from the Svalbard area and found that fish caught in locations with a high presence of *P. borealis* were mainly feeding on *B. saida* and *G. morhua*. Small pelagic fish have been described to contain some of the highest energy densities as they mature at small lengths and require high lipid concentrations for buoyancy in the water column (Anthony et al., 2000; Elliott & Gaston, 2008). In Arctic waters, this is the case of *B. saida*, which was defined as one of the most energy-rich prey species in many ecosystems (Cairns, 1984; Elliott & Gaston, 2008; Harter et al., 2013; Weslawski et al., 1994). In the present study, *B. saida* was a major prey in the WAZ (Figure 4). The relatively high contribution of this prey to the diet of *R. hippoglossoides* compared with its relative abundance in the environment suggests a preference for the species in this zone. In 2017, the biomass of *B. saida* was estimated at c. 20,000 t (DFO, 2020a), compared to c. 55,000 t of fishable *Pandalus* shrimp in the same year (DFO, 2021b). Given that catches from the NSRF survey target bottom-dwelling *B. saida*, these numbers undoubtedly underestimate the total biomass in the system as this species distributes throughout the water column (Walkusz et al., 2019). Moreover, the percentage of empty stomachs in the WAZ was low (Table 1), indicating high feeding intensity (Vollen et al., 2004), likely attributable to the presence of highly abundant, attractive prey in the zone such

as the high-energy content *B. saida*. Results support those from a growing body of literature that documented the predominance of *B. saida* in the diet of *R. hippoglossoides* in cold-water areas such as Hudson Strait (Astthorsson, 2012; Logerwell et al., 2011; Majewski et al., 2016). Moreover, several studies confirmed the high importance of the contribution of pelagic sources to the diet of *R. hippoglossoides* (Dennard et al., 2009; Giraldo et al., 2018; Solmundsson, 2007; Vollen & Albert, 2008). Thus, the pelagic portion of the *B. saida* population, for which the biomass remains unknown, could represent a major source of energy for *R. hippoglossoides* in the WAZ.

Results indicated a relatively low interannual variability in the diet of *R. hippoglossoides*. However, due to the sampling issues of the 2020 campaign, interannual comparisons with that year have to be made very carefully. Therefore, the effect of the sampling year on the diet of larger specimens cannot be studied. Nevertheless, interesting results were obtained at other size classes. As there was nearly no *Sebastes* sp. in the diet in 2018 and 2019, it became the main prey for the 30–39.9 cm fish in 2020, particularly in SFA 4 (Figure 4). *Sebastes* sp. has often been documented as a major prey for *R. hippoglossoides* in other areas (Bowering & Lilly, 1992; Chumakov & Podrazhanskaya, 1986; Gauthier et al., 2020; Pedersen & Riget, 1993; Vollen & Albert, 2008). Some of these studies noted the presence of larger specimens of *Sebastes* sp. (>20 cm) in the diet of large *R. hippoglossoides* (>60 cm) feeding at great depths (>500 m) (Chumakov & Podrazhanskaya, 1986; Gauthier et al., 2020; Vollen & Albert, 2008). In the present study, *Sebastes* sp. ingested by *R. hippoglossoides* were small specimens. They were found in stomachs of fish caught at relatively shallow depths, and no *R. hippoglossoides* larger than 48.5 cm were caught in 2020, which could partly explain the lack of bigger *Sebastes* sp. specimens in the diet. In 2020, DFO surveys and fishing vessels operating on the Labrador shelf reported a very high abundance of small *Sebastes* sp. in the zone, which could be an indicator of a recent strong recruitment event, similar to that recently observed in the Gulf of St. Lawrence (Burns et al., 2020; DFO, 2022b). The size of *Sebastes* sp. ingested by *R. hippoglossoides* could correspond to fish aged >1 year (Saborido-Rey et al., 2004; Senay et al., 2021), and the narrow length range suggests that they were from the same cohort, presumably that of 2019. The incorporation of this newly available prey into the diet of *R. hippoglossoides* suggests opportunistic feeding and the potential to use *R. hippoglossoides* diet as an ecosystem indicator. As pointed by Dwyer et al. (2010), the consideration of *R. hippoglossoides* diet, in conjunction with other indices, could complement information obtained from research surveys to facilitate the implementation of an ecosystem approach to resource assessment and management.

4.3 | Greenland halibut trophic ecology in a changing environment

Results showed that *Pandalus* spp. shrimp were important prey in the diet. However, they were not selected by *R. hippoglossoides* over other potential prey. Ocean warming can reduce thermal habitat for shrimp and alter the phenological match between egg hatching and the spring

phytoplankton bloom, which makes these species very sensitive to climate-associated changes (Greene et al., 2009; Koeller et al., 2009). In the northwest Atlantic, these changes were seen in the community structure by the mid-late 2000s, as fish functional groups began to show increases in biomass and crustaceans started to decline (DFO, 2014). Recently, Leung et al. (2023) found that *P. borealis* lacked genetic variation, explaining thermal plasticity. Their results suggest a limited potential of this species for evolutionary thermal plasticity, increasing its vulnerability to future global changes. Thus, the contribution of Pandalid shrimp to the diet of *R. hippoglossoides*, and especially *P. borealis*, could decrease in the future, as water temperatures increases in the Arctic and environmental conditions become less favorable for these species (Le Corre et al., 2021; Ouellet et al., 2017).

Recently, there has been a significant warming trend in Arctic marine ecosystems, including the Labrador Sea (DFO, 2020c). Although these altered environmental conditions are expected to be detrimental to shrimp, they could still be suitable habitats for groundfish, including *R. hippoglossoides*. Previous studies showed that *R. hippoglossoides* can migrate in relation to water temperature (Morgan et al., 2013; Wheeland & Morgan, 2020), which could give them the ability to better adapt to changing ecosystem conditions. In the Gulf of St. Lawrence, however, *P. borealis* and *R. hippoglossoides* stocks show a parallel decrease likely due to the warming and oxygen depletion in the bottom layer (DFO, 2021d). Despite the fact that deep waters of the Labrador Sea, Hudson Strait, and Davis Strait are still colder than those of the Gulf of St. Lawrence (Galbraith et al., 2022), the decrease in these two stocks in this region can provide us an insight into future Arctic conditions. Additionally, in the Gulf of St. Lawrence, warming conditions have favored *Sebastes* sp. recruitment, with the production of multiple strong cohorts in the last decade, which substantially increased predation on *P. borealis* (DFO, 2022a). Recent reports of small *Sebastes* sp. in the Labrador Sea suggest a similar strong recruitment event. This deep-water fish has a diverse diet, but larger individuals (≥ 30 cm) have also been described as a major shrimp predator (Brown-Vuillemin et al., 2022, 2023). Thus, the biomass increase in this species could be of great concern for Arctic shrimp stocks in the near future, especially if larger individuals become abundant. Along with the *Sebastes* sp. abundance growing, competition for resources can have a considerable impact on *R. hippoglossoides* stock productivity (DFO, 2020b; Senay et al., 2021). Overall, the resurgence of *Sebastes* sp. in the studied area coupled with unfavorable environmental conditions could be contributing to a potential decline in the *P. borealis* and *R. hippoglossoides* resources in the future, as currently observed in the Gulf of St. Lawrence.

R. hippoglossoides diet was significantly influenced by zone, temperature, depth, year, and predator length. Although a large proportion of the variance in diet composition remained unexplained, the most important variables affecting diet composition were location and predator size. The diet of *R. hippoglossoides* differed among zones, potentially driven by differences in community structure and prey availability mediated by local oceanographic conditions. In zones with

high abundance of fish species such as *B. saida* and *Sebastes* sp., selection toward these high-energy prey was observed. Pursuing the ongoing monitoring of the energetic content of *R. hippoglossoides* in relation to their diet would be helpful to predict future stock conditions in response to the changing environment.

AUTHOR CONTRIBUTIONS

Félix Tremblay-Gagnon, David Deslauriers, Dominique Robert, and Wojciech Walkusz conceived the project objectives and methodology. Hannah Polaczek and Félix Tremblay-Gagnon performed analysis of stomach contents. Félix Tremblay-Gagnon conducted data analyses and wrote the first draft of the manuscript. All authors have contributed to the revision and improvements of the manuscript and take responsibility for its content.

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SUPPORTING INFORMATION

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