Diet composition of redfish (*Sebastes* sp.) during periods of population collapse and massive resurgence in the Gulf of St. Lawrence

Sarah Brown-Vuillemin[1]*, Denis Chabot[2], Claude Nozères[2], Réjean Tremblay[1], Pascal Sirois[3] and Dominique Robert[1]

[1]Institut des Sciences de la Mer, Université du Québec à Rimouski, Rimouski, QC, Canada,
[2]Institut Maurice-Lamontagne, Pêches et Océans Canada, Mont-Joli, QC, Canada,
[3]Département des sciences fondamentales, Université du Québec à Chicoutimi, Chicoutimi, QC, Canada

Redfish (*Sebastes mentella* and *S. fasciatus*) are back at spectacular record high levels in the Gulf of St. Lawrence (GSL) and the effects of this massive resurgence on other components of the food web remain largely unknown. To better understand the trophic implications of the surging redfish biomass within the GSL ecosystem, 3,690 stomachs containing food were collected during two periods: one characterised by low redfish abundance (1993–1999) and the other during a period of record abundance (2015–2019). Taxonomical analysis of stomach contents from individuals of different sizes from three subareas of the GSL was carried out to determine diet composition during both periods. Zooplankton represented the main prey category for small redfish (< 20 cm), which was driven by a predation on amphipods, mostly *Themisto* sp. in North-East Gulf, in the 1990s and on copepods of the genus *Calanus* in the deep channels and euphausiids in North-West Gulf in the 2010s. *Themisto* sp. still dominated the diet of medium (20–30 cm) redfish in the 1990s while the copepods were predominant during the 2010s. Shrimp consumption increased with redfish size and two species were particularly important in large redfish diet (≥ 30 cm) during both periods: pink glass shrimp (*Pasiphaea multidentata*), mostly in the Laurentian Channel and northern shrimp (*Pandalus borealis*), especially in North-East Gulf. Redfish predation on shrimp represents a major concern for the dynamics of the northern shrimp which supports a valuable fishery in the GSL but has been declining in abundance since several years. Piscivory was observed in large redfish diet, with capelin (*Mallotus villosus*)

being the major fish prey in the 1990s and redfish (cannibalism) in the 2010s, suggesting density-dependent control at high density of small redfish. By presenting a detailed overview into the redfish diet composition and its temporal variability, the present study offers a first look into the possible future trophic impacts of a resurging groundfish in the GSL ecosystem.

1 Introduction

Knowledge of feeding ecology and prey-predator interactions is essential to appraise the respective roles of the mosaic of species that compose ecological communities (Arditi and Ginzburg, 2012). Information on trophic linkages, which have often been recognized as being ecosystem-specific, is essential for the robust implementation of ecosystem-based management strategies (Hanson and Chouinard, 2002; Crowder and Norse, 2008; Glaser et al., 2015). Stomach content analysis is a well-established method for the detailed assessment of individual diet composition. At the population level, stomach content data enable the determination of the contribution of the different prey species to the diet and how diet composition varies according to factors such as abundance, ontogeny or predator size (e.g., Hyslop, 1980; Baker et al., 2014; Amundsen and Sánchez-Hernández, 2019; Sánchez-Hernández et al., 2019). Stomach content data are particularly relevant to assess fish trophodynamics because fish generally swallow their prey whole, allowing for robust inferences on biological traits such as feeding mode, as well as ecological characteristics such as habitat preference (Braga et al., 2012; Amundsen and Sánchez-Hernández, 2019). Annual fishery-independent surveys offer the opportunity to collect stomachs from a wide size range and over the large part distribution of a species population. Moreover, long time series of stomach content data collected during yearly surveys can reveal major trophic changes in the ecosystem over time (e.g., Fahrig et al., 1993; Hanson and Chouinard, 2002; Dwyer et al., 2010).

Over the past three decades, the Gulf of St. Lawrence (GSL, Canada) ecosystem has undergone profound changes in species composition. In the early 1990s, several groundfish species, such as Atlantic cod (*Gadus morhua* Linnaeus 1758), American plaice (*Hippoglossoides platessoides* Fabricius 1780) and redfish (*Sebastes* sp. Cuvier 1829), collapsed as a result of overfishing during a period of low productivity and recruitment associated with exceptionally cold water temperatures (Murawski, 1997; Brêthes, 1998; Gascon, 2003), resulting in the implementation of fishing moratoria. Meanwhile, the abundance of boreal species

such as northern shrimp (*Pandalus borealis* Krøyer 1838), snow crab (*Chionoecetes opilio* Fabricius 1788) and Greenland halibut (*Reinhardtius hippoglossoides* Walbaum 1792) increased to record high levels driven by cooling waters and reduced competition and predation pressure (Brêthes, 1998; Savenkoff et al., 2006). After a relative stability over two decades, the deep waters of the GSL warmed during the 2010s, resulting in a decline of dominant cold water species and the concurrent, unprecedented recruitment of the redfish, spelling a massive return of this fish in the GSL (Bourdages et al., 2017; Brassard et al., 2017; Galbraith et al., 2019). In the GSL, two sympatric redfish species coexist: the Acadian redfish *Sebastes fasciatus* (Storer 1854) and the deepwater redfish *Sebastes mentella* (Travin 1951) (Senay et al., 2019). These species are morphologically similar, which makes species identification difficult and nearly impossible by cursory examination (e.g., Gascon, 2003; Cadrin et al., 2010). As a result, *S. mentella* and *S. fasciatus* from the GSL have traditionally been managed as a single stock and have not been identified to species in historical databases. In the present study, the two species have thus not been discriminated and are both comprised under the name 'redfish'.

In recent years, the annual research bottom trawl survey of the estuary and northern GSL, carried out by the Department of Fisheries and Oceans (DFO, Canada), revealed that redfish had become by far the most common taxon in the captures, accounting for 90% of the total biomass caught in 2019, compared to 15% in 1995–2012 (Senay et al., 2021). This represented a 72% redfish biomass increase from the 2017 estimate. The most recent redfish assessment report estimated an average minimum trawlable biomass of 113 kt in 1993–1999 and 2,423 kt in 2015–2019 (Senay et al., 2021). In 2019, total minimum trawlable biomass was estimated to be 4,365 kt, the highest value ever observed in the time series since 1984 (Senay et al., 2021). Redfish exploitation is still under moratorium, but this unprecedented increase in abundance, supported by the 2011–2013 cohorts, is expected leading to a rapid increase of spawning biomass, which will support a commercial fishery in the coming years. This increase in biomass also represents a

major concern for the dynamics of forage species, including the northern shrimp, which supports a major fishery in the GSL (DFO, 2020). The growing redfish cohorts could exacerbate the ongoing regime shift within the GSL, but their potential impact on other components of the food web remains largely speculative as knowledge of redfish trophic ecology is scarce.

The objective of this study is to describe and quantify the GSL redfish diet composition over two time periods of contrasting population dynamics (the 1990s, collapse and the 2010s, resurgence) to provide an overall assessment of the potential changes and discuss possible implications of redfish predation within the GSL food web. For the entire 1990–2019 period, redfish were caught relying on the same methodology through an annual Research Vessel (RV) bottom trawl survey (Bourdages et al., 2007; Senay et al., 2019). Redfish stomachs were collected during two periods, 1993 to 1999 and 2015 to 2019, thus offering a unique opportunity to evaluate redfish feeding and assess decadal changes in feeding habits and prey preferences. Considering the shifting oceanographic and ecological characteristics of the GSL from a cold-water ecosystem during the 1990s to a warmer water ecosystem in the 2010s, combined with the contrast in redfish abundance between these two periods, marked decadal differences are expected in the redfish diet composition. By offering a unique glimpse into the temporal variability that exists in the diet composition of a dominant groundfish resource through ontogeny and across subareas of the GSL, the present study also provides insight into the implication of the surging redfish predation pressure on the northern shrimp.

2 Materials and methods

2.1 Study area and trawl survey

The GSL is a stratified, semi-enclosed sea connected to the North Atlantic Ocean through the Cabot Strait to the southeast and the Strait of Belle-Isle to the northeast. Redfish were captured during annual summer trawl research surveys conducted by DFO using a stratified-random survey design covering the estuary and northern GSL (Figure 1). From 1990 to 2005, the survey was conducted onboard the Canadian Coast Guard Ship (CCGS) *Alfred Needler* using a URI trawl with a 19-mm liner in the cod-end (24-min tows). Since 2004, the survey has been conducted with the CCGS *Teleost* equipped with a Campelen 1800 trawl with a 13-mm liner (15-min tows). Based on comparative fishing experiments held in 2004 and 2005, data for most species, including redfish, were corrected for differences in catchability between the two periods. Details of bottom trawl surveys, sampling, protocol and conversion factors between the two trawl types can be found in Bourdages et al. (2007).

2.2 Redfish stomach collection

The annual surveys were similar among years, taking place from August into early September, thus avoiding seasonal effects in the estimation of redfish abundance and their diet in each of the two time periods. At each haul (exceptions were 2015, when redfish stomachs were sampled only on hauls with even numbers, and in 2016, when they were sampled only on hauls with odd numbers), the biomass of redfish captured by the trawl was estimated. A sub-sample of redfish was measured (fork length, FL, in cm in the 1990s, in mm converted to cm in the 2010s) and weighed (g). This sub-sample also allowed the estimation of the number of fish of each 1 cm length class in the catch. From these, a length-stratified sub-sample was chosen for stomach collection and redfish that showed obvious signs of regurgitation were rejected, a common consequence of barotrauma for these fish, or feeding within the trawl. Smaller specimens (FL < 15 cm) were collected whole to optimize sample collection at sea, while the stomachs of larger specimens, quicker to dissect, were excised at sea. Each sample was placed in a plastic bag with an identification label and kept frozen (-40°C) until examination.

2.3 Stomach analysis and taxonomic identification

In the laboratory, each stomach was opened to remove and weigh its content. All prey present in the stomach were sorted, weighted, and identified to the most precise taxonomic level possible with a binocular microscope and using keys, identification guides (e.g., Squires, 1990; Campana, 2004; Vassilenko and Petryashov, 2009; ICES, 2014) and the help of specialists. A number of different personnel carried out the analyses over the years but always followed the same protocol in recognizing common GSL fish and invertebrate species. It was however noted that less effort was dedicated in the 1990s than in the 2010s at identifying heavily digested prey. Stomachs from the 1990s were usually analysed within a few years of capture whereas those from the 2010s were analysed within a few months of capture. Frozen samples dating from 1997 to 1999 were still available to be analysed in 2019 to increase sample size of the 1990s and assess the impact of methodology (difference in effort for taxonomical resolution of very digested prey) on the results (Supplementary Figure 1).

2.4 Redfish barotrauma

Redfish are physoclist fish that have a closed swim bladder and therefore cannot adapt to rapid changes in depth. As a result, redfish are extremely sensitive to barotrauma when

FIGURE 1
Map of the study area showing sampling hauls (1993–1999; *n* = 450 and 2015–2019; *n* = 447) where redfish stomachs containing prey were sampled (*n* = 3,690) from each period (1993–1999; *n* = 1,366 and 2015–2019; *n* = 2,324). The grey line indicates the 250 meters isobath. The three subareas considered for the analysis are delimited by the dotted lines with North-West Gulf (NWG), Laurentian Channel (LC) and North-East Gulf (NEG).

caught in deep water and brought to the surface rapidly (Jarvis and Lowe, 2008). Although redfish showing signs of regurgitation (food in their mouth or evaginated stomach) were discarded during sea sampling, decompression likely resulted in partial or total regurgitation in several sampled fish. Thus, the proportion of empty stomachs, a common measure of feeding intensity, was deemed unreliable for redfish. For this reason, empty stomachs were excluded from the analyses. Furthermore, it was necessary to assume that the probability of regurgitation was similar for all taxa when assessing the importance of different prey taxa or categories in redfish diet, a reasonable assumption considering the barotraumatic cause of regurgitation.

2.5 Size classes and spatial analysis

For both periods, redfish diet composition was analysed as a function of redfish size using 5 cm size classes, a uniform cut-off to visualize general trends as follows: < 10.0 cm, 10.0–14.9 cm, 15.0–19.9 cm, 20.0–24.9 cm, 25.0–29.9 cm, 30.0–34.9 cm, 35.0–39.9 cm and ≥ 40.0 cm. Since the GSL is physically and topographically heterogeneous (Koutitonsky and Bugden, 1991; Therriault, 1991; Rodrigues et al., 1993; Galbraith et al., 2019), three distinct subareas were distinguished and compared in this study: (1) the deepest part of the Laurentian Channel (LC) which extends from Cabot Strait to the centre of the Gulf and can reach a maximum water depth of about 550 m, (2) the North-East Gulf (NEG) including the Esquiman (maximum depth of about 285 m) and Anticosti (maximum depth of about 335 m) Channels and (3) and the North-West Gulf (NWG) comprising the estuary and the western part of the Laurentian Channel (maximum depth about 300 m) (Figure 1). In order to describe redfish diet during both periods in each subarea within the GSL and maintain sufficient sample sizes, it was necessary to regroup the 5-cm size classes into three major size classes (small < 20, medium 20–30 and large redfish ≥ 30 cm) (Table 1).

TABLE 1 Number of redfish stomachs analysed, percentage of empty stomachs, number of non-empty stomachs, total number in the catch and percent of stomachs of redfish caught in the GSL during annual DFO trawl research surveys according to subareas and three size classes for the periods 1993–1999 and 2015–2019.

| | | | Stomachs containing prey | | | | | | | | | | | | |
| | | | Total GSL | | | | NWG | | | LC | | | NEG | | |
	Stomachs analysed	% Empty stomach	All size classes	< 20	20—30	≥ 30	< 20	20—30	≥ 30	< 20	20—30	≥ 30	< 20	20—30	≥ 30
1993	886	63	332	101	57	174	17	8	11	47	30	70	37	19	93
1994	461	64	167	54	16	97	23	3	11	29	12	49	2	1	37
1995	258	59	106	24	9	73	13	4	3	9	4	38	2	1	32
1996	323	29	230	78	36	116	17	4	1	56	31	85	5	1	30
1997	357	80	70	27	8	35	11	2	1	13	5	21	3	1	13
1998	348	47	183	66	22	95	3	0	1	36	18	78	27	4	16
1999	496	44	278	108	27	143	10	2	1	35	21	98	63	4	44
1993—1999	**3129**	**56**	**1366**	**458**	**175**	**733**	**94**	**23**	**29**	**225**	**121**	**439**	**139**	**31**	**265**
Total number caught			*68486*	*29195*	*16989*	*22303*	*1309*	*687*	*1790*	*22546*	*15022*	*13410*	*5340*	*1280*	*7103*
Proportion of stomachs/catches (%)			*1.99*	*1.57*	*1.03*	*3.29*	*7.18*	*3.35*	*1.62*	*1.00*	*0.81*	*3.27*	*1.76*	*1.80*	*0.41*
2015	1003	33	675	403	60	212	105	12	7	131	18	137	167	30	68
2016	579	41	342	217	58	67	54	12	7	79	19	43	84	27	17
2017	564	38	347	172	99	76	41	34	7	71	41	50	60	24	19
2018	974	48	511	215	191	105	45	49	1	79	75	74	91	67	30
2019	709	37	449	153	224	72	71	29	6	40	93	42	42	102	24
2015—2019	**3829**	**39**	**2324**	**1160**	**632**	**532**	**316**	**136**	**28**	**400**	**246**	**346**	**444**	**250**	**158**
Total number caught			*4187545*	*2235518*	*1941125*	*10902*	*322656*	*91811*	*205*	*1063270*	*599946*	*7411*	*849591*	*1249368*	*3286*
Proportion of stomachs/catches (%)			*0.06*	*0.05*	*0.03*	*4.88*	*0.10*	*0.15*	*13.66*	*0.04*	*0.04*	*4.67*	*0.04*	*0.01*	*0.85*
TOTAL	**6958**	**47**	**3690**	**1618**	**807**	**1265**	**410**	**159**	**57**	**625**	**367**	**785**	**583**	**281**	**423**

Bold indicates total.

2.6 Diet analysis

Developing reliable indices of diet composition over different time periods based on stomach content analysis requires the consideration of several key issues. While stomach contents reveal information about one or a few recent meals when a fish was sampled, it is only a snapshot of an individual's feeding habits, which needs to be considered when deriving indices that are representative of the predator's diet. Stomach content data can be used to derive several types of diet indicators (Hyslop, 1980). Basic indicators include methods based on prey numbers, prey mass or volume, and frequency of occurrence. Composite indices (e.g., Index of Relative Importance, IRI) have also been developed to integrate two or more of the basic indicators. In a modelling experiment, Ahlbeck et al. (2012) clearly demonstrated that basic indicators based on prey mass or volume provide the best estimates of diet for a wide array of feeding strategies, while composite indices were less robust. Further, the basic currency to describe the contribution of different prey to the diet of a predator is energy, which is directly related to mass and energy density of prey.

In the present study, three measures were used to describe the redfish diet. First, the partial stomach fullness index (PFI)

(Lilly and Fleming, 1981; Orr and Bowering, 1997) was calculated for each prey taxa in the redfish stomach according to the equation:

$$PFI_{ij} = M_{ij} \times L_j^{-b} \times 10^4 \tag{1}$$

where M_{ij} is the mass of prey i in redfish j, L_j is the FL (cm) of redfish j and b is the specific allometric exponent calculated for redfish (b = 3.19), corresponding to the slope of the linear relationship of log(mass) and log(FL) of redfish collected for this study during the 1993–1999 and 2015–2019 surveys (n = 6958; r^2 = 0.99, P < 0.001). The PFI adjusts the amount of each prey taxon found in a stomach for the effect of predator size. The mean PFI of prey i in the sample (period, size class and/or subarea) was then obtained as follows:

$$PFI_i = \frac{1}{N} \times \sum_{j=1}^{N} PFI_{ij} \tag{2}$$

where N is the number of redfish in the sample. Second, in order to assess the proportion of the contribution of prey in the diet of redfish, PFI_i was transformed into a percentage (%FI_i, percentage fullness index, Bernier and Chabot, 2012) and calculated as:

$$\%FI_i = \frac{PFI_i}{TFI} \times 100 \qquad (3)$$

where total stomach fullness index (TFI_j) was the sum of all PFI_i for a fish j.

TFI was calculated as:

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

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

where I represents the number of different prey taxa found in the sample. Third, to qualitatively indicate whether a small or large proportion of redfish fed on a given prey, the percentage of occurrence (%O) of prey i was also calculated (Hyslop, 1980) as follows:

$$\%O = \frac{N_i}{N} \times 100 \qquad (6)$$

where N_i is the number of stomachs in the sample containing prey i.

To gain further insight on the importance of each prey category in the diet of redfish, we used Amundsen diagrams, a modification of Costello's graphical method (Costello, 1990; Amundsen et al., 1996) which is a two-dimensional representation of prey-specific abundance in stomach fullness index ($\%FI_{spe}$) and percentage of occurrence (%O). Prey-specific abundance is defined as the percentage of a specific prey over all prey items, but only for those predators in which that prey occurs. Thus, prey-specific abundance in stomach fullness index for prey category i, $\%FI_{spe\_i}$, was obtained exactly as $\%FI_i$ (Eq. 3), but instead of using all N stomachs in a sample, using only the K stomachs containing prey category i:

$$\%FI_{spe\_i} = \frac{PFI_{spe\_i}}{TFI_{spe\_i}} \times 100 \qquad (7)$$

where PFI_{spe_i} is the average fullness index for prey i for the stomachs containing prey i, and TFI_{spe_i} is the average total fullness index for the stomachs containing prey i. Prey categories scoring 25–50% in prey-specific abundance and ≥ 25%O were considered important, those with ≥ 50% in prey-specific abundance and 25–50%O were very important, and prey categories with ≥ 50% on both axes were considered dominant. Prey with high prey-specific abundance (≥ 50%) and just short of 25%O were considered « noteworthy ».

2.7 Diet data weighting

A particular consideration must be made with samples collected in RV surveys such as those considered in the present study. Typically, research survey protocols request a fixed number of stomachs to be taken in each haul where the predator is present, usually stratified in a number of predator size classes. As long as there are enough fish of the target species to fill the stratification, the number of stomachs becomes independent of the number of fish in the catch. In the present study, the number of non-empty stomachs sampled per haul ranged between 1 and 44. However, the abundance of redfish varied widely among hauls, in particular during the recent period of population recovery where total estimated numbers caught varied between 1 and 250,047 (1 and 10,745 for the 1990s). The subsampling design, combined to the difference of up to 5 orders of magnitude in redfish abundance among hauls, implies the risk of widely overrepresenting the diet of fish captured in subareas of relatively low abundance relative to those from the heart of the distribution. To account for this issue, we followed the recommendations of Chipps and Garvey (2006) and weighted the stratified diet data by the relative proportion of individuals actually caught within each size class at a given haul. Capture data and the subsample of redfish measured in each haul were used to estimate the number of redfish of each 1-cm length class in the catch. Mass of each stomach of length class 1 was then estimated according to the number of fish of length class 1 in the catch divided by the number of stomachs of that same class. Only weighted results are shown. Description of the prey taxon contributions to diet, before weighting for abundance in the catches, is provided in Supplementary Table 1 for the two periods.

2.8 Statistical analysis

Cumulative prey curves (Ferry and Cailliet, 1996) were calculated to assess whether the number of redfish samples was sufficient to describe the diet. Prey curves were generated after 100 randomizations of the original data (%FI) calculated according to the number of prey categories considered in further analyses. The slope of the linear regression (b) through the last five subsamples validated the sample size, where $b \leq 0.05$ signified acceptable levelling off of the prey curve for diet analyses (Brown et al., 2012).

Differences in percentage fullness index (%FI) between (1) the two periods according to redfish size (< 20, 20–30 and ≥ 30 cm) and (2) among sizes classes over periods and GSL subareas (NWG, LC and NEG) were investigated. A nonparametric distanced-based permutation multivariate analysis of variance was conducted on the Bray-Curtis distance matrix (PERMANOVA, Anderson, 2014), calculated on average stomach contents per haul expressed as %FI: stomachs from the same major size class were averaged for each haul because they cannot be considered independent. Following significant test results (PERMANOVA), *post hoc* tests using pairwise multiple comparisons were used to identify differences between means. Similarity percentage analysis (SIMPER, Clarke, 1993) was used

to identify the prey explaining most of the dissimilarities between factors. All analyses were performed with the software R version 4.0.1 (R Core Team, 2020) using packages 'vegan' (Oksanen et al., 2019), 'plyr' (Wickham, 2011), 'ggplot2' (Wickham, 2016) and 'ggpubr' (Kassambara, 2020).

3 Results

3.1 Stomach dataset overview

A total of 6,958 stomachs were collected throughout the GSL and examined, of which 3,690 contained prey (47% of empty stomach), from a total of 897 hauls, with 1,366 and 2,324 stomachs for 1993–1999 and 2015–2019, respectively (Figure 1, Table 1). In 2015–2019, the number of redfish in the catch was 61 times higher, for the entire GSL, than during 1993–1999, and captures of small and medium redfish (< 20 and 20–30 cm) were 77 and 114 times higher, respectively, in the recent period, reflecting the strong recruitment of the 2011–2013 cohorts. The total number of large individuals ≥ 30 cm captured was approximately equal during both periods and a similar sampling intensity was obtained (3.29 and 4.88% of captured fish were sampled). Sampling intensity was similar (1.57 and 1.03% of captured fish) for small and mid-size fish in the 1990s. Despite a larger number of stomachs collected for these same size classes in the 2010s, sampling intensity was much less (0.05 and 0.03% of captured fish) due to the surging abundance of small and mid-sized individuals in recent years relative to the 1990s (Table 1). Even if the proportion of individuals sampled for stomach contents was small for some groups, most cumulative prey curves calculated for both periods according to three major size classes and subareas reached a stable asymptote, indicating sufficient sample sizes for an accurate description of the redfish diet (Supplementary Figures 2, 3). The only exceptions where an asymptote was not reached was for large redfish (≥ 30 cm) in NWG for both periods, as well as for mid-sized redfish (20–30 cm) in NEG in the 1990s (Supplementary Figure 3).

The range of redfish sizes for stomach collection was 7–50 cm in both periods (Figure 2), median (25th and 75th percentiles) FL was 31 (17 and 37) cm in the 1990s and 20 (16 and 28) cm in the 2010s. Size classes with largest sample sizes for stomachs were 35–38 and 17–20 cm in the 1990s and 2010s, respectively. For both periods, the NWG was characterised by a scarcity of large individuals sampled compared to other subareas, both in the number of stomachs and in the catch (Figure 2, Table 1). Most of redfish samples were collected from the deep channels (Laurentian, Esquiman and Anticosti, Figure 1, Table 1) of the GSL. In the 1990s, median depth (25th and 75th percentiles) where the stomachs with prey were obtained was 299 (255 and 315) m, 318 (256 and 382) m and 271 (248 and 288) m for the NWG, LC and NEG, respectively, and in the 2010s,

median depth was 250 (181 and 316) m, 329 (245 and 391) m and 228 (177 and 276) m, for the three subareas, respectively.

3.2 Taxonomic considerations

To provide and facilitate the description of the redfish diet for both periods, prey items were assigned to one of eight broad taxonomic categories under the common denomination: Fish, Shrimp, Amphipod, Copepod, Mysid, Euphausiid, Other Invertebrates and Unidentified Material. The TFI (sum of all PFIs) and the three measures for the assessment of prey contribution to redfish diet (PFI, %FI and %O) based on the entire stomach dataset for each period are presented in Table 2 and showed the eight broad dietary categories and each of the 58 and 93 different prey items found in stomachs collected in 1993–1999 and 2015–2019, respectively.

As far as possible, prey that showed important signs of digestion, but which were identifiable by distinguishing features (e.g., telson for shrimp) were assigned to one of the eight categories with the name "digested". The category Other Invertebrates was comprised mostly of remains of crustaceans, along with traces of identified groups from several classes of invertebrates that were rarely encountered in redfish stomach. Overall, only a few of the prey types identified at the genus or species level had important dietary contributions and were consumed regularly during both periods (taxon identified by an asterisk, Table 2). Capelin and redfish were the most frequent fish, while shrimp were most often represented by northern shrimp *P. borealis* and pink glass shrimp *P. multidentata*. Among amphipods, the greatest contributions were from unspecified *Themisto* sp. along with *T. abyssorum*, *T. compressa* and *T. libellula*. Of the copepods, unspecified *Calanus* sp. and *C. hyperboreus* were most important, while among euphausiids, the northern krill, *Meganyctiphanes norvegica*, was the main contributor. Another major zooplankter was the deepwater mysids of genus *Boreomysis*, though these were not significant enough to be major prey. These important taxa were retained in the following analyses, except that all four *Themisto* taxa were grouped into *Themisto* sp. since the three identified species contributed similarly to the diet. Other prey taxa were grouped together according to broad taxonomic categories, resulting in fifteen prey groups of interest (see Figure 3).

Prey that could not be identified to a chosen taxonomic group were classified in the category Unidentified Material. Compared to the 2010s, the 1990s were characterised by a higher contribution and occurrence of Unidentified Material (the 1990s: %FI = 18.99, %O = 18.38; the 2010s: %FI = 1.93, %O = 11.17, Table 2). Some stomachs from the 1990s were analysed in 2019, allowing the assessment of the impact of protocol adjustments and differences in taxonomic expertise between the two periods. For example, the stomachs from the 1990s that were examined in 2019 had virtually no Unidentified Material, in contrast to the other stomachs from
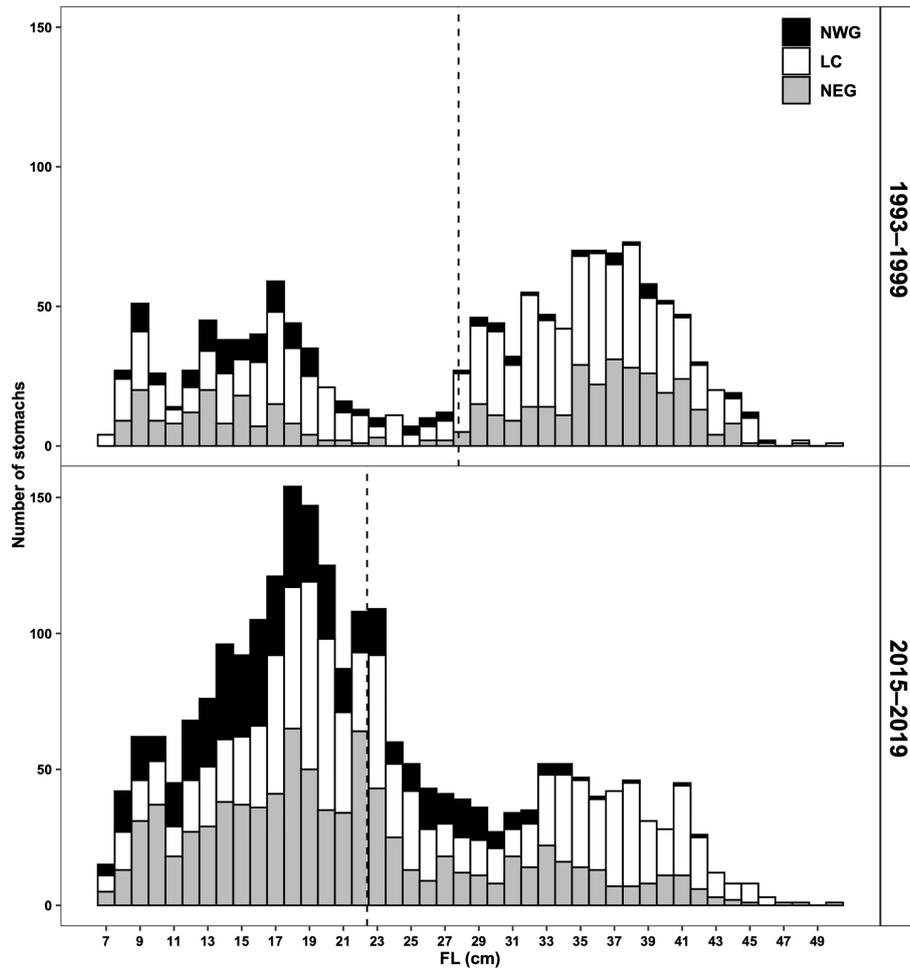
FIGURE 2
Size frequency distribution of redfish with stomachs containing prey collected in the GSL during 1993–1999 and 2015–2019 according to each defined subarea. Dashed lines represent the FL mean value for each period.

the 1990s that had been examined during that period (Supplementary Figure 1). Removal of the category Unidentified Material reveals similar trends in diet of the 1990s, regardless of when the stomachs were analysed, with two exceptions: amphipods and shrimp. For amphipods, the category Other Amphipods was more abundant in the stomachs from the 1990s analysed in the 1990s, whereas those examined in 2019 contained more *Themisto* sp. taxa. However, for the entire dataset, all identifiable Amphipod taxa were present as traces only, except *Themisto* taxa. Therefore, a major part of Other Amphipods in stomachs analysed in the 1990s were likely *Themisto* sp. and the trends for Amphipods very similar for stomachs from the 1990s regardless of when the stomachs were analyzed. For Shrimp prey, stomachs from the 1990s examined in 2019 did show more *P. multidentata* and less *P. borealis* than stomachs analysed in the 1990s. This switch in shrimp species likely represents interannual differences in diet, as most stomachs examined in the 1990s were collected in 1997 or before, and all

stomachs from the 1990s analysed in 2019 were collected in 1997 and after. Both subsets of stomachs from the 1990s were considered comparable and combined for further analysis, and the category Unidentified Material was removed from the data for both the 1990s and 2010s, because differences in the importance of this group appeared to be caused by methodological differences (Supplementary Figure 1). This adjustment slightly reduced sample size by 111 for the 1990s and 35 for the 2010s (mainly for small individuals < 20 cm; $n = 64$ and $n = 20$, for both periods respectively) (Supplementary Table 2).

3.3 Effect of redfish size on diet composition

For both periods, zooplankton dominated the diet of the smallest redfish. With increasing predator size, their importance

TABLE 2 Diet composition of GSL redfish expressed in partial stomach fullness index (PFI), percentage fullness index (%FI) and percentage of occurrence (%O) according to period.

		PFI		%FI		%O	
	Periods	1993–1999	2015–2019	1993–1999	2015–2019	1993–1999	2015–2019
	n	1366	2324				
Prey	TFI	0.422	0.095				
FISH		0.033	0.002	7.804	2.322	6.257	0.548
	Fish eggs	T	T	T	0.002	0.005	0.001
	Digested Fish	0.025	T	5.980	0.233	5.399	0.327
Anguilliformes	*Nemichthys scolopaceus*	-	T	-	0.005	-	0.000
Aulopiformes	*Arctozenus risso*	T	T	0.022	0.043	0.021	0.004
	Paralepis sp.	T	-	0.008	-	0.009	-
Clupeiformes	*Clupea harengus*	-	T	-	T	-	0.002
Gadiformes	*Nezumia bairdii*	T	T	0.020	0.001	0.056	0.000
	Gadus sp.	-	T	-	0.001	-	0.001
Gasterosteiformes	*Gasterosteus aculeatus*	T	-	0.007	-	0.010	-
Myctophiformes	*Notoscopelus kroyeri*	-	T	-	0.003	-	0.000
	Myctophidae	-	T	-	0.004	-	0.000
Osmeriformes	*Mallotus villosus**	0.007	0.002	1.709	1.871	0.513	0.195
Perciformes	*Lumpenus fabricii*	-	T	-	0.001	-	0.002
	Melanostigma atlanticum	T	T	0.047	0.008	0.290	0.010
	Zoarcidae	T	-	0.001	-	0.016	-
Pleuronectiformes	Digested Pleuronectiformes	-	T	-	0.001	-	0.001
Scorpaeniformes	*Sebastes* sp.*	T	T	0.010	0.149	0.010	0.012
SHRIMP		0.152	0.018	35.969	19.069	30.136	2.282
	Digested Shrimp	0.008	0.001	1.992	0.727	5.199	0.751
Crangonidae	*Sabinea septemcarinata*	-	T	-	0.031	-	0.006
	Pontophilus norvegicus	T	-	T	-	0.005	-
Thoridae	*Eualus fabricii*	-	T	-	0.001	-	0.000
	Eualus gaimardii	-	T	-	0.009	-	0.002
	Eualus macilentus	T	T	0.006	0.002	0.032	0.000
	Spirontocaris spinus	-	T	-	0.001	-	0.000
	Digested Hippolytidae	-	T	-	0.003	-	0.001
Pandalidae	*Pandalus borealis**	0.058	0.001	13.772	1.163	5.198	0.063
	Pandalus montagui	0.003	T	0.610	0.095	0.177	0.007
	Pandalus sp.	0.002	0.001	0.447	0.691	0.553	0.109
Pasiphaeidae	*Pasiphaea multidentata**	0.079	0.016	18.694	16.346	19.601	1.395
	Pasiphaea sp.	0.002	T	0.448	T	0.493	0.001
AMPHIPOD		0.100	0.011	23.679	11.971	46.132	19.667
	Digested Amphipod	0.041	T	9.725	0.009	7.981	0.027
Ampeliscidae	*Byblis* sp.	-	T	-	0.001	-	0.001
Eusiridae	*Rhachotropis aculeata*	-	T	-	T	-	0.000
Gammaridea	Digested Gammaridea	T	T	T	0.015	0.010	0.313
Hyperiidae	*Hyperia galba*	-	T	-	0.151	-	0.185
	Hyperia sp.	-	T	-	0.006	-	0.003
	Hyperoche medusarum	T	-	T	-	0.007	-
	Themisto abyssorum*	0.010	T	2.344	0.235	7.066	2.359

(Continued)

TABLE 2 Continued

	Periods	PFI		%FI		%O	
		1993–1999	2015–2019	1993–1999	2015–2019	1993–1999	2015–2019
	*Themisto compressa**	0.008	0.002	1.836	2.498	3.928	3.437
	*Themisto libellula**	0.007	0.003	1.549	3.317	2.669	2.133
	Themisto sp.*	0.025	0.005	5.843	5.514	26.944	12.880
	Digested Hyperiidae	0.010	T	2.377	0.173	4.560	1.106
Lysianassidae	*Hippomedon* sp.	-	T	-	T	-	0.003
	Digested Lysianassidae	-	T	-	0.011	-	0.060
Maeridae	*Maera loveni*	-	T	-	0.001	-	0.001
Melitidae	*Melita* sp.	-	T	-	T	-	0.000
Oedicerotidae	*Monoculodes* sp.	-	T	-	T	-	0.001
Phoxocephalidae	*Harpinia* sp.	-	T	-	T	-	0.003
Scinidae	*Scina borealis*	T	T	T	0.037	0.014	0.236
Unciolidae	*Neohela monstrosa*	T	T	0.006	T	0.010	0.000
Uristidae	*Tmetonyx cicada*	-	T	-	0.001	-	0.009
COPEPOD		**0.010**	**0.034**	**2.465**	**35.286**	**15.761**	**74.787**
	Digested Copepod	0.007	0.002	1.751	2.296	11.245	12.210
Aetideidae	*Bradyidius similis*	T	T	T	0.007	0.018	0.089
	Chiridius gracilis	-	T	-	0.002	-	0.170
	Digested Aetideidae	-	T	-	0.168	-	1.881
Calanoida	Digested Calanoida	T	0.009	0.085	9.889	0.137	25.567
Calanidae	*Calanus finmarchicus*	T	T	0.004	0.002	0.188	0.156
	Calanus glacialis	-	T	-	T	-	T
	*Calanus hyperboreus**	0.001	0.006	0.250	6.511	3.260	25.476
	Calanus sp.*	0.001	0.015	0.325	15.640	2.143	26.367
Euchaetidae	*Paraeuchaeta norvegica*	T	T	0.025	0.449	0.559	9.485
	Euchaeta sp.	T	-	T	-	0.035	-
Metridinidae	*Metridia longa*	T	T	0.001	0.002	0.138	0.065
	Metridia lucens	T	T	0.004	0.001	0.058	0.013
	Metridia sp.	T	T	0.019	0.318	0.490	2.413
Scolecitrichidae	*Scolecithricella* sp.	-	T	-	T	-	0.107
MYSID		**0.007**	**0.001**	**1.774**	**1.410**	**6.882**	**1.784**
	Digested Mysid	-	T	-	0.001	-	0.013
Mysidae	*Boreomysis arctica*	0.001	T	0.156	0.289	0.375	0.118
	Boreomysis tridens	T	T	0.039	0.014	0.127	0.022
	Boreomysis sp.	0.005	0.001	1.091	1.025	5.666	1.428
	Erythrops erythrophthalma	-	T	-	0.024	-	0.026
	Erythrops sp.	-	T	-	0.001	-	0.005
	Mysis mixta	T	-	0.007	-	0.029	-
	Mysis sp.	-	T	-	0.036	-	0.057
	Pseudomma roseum	-	T	-	0.002	-	0.001
	Pseudomma sp.	T	T	0.015	0.012	0.019	0.079
	Stilomysis sp.	-	T	-	0.001	-	0.002
	Digested Mysidae	0.002	T	0.466	0.005	1.139	0.045
EUPHAUSIID		**0.016**	**0.016**	**3.825**	**17.233**	**9.573**	**5.038**
	Digested Euphausiid	T	T	0.001	0.010	0.113	0.192
Euphausiidae	*Meganyctiphanes norvegica**	0.013	0.004	3.161	3.710	8.741	2.241

(Continued)

TABLE 2 Continued

		PFI		%FI		%O	
	Periods	1993–1999	2015–2019	1993–1999	2015–2019	1993–1999	2015–2019
	Thysanoessa inermis	T	T	T	0.001	0.014	0.000
	Thysanoessa raschii	T	T	0.001	0.083	0.120	0.105
	Thysanoessa sp.	-	0.005	-	5.531	-	0.917
	Digested Euphausiidae	0.003	0.008	0.661	7.897	1.054	2.126
OTHER INVERTEBRATES		**0.023**	**0.010**	**5.496**	**10.781**	**16.269**	**23.472**
	Invertebrate egg	T	-	T	-	0.023	-
	Digested invertebrate	0.001	T	0.175	0.015	1.659	0.063
Anomalodesmata	*Cuspidaria* sp.	T	-	0.001	-	0.010	-
Cephalopoda	*Rossia* sp.	-	T	-	0.001	-	0.001
Cumacea	Digested Cumacea	-	T	-	0.039	-	0.922
Crustacea	Digested Crustacea	0.022	0.010	5.268	10.679	14.532	22.639
Decapoda	*Chionoecetes opilio*	-	T	-	T	-	0.001
	Hyas sp.	-	T	-	T	-	0.002
	Digested Brachyura	-	T	-	0.003	-	0.025
Gastropoda	*Limacina* sp.	-	T	-	T	-	0.004
	Digested Gastropoda	-	T	-	T	-	0.001
Isopoda	*Syscenus infelix*	-	T	-	T	-	0.000
	Digested Isopoda	T	-	T	-	0.005	-
Malacostraca	Digested Malacostraca	T	-	0.052	-	0.073	-
Mollusca	Digested Mollusca	-	T	-	0.001	-	0.044
Ostracoda	Digested Ostracoda	-	T	-	0.022	-	0.254
Polychaeta	*Aphrodita hastata*	-	T	-	0.019	-	0.002
	Digested Polychaeta	-	T	-	T	-	0.007
UNIDENTIFIED MATERIAL		**0.080**	**0.002**	**18.988**	**1.929**	**18.379**	**11.168**
	Egg	T	T	T	0.003	0.005	0.031
	Item	0.080	0.002	18.988	1.926	18.379	11.137

T, Trace. The contribution of the eight broad taxonomic categories is in bold. *= Main prey taxa.

decreased while the proportion of shrimp and fish increased, according to all three diet measures (Figure 3). This same major shift in the diet of redfish is observed around 25 cm for the 1990s and 30 cm for the 2010s. Although the contribution of zooplankton in terms of %FI decreased drastically for large specimens, occurrences remained high, especially for amphipods in the 1990s and for copepods in the 2010s. For both periods, pink glass shrimp and northern shrimp were found in high proportion and occurrence in large redfish, although the contributions in %FI and %O of pink glass shrimp were greater than that of northern shrimp. For both periods, the specific contribution of northern shrimp was greatest for 30–35 cm redfish (%FI = 32.66 in the 1990s and 26.79 in the 2010s, Figure 3). Although the two periods were characterised by the same overall diet trends in relation to redfish size, differences in the importance of specific prey were observed. Diet composition based on %FI of the fifteen prey groups was influenced by the interaction between periods and size classes (PERMANOVA, $p = 0.001$, Table 3).

Amphipod groups, principally of *Themisto*, dominated the diet of small (< 20 cm) redfish in the 1990s, while euphausiid and copepod groups dominated during the recent period (Figure 3). SIMPER analysis revealed that for small redfish, differences between the two periods were explained at 47% by the relative abundance in the diet of *Themisto* sp. and Other Amphipods (more abundant in the 1990s), as well as Other Copepods and *Calanus* sp. (more abundant in the 2010s), whereas Other Invertebrates and Mysids, more abundant in the 1990s, contributed another 30% (Table 3).

Themisto sp. still dominated the diet of medium (20–30 cm) redfish in the 1990s while the three Copepod categories were predominant during the 2010s with *C. hyperboreus* as the species identified most frequently, though it was nearly absent in the 1990s (Figure 3). According to SIMPER analysis, Other Amphipods, *Themisto* sp., Other Copepods and *C. hyperboreus* accounted for 36% of the differences between medium redfish from the two periods, whereas Other Invertebrates, Mysids and
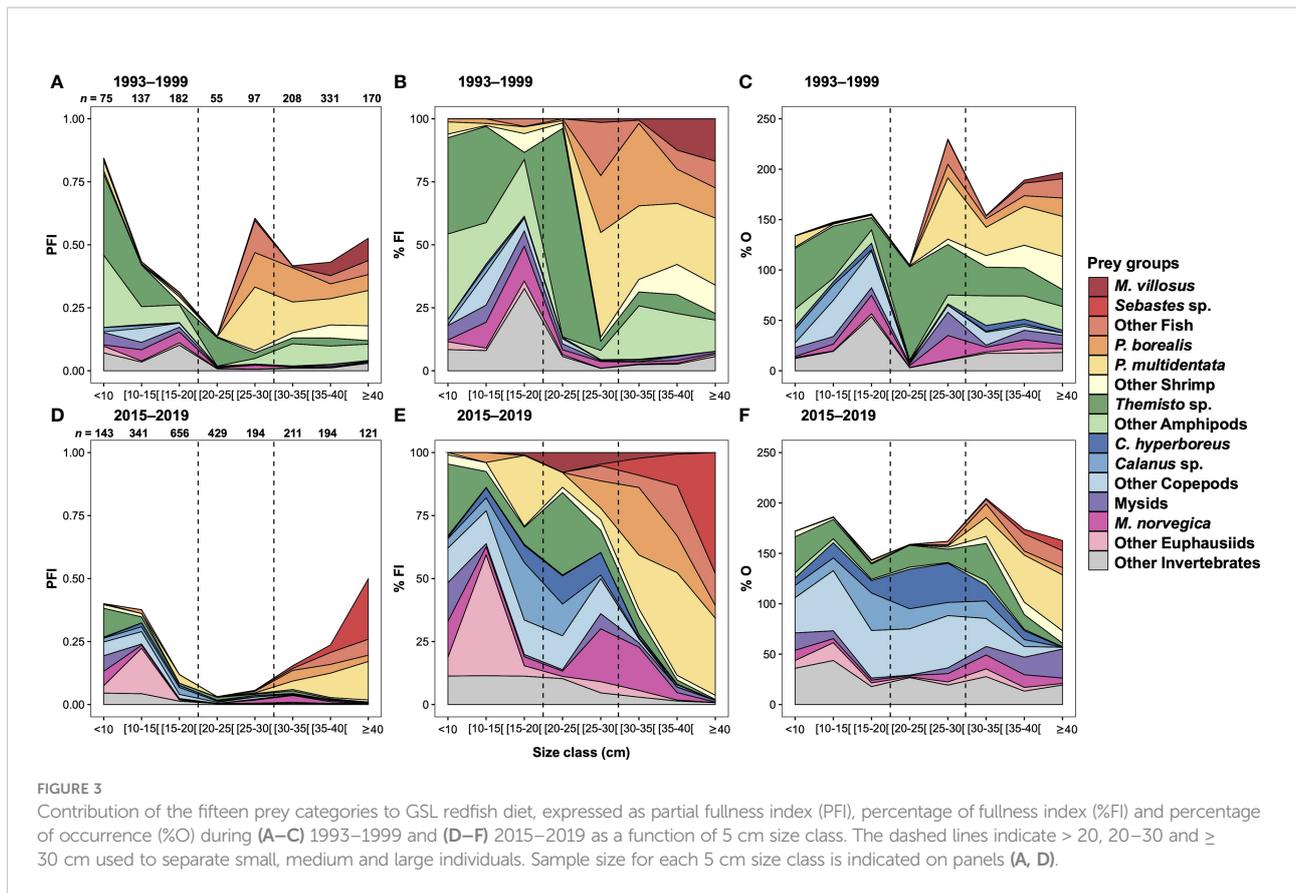
FIGURE 3
Contribution of the fifteen prey categories to GSL redfish diet, expressed as partial fullness index (PFI), percentage of fullness index (%FI) and percentage of occurrence (%O) during **(A–C)** 1993–1999 and **(D–F)** 2015–2019 as a function of 5 cm size class. The dashed lines indicate > 20, 20−30 and ≥ 30 cm used to separate small, medium and large individuals. Sample size for each 5 cm size class is indicated on panels **(A, D)**.

Other Shrimp, slightly more abundant in the 2010s, contributed another 31% (Table 3). In the 1990s, there was a peak in the proportion of *P. multidentata* in the diet (41.51%) for 25–30 cm redfish (Figure 3) and this prey contributed 7% to the difference in the diet of the two periods for medium size redfish (Table 3).

Although the Shrimp groups were important in both periods in the diet of large (≥ 30 cm) redfish (%FI = 61.71 in the 1990s

and 50.48 in the 2010s), the relative proportion of the three categories changed between periods (Figure 3) and contributed 45% to the differences in diets (Table 3). In terms of %FI, the diet of the largest redfish (≥ 40 cm) in the 2010s was almost exclusively based on shrimp and fish groups (%FI = 89.69) (Figure 3). Capelin was the most important fish prey consumed in large redfish in the 1990s, while a shift to cannibalism was

TABLE 3 PERMANOVA, pairwise comparisons and SIMPER results testing the dissimilarities in redfish diet composition based on percentage fullness index (%FI) of the fifteen prey categories between periods and for three size classes.

Source	DF	Pseudo-F	P-value	
Period x Size	2	7.755	**0.001**	
Residuals	1416			

	Levels	P-value	Contribution (%) to dissimilarity
	< 20 cm		
	1990s:2010s	**0.001**	Other Invertebrates (17); *Themisto* sp. (15); Other Copepods (13); Mysids (13); *Calanus* sp. (11); Other Amphipods (8)
	20–30 cm		
	1990s:2010s	**0.001**	Other Invertebrates (13); Other Amphipods (11); Mysids (10); Other Copepods (10); *Themisto* sp. (8); Other Shrimp (8); *C. hyperboreus* (7); *P. multidentata* (7)
	≥ 30 cm		
	1990s:2010s	**0.001**	*P. multidentata* (22); *P. borealis* (12); Other Shrimp (11); Other Fish (10); Other Amphipods (9); *Themisto* sp. (8)

Bold indicates significant values adjusted (P < 0.05). DF, degrees of freedom.

observed for the same size class in the 2010s (Figure 3), but these changes did not contribute strongly to the differences between periods shown in Table 3. Amphipods remained important in the diet of large redfish during the 1990s, while their contribution was negligible during the 2010s (Figure 3), explaining 17% (Other Amphipods and *Themisto* sp.) of the differences between periods.

3.4 Spatial variability in diet composition and feeding strategy

Diet composition was also influenced by the interaction among size classes (< 20, 20–30, ≥ 30 cm) over periods (1990s and 2010s) and subareas (NWG, LC, NEG) (PERMANOVA, p = 0.003). Pairwise comparisons indicated redfish diets differences, except for redfish ≥ 30 cm in the NWG (Table 4). The absence of difference for ≥ 30 cm redfish in the NWG should be interpreted with caution given the low numbers of large individuals in this subarea during both periods. Amundsen diagrams were used to depict the feeding strategy of redfish during both periods (Figures 4, 5). Overall, only the prey groups of Other

Amphipods, Mysids, and *P. borealis* appeared as dominant, and then only in the 1990s (Figure 4).

The diets of small (< 20 cm) redfish during the 1990s were characterised by Mysids (i.e., *Boreomysis* sp., Table 2) as the dominant prey in NWG and by very important prey groups in the three subareas: Other Invertebrates (NWG), and Other Copepods and *Themisto* sp. (LC and NEG) (Figure 4). In the 2010s, the diets of small redfish were characterised by very important prey categories: Other Invertebrates in NWG, *Calanus* sp. in LC and NEG, and Other Copepods being important prey in the same two subareas. Other Euphausiids and *Calanus* sp. were noteworthy in NWG (Figure 5). Mysids (25% in NWG), Other Invertebrates (12–25% in the three subareas), *Themisto* sp. (23% in NEG) and Other Copepod (6–17% in the three subareas) explained the most of the dissimilarities observed in pairwise comparisons over periods and spatial subareas (Table 4).

In medium (20–30 cm) redfish diet and during the 1990s, only northern shrimp was the dominant prey type in NEG while Mysids, *P. multidentata* and Other Amphipods were very important in NWG, LC and NEG, respectively, and *Themisto* sp. was important in LC (Figure 4). In the 2010s, Other Copepods, Other Invertebrates

TABLE 4 PERMANOVA, pairwise comparisons and SIMPER results testing the dissimilarities in redfish diet composition based on percentage fullness index (%FI) of the fifteen prey categories among size classes over periods and subareas.

Sources	DF	Pseudo-F	*P*-value
Periods x Size x Subareas	4	1.681	**0.003**
Residuals	1404		

Levels		*P*-value	Contribution (%) to dissimilarity
1990s:2010s	**< 20 cm**		
	NWG	**0.001**	Mysids (25); Other Invertebrates (25); Other Euphausiids (13); Other Amphipods (6); Other Copepods (6)
	LC	**0.001**	Other Invertebrates (16); Other Copepods (15); *Themisto* sp. (14); *Calanus* sp. (13); Mysids (12); Other Amphipods (10)
	NEG	**0.001**	*Themisto* sp. (23); Other Copepods (17); *Calanus* sp. (13); Other Invertebrates (12); Other Amphipods (9)
1990s:2010s	**20–30 cm**		
	NWG	**0.001**	Mysids (29); Other Invertebrates (15); *P. borealis* (12); Other Fish (8); Other Amphipods (7)
	LC	**0.001**	Other Invertebrates (14); Other Copepods (11); *C. hyperboreus* (10); *P. multidentata* (10); Other Shrimp (9); Mysids (8), *Calanus* sp. (8); Other Amphipods (7)
	NEG	**0.001**	Other Amphipods (24); *Themisto* sp. (15); Other Copepods (11); Other Invertebrates (10); Other Shrimp (8); *Calanus* sp. (7)
1990s:2010s	**> 30 cm**		
	NWG	0.442	
	LC	**0.001**	*P. multidentata* (26); Other Shrimp (13); Other Fish (11); Other Invertebratse (8); *Themisto* sp. (7); *P. borealis* (7)
	NEG	**0.001**	*P. borealis* (19); *P. multidentata* (16); Other Amphipods (15); *Themisto* sp. (11); Other Shrimp (8); Other Fish (7)

Bold indicates significant values adjusted (P < 0.05). DF, degrees of freedom.

FIGURE 4

Feeding strategy of GSL redfish in the 1990s for three subareas and three major size classes. Prey-specific abundance in stomach fullness index (%FI$_{spe\_i}$) is plotted against percentage of occurrence (%O).
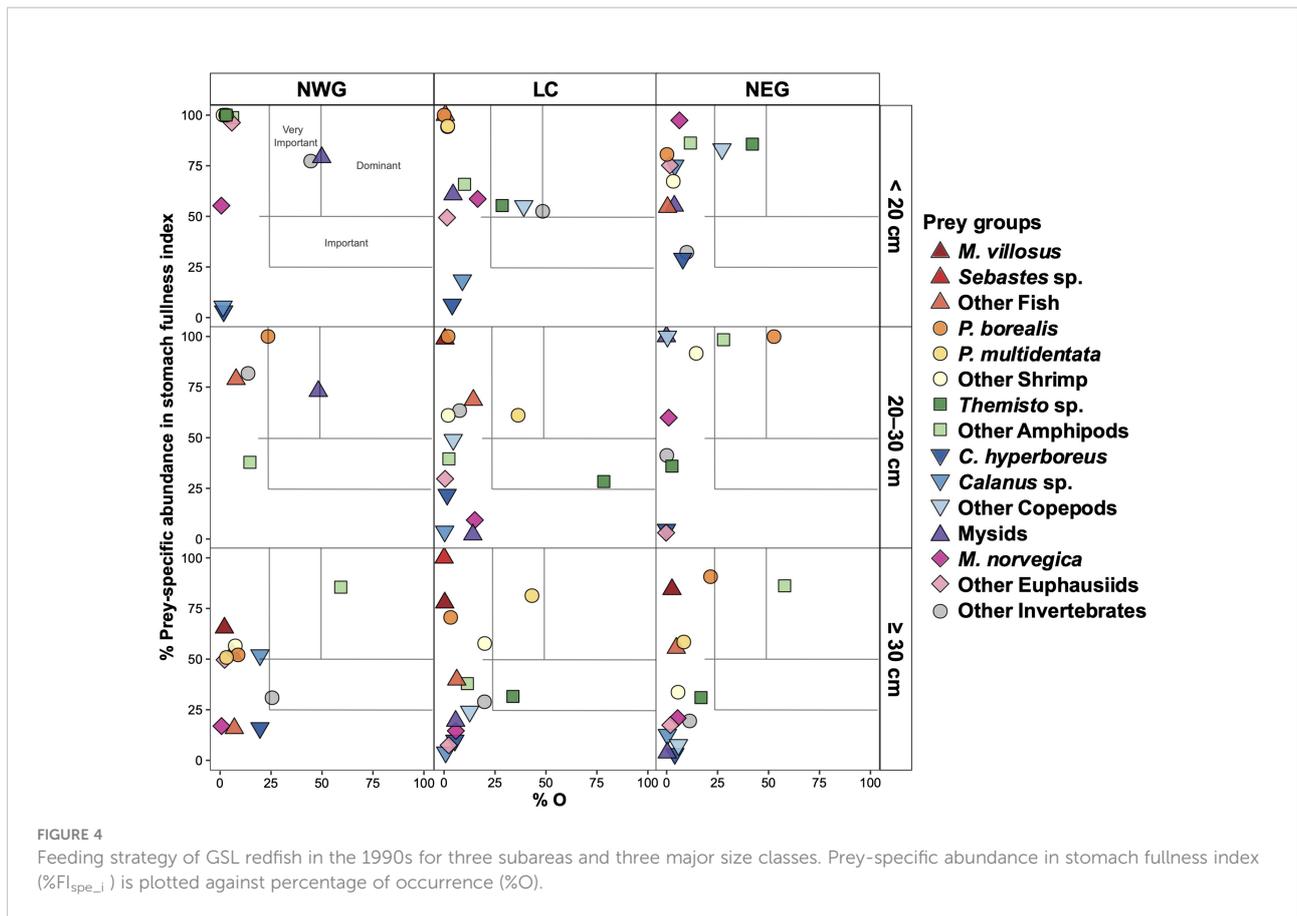
(e.g., digested crustaceans, Table 2) and *Themisto* sp. were very important groups in NWG, LC and NEG, respectively. *C. hyperboreus* was important in all three subareas and Other Copepods were important in LC and NEG, whereas Other Invertebrates were important in NEG (Figure 5). Mysids explained 29% of the dissimilarity in NWG while Other Invertebrates and Other Amphipods respectively explained 14 and 24% in LC and NEG subareas, observed in pairwise comparisons (Table 4).

In the large (≥ 30 cm) redfish diet in the 1990s, Other Amphipods dominated the diet in NWG and NEG, and *P. multidentata* was a very important prey in LC, whereas *Themisto* sp. was important in LC as well as Other Shrimp and *P. borealis* were noteworthy in LC and NEG, respectively (Figure 4). In the 2010s, a single very important prey, *P. multidentata*, was observed in LC. Mysids and *M. norvegica* were important prey categories in NWG and NEG, respectively, and *P. borealis* was a noteworthy prey in NWG and NEG (Figure 5). Fish prey were noteworthy in large redfish diet for both time periods (Figure 3); these were important despite their low occurrence because they often consisted of large meals (high fullness index) (Figures 4, 5). The two shrimp species explained together 25% of the dissimilarity observed in NEG and *P. multidentata* explained 26% of the differences between periods in LC (Table 4).

4 Discussion

4.1 Stomach content analysis and the measure of diet composition over long time periods

The potential variability in stomach content data means that large sample sizes may be required to obtain a representative portrait of diet composition for a given category of fish, area or time period. This is particularly true for predators that often have regurgitated stomachs when sampled, as is seen with Greenland halibut and redfish. In a literature review, Baker et al. (2014) concluded that samples comprising ≥ 100 individuals generally provide a reliable depiction of diet composition. The validity of sample sizes can be assessed using prey accumulation curves. In cases when the asymptote is not reached (Supplementary Figure 3), the reliable depiction of diet composition can be further assessed by evaluating the convergence of diet indicators based on mass or volume (e.g., %FI) and %O. In the present study, we considered a total number of 6,958 stomachs, of which 3,690 contained prey taxa. Within a given period, each 5 cm size class comprised between 55 and 656 individual redfish stomachs. Even though there were only 55

FIGURE 5

Feeding strategy of GSL redfish in the 2010s for three subareas and three major size classes. Prey-specific abundance in stomach fullness index (%FI$_{spe\_i}$) is plotted against percentage of occurrence (%O).
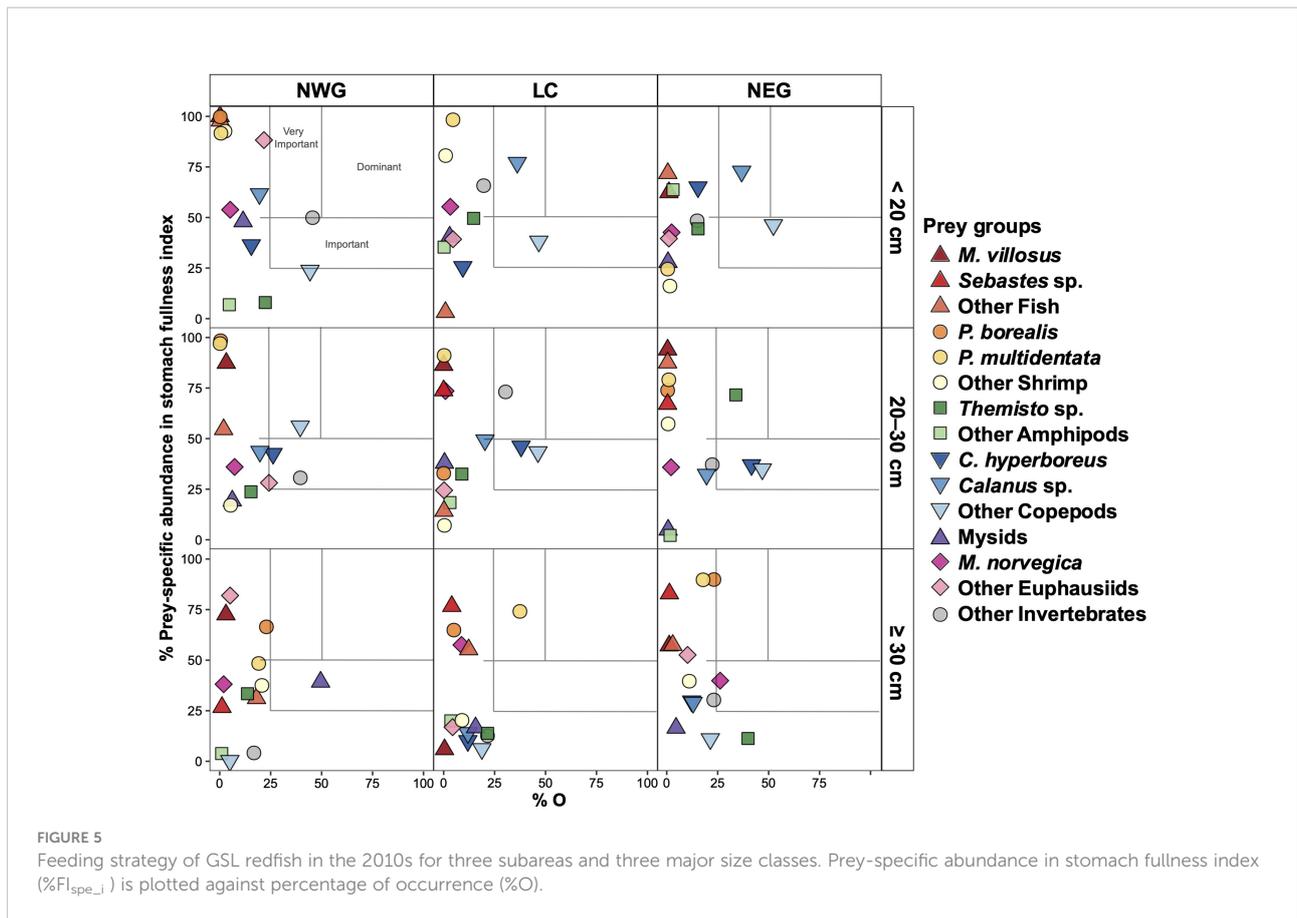
stomachs available for 20–24.9 cm redfish in the 1990s, the progressive diminution of small prey items with increasing fish length is clearly visible using all three measures (PFIs, %FI, and %O) and the relative abundance of Amphipods and Copepods was coherent with other size classes of the 1990s, and different from their relative abundances in the 2010s (Figure 3). In some instances, smaller sample sizes were considered when splitting samples into subareas (e.g., NWG in the 1990s, Table 1), but for the large majority of subgroups (combination of size classes, period and geographic subarea) well above 100 stomachs with food were available, making us confident that our sample sizes and choice of diet indicators allowed for a representative description of the redfish diet and robust comparisons of redfish diet composition between periods and among subareas within the GSL.

4.2 Size-related changes in diet composition of redfish

For both periods considered in the present study, analysis of redfish diet composition revealed similar patterns of dietary shifts with size. Overall, zooplankton dominated the diet of small redfish (< 20 cm), but generally showed decreasing importance with increasing predator size as it was replaced by shrimp and

fish. Size-related shifts in diet composition are commonly observed in fishes (e.g., Hovde et al., 2002; Buckley and Whitehouse, 2017; Sánchez-Hernández et al., 2019), given that body size often increases by more than one order of magnitude from the early juvenile to the late adult stages. Shifts in prey are generally linked to the combination of predator size, mouth opening and swimming ability, as well as changes in vertical distribution and habitat use (Cook and Bundy, 2010; Sánchez-Hernández et al., 2019).

Redfish occupy various depth strata during ontogeny. Larvae develop in surface waters then migrate to deeper waters as they develop (Templeman et al., 1959; Senay et al., 2021). Juveniles and adult redfish are bentho-pelagic, distributed near the sea floor at depths ranging between 40 and 500 m in the GSL, older fish occupying generally deeper waters than younger fish, then migrating vertically to feed on pelagic preys (e.g., Steele, 1957; Lambert, 1960; Planque et al., 2013; Senay et al., 2021; Froese and Pauly, 2022).

Our study provides a robust confirmation of trends observed in a preliminary analysis based on raw data, showing a dietary shift from zooplankton to shrimp and fish (Senay et al., 2021). Such a transition was also reported in both Barents (Dolgov and Drevetnyak, 2011) and Irminger (González et al., 2000) seas, as well as on the Flemish Cap (Albikovskaya and Gerasimova,

1993). Moreover, the main groundfish species co-occurring with redfish in the GSL, namely the Greenland halibut, Atlantic cod and white hake (*Urophycis tenuis* Mitchill 1814), are also characterised by a dietary shift from zooplankton to shrimp at sizes ranging between 20–25 cm, and then to piscivory at larger sizes (Ouellette-Plante et al., 2020).

4.3 Redfish: Selective predator or indicator of ecosystem change?

Our capacity to detect whether the diet of a given species is either selective or reflects changes in the relative abundance of potential prey taxa requires sampling across the distribution of a given species that may vary between periods in relation to prey availability (Fahrig et al., 1993; Dwyer et al., 2010; Buckley and Whitehouse, 2017) and abiotic conditions, such as temperature (Cook and Bundy, 2010).

Since the early 2010s, changes have been noticed in the GSL environment and ecosystem. Deep waters have warmed from the inflow of oceanic water through Cabot Strait, contributing to a worsening of acidification and hypoxia of this deeper water layer (Mucci et al., 2011; Galbraith et al., 2019; Blais et al., 2021). This continuing warming of the deeper water layers will impact on species distribution and composition, such as the decline of dominant cold-water species like northern shrimp, snow crab, and Greenland halibut, and the increase of warm-water species like redfish and cod (Bourdages et al., 2017; Brassard et al., 2017; Galbraith et al., 2019). In the present study, the geographic coverage of the redfish stomach collection on trawl research surveys was relatively extensive and similar between both periods, allowing us to detect temporal changes among the three spatial subareas of the GSL. Moreover, weighting of diet composition to account for spatial variability in redfish abundance allowed us to document dietary changes between the two periods characterised by different regimes, considering redfish local abundance.

In addition to considering variability in redfish spatial distribution, a robust assessment of feeding strategies would be facilitated by information on prey availability over the full time series considered. DFO's Atlantic Zone Monitoring Program (AZMP) provides abundance indices for mesozooplankton taxa such as copepods, and some information on macrozooplankton taxa, such as amphipods, euphausiids and mysids, but the program only started its large-scale monitoring activities in 2000 (Blais et al., 2021), i.e., after the first period considered in the present study. For shrimp, abundance of the commercially exploited northern shrimp has been assessed over the full time series. Data on pink glass shrimp are only partial, obtained by sampling from the annual bottom trawl survey. Compared with northern shrimp, pink glass shrimp is mostly pelagic and catch quantities are orders of magnitude lower (kilotons vs. kg; Bourdages et al., 2020b) on the trawl survey, representing an

unknown fraction of the available biomass in the water column. The frequent presence of pink glass shrimp in redfish stomachs suggests it could be present at a similar scale of biomass as northern shrimp. In the 2015–2017 groundfish stomach contents summary by Ouellette-Plante et al. (2020), among deepwater predators, pink glass shrimp is ranked first in contributed prey for redfish, black dogfish (*Centroscyllium fabricii*), longfin hake (*Phycis chesteri*) and is significant in Greenland halibut, thus suggesting that it is widely available and abundant in the deep channels of the GSL. Regarding fish prey, small redfish has been monitored over the whole time series, while capelin is not assessed in the same manner in the GSL because the trawl research surveys has limited catchability for pelagic species, akin to the situation with pink glass shrimp noted above (Bourdages et al., 2020b). Even though several key prey species are mostly pelagic and abundance indices are not currently generated from the annual bottom trawl survey, complementary information based on specific research initiatives can be used to make robust inferences on redfish feeding strategies within the three main size classes considered.

4.3.1 Small-sized redfish: Zooplankton consumption based on the relative abundance of key taxa

Marked variability in diet composition was observed in small (< 20 cm) redfish diet, reflected by the dominance of different zooplankton prey taxa between periods and among subareas of the GSL. These differences were primarily driven by a dominance of amphipods (*Themisto* sp.) in the 1990s, in particular in the diet of North-East Gulf redfish, while in the 2010s, copepods (*Calanus* sp., especially large *C. hyperboreus*) and euphausiids (mostly *M. norvegica*) respectively dominated diet composition in the Laurentian Channel and the North-West Gulf. Information available on spatiotemporal variations of zooplankton taxa within the GSL suggests that small redfish diet composition was proportional to the relative abundance of main zooplankton taxa in time and space. For example, as Mysids were mostly composed of *Boreomysis arctica* and *Boreomysis* sp., their importance in the diet of NWG redfish was not surprising as their distribution is mostly in NWG, spilling over into the southwest part of LC (Chabot et al., 2007). This pattern may be similar to that with Atlantic cod, with their diet reflecting available prey (and thus a good sampler of the ecosystem, Link, 2004), possibly in contrast to Greenland halibut, which exhibit prey preferences and may thus not select alternate prey when preferred ones are less available (Ouellette-Plante et al., 2020).

In the 1990s, the massive intrusion of the cold Labrador Current waters into the GSL *via* the Strait of Belle Isle led to a sharp increase of the abundance of the arctic *Themisto libellula* and subarctic *T. abyssorum* into the ecosystem (Harvey et al., 2004; Harvey and Devine, 2009; Kraft et al., 2013). These two amphipod species were five times more abundant in 1998,

corresponding to the end of the cold period, compared to 2000–2001 (Descroix et al., 2005). The importance of cold water amphipods in the GSL in the 1990s was also confirmed by Starr et al. (2002), who found strong concordance between their relative abundance in the environment to their importance in the diet of Atlantic cod between 1994 and 2001 in the North-West Gulf. This previous study, as well as our own results, suggest that small cod and redfish consume *T. libellula* in proportion to their availability in the environment. Since 2005, *T. libellula* abundance has strongly declined (Harvey and Devine, 2009), which is consistent with their reduced importance in the diet of redfish during the 2010s.

Calanus spp. copepods represent a large proportion of the mesozooplankton community in the GSL (Plourde et al., 2003; Harvey and Devine, 2009). They are distributed near the surface during the productive season but sink in the deep channels diapausing from August to early spring (Harvey et al., 2004; Dufour and Ouellet, 2007) where they become a major prey for redfish. The AZMP has revealed that peak abundance of *C. hyperboreus* has been recorded in recent years (Blais et al., 2021). Given its large body size, Devine et al. (2017) estimated that *C. hyperboreus* recently represented up to 80% of the total *Calanus* sp. biomass in the GSL. The current trends of increasing *Calanus* sp. biomass in the GSL is consistent with the higher contribution of this taxon to small redfish diet in the 2010s compared to the 1990s.

Euphausiids also contributed importantly to the diet of smaller redfish in the 2010s, with the highest contribution in 10–15 cm redfish. Between 1994 and 2007, the abundance of the two main species of euphausiids, *Thysanoessa raschii* and *Meganyctiphanes norvegica*, was estimated to have decreased (Harvey and Devine, 2009). However, acoustic surveys suggest that traditional sampling methodologies strongly underestimate actual abundances (McQuinn et al., 2015). Moreover, there are no data available to contrast euphausiid abundance between the 1990s and the 2010s, so it is not possible to determine whether euphausiids were consumed according to their relative abundance in the environment. Even though krill consumption by redfish requires further investigation, our results and available evidence relative to amphipod and copepod abundance in the GSL strongly suggest that small redfish consume their zooplankton prey in an opportunistic fashion, based on the relative availability of the main taxa in the environment, in particular near the sea bottom.

4.3.2 Medium-sized and adult redfish: Transition to shrimp selection and piscivory

During both periods considered, redfish shifted from a zooplankton-based diet to a shrimp-dominated diet around sizes of 25 cm in the 1990s and 30 cm in the 2010s. Even if the relative proportion of the Shrimp categories contributed to variability between periods according to statistical analysis, two shrimp species stood out, northern shrimp and pink glass

shrimp, which showed high relative importance in both periods. The commercially important northern shrimp is by far the most abundant shrimp species sampled across the DFO bottom trawl survey (on the order of kilotons) and its abundance has been estimated annually since 1990 in the GSL. The abundance of northern shrimp was high through the 1990s, peaked in the mid-2000s, after which it started to decline to reach a record-low value in 2017 (Bourdages et al., 2020a). In contrast, the abundance for pink glass shrimp sampled on the trawl survey is on the order of several dozen kilograms, reflecting the pelagic nature of the shrimp, with adult stages predominantly available on the bottom and which does not allow for an estimate of their population in the GSL.

Data from northern shrimp suggest that redfish systematically transition to preying on shrimp independent of predator or prey abundance. In the 2010s, average northern shrimp biomass throughout the northern Gulf survey region was estimated to be at half the levels estimated in the 1990s (Bourdages et al., 2020a) while mid-size redfish were estimated to be 114 times more abundant (Table 1). However, these contrasting numbers had little effect on the contribution of shrimp to diet, which suggests that redfish exhibit prey selectivity during this feeding transition, after the initial period when they fed more opportunistically on available zooplankton taxa, probably because there were no other large crustacean prey available in sufficient numbers. It is possible that medium size redfish would ingest more pink glass shrimp if the abundance of northern shrimp dropped below a yet to be determined level.

Large redfish ≥ 30 cm in length retained shrimp as main prey, accounting for more than 50% for each of the various feeding indices. The contribution of the mesopelagic *P. multidentata* to redfish diet gained in importance with increasing redfish size in recent years, but both shrimp species continued to contribute importantly to the diet of redfish of increasing size in the 1990s (Figure 3). The large contribution of pink glass shrimp to redfish diet in both periods, at similar or even greater levels than northern shrimp in the presented results, is evidence that this pelagic species is more widely available than indicated from the trace catches observed in the bottom trawl survey and that a large distributional overlap exists between large redfish and *P. multidentata* in the deep channels of the GSL. However, we have not speculated on pink glass shrimp selectivity since the population size and thus its importance or temporal trends cannot be estimated. Mean biomass of northern shrimp in the region has been estimated at 1,475 kg/km^2 while pink glass shrimp was 70 kg/km^2 from the trawl survey conducted by the DFO between 1990 and 2011 (Savard and Nozères, 2012) indicating that these two shrimp species were as much as 20:1 in survey catches compared to near 1:1 level in redfish diet. Though in recent years this ratio has been reduced (6:1 in 2020), because of large declines in northern shrimp survey catches while glass shrimp catches have displayed little or no declines (Bourdages et al., 2021), this could be evidence

that the trawl survey is under sampling a pelagic species while adequately sampling a targeted species (northern shrimp).

Fish were the second most important prey category consumed by large adult redfish for both periods. Capelin was the main fish prey in the 1990s, although it was observed eaten by a very small proportion of redfish, constituting the majority of the stomach content when eaten. However, most fish prey were also not identified during that period, which may have led to an underestimation of capelin in the diet of large redfish in the 1990s, digested capelin being considered "Other Fish". In recent years, digested fish was often identified to species by using otoliths and partial remains. Piscivory was more prevalent in the 2010s, primarily from cannibalism of small redfish. The high occurrence of cannibalism in the 2010s suggests density-dependent control at high redfish abundance and opportunistic selection of fish prey based on availability. Cannibalism is expected to intensify as the strong 2011–2013 year classes grow larger, if small redfish continue to recruit in high numbers. Given that redfish currently represent the vast majority of the biomass in the demersal habitats of the GSL (90% of sampled biomass in the 2019 trawl survey, compared to 15% from 1995–2012, Senay et al., 2021), cannibalism is expected to become an important source of mortality for early juveniles, which could prevent the emergence of strong year classes in the mid-term. In a previous study on GSL redfish predation mortality, Savenkoff et al. (2006) estimated that cannibalism represented 11–15% of total mortality, during a period when small redfish only constituted 2% of the diet of large piscivorous redfish. The anticipated high mortality rates of juvenile redfish attributable to cannibalism will have to be quantified for accurate projections of population dynamics.

4.4 Redfish impact on the northern shrimp and implications for the demersal community

The northern shrimp is a key forage species in the GSL demersal ecosystem and also sustains an important commercial fishery. There is growing evidence across multiple North Atlantic ecosystems that northern shrimp populations are impacted by bottom-up effects associated with regional warming (Ouellet et al., 2007; Koeller et al., 2009; Bourdages et al., 2020a). In the GSL, the warming of both surface and deep waters negatively affect northern shrimp recruitment from the larval stage until juvenile settlement in the demersal habitat (Bourdages et al., 2020a). Even though recruitment prospects are generally negative, Brosset et al. (2019) suggested that moderate warming could favour recruitment and abundance in the Esquiman Channel (NEG), which hosts one of the main northern shrimp aggregations in the GSL. However, these authors recognized that the potential northern shrimp abundance increase in Esquiman is conditional to the stability of current predation pressure in the area. Our results indicate that in the 2010s, the contribution of northern shrimp to diet of large

redfish was highest in the NWG and NEG subareas, corresponding to known shrimp density hot spots. These results suggest that the potential northern shrimp population growth in the Esquiman Channel (NEG) will be buffered by the increasing biomass of large redfish in the subarea.

Redfish are slow-growing and long-lived species that can reach the size of 42 cm at an age of 40 years. Redfish minimal trawlable biomass was estimated at 4.4 million tons in 2019 with modal size at 23 cm (Senay et al., 2021). Senay et al. (2021) estimated the annual northern shrimp consumption by redfish was ca. 9,500 t during the 1997–1999 period, compared to 81,000 t for the 2017–2019 period, representing an 8.5 fold increase. Given that redfish are currently reaching the size corresponding to a shift between a zooplankton-dominated diet to one primarily based on fish and shrimp, consumption is expected to quickly rise in the short term, with important implications for the development of management strategies of commercial stocks such as the GSL northern shrimp. Apart from the impact on juvenile redfish and northern shrimp, the large redfish will also be expected to affect other pelagic prey such as pink glass shrimp and capelin (also a commercial species), with unknown consequences to the ecosystem for these important forage species to other predators such as Greenland halibut, Atlantic cod, marine mammals and seabirds.

Northern shrimp is an important prey for several other groundfish species besides redfish. Stomach content data collected between 2015–2017 in the GSL revealed that the contribution of northern shrimp and pink glass shrimp was important for medium-sized Greenland halibut (20–40 cm), Atlantic cod (30–55 cm) and white hake (< 35 cm) (Ouellette-Plante et al., 2020). The increased predation pressure on shrimp linked to the surge in large redfish biomass could result in competition interactions that will be detrimental to the condition and growth of several other large fish species. Greenland halibut currently constitutes an important valuable groundfish fishery in the GSL, and the rebuilding Atlantic cod stock in the northern GSL is also characterised by high cultural and commercial importance. In the GSL, white hake has experienced a past collapse and was conferred a "threatened" status by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2013. Through competition for northern shrimp, redfish could thus contribute to the current ecosystem shift by impacting other commercially important and threatened groundfish species. These considerations should be explored further by modelling shrimp consumption and population dynamics under various redfish predation intensity scenarios and considered in the current efforts of developing ecosystem-based approaches to fishery management in the GSL.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical review and approval was not required because the study was conducted in the field using animals killed during surveys.

Author contributions

All authors conceived the project objectives and methodology. DC designed and initiated the stomach collection program and the database. SB-V and CN analysed many of the stomach content. SB-V, DC, and RT conducted the data analyses. SB-V 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. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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