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ABSTRACT

Arctic and sub-Arctic marine ecosystems are experiencing some of the highest sea surface warming in the world, which has intensified water column stratification and subsequently reduced phytoplankton production and particulate organic matter quality. However, the effects of these changes on benthic food webs and the transfer of organic matter to higher trophic levels are still poorly understood. This study examines the spatial and temporal variability of food web structure in a sub-Arctic benthic community exposed to contrasting thermal stratification conditions. The study hypothesizes that during stratified periods, oceanographic conditions would have a limited effect on benthic invertebrates located above/at the thermocline due to their direct access to surface/subsurface primary production. On the other hand, organisms below the thermocline may be more sensitive to increased stratification because they do not have direct access to these food resources. To test this hypothesis, we sampled benthic invertebrates and several fish species on the Newfoundland Shelf along a cross-shore transect (2 shallow stations versus 2 deep stations above and below the thermocline, respectively) over two seasons. We used isotopic analyses (δ^{13}C and δ^{15}N) to study the structure of the food web and the transfer of organic matter. No temporal variation and little spatial variability in food web structure was observed, resulting in a 73.2% overlap between isotopic niches of shallow and deep stations. At all stations, most primary consumers were characterized by high trophic plasticity, feeding on both phytoplankton and benthic organic matter (mean dependence on benthic sources = 46.7%). In the context of global warming and increased thermal stratification, we hypothesize that benthic primary production may be less vulnerable to nutrient depletion than phytoplankton. We suggest that an increased contribution of benthic primary producers to organic matter fluxes in shallow coastal food webs could significantly enhance the resilience of the benthic food web to stratification intensification.

1. Introduction

Arctic and sub-Arctic shelves usually harbor large benthic biomass on the seafloor (Grebmeier et al., 1988; Dunton et al., 2005; Piepenburg, 2005), resulting from the tight pelagic-benthic coupling at high latitudes (Ambrose and Renaud, 1995; Fortier et al., 2002; Cochrane et al., 2009; Grebmeier, 2012). These benthic invertebrates play a key role in marine food webs by providing large carbon stocks for benthic fish (e.g.

Hippoglossoides platessoides (Fabricius, 1780), *Pleuronectes platessa* Linnaeus, 1758, Sherwood and Rose 2005; Silberberger et al., 2018), seabirds (e.g. common eiders (*Somateria mollissima borealis* (Brehm, CL, 1824; Blicher et al., 2011), and marine mammals (e.g. walrus (*Odobenus rosmarus* (Linnaeus, 1758)), Born et al., 2003). This entire food web also constitutes an important food resource on which some human populations depend (Grebmeier et al., 2006; Darnis et al., 2012). However, the intensity of pelagic-benthic coupling is related to a variety of factors,

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including phytoplankton productivity, grazing pressure, activity of pelagic microbial communities, as well as sedimentation of phytoplankton cells (Renaud et al., 2008; Kędra et al., 2015, Turner, 2015). In the Arctic, the evolution of this coupling will also depend on the fate of sea ice, which directly controls the production and phenology of ice algae, and thus the timing and intensity of sympagic-pelagic-benthic coupling (Leu et al., 2011, Niemi et al., 2024). Any future environmental changes, such as the projected warming of surface seawaters, that would affect the strength of the pelagic-benthic coupling and/or the intensity of primary production are thus expected to ultimately affect the benthic stocks.

In recent decades, the Arctic and sub-Arctic latitudes have experienced significant warming, about 2–3 times higher than the global average (AMAP, 2017). It is widely accepted that the associated continued increase in seawater temperatures and ice melt (from sea-ice and ice sheets) will greatly increase stratification during the xxi century (Capotondi et al., 2012; Nummelin et al., 2016). Several studies have demonstrated that such impending changes will significantly affect pelagic-benthic coupling in future Arctic seas (e.g. Wassmann and Reigstad, 2011; Ardyna and Arrigo, 2020; Wassmann et al., 2020). Decreases in vertical nutrient fluxes associated with increased stratification may directly limit primary production by limiting nutrient concentrations in surface waters (Tremblay and Gagnon, 2009; Tremblay et al., 2015). In addition, nutrient depletion in surface waters is expected to shift the size structure of phytoplankton communities toward smaller cells (e.g. Li et al., 2009), which in turn affects phytoplankton sedimentation rates and may decrease the quantity/quality of organic matter reaching the seabed (Bopp, 2005, Turner, 2015). Considering the critical role of food quantity and quality on benthic biomass and food web structure (e.g. Campanyà-Llovet et al., 2017), stratification should affect both pelagic primary production and organic matter quality, thereby influencing benthic ecosystem dynamics. However, little is known about the role of water column stratification on organic matter transfer to coastal benthic food webs up to predators, including commercial fish species.

In this context, this study investigated benthic food web structure and organic matter transfers to several fish species under contrasting stratification conditions in a sub-Arctic coastal ecosystem (Saint-Pierre-et-Miquelon archipelago – Newfoundland Shelf). We identified the Newfoundland Shelf as an exceptional study area for such an investigation because seawater temperatures have experienced one of the largest warmings in the world in recent decades (+0.37 °C per decade between 1982 and 2018, Belkin, 2009; Chen et al., 2020), resulting in a significant increase in stratification (Cyr et al., 2020). In addition, the Scotian/Newfoundland Shelf is an important region for fisheries providing an important economic resource for Canada's maritime population, employing approximately 80 000 people (Baum and Fuller, 2016). In 2021, landings of benthic invertebrates (e.g. *Homarus americanus* H. Milne Edwards, 1837, *Placopecten magellanicus* (Gmelin, 1791)) from the Canadian Atlantic coast reached 385 000 metric tons and were valued at $3.9 billion, while benthic fish landings (e.g. *Hippoglossus* (Linnaeus, 1758), *Melanogrammus aeglefinus* (Linnaeus, 1758), *Reinhardtius hippoglossoides* (Walbaum, 1792)) reached 84 000 metric tons and were valued at $232 million (DFO, 2021). Therefore, predicting how primary production and pelagic-benthic coupling will respond to increasing ocean stratification is essential to ensure the economic and ecological sustainability of fisheries.

The primary objectives of this study were to: (1) describe the spatial and temporal variability in the structure of associated food webs, and (2) assess the effects of stratification on organic matter transfers. To this end, we sampled benthic assemblages during either low or high stratification periods along a cross-shore transect. Shallow stations of this transect (i.e. 11 m and 25 m) represent unstratified stations because they are always located above/at the thermocline (≈15–25 m, Bridier et al., 2021), whereas deeper stations (i.e. 60 m and 88 m) are considered stratified stations because they remained below the thermocline during

the stratification period. We hypothesize that during the stratified season, benthic invertebrates from shallow stations above/at the thermocline could have a direct access to food sources from the surface/subsurface primary production, while organisms from deep stations may be more sensitive to increased stratification because they do not have direct access to these food resources.

2. Materials and methods

2.1. Study site

The study was conducted in Saint-Pierre-et-Miquelon (46°50′N, 56°20′W), a sub-Arctic Archipelago located on the Newfoundland Shelf (Fig. 1). This site is characterized by large seasonal variations in surface temperatures (i.e. ranging from 0°C to 2°C in March–April up to 18 °C in August–September), but annually stable temperatures in deeper waters (<80 m depth, Lazure et al., 2018; Poitevin et al., 2018). These decoupled seasonal variations in seawater temperatures lead to the formation of a sharp thermocline in late summer, which occurs at depths between 20 m and 40 m (Lazure et al., 2018). This results in a significant reduction in Particulate Organic Matter (POM) quantity/quality and pelagic-benthic coupling strength (Bridier et al., 2021). The temporal dynamics of pelagic primary production is typically characterized by a single bloom that occurs in March–April (Harrison et al., 2013; Pepin et al., 2017), although there may be a secondary phytoplankton bloom in late fall (Pepin et al., 2017; Bridier et al., 2021).

The four sampling stations are distributed along a small cross-shore gradient (L1, L2, L3 & L4 depths = 11 m, 25 m, 60 m and 88 m, respectively, Fig. 1). The sediment grain size distribution was similar along the gradient and dominated by fine sand particles (85 % of the grain size fraction is between 100 μm and 200 μm, Robin, 2007). The sampling stations are exposed to contrasting thermal conditions, with the shallow area (10–30 m) experiencing strong seasonal thermal variations (ranging from 1 °C in March/April to 18 °C in August/September), while the seawater temperature in the deeper area (60 m–80 m) remains stable and cold (below 2 °C) throughout the year (Poitevin et al., 2018; Lazure et al., 2018). Benthic assemblages respond to such contrasting thermal conditions with boreal species (e.g. *Arctica islandica* (Linnaeus, 1767)) colonizing the shallow zone, whereas polar species (e. g. *Astarte montagui* (Dillwyn, 1817)) are restricted to the deeper stations (J. Grall and F. Olivier, pers. com.).

2.2. Sampling

Sampling was conducted over two consecutive years (2017 and 2018) to detect any interannual variability in the benthic food web structure. Benthic organisms were collected using a Rallier du Baty dredge (1 mm square mesh size) on August 30, 2017, and July 10, 2018. All collected species were identified directly on board at the lowest taxonomic level possible and then immersed in seawater at 4 °C for 6 h to eliminate gut contents. All species were either dissected or not, depending on their size, separately wrapped in aluminum foil, and then stored at − 20 °C prior to analysis (see Table S1 for more details on tissue selection).

Main sources of organic matter were collected to identify carbon pathways in the benthic food web. Particulate Organic Matter was collected at 1 m above the seafloor at each station (i.e. 10, 24, 59, and 87 for L1, L2, L3, and L4 stations, respectively) using a 10-L Niskin bottle. Water samples were then filtered through GF/F microfiber filters (pore = 0.7 μm). The upper sediment surface (≈ first 0–3 mm) was collected for SOM samples at shallow stations (L1 & L2 in August 2017, L2 in July 2018) using a 450 mL syringe operated by scuba divers. Sediment samples (i.e. consisting of a mixture of microphytobenthos, various detritus and inorganic particles) were mixed with 1 L of filtered seawater and left to settle for 1 h before the suspended SOM was filtered through GF/F filters. Finally, several dominant and palatable macroalgae species
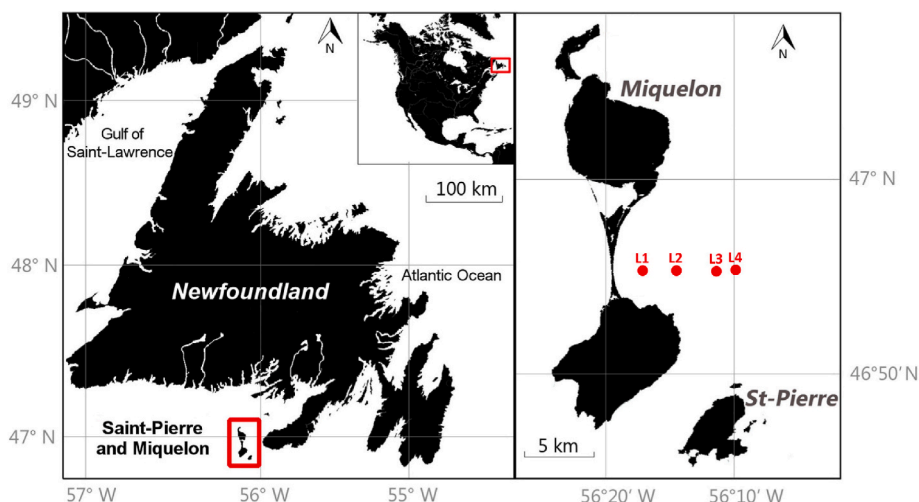
Fig. 1. Localization of the Saint-Pierre-et-Miquelon Archipelago relative to Newfoundland (left) and geographical locations of the four sampled stations (right, modified from Poitevin et al., 2018).

were sampled by scuba divers in 2017, namely *Agarum clathratum* Dumortier, 1822, *Desmarestia viridis* (O.F.Müller) J.V. Lamouroux, 1813, *Halosiphon tomentosus* (Lyngbye) Jaasund, 1957, *Porphyra* spp., *Saccharina latissima* (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W. Saunders, 2006. Among these macroalgae, A. *clathratum* and S. *latissima* were the most abundant species along the studied transect (Bridier et al., 2021). Microphytobenthos was not sampled in this study, but we examined its role in the benthic food web by using an average of 26 microphytobenthos stable isotope values from the literature ($\delta^{13}C = -16.9$, $\delta^{15}N = 6.4$, see McTigue and Dunton, 2017).

Several environmental parameters were recorded to ensure that the two sampling periods were characterized by different stratification levels but similar primary production conditions. Water column stratification was assessed at each station in both seasons (except at station 4 in July 2018, due to logistical constraints) by recording vertical temperature profiles using CTD probes (Seabird 911 plus). Surface primary production dynamics were estimated using chlorophyll-a data measured monthly by the MODIS satellite over the area $46.90–47.00°N/56.15–56.23°W$.

2.3. Laboratory analyses

All animal tissues and macroalgae were freeze-dried at $-50\ °C$ for at least 48 h. Dried tissues were then ground into fine powder using a ball mill (30 Hz, 10-min cycles). Carbonate-rich tissues were divided into two parts: one half was acidified to avoid carbonate-related bias on $\delta^{13}C$ analyses (Søreide et al., 2006), while the other half was not acidified to avoid the effect of this treatment on $\delta^{15}N$ analyses (Jacob et al., 2005). No lipid extraction was performed considering the usually low lipid concentration in benthic invertebrates (Clarke and Peck, 1991) and the potential bias of lipid extractions on $\delta^{15}N$ values (Bodin et al., 2007; Post et al., 2007). In addition, no mathematical corrections were applied due to the inaccuracy of lipid normalization equations that use a constant lipid $\delta^{13}C$ value, despite the large variability in $\delta^{13}C$ lipid bulk signatures in Arctic marine species (Mohan et al., 2016). Carbon and nitrogen isotope ratios are expressed in parts per thousand (‰) and follow the notation of Peterson and Fry (1987):

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 1000$$

Where δX is $\delta^{13}C$ or $\delta^{15}N$ and R is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio.

2.4. Data analyses

2.4.1. Statistical tests and standard ellipses

Univariate two-way PERMANOVAs were performed for all species to test the effect of station (S), year (Y) and the interaction of these two factors (S * Y) on stable isotope signatures ($\delta^{13}C$, $\delta^{15}N$). This permutational analysis was preferred to ANOVAs because of its robustness to normality and homoscedasticity issues (Anderson and Walsh, 2013). In addition, univariate pairwise PERMANOVAs were performed when one factor showed a significant effect to identify which pairs of factors were significantly different from each other. The same procedure was applied to each trophic guild to examine whether trends observed at the community level were generalizable to trophic guilds. Benthic organisms were grouped into three trophic guilds based on their trophic ecology (Fauchald and Jumars, 1979; Macdonald et al., 2010; Degen and Faulwetter, 2019) using the classification of Włodarska-Kowalczuk et al. (2019): suspension-feeders, deposit feeders (i.e. surface/subsurface deposit-feeders and grazers), and carnivores (i.e. predators and scavengers). Stable isotope signatures from factor pairs without significant differences between them were pooled together in subsequent statistical analyses. Stable isotope signatures and standard ellipses from each significant pair of factor levels were plotted in a δ-space to visualize the dimension of their trophic niche (i.e. food web length and basal food source diversity). Standard ellipse overlap (defined as the percentage of δ-space shared between two ellipses relative to the smallest ellipse) was then assessed to identify shifts in the contributions of food source fueling benthic food webs.

2.4.2. Reliance on benthic sources

To distinguish the relative contribution of phytoplankton and benthic primary production to primary/secondary consumers (i.e. benthic invertebrates and fish), we estimated the reliance of each taxon on benthic carbon sources. The percentages of reliance on benthic carbon sources were calculated using the following equation (see Fig. 2), adapted from Vander Zanden and Vadeboncoeur (2002), Sherwood and Rose (2005) and Le Loc'h et al. (2008) for a primary producer baseline.

The carbon isotope signature of pelagic sources ($\delta^{13}C$ pelagic sources) was chosen as the average value of POM $\delta^{13}C$ from both shallow and deep stations. The carbon isotopic signature of benthic sources ($\delta^{13}C$ benthic sources) was calculated from the average between *Saccharina latissima* and microphytobenthos $\delta^{13}C$ signatures. The red alga *Porphyra* spp. Was not included as an end-member in our mixing model because its δ13C signature was too depleted compared to that of benthic consumers to expect a contribution of this organic matter source to their
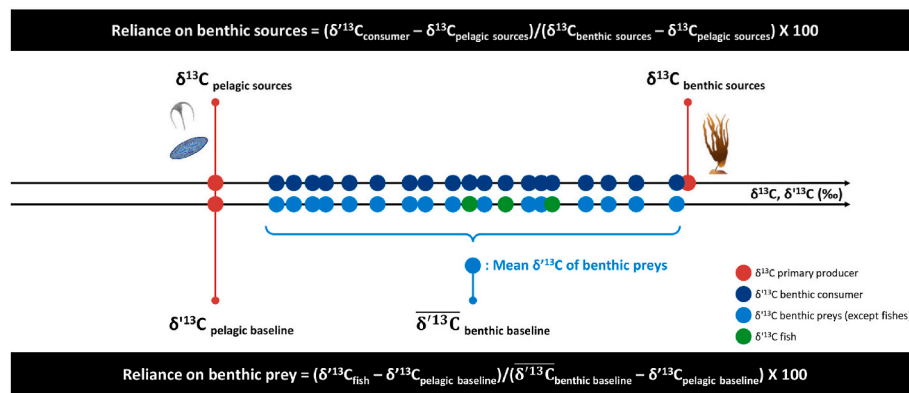
Fig. 2. Conceptual diagram showing the selection of benthic baseline $\delta'^{13}C$ values for the calculation of the reliance on benthic sources (equation I, top) and benthic prey (equation II, bottom).

diet. We also excluded *Agarum clathratum* from this mixing model because we could not clearly distinguish its $\delta^{13}C$ signature from that of the POM pool. It is recommended in mixing models to avoid integrating multiple sources with overlapping isotopic signatures (Phillips et al., 2014). All $\delta^{13}C$ stable isotope signatures were corrected individually for each taxon ($\delta^{13}C$) to standardize all consumers at the same trophic level (i.e. primary producer baseline, i.e. TL = 1), assuming a fractionation factor of 1 ‰ per trophic level (Post, 2002):

$$\delta'^{13}C_{consumer} = \delta^{13}C_{consumer} - (TL_{consumer} - 1) \times 1‰$$

where $TL_{consumer}$ is the trophic level of a consumer relative to primary producer baselines:

$$TL_{consumer} = 1$$
$$+ \frac{\delta^{15}N_{consumer} - \left(\delta^{15}N_{benthic\ sources} \times 0.5 - \delta^{15}N_{pelagic\ sources} \times 0.5\right)}{\Delta^{15}N}$$

With $\Delta^{15}N$ corresponding to the trophic enrichment in $\delta^{15}N$ observed between two trophic levels, based on a fractionation factor of 3.4 ‰ per trophic level (Post, 2002; DeNiro and Epstein, 1981).

2.4.3. Reliance on benthic prey

Fish reliance on benthic prey was calculated to assess the connectivity of fish species to pelagic and benthic food webs. The equation for fish reliance on benthic prey (see Fig. 2) is derived from the previous equation but uses benthic prey (i.e. all benthic consumers except fish) as the benthic baselines. The pelagic baseline corresponds to a virtual $\delta^{13}C$ signature of a pelagic primary consumer (i.e. $\delta'^{13}C = \delta^{13}C - 1$) feeding exclusively on POM (i.e. $\delta^{13}C$ pelagic baseline = $\delta^{13}C$ POM). The benthic baseline was defined following the equation used by Vander Zanden and Vadeboncoeur (2002) and Scherwood and Rose (2005) by averaging all benthic consumer $\delta^{13}C$ signatures (i.e. $\overline{\delta'^{13}C}$). When a fish $\delta'^{13}C$ signature is outside the range of the pelagic and benthic baselines (i.e. either $\delta'^{13}C$ fish < $\delta^{13}C$ pelagic baseline or $\delta'^{13}C$ fish > $\overline{\delta'^{13}C}$ benthic baseline), we set its reliance to either 0 % or 100 %. Fish with a reliance on benthic prey of less than 25 % or greater than 75 % were considered to be exclusively linked to pelagic and benthic food webs, respectively (Sherwood and Rose, 2005). A fish showing an intermediate reliance was considered to be part of both pelagic and benthic food webs (Sherwood and Rose, 2005).

3. Results

3.1. Environmental conditions

Temperature measurements revealed strong differences in stratification between the two sampling periods (see Fig. 3a and b). The water column was highly stratified in late August 2017, with temperatures above 16 °C at the surface and below 1 °C at 80 m (Fig. 3a). A thermocline was observed at 20–30 m, where temperatures dropped from 11 to 7 °C (Fig. 3a). In early July 2018, no thermocline was observed, as temperatures gradually decreased with depth from 9 °C at the surface to 2 °C at 60 m (Fig. 3b). Surface primary production dynamics measured by MODIS satellites showed a small phytoplankton bloom in May 2017 and April 2018 (Fig. 3c), with greater intensity in 2017 than in 2018 (i.e. [chlorophyll-a] = 3.0 and 1.4 µg.L^{-1}, respectively). A second fall bloom was observed in October 2017 (i.e.
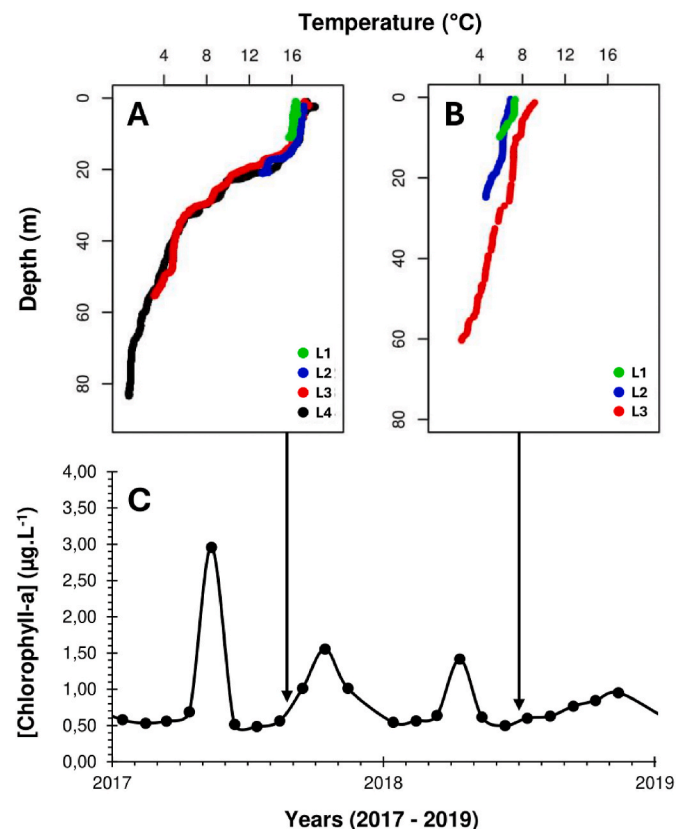

Fig. 3. Temperature profiles (A, B) and chlorophyll *a* concentration over the two sampling periods in Miquelon. The upper plots show vertical temperature variations recorded at stations L1, L2, L3, and L4 in late August 2017 (A) and early July 2018 (B). The bottom plot (C) represents the dynamics of surface chlorophyll *a* concentration from 2017 to 2019 (monthly averages).

[Chlorophyll-a] = 1.6 µg.L^{-1}) but not in 2018 (Fig. 3c). Surface chlorophyll-a concentrations measured during the sampling of benthic invertebrates and food sources were of the same order of magnitude in both years (i.e. [Chlorophyll-a] = 0.66 and 0.54 µg.L^{-1} for late August 2017 and early July 2018, respectively).

3.2. Benthic food web structure

We observed no differences in the structure of the entire benthic food web between 2017 and 2018 (p < 0.05, two-way PERMANOVAs, Table 1). Weak spatial variations were detected in δ^{15}N signatures (p < 0.05, two-ways PERMANOVAs), while none occurred for δ^{13}C signatures. According to pairwise PERMANOVAs, δ^{15}N values were significantly lower in tissues from the L1 station compared to those from the L3-L4 stations (p < 0.05). Based on these results, we decided to pool the stable isotope signatures into two groups representing "shallow stations" (L1 & L2) and "deep stations" (L3 & L4) from both seasons. Despite this new data arrangement, the standard ellipses of both communities still show high overlap (i.e. 73.2 %), confirming the relatively low spatial variability along the transect (Fig. 4a). The position of the standard ellipse of the community from the deep stations was slightly higher on the δ^{15}N axis than that of the shallow benthic community (Fig. 4a, p < 0.05, two-way PERMANOVAs). Statistical analyses conducted separately for each trophic group yielded results similar to those for the entire benthic community. No temporal variations were observed, and spatial variations were significant only for δ^{15}N signatures, except for deposit-feeders for which significant spatial variations were observed for both δ^{13}C and δ^{15}N signatures (p < 0.05, two-way PERMANOVAs, Table 1). Furthermore, all trophic groups from deep stations showed a higher position on the δ^{15}N axis than those from shallow stations (Fig. 4b). Deposit-feeder standard ellipses showed the lowest overlap between shallow and deep stations (i.e. 46.6 %, Fig. 4b).

Table 1
Results of PERMANOVA analyses performed on the δ^{13}C and δ^{15}N signatures of all species as well as each trophic group (suspension-feeders, deposit-feeders and carnivores). Two sources of variation were tested: Station (S, fixed with 4 levels) and Year (Y, fixed with two levels). Significant p-values (p) are presented in **bold**.

Feeding group	Isotope ratio	Effect	F-statistic (df)	p-perm
All fauna	δ^{13}C	S	1.09 (3)	0.36
		Y	1.19 (1)	0.27
		S * Y	0.59 (3)	0.62
	δ^{15}N	S	2.73 (3)	**< 0.05**
		Y	1.81 (1)	0.18
		S * Y	0.19 (3)	0.90
Suspension-feeders	δ^{13}C	S	2.30 (3)	0.09
		Y	1.43 (1)	0.24
		S * Y	0.18 (3)	0.91
	δ^{15}N	S	4.70 (3)	**0.01**
		Y	0.49 (1)	0.48
		S * Y	0.33 (3)	0.81
Deposit-feeders	δ^{13}C	S	3.60 (3)	**0.03**
		Y	0.00 (1)	0.99
		S * Y	0.88 (3)	0.47
	δ^{15}N	S	3.08 (3)	**0.04**
		Y	0.03 (1)	0.86
		S * Y	1.00 (3)	0.40
Carnivores	δ^{13}C	S	0.98 (3)	0.41
		Y	0.16 (1)	0.69
		S * Y	0.67 (3)	0.57
	δ^{15}N	S	2.94 (3)	**0.03**
		Y	0.78 (1)	0.38
		S * Y	0.15 (3)	0.93

3.3. Reliance on benthic resources and benthic prey

Stable isotope signatures of benthic organisms from both shallow and deep stations showed an overall large range across the δ^{13}C and δ^{15}N axes (Fig. 4a and b). Based on a common δ^{15}N enrichment factor of 3.4 ‰, food web length spanned nearly three trophic levels at both stations (Δ δ^{15}N range = 9.1 ‰ and 9.2 ‰ in shallow and deep stations, respectively). The wide range of stable isotope signatures across the δ^{13}C axis was also reflected by substantial variation in the reliance on benthic sources among benthic consumers (Fig. 5). Reliance on benthic sources ranged from 0 % (Caprellidae) to 96.4 % (*Buccinum undatum* Linnaeus, 1758) at shallow stations and from 4.7 % (Pycnogonida) to 82.5 % (Turritellidae) at deep stations (Fig. 5a). The ranges of reliance on benthic sources were homogeneous among trophic groups and varied mainly from 20 % to 80 % (mean reliance = 51.0 % and 43.9 % for shallow and deep stations, respectively). The percentages of fish reliance on benthic sources showed a moderate reliance of fish on the benthic primary production. Almost all estimates were below 50 %, ranging from 9.0 % for *Eumicrotremus spinosus* (Fabricius, 1776) to 52.5 % for *Hippoglossoides platessoides* (mean reliance = 36.8 %, Fig. 5b–Table 2). In contrast, percentages of fish reliance on benthic prey were much higher, ranging from 59.8 for *Cyclopterus lumpus* Linnaeus, 1758 to 100 % for *Hippoglossoides platessoides* (mean reliance = 77.2 %), except for *Eumicrotremus spinosus* (19.3 %, Fig. 5c–Table 2).

4. Discussion

4.1. Structure of the benthic food web of Saint-Pierre-et-Miquelon

4.1.1. Year-to-year variations in the benthic food web structure
Despite strong seasonal variations in trophic conditions (Bridier et al., 2021), benthic food web structure did not differ between low and high stratification periods. While some might suggest that these results imply that seasonal stratification has no effect on the structure of benthic food webs, we believe that they are more likely related to the isotopic turnover rates of animal tissues. Previous temporal studies have shown that benthic invertebrates can exhibit highly variable integration times (ranging from one month, e.g. Nordström et al., 2009, Rodil et al., 2020, to one year or more, e.g. Fry, 2006, Wing et al., 2012), depending on tissue type, animal growth rate, or ambient temperature (Vander Zanden et al., 2015). Therefore, the slow growth rates of long-lived benthic invertebrates in cold polar/sub-polar waters are likely associated with low turnover rates (i.e. long integration times) exceeding several months or a year (Wing et al., 2012; McMeans et al., 2015). Therefore, we hypothesize that the time lag between low and high stratification conditions (i.e. ≈ 2 months) is too short for benthic invertebrates to reach their isotopic equilibrium. In addition, the extent to which food availability and quality may influence rates of isotopic incorporation into animal tissues could be questioned (Martínez del Rio et al., 2009). High food quality and availability during the phytoplankton bloom (Martínez del Rio et al., 2009) may lead to a higher food assimilation and isotopic incorporation in invertebrate tissues than during periods outside of phytoplankton blooms. Isotopic signatures of benthic invertebrates from both low and high stratification periods could then reflect trophic conditions during the previous phytoplankton bloom. This hypothesis could be tested through more regular sampling of benthic invertebrates or by stable isotope analyses associated with complementary trophic markers (e.g. fatty acids, e.g. Amiraux et al., 2021).

4.1.2. Benthic food web vertical structure
The vertical structure of the benthic food web showed little spatial variation in δ^{15}N signatures along the cross-shore transect. The length of the benthic food web (from primary producers to uppermost predators) was estimated to be ≈ 3.7–3.8 trophic levels in both shallow and deep stations, a common value among those known in marine food webs
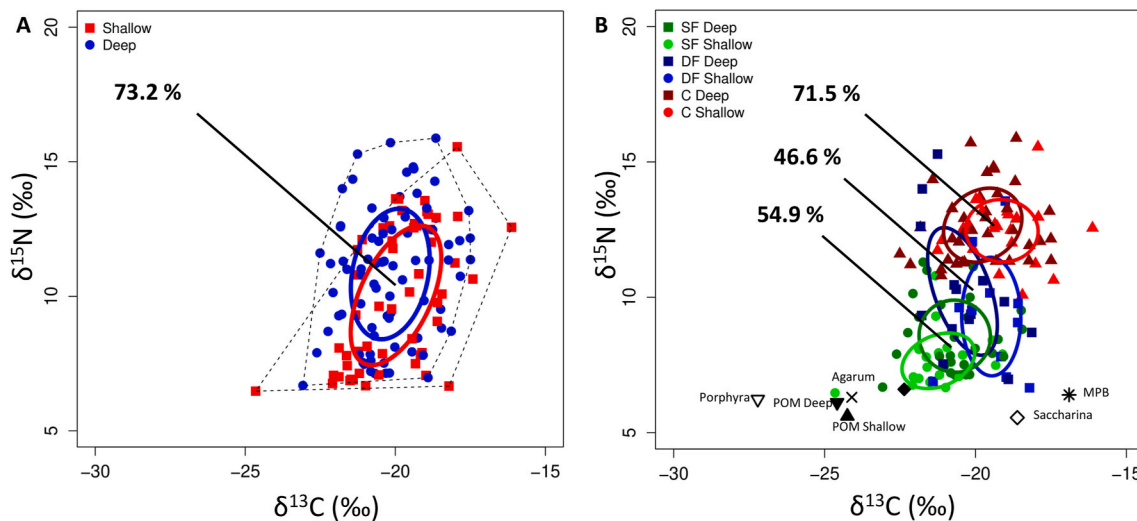
Fig. 4. Standard ellipses (solid lines) and convex hulls (dashed lines) of shallow and deep benthic assemblages based on either A) all species or B) each trophic group (suspension-feeders SF, deposit-feeders DF, carnivores C).

(Vander Zanden and Fetzer, 2007). However, the majority of suspension-feeder signatures surprisingly remained below their presumed trophic level (i.e. TL primary consumer range = 1.07–2.34 and 1.13–2.49, mean = 1.42 and 1.69, in shallow and deep stations, respectively). Several factors could explain such unexpected observations. First, the $\delta^{15}N$ fractionation factor used here ($\Delta\delta^{15}N$ = 3.4 ‰, Post, 2002) may be somewhat high compared to the effective fractionation in aquatic invertebrates as reported by McCutchan et al. (2003) and Vanderklift and Ponsard (2003). The McCutchan factor ($\Delta\delta^{15}N$ = 2.3 ‰, McCutchan et al., 2003) seems to be effectively closer to the observed $\delta^{15}N$ fractionation between primary producers and primary consumers. However, this factor seems paradoxically inappropriate for upper trophic levels, since the mean $\delta^{15}N$ fractionation between primary and secondary consumers in our study ranges between 3.5 ‰ and 4.5 ‰ (i.e. ≈ 1.5 to 2 times higher than the McCutchan factor). This trend is somewhat contradictory to what is typically observed in marine food webs, as isotope discrimination generally decreases at higher trophic levels (Hussey et al., 2014). It is therefore unlikely that the fractionation factor explains the low trophic level observed in suspension-feeders.

On the other hand, low trophic positions in suspension-feeders have been already reported from other locations and interpreted as a possible indicator of food selection. Some suspension-feeders may indeed select for a specific particle type/size, depending on their anatomy as well as on the quality and/or availability of suspended organic matter, and thus exhibit a distinct (depleted) $\delta^{15}N$ signature from the POM bulk (Fry, 1988; Iken et al., 2005; Le Loc'h et al., 2008).

Finally, an alternative hypothesis is that the $\delta^{15}N$ signatures of organic matter sources sampled during this study are higher than those of organic matter sources assimilated by benthic invertebrates during previous periods (months to years). Stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of trophic baselines (e.g. phytoplankton, macroalgae) are rarely stable over the whole season/year (e.g. Nordström et al., 2009; Dethier et al., 2013). As a result, the isotopic signatures of benthic consumers are not always in equilibrium and can sometimes reflect the isotopic signature of trophic baselines from the previous season (Woodland et al., 2012; McMeans et al., 2015). Time-lagged sampling of trophic baselines and primary consumer tissues, as recommended by McMeans et al. (2015), may have revealed more consistent fractionation between primary producers and primary consumers. The slight variations in POM $\delta^{15}N$ signatures observed between 2017 and 2018 ($\delta^{15}N$ = 6.6 ‰ and 4.4 ‰, respectively) could validate this hypothesis. These results may imply that the benthic food web of Saint-Pierre-et-Miquelon is actually one trophic level higher than our estimate.

4.1.3. Benthic food web horizontal structure

The horizontal dimension of the benthic food web is similar in both stations and shows a large extent on the $\delta^{13}C$ axis (over 8.5 ‰), reflecting the contribution of several food sources with contrasting $\delta^{13}C$ signatures (Layman et al., 2007). According to the percentages of reliance on benthic sources, many benthic consumers actually feed on a mixed diet of both pelagic (i.e. POM) and benthic (i.e. macroalgae and/or microphytobenthos) sources (i.e. 85 % of benthic consumers relied between 20 % and 80 % on benthic sources). In contrast, some species seem to feed exclusively on pelagic (such as Caprellidae, Cumaceae) or benthic sources (e.g. *Lacuna vincta* (Montagu, 1803), *Siphonoecetes* sp., *Tellina* sp.).

The lack of spatial variation in the horizontal structure of the benthic food web suggests that species assemblages from both shallow and deep stations are based on the same organic matter sources. This result may be surprising in light of previous cross-shelf studies showing that benthic primary production and stratification conditions can induce strong spatial variation in the $\delta^{13}C$ and $\delta^{15}N$ signatures of primary consumers between shallow and deep stations. For instance, the relative increase in benthic primary production over phytoplankton production in shallow areas is usually associated with an increase in the $\delta^{13}C$ signature of primary consumers (e.g. Miller et al., 2008; Nérot et al., 2012; Carlier et al., 2015). In our study, the absence of such a spatial shift could therefore imply that the contribution of benthic sources (i.e. macroalgae and microphytobenthos) is homogeneous along the cross-shore transect. Furthermore, previous studies have shown that contrasting stratification conditions along cross-shelf gradients can lead to differences in trophic functioning between weakly and highly stratified areas (e.g. González et al., 2013; Chouvelon et al., 2015; Day et al., 2019). For example, Chouvelon et al. (2015) observed a decrease in the $\delta^{13}C$ signature of primary consumers along a cross-shelf transect, which they attribute to a shift in trophic functioning from a microalgae-based system at low stratified stations to a microbial-based system at high stratified stations.

Although strong variations in the trophic environment were observed between shallow and deep stations (in terms of organic matter availability, sources and quality, Bridier et al., 2021), they did not induce subsequent variations in primary consumer $\delta^{13}C$ signatures or benthic food web structure. We propose two hypotheses to explain this lack of spatial variation in the food web structure, which will be discussed in the next section: (1) the impact of stratification on benthic food webs may vary according to the synchronization/desynchronization between phytoplankton blooms and stratification onsets, and (2) the contribution of alternative organic matter sources to the pelagic trophic
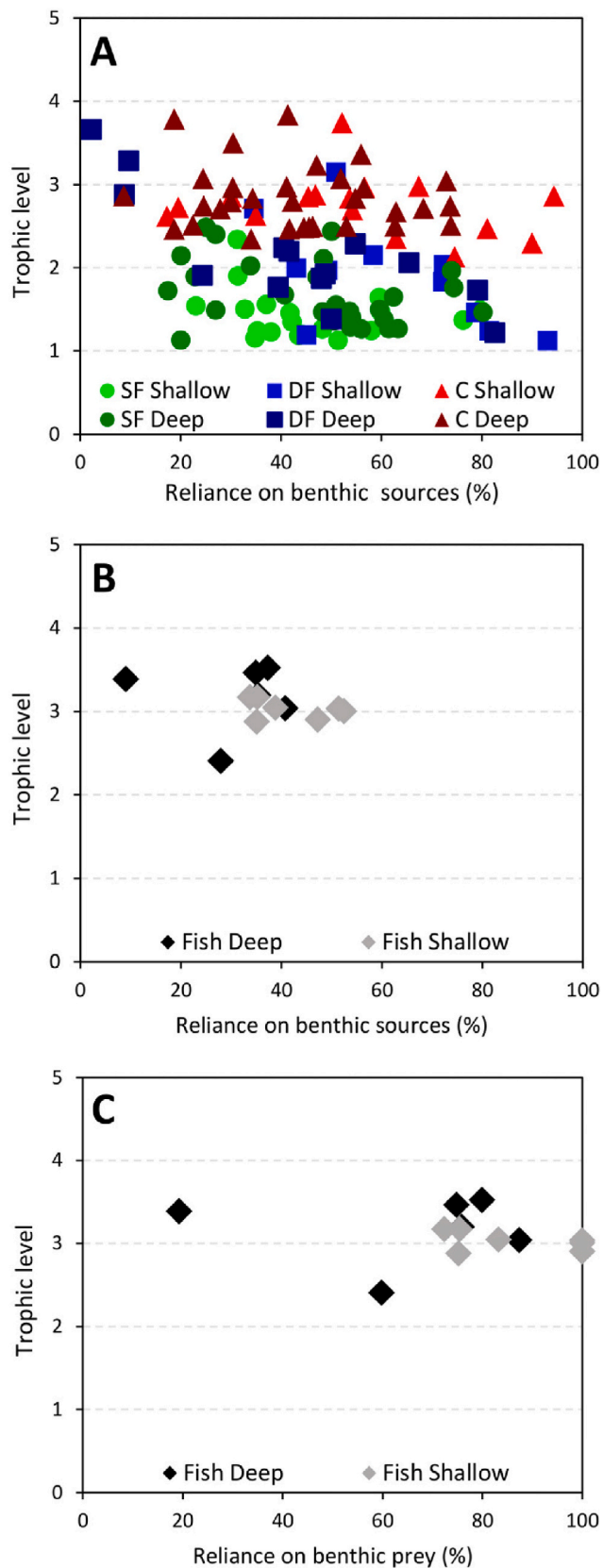
Fig. 5. Plots representing the reliance of each taxon on benthic sources/prey and its associated trophic level. Upper plot (A) show the reliance on benthic sources of all benthic species (except fish) from shallow and deep stations according to their feeding groups (suspensive feeders SF, deposit feeders DF and carnivores C). Middle and lower plots show the reliance of fish on benthic sources (B) and benthic prey (C).

Table 2

Percentages of fish reliance on benthic sources and prey with associated a priori and δ13C-derived assignments.

Species	Reliance on benthic sources (%)	Reliance on benthic prey (%)	A priori trophic assignment	δ13C-derived trophic assignment
Eumicrotremus spinosus	9.0	19.3	pelagic	pelagic
Cyclopterus lumpus	27.9	59.8	mixed	mixed
Pholis gunnellus	33.7	72.4	mixed	mixed
Artediellus uncinatus	34.9	74.8	benthic	mixed
Cottidae (Shallow)	35.0	75.2	benthic	benthic
Myoxocephalus scorpius	35.2	75.5	mixed	benthic
Hippoglossoides platessoides (Deep)	35.3	75.8	benthic	benthic
Gymnocanthus tricuspis	37.2	79.9	mixed	benthic
Gadus morhua	38.8	83.2	mixed	benthic
Cottidae (Deep)	40.7	87.4	benthic	benthic
Zoarces americanus	47.2	100	benthic	benthic
Lumpeninae	51.4	100	benthic	benthic
Hippoglossoides platessoides (Shallow)	52.5	100	benthic	benthic
Total mean	36.8	77.2		

environment may also limit the consequences of stratification on benthic food webs.

4.2. Mismatch between phytoplankton bloom and stratification onsets

The effect of trophic constraints may depend strongly on the onset of stratification and, in particular, its duration. First, although the Newfoundland Shelf is one of the most highly stratified marine systems at sub-Arctic latitudes (e.g. Harrison et al., 2013), the duration of such extreme events is quite limited in time. Moderate stratification conditions are typically observed on the Newfoundland Shelf in May/June and October/November, while strong stratification conditions are observed in the summer only from July to September (Craig and Colbourne, 2002; Harrison et al., 2013; Cyr et al., 2020). Outside of this timeframe, all the stations in Saint-Pierre-et-Miquelon have access to the same water mass and are likely to feed on the same POM pool. Therefore, the duration of trophic forcing associated with high stratification conditions may not be long enough in time to have a detectable effect on the structure of the benthic food web. In addition, and perhaps even more importantly, the short duration of strong stratification conditions in Saint-Pierre-et-Miquelon may not correspond to a period of high pelagic primary productivity. In fact, most of the annual pelagic primary production on the Newfoundland Shelf is actually due to a single bloom that occurs in March–April (i.e. three months before the high stratification period, Harrison et al., 2013; Pepin et al., 2017; Maillet et al., 2019). Consequently, we believe that benthic organisms in Saint-Pierre-et-Miquelon may be relatively unaffected by harsh trophic conditions during the period of high stratification, as they are likely to assimilate most of their annual carbon requirements before the stratification onset. Such hypothesis suggests therefore that the coupling between stratification and the appearance of phytoplankton blooms could be a key factor controlling the impact of stratification on benthic food webs especially if organic matter transfers mainly imply the use of pelagic sources. Under climate changes, the sub-Arctic zones characterized by a similar mismatch between phytoplankton blooms and high stratification period could therefore be relatively unaffected by future increases in thermal stratification. On the other hand, a large part of the

annual primary production in high-Arctic areas is triggered by a match between sea ice retreat and high stratification conditions (e.g. Wassmann and Reigstad, 2011; Holding et al., 2019). In such case, forthcoming strengthening in stratification should thus have a deeper impact on the annual primary production budget.

4.3. Contribution of the benthic primary production and its role in coastal ecosystems

The present work emphasizes a strong contribution of benthic sources (i.e. macroalgae and microphytobenthos) to the diet of benthic consumers at both shallow and deep stations, which could explain the lack of spatial variation in the food web structure. The percentages of reliance on benthic sources reveal that benthic primary production provides at least half of the community's carbon requirements. However, there is strong variation among benthic consumers, with some species feeding exclusively on pelagic sources and others feed feeding exclusively on benthic sources. These percentages of reliance on benthic sources should be considered as low estimates in this study because our mixing model does not include macroalgae with less enriched isotopic signatures (e.g. *Agarum clathratum* Dumortier, 1822was not include because we cannot distinguish this source from the POM pool). Such a high macroalgal contribution along the cross-shore transect may be surprising, as a previous study showed that the contribution of macroalgae to the POM pool was limited to the shallowest stations (Bridier et al., 2021). However, macroalgae erosion and detritus export to the POM can potentially be higly variable in space and time, depending on numerous local abiotic and biotic factors (Krumhansl and Scheibling, 2011, 2012; Wernberg and Filbee-Dexter, 2018). In addition, POM composition is usually highly variable over time (i.e. from few hours to few days) in shallow areas because the particles present in the water column at the time of sampling are strongly influenced by coastal hydrological processes (i.e. tidal cycles, short upwelling/downwelling events, e.g. Moynihan et al., 2016; David et al., 2019; Dyer et al., 2019). This may be particularly true in Saint-Pierre-et-Miquelon, where diurnal internal waves (see Lazure et al., 2018) can rapidly change the nearshore POM composition by bringing deep water to the surface or surface water to the bottom (Woodson, 2018). Our sampling strategy, based on a single sampling date per station, would not detect variations in POM composition and sporadic pulses of macroalgal detritus.

The high contributions of macroalgae and microphytobenthos along the cross-shore transect suggest that most benthic consumers may be relatively independent of pelagic primary production and potentially less sensitive to changes in POM quality/quantity that occur under highly stratified conditions. While several authors predict that increased stratification should reduce both primary production and organic matter quality in the pelagic compartment (e.g. Wassmann and Reigstad, 2011; Turner, 2015; Bridier et al., 2021), the impact on the benthic compartment remains uncertain. For example, microphytobenthos is well adapted to pelagic nutrient depletion because benthic diatoms can utilize nutrients released directly from the seabed and benefit from lower seawater turbidity due to reduced phytoplankton biomass (MacIntyre et al., 1996; Glud et al., 2009; Griffiths et al., 2017). In addition, perennial macroalgae are less sensitive to pelagic nutrient depletion because they require fewer nutrients for optimal growth than phytoplankton species (Pedersen and Borum, 1996). As a result, the relative importance of benthic and pelagic primary production in coastal ecosystems is often set by local nutrient regimes, with oligotrophic conditions favoring the former and eutrophic conditions favoring the latter (Duarte, 1995; Cloern, 2001; Riemann et al., 2016). This paradigm suggests that future increases in stratification may have contrasting effects on Arctic ecosystems, depending on stratification characteristics (i. e. either haline or temperature-based stratification, but see in Ardyna and Arrigo, 2020). In shallow nearshore areas exposed to enhanced temperature-based stratification (e.g. Saint-Pierre-et-Miquelon), benthic primary production could be crucial for the resilience of benthic ecosystems to higher nutrient depletion. Benthic primary producers may provide an alternative source of organic matter to the pelagic organic matter pool, and their relative contribution to benthic food webs might even be expected to increase as pelagic primary production decreases. However, the contribution of benthic primary producers is more uncertain in Arctic ecosystems facing increased haline-based stratification, as the high turbidity associated with freshwater inputs (e.g. Murray et al., 2015) could affect both pelagic and benthic primary production (Bridier et al., 2019).

4.4. Fish connectivity to the benthic food web

According to estimates of fish reliance on benthic sources in this study, benthic primary producers are an important source of organic matter for fish (mean benthic reliance = 37 %, range = 9–53 %). This likely reflects a tight coupling in shallow areas, as studies conducted in deeper regions (i.e. > 100 m) generally show a dominant reliance on phytoplankton (e.g. Le Loc'h et al., 2008, Cresson et al., 2020). Previous studies have highlighted a major contribution of benthic primary producers to fish food webs in shallow zones, such as the eastern English Channel (≈50 %, Kopp et al., 2015; Cresson et al., 2020), the western Norwegian (33–68 %, Fredriksen, 2003) and northwestern American (32–89 %, von Biela et al., 2016) coasts, the Wadden Sea (Christianen et al., 2017) or the Svalbard coast (McGovern et al., 2018). The differences in benthic reliance between Saint-Pierre-et-Miquelon and the other sites may be related to depth, as the previously cited studies were conducted in shallower areas compared to the present work.

Estimates of fish reliance on benthic prey indicate that almost all fish feed exclusively on benthic prey (benthic reliance >75 %), except for the lumpfish *Cyclopterus lumpus* and the Atlantic spiny lumpsucker *Eumicrotremus spinosus*. The mixed reliance of *Cyclopterus lumpus* on benthic and pelagic prey (benthic reliance = 59 %) is consistent with previous data showing that lumpfish feed on both benthic harpacticoids and pelagic calanoids (Daborn and Gregory, 1982; Ingólfsson and Kristjánsson, 2002). In contrast, Roshchin (2006) and Berge and Nahrgang (2013) observed that *Eumicrotremus spinosus* feeds primarily on *Themisto* spp. Amphipods, which may explain its exclusive feeding on pelagic prey in Saint-Pierre-et-Miquelon (benthic reliance <25 %). It could be argued that the present study underestimates the contribution of phytoplankton and pelagic prey to the overall fish food web because our sampling did not include strictly pelagic fish species. However, previous studies have shown that the distinction between pelagic and benthic fish is less relevant in shallow habitats where pelagic and benthic prey are present in the same habitat (Kopp et al., 2015; Giraldo et al., 2017). It is therefore possible that benthic primary production may also benefit pelagic fish to some extent if they feed partly on benthic prey.

The future of sub-Arctic fisheries will obviously depend primarily on the regulation of the fishing industry and the implementation of new management policies to control fishing pressure (e.g. Jørgensen et al., 2017). However, it may be interesting to investigate to what extent the evolution of sub-Arctic fisheries may also depend in part on the evolution of benthic and pelagic sources in a warmer and more stratified ocean.

CRediT authorship contribution statement

Guillaume Bridier: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Frédéric Olivier:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Laurent Chauvaud:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Vincent Le Garrec:** Writing – review & editing, Methodology, Investigation. **Gabin Droual:** Writing – review & editing, Methodology, Investigation. **Jacques Grall:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108982.

Data availability

Data will be made available on request.

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