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Icelandic intertidal fish communities and effects of knotted wrack (*Ascophyllum nodosum*) harvesting

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Research Article

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Abstract

In Iceland, sheltered rocky intertidal zones like Breiðafjörður bay are dominated by monospecific stands of *Ascophyllum nodosum*, providing key habitats for marine organisms. Increasing demand for *A. nodosum* has led to its commercial exploitation, yet impacts on fish assemblages remain poorly known. Using a novel multi-mesh netting approach, we characterised seasonal patterns in fish composition, abundance, size structure, age, and diet. Additionally, to assess the local effects of seaweed harvesting, commercial harvesting was conducted, with comparisons being made between treatment and control unharvested areas during different seasons. Nine fish species were identified, with *Pollachius virens, Myoxocephalus scorpius*, and *Gadus morhua* being the most common. Fish abundance peaked in summer, and declined the following spring, suggesting cohort turnover with juvenile gadoids relying on these habitats as nurseries. *P. virens* showed increased length through seasons, whereas no trends in length or abundance were observed for *M. scorpius*. Effects of seaweed harvesting were minimal, although fish diversity was slightly higher and *G. morhua* significantly larger in control plots. Stomach contents exhibited a greater diversity of prey types in harvested sites, suggesting potential impacts on trophic dynamics. These findings underscore the importance of *A. nodosum*-dominated habitats as nursery grounds for commercially valuable gadoids and highlight the need for a precautionary approach to seaweed harvesting to maintain ecosystem health.

Introduction

Rocky intertidal areas are diverse and productive ecosystems, providing valuable habitat for both adult and juvenile fish populations (Compaire *et al.*, 2016; Dias *et al.*, 2014). Historically, most attention has been given to sandy beaches and mudflats in tropical and temperate areas as nursery grounds for fish (Gibson, 1973; Marley *et al.*, 2020; Tse *et al.*, 2008). However, there is growing evidence of the importance of the rocky intertidal zone as a fish nursery (Dias *et al.*, 2016, 2014; Studebaker, 2006; Studebaker *et al.*, 2009). Intertidal fish communities have been studied extensively worldwide, particularly within rocky estuaries (Carminatto *et al.*, 2020) and tidepools (Bezerra *et al.*, 2017; White *et al.*, 2015), but much of this work has been in lower latitudes (Choat, 1982; Dias *et al.*, 2014). In contrast, our understanding of fish assemblages at higher latitudes remains limited (Gibson, 1972; Henriques and Almada, 1998; Pihl and Wennhage, 2002). These little studied systems are subjected to several anthropogenic stressors such as pollution (Crowe *et al.*, 2000), introduced alien species (Magnússon *et al.*, 2024), and extensive exploitation of living resources (Boaden and Dring, 1980), all of which are exacerbated by overarching effects of global change (Hawkins *et al.*, in press; Thompson *et al.*, 2002).

Rocky shores, particularly sheltered rocky shores, provide abundant refuges, such as crevices, rockpools, and spaces beneath boulders and algae, hosting both transient juvenile marine fish species that use these habitats as nurseries (Henriques and Almada, 1998) and resident intertidal fish species (Horn *et al.*, 1998). Amongst the transient species are cod (*Gadus morhua* Linnaeus, 1758) and saithe (*Pollachius virens* [Linnaeus, 1758]), two common species of boreal waters of the North Atlantic (Dutil and Brander, 2003; ICES, 2020; Saha *et al.*, 2015) of commercial importance (Astthorsson *et al.*, 2007). Various aspects of the ecology of these species have been well studied, such as distribution (Armannsson *et al.*, 2007; Begg and Marteinsdottir, 2002; Rose *et al.*, 2000), abundance (McCain *et al.*, 2016), feeding ecology (Jaworski and Ragnarsson, 2006; Jónsson, 1997; Nedreaas, 1987; Pálsson, 1997), or foraging behaviour (Pálsson, 1983), but

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very few studies have focused on their use of the rocky intertidal zone (Elliott *et al.*, 2016; Pihl and Wennhage, 2002; Rangeley and Kramer, 1995a, 1995b). In contrast, more is known about resident species such as the shorthorn sculpin (*Myoxocephalus scorpius* [Linnaeus, 1758]), a common inhabitant of the Icelandic rocky intertidal zone (Jónsson and Pálsson, 2006). It has various adaptations to deal with tide-out emersion and hypoxia in rock pools (Nonnotte and Kirsch, 1978; Sundell *et al.*, 2021) and is a sit-and-wait predator that feeds on seaweed associated prey such as small crustaceans (Sawyer, 1967; Shorty and Gannon, 2013) and fish (Cardinale, 2000; Dick *et al.*, 2009; Hauksson, 1999; Landry *et al.*, 2018).

Ascophyllum nodosum (L.) Le Jolis is a large canopy-forming alga found on both sides of the North Atlantic (Jenkins *et al.*, 2008). It provides critical shelter and habitat for a diverse array of associated sessile and mobile species (Magnússon *et al.*, 2024; Pereira *et al.*, 2020; Phillippi *et al.*, 2014; Pocklington *et al.*, 2018). Increases in demand and access to large quantities of *A. nodosum* in Canada, Ireland, Scotland, Norway, and Iceland have led to commercial exploitation for various uses such as alginates, food, or fertilisers (Gunnarsson *et al.*, 2019; Mac Monagail *et al.*, 2017; Pereira *et al.*, 2020). *Ascophyllum nodosum* has been commercially harvested in Breiðafjörður for several decades, with current extraction estimates ranging between 13,000 and 15,000 tonnes per annum (Icelandic Directorate of Fisheries, 2025). Mechanical harvesting in the area typically removes approximately 30–66% of the standing biomass, cutting the fronds above the holdfast to allow regrowth (Gunnarsdóttir, unpublished data). Intensive harvesting can exert profound effects on the targeted alga and associated biota (Fegley, 2001; Pereira *et al.*, 2020; Phillippi *et al.*, 2014; Seeley and Schlesinger, 2012). Recovery rates vary depending on the extent and type of biomass removal. After complete removal, including holdfast complexes, regeneration can be particularly slow taking up to 20 years (Gendron *et al.*, 2018; Ingólfsson and Hawkins, 2008; Jenkins *et al.*, 2004). In contrast, when a lower proportion of the biomass is harvested by cutting fronds above the holdfast, recovery is faster (Johnston *et al.*, 2023; Lauzon-Guay *et al.*, 2021; Ugarte *et al.*, 2007).

The usage and role of fishes within canopy-forming fucoid assemblages such as *A. nodosum* beds in the rocky intertidal zone is also understudied (Rangeley, 1994). Moreover, the impacts of harvesting large fucoids on mobile fish assemblages and populations have received little attention (Pereira *et al.*, 2020). Fish widely forage over the intertidal zone, thereby influencing community structure (Choat, 1982), linking algae-dominated areas with other marine habitats, through migration (Fulton *et al.*, 2020; Kang *et al.*, 2015). Various studies have explored the role of fish in intertidal food webs through stomach content analysis (Da Silveira *et al.*, 2020), from which most current understanding of trophic ecology is derived (Braga *et al.*, 2012). These have yielded valuable insights into fish diet and food-webs within intertidal communities (Hadwen *et al.*, 2007; Mendonça *et al.*, 2019).

Our overall aim was to investigate the fish assemblages across seasons in the *Ascophyllum nodosum* covered intertidal rocky shores in Breiðafjörður, Iceland, and experimentally assess impacts of commercial harvesting. We compared harvested areas with adjacent control areas using a multi-mesh netting approach, to characterise fish assemblage composition, population abundance, size/age structure and feeding ecology of the most caught resident species (*M. scorpius*) plus those using the intertidal as feeding or nursery grounds (*G. morhua* and *P. virens*). Thus, we explored whether current harvesting practices impact fish assemblages and the provision of ecosystem services such as feeding and nursery grounds.

Materials and methods

Study area and experimental design

The study was made between June 2019 and June 2020 at Borg, in the inner reaches of Breiðafjörður bay, a large semi-enclosed bay in North-West Iceland with a mean tidal amplitude at spring tide of 4.3 m.

Four experimental plots were randomly interspersed at the study site: two control plots in areas without *A. nodosum* harvesting (labelled C1 65°28.52 N, 22°00.91′ W and C2 65°28.48′ N, 22°00.88′ W), and two harvested plots (labelled H1 65°28.58′ N, 22° 00.91′ W and H2 65°28.46′ N, 22°00.91′ W) (Figure 1, Supp. Fig.1) using an Aquamarine™ floating aquatic plant harvesters operating in the area. Prior to harvesting, *A. nodosum* cover was visually assessed to be 100% in all plots. The study area had no prior history of commercial cutting, ensuring that any observed effects resulted from the experimental treatment. Harvesting was done once on the 1st of July 2019, following standard commercial practices. Commercial harvesting operations run from spring to autumn, using a rotation system in which areas are left untouched for 4–6 years between harvesting events. Harvesters will also typically leave large patches of untouched *A. nodosum* next to harvested areas. Both harvested plots were treated and cut equally, leaving the holdfasts intact, matching harvesting practices in the region (Gunnarsdóttir, unpublished data).

In each plot, two multi-mesh nets equipped with floats (one 4 m in length and the other 5 m) were deployed. The nets had 1 × 1 m panels with different mesh sizes in the following order: the 4 m net had 29, 35, 24, and 19.5 mm mesh-size panels; the 5 m net had 15.5, 10, 19.5, 12.5, and 8 mm mesh-size panels (mesh sizes recommended by Einarsson, Marine and Freshwater Research Institute of Iceland, personal communication). The nets were fixed to large boulders on the substratum, using bolted eye nuts and carabiners, floating upright on the flooding tide. To prevent algae from entangling the nets, a narrow 4 or 5 m long, 1 m wide strip of larger algae around each net was cleared at both control and harvested sites. Only the fronds immediately adjacent to the nets were trimmed, meaning that this clearing was minimal and localised, not comparable in scale to commercial harvesting. The nets were set during the evening low tide and then emptied on the next low tide at midday for three consecutive nights. Three sets of bolted nets were set in two control areas and two harvested areas on the following dates: 3–5 June 2019 (before first harvest), 3–5 July 2019, 3–5 September 2019, 23–24 February 2020, 5–8 May 2020, and 2–5 June 2020 (once per season post-harvest). In February 2020, most of the nets were damaged by a storm, consequently, data from that season were excluded from the analysis. The length of each fish captured was measured to the nearest 0.5 cm. Weight was recorded to the nearest gram using a digital hanging scale. Each specimen was photographed, and otoliths were extracted for subsequent age determination.

Fish ageing

The sagittal otolith pairs obtained from the fish caught were used to age the most abundant species in the catch (*Pollachius virens, Gadus morhua, Myoxocephalus scorpius*). *P. virens* and *G. morhua* were aged by embedding the otoliths in resin and cutting a 1 mm

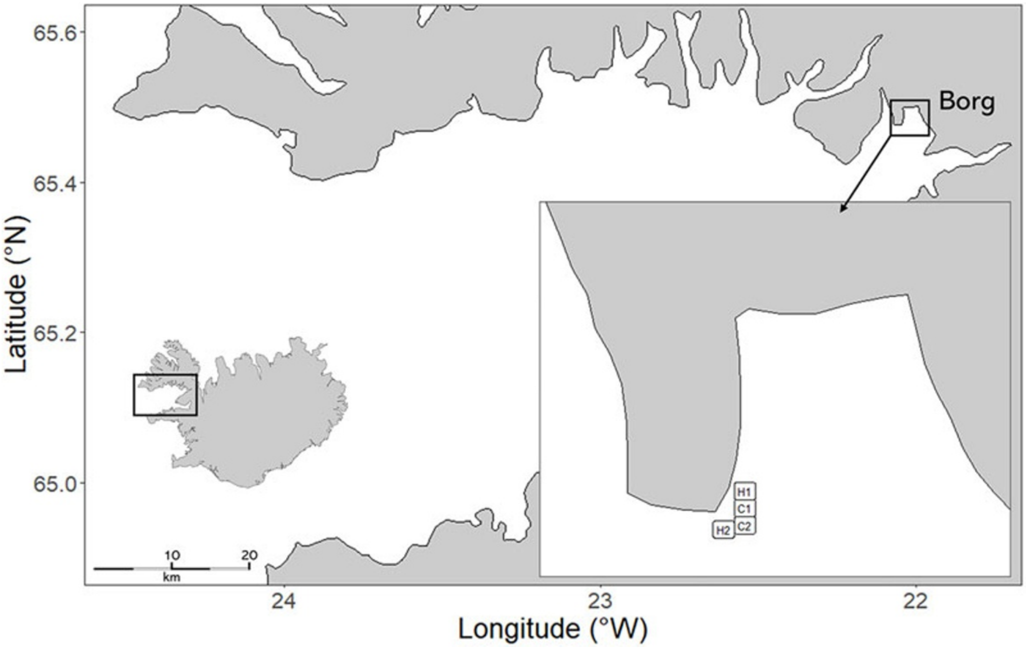


Figure 1. Breiðafjörður bay with insert showing the sampling area at Borg and all plots. Sampling plots included two harvested sites (H1 and H2) and two control sites (C1 and C2), all located within the same intertidal zone.

transverse section for subsequent examination under a dissecting microscope. The dark lines representing winter growth were counted in one of the pair of otoliths. *M. scorpius* ageing was based on the methods used in Ennis (1970).

Stomach content

All prey present in the fish stomachs were sorted, counted, and identified to the most precise taxonomic level possible. Relative diet composition was investigated through frequency of occurrence (f_i; number of individuals with the respective prey item, expressed as a frequency of the total number of non-empty stomachs) and relative prey abundance (p_i; mean percentage of stomach contents of all predators that had each prey type) (Amundsen *et al.*, 1996; Hyslop, 1980). Where: $f_i = N_i/N$ and $p_i = \sum S_i/\sum ST$ and N_i is the number of predators with prey type i in their stomach; N is the total number of predators with stomach contents; S_i is the amount of stomach contents composed by prey type i; and ST is the total amount of all prey types present in each stomach of the sample (Amundsen and Sánchez-Hernández, 2019). Partially digested prey that were still identifiable as fish were assigned to the category 'Digested fish'. Other prey taxa were grouped into broad taxonomic categories. Prey that could not be identified to a chosen taxonomic group due to advanced stages of digestion were classified as 'Unidentified remains'.

Statistical analysis

Biodiversity parameters (Shannon entropy, Shannon diversity, Simpson diversity, Pielou evenness, and Simpson evenness) were calculated with the 'diversity' function from the 'vegan' R package. Unconstrained ordination of treatment and date was performed by non-metric multidimensional scaling (NMDS) with the Bray–Curtis dissimilarity index using the vegan 'metaMDS' function (R Core Team, 2024).

A permutational multivariate analysis of variance (PERMANOVA) using Bray–Curtis dissimilarity with 999 permutations were performed to test for differences between species composition and stomach contents in the control and harvested areas, using the function 'adonis' in the 'vegan' R package (Oksanen, 2015).

Cumulative frequency curves were used to visualise and compare fish size structure in harvested and control areas. As conditions for parametric tests were violated, non-parametric tests were used (Wilcoxon signed-rank test). Non-parametric Kruskal–Wallis test was also performed to test for differences of fish length between seasons. Finally, fish population size structures between harvested and non-harvested areas were compared with the Kolmogorov–Smirnov (K-S) test.

For stomach content analysis, a Bray–Curtis similarity matrix was constructed using fourth-root transformed data (Clarke, 1993). The similarity percentages (SIMPER) routine was used to identify the contributions of prey species to the differences detected between harvested and control areas. Food webs were constructed from the fish gut content analysis.

All tests were performed by using R and RStudio 'Ghost Orchid' (version 2021.9.2.382) (R Core Team, 2024; RStudio Team, 2024).

Results

Catch

A total of 303 individuals ($n_{\text{control}} = 106$, $n_{\text{harvest}} = 197$) of nine fish species were caught using multi-mesh nets (Supp. Fig. 2). The number of fish caught across the mesh size spectrum was not significantly different between treatments (K-S test; $n = 9$, $p= 0.7$, and $D = 0.3$). However, the 12.5-mm mesh size captured the highest quantity of fish in harvested areas, driven by a large catch of *P. virens* in September 2019. Whereas in control areas, the 19.5-mm mesh size yielded the greatest catch.

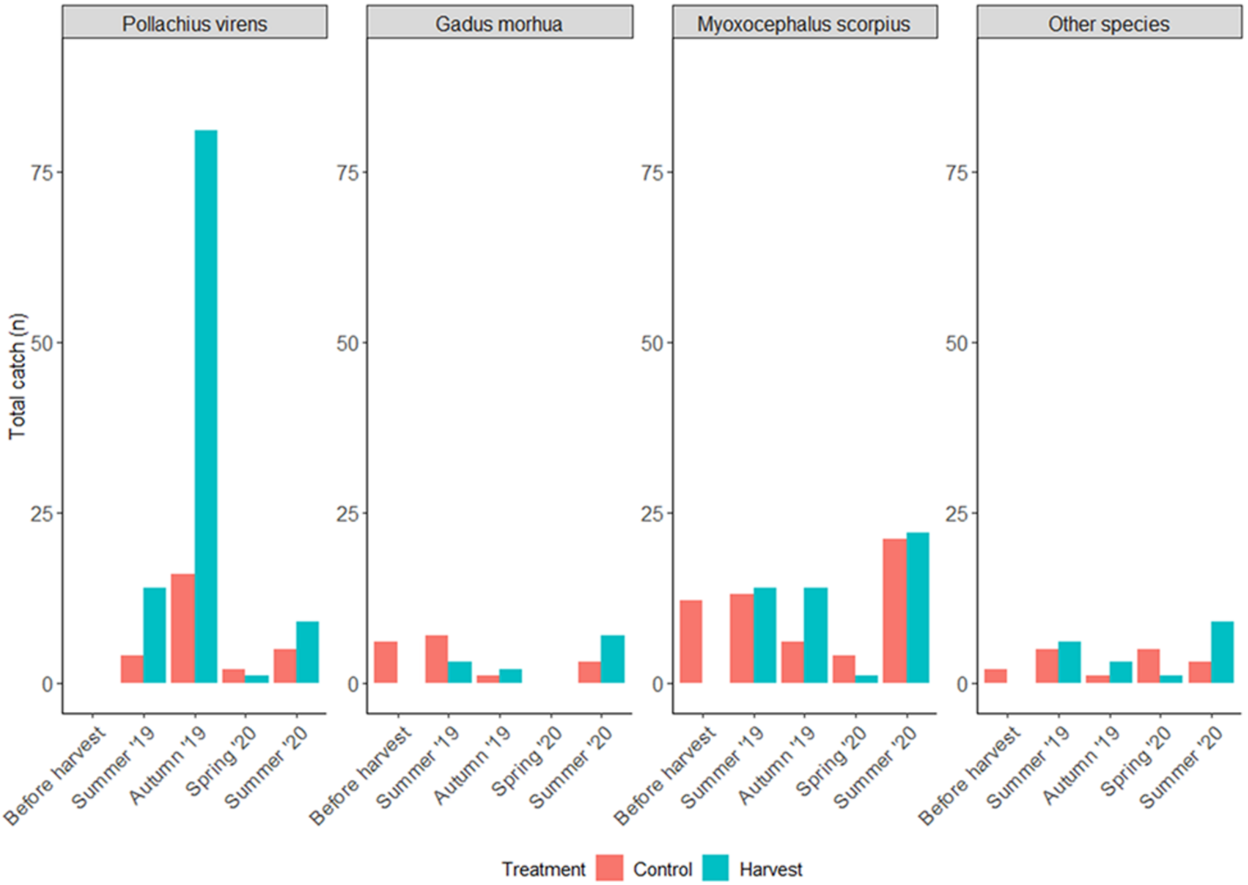


Figure 2. Total catch per season and treatment of the three most commonly caught species: Pollachius virens, Gadus morhua, and Myoxocephalus scorpius as well as the total of other species in harvested (H) and control (C) plots.

The most common species were *P. virens* [saithe, $n = 132$, 43.6%], *M. scorpius* [sculpin, $n = 107$, 35.3%] and *G. morhua* [cod, $n = 29$, 9.6%], followed by *Pleuronectes platessa* Linnaeus, 1758 [European plaice, $n = 13$, 4.3%], P. *gunnellus* [butterfish, $n = 11$, 3.6%], *Platichthys flesus* (Linnaeus, 1758) [European flounder, $n = 4$, 1.3%], *Salvelinus alpinus* (Linnaeus, 1758) [Arctic charr, $n = 3$, 1%], *Gasterosteus aculeatus* Linnaeus, 1758 [three-spined stickleback, $n = 2$, 0.7%] and *Limanda limanda* (Linnaeus, 1758) [common dab, $n = 2$, 0.7%] (Supplementary Table S1). Fish diversity was higher in the control areas than in the harvested areas (Control: Shannon entropy = 1.4, Shannon diversity = 4.2, Simpson diversity = 3.2; Harvest: Shannon entropy = 1.3, Shannon diversity = 3.5, Simpson diversity = 2.6), driven by differences in evenness (Control: Pielou evenness = 0.6, Shannon evenness = 0.5 and Simpson evenness = 0.7; Harvest: Pielou evenness = 0.4, Shannon evenness = 0.3 and Simpson evenness = 0.6), as species richness was low and similar (7 in control, 8 in harvested). Higher numbers of total fish were caught in late summer and early autumn, with lower numbers recorded the following spring (Figure 2 & Supp. Fig. 3). Harvested areas yielded higher catches than control areas in July 2019, September 2019, and June 2020; whereas higher catches were made in June 2019 and May 2020. An increase in abundance was also observed during the summer months for the most caught species. Notably, September 2019 saw a high capture of *P. virens*.

A PERMANOVA using distance matrices was used to compare fish communities in harvested and non-harvested areas, showing no significant differences ($\Pr(>F) = 0.6$, F model $= 0.8$, $df = 9$). Nevertheless, the NMDS plot (Figure 3) shows that the assemblages are trending towards two clear treatment groups in the NMDS space, except for autumn 2019 (control) and summer 2019 (harvest), which fall within the ellipses of the opposite treatment group.

Size and age

Significant seasonal variations in median length over the study period can be observed for *P. virens* (Kruskal–Wallis; $\chi^2 = 71.7$, $df = 3$, $p < 0.01$) (Figure 4). There was a sharp decrease in length from July 2019 to May 2020, followed by an increase in June 2020, consistent across treatments. Given the small sample sizes, no pattern was observable for *G. morhua*. *M. scorpius* maintained a relatively consistent length across both treatments and seasons.

Cumulative frequency curves were used to compare fish size structure in harvested and control areas (Figure 5). For *P. virens* (Harvest average length: 12.6 cm, median length: 11.5 cm; Control average length: 13 cm, median length: 11.5 cm), there were no significant differences between treatments in terms of median length (Wilcoxon rank sum test; $n = 142$, $W = 1528$, $p = 0.5$) and size distribution (K-S test; $p = 0.7$ and $D = 0.2$). In *G. morhua* (Harvest average length: 13.1 cm, median length: 13.5 cm; Control average length: 16.12 cm, median length: 16.5 cm), there were significant differences in median length (Wilcoxon rank sum test; $n = 29$, $W = 163$, $p < 0.01$) but not for size distribution (K-S test; $p = 0.08$, $D = 0.5$) between harvested and control areas, with control areas tending to have slightly bigger fish. However, it is important to

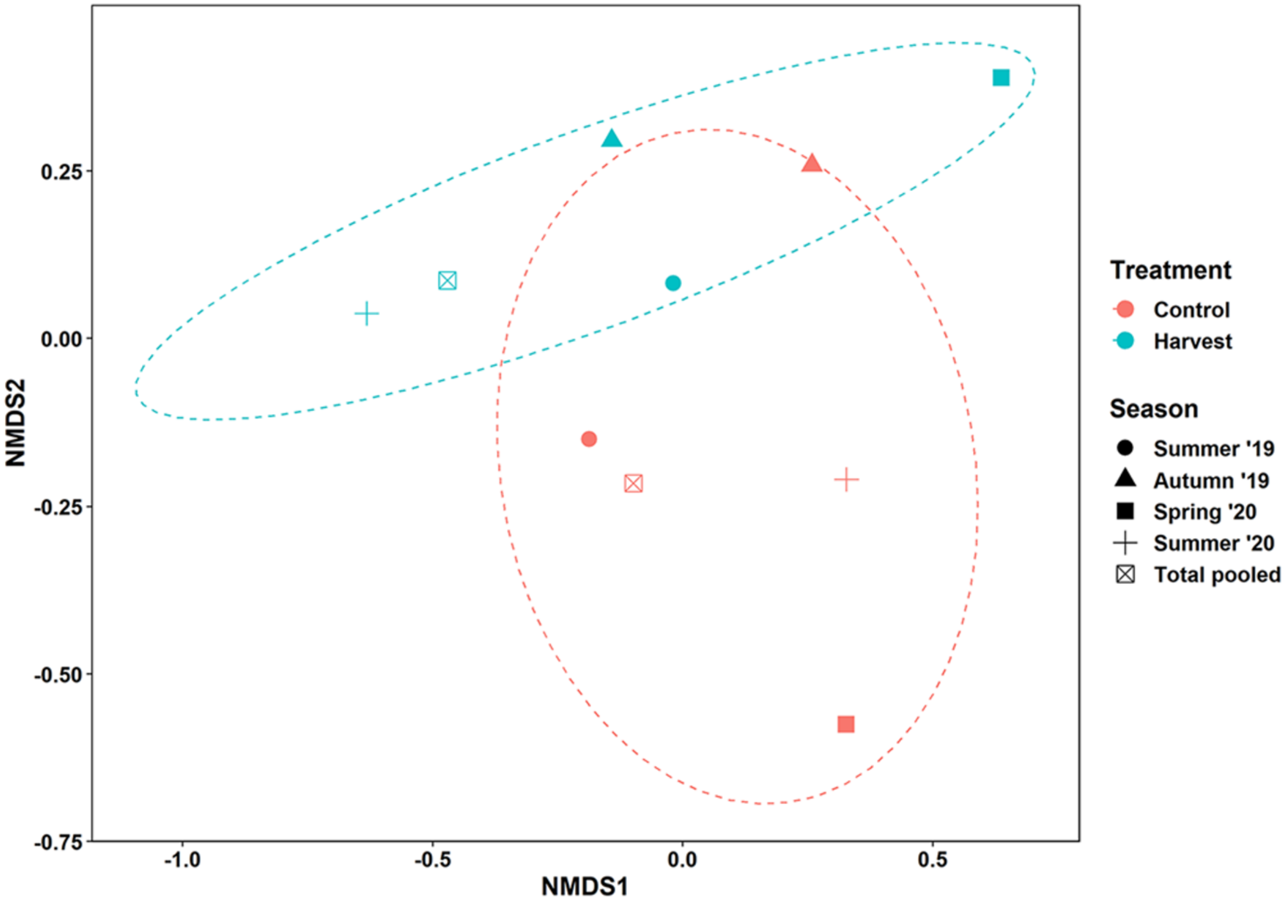


Figure 3. Non-metric multidimensional scaling (NMDS) of the fish assemblages at different seasons separated by treatment (all sampling occasions pooled). Stress = 0.07.

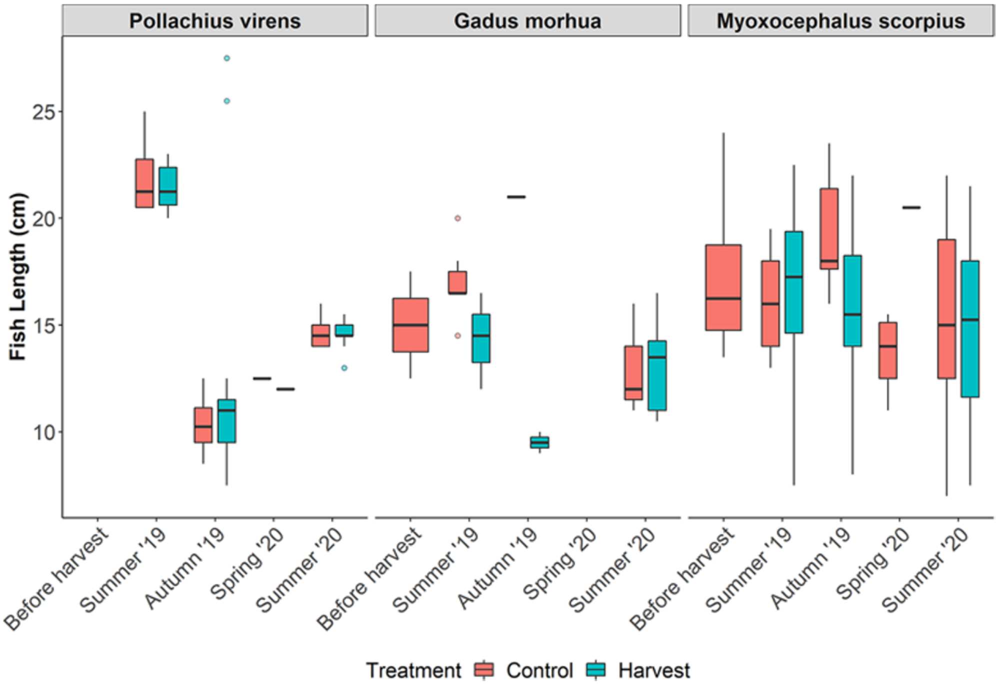


Figure 4. Size (length; cm) of the most represented fish species (Pollachius virens, Gadus morhua, and Myoxocephalus scorpius; bottom) separated by treatment and season. Each boxplot represents the interquartile range, the median (bold horizontal line) and two whiskers (1.5 times the interquartile range), with individual outliers shown as points.

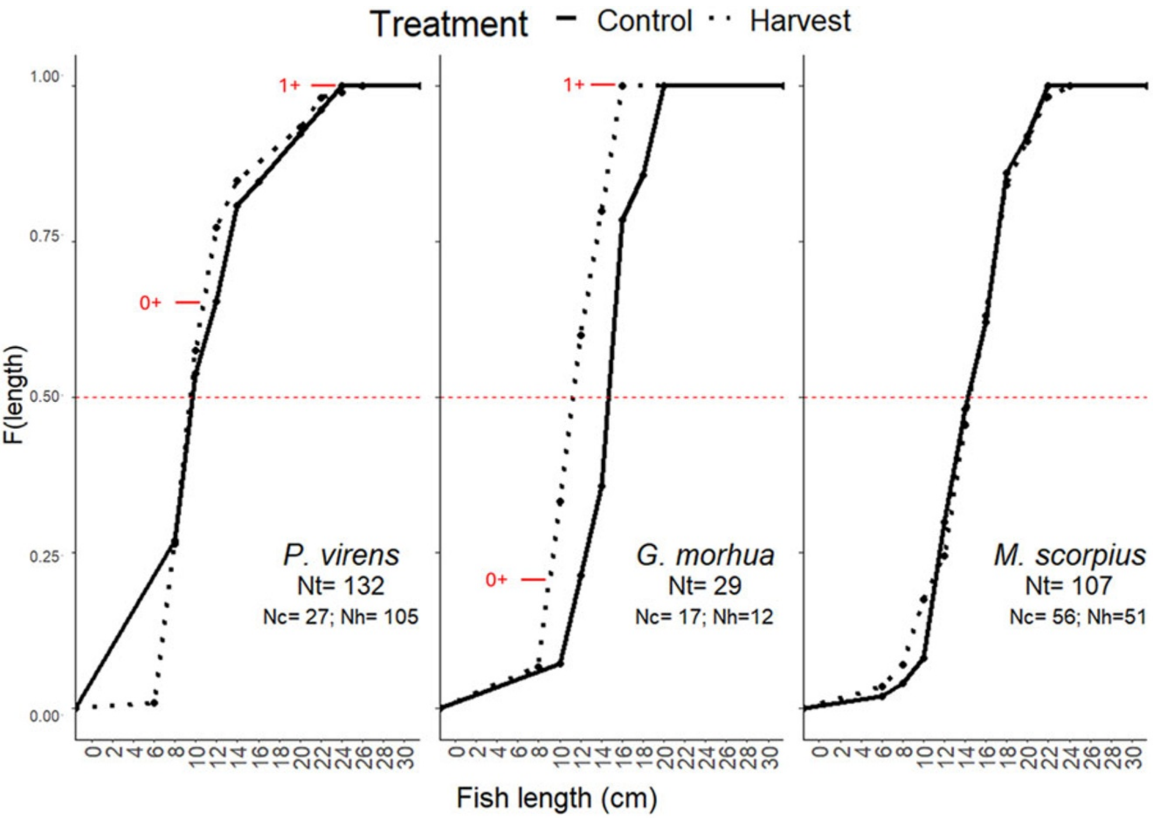


Figure 5. Cumulative frequency curves of length of the three species most represented in the catch separated by treatment and pooled across sampling occasions. nt = total number (n), nc = n for control areas and nh = n for harvested areas. Red lines marks the difference between 0+ and 1+ cohorts.

interpret these results cautiously, due to the relatively small sample size ($n_{\text{harvest}} = 12$ and $n_{\text{control}} = 17$). For *M. scorpius* (Harvest average length: 16 cm, median length: 16.5 cm; Control average length: 16.1 cm, median length: 16 cm) no differences in size distribution (K-S test; $p = 0.6$, $D = 0.2$) or median length (Wilcoxon rank sum test; $n = 107$, $W = 1407$ $p = 0.9$) were found between treatments.

Resident *M. scorpius* had a much larger age range with up to 5 years, than the transient visitors *P. virens* (mostly 0+ and 1+) and *G. morhua* (mostly 0+) as they use the intertidal zone throughout their lifespan (Supplementary Table S2).

Stomach contents

Of the 303 stomachs examined, 50 were empty (16.5%) and 253 contained prey (83.5%). Thirty-one different prey items were identified. Pooling across all species, the most common taxa eaten was Amphipoda, found in half of the stomachs examined (Table S3). This was followed by the broad category of 'Unidentified remains' (34.8%) and *Idotea granulosa* Rathke, 1843 (15.2%). Control areas had a 13% higher frequency of occurrence for amphipods and I. granulosa; otherwise, no notable differences were observed. Fish in harvested plots exhibited significantly greater prey richness (Wilcoxon rank sum test; $n = 172$, $W = 4205$, $p < 0.05$), but prey diversity did not differ significantly between treatments (Wilcoxon rank sum test; $n = 172$, $W = 4201$, $p = 0.06$).

The diet of *P. virens* stomachs was mainly composed of amphipods (63%), followed by unidentified prey, categorised as 'Unidentified remains' (9.8%), and partially digested fish (5.3%). The diet of *G. morhua* was dominated by amphipods (93%), with 'Unidentified remains' comprising a minor portion (2.4%). In the case of *M. scorpius*, amphipods also constituted the largest dietary component (53%), followed by *I. granulosa* (18%) (Table 1). Trophic diagrams were created for fish from both harvested and control areas based on these dietary data (Figure 6). The primary dietary components both for harvested and control areas were amphipods, followed by unidentified remains, and the isopod *I. granulosa* which was particularly important for *M. scorpius* and *P. virens*. Harvested areas had a broader variety of prey types, and unidentified gastropods and sand eels (Ammodytidae) appeared as important food for *P. virens* (Table 1).

When comparing fish diet in harvested and control areas for each species with PERMANOVA, no differences were found (*P. virens*: $\Pr(>F) = 0.4$, F model $= 1.01$, $df = 83$; *G. morhua*: $\Pr(>F) = 0.2$, F model $= 1.6$, $df = 20$ and *M. scorpius*: $\Pr(>F) = 0.3$, F model $= 1.2$, $df = 66$). Nevertheless, SIMPER analyses revealed dietary dissimilarities across species between harvested and control areas. For *P. virens*, average dissimilarity was 69.8% between treatments, with Amphipoda contributing most to this difference (42% contribution), followed by 'Unidentified remains' (20% contribution) and unidentified digested fish (13% contribution). Similarly, between treatment dissimilarity for *G. morhua* was 70.7%, primarily driven by Amphipoda (64% contribution) and, to a lesser extent, unidentified digested fish and 'Unidentified remains' (13% contribution each). *M. scorpius* exhibited the highest level of dissimilarity at 90.3%, with

Table 1. Stomach content of three most common species, separated by treatments and pooled across sampling occasions

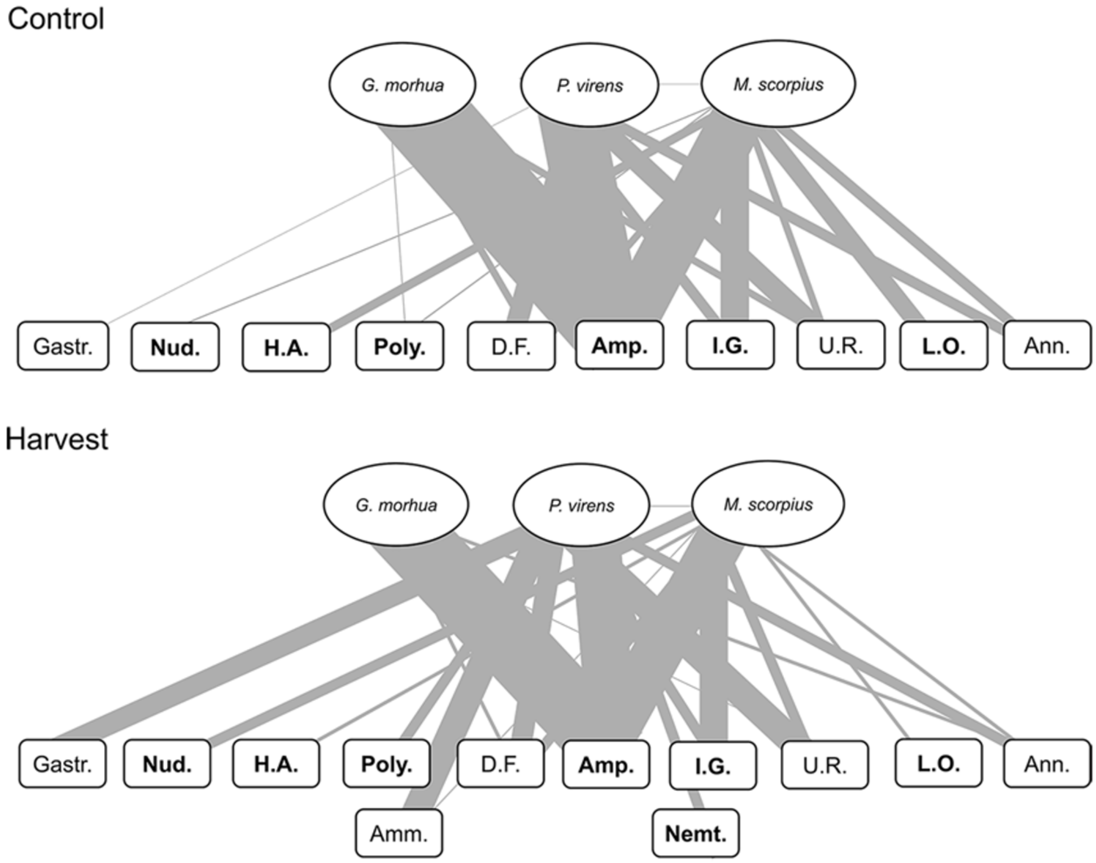
	P. virens				*G. morhua*				*M. scorpius*			
	Harvest		Control		Harvest		Control		Harvest		Control	
Taxa	f_i	p_i	f_i	p_i	f_i	p_i	f_i	p_i	f_i	p_i	f_i	p_i
Number of stomachs	64		20		8		13		28		39	
Teleostei												
Pollachius virens	0	0	0	0	0	0	0	0	2.5	0.7	2.6	0.5
Ammodytidae	1.9	6	0	0	0	0	0	0	2.5	0.7	0	0
Pholis gunnellus	1.9	1.7	0	0	0	0	0	0	0	0	0	0
Digested/unid. fish	11.3	4.7	20	7.4	16.7	3	23.1	2.2	22.5	6.5	10.5	2
Arthropoda												
Amphipoda	43.4	59.9	60	75.7	58.3	91	84.6	94	47.5	55.2	57.7	53.7
Idotea granulosa	6.6	2.4	16	2.9	0	0	0	0	22.5	13	36.8	21.9
Hyas araneus	0	0	0	0	0	0	0	0	10	2.6	10.5	3.5
***Jaera* spp.**	0	0	0	0	0	0	0	0	0	0	2.6	0.5
Pygnoconida	0	0	0	0	0	0	0	0	2.5	1.3	0	0
Euphausiacea	0	0	0	0	0	0	0	0	0	0	2.6	1
Calanus finmarchicus	0.9	0.2	0	0	0	0	0	0	0	0	0	0
Decapoda (unid.)	0	0	0	0	8.3	1.5	0	0	0	0	2.6	0.5
Mollusca												
Littorina obtusata	0	0	0	0	0	0	0	0	7.5	2	7.9	4.5
Lacuna vincta	0	0	4	0.7	0	0	0	0	0	0	0	0
Nucella lapillus	0	0	0	0	0	0	0	0	2.5	0.7	0	0
Littorina saxatilis	0	0	0	0	0	0	0	0	0	0	2.6	0.5
Gastropoda (unid.)	3.8	4.5	4	0.7	0	0	0	0	0	0	0	0
Nudibranchia	0	0	0	0	0	0	0	0	2.5	5.2	2.6	0.5
Bivalvia (unid.)	0	0	0	0	0	0	0	0	0	0	2.6	0.5
Annelida												
Sipunculida	0	0	0	0	8.3	1.5	0	0	5	1.3	2.6	1.5
Polychaeta	0.9	2.3	0	0	0	0	7.7	0.8	0	0	2.6	0.5
Annelida (unid.)	13.2	3.2	8	3.7	8.3	1.5	0	0	10	2.6	10.5	4.5
Echinodermata												
Ophiuroidea	0	0	0	0	0	0	0	0	2.5	0.7	2.6	0.5
Holothuria	1.9	0.4	0	0	0	0	0	0	2.5	0.7	0	0
Other												
Nematoda	1.9	0.6	0	0	0	0	0	0	0	0	2.6	1

(*Continued*)

Table 1. (*Continued.*)

	P. virens				*G. morhua*				*M. scorpius*			
	Harvest		Control		Harvest		Control		Harvest		Control	
Taxa	f_i	p_i	f_i	p_i	f_i	p_i	f_i	p_i	f_i	p_i	f_i	p_i
Nemertea	0.9	2.4	0	0	0	0	0	0	0	0	0	0
Priapulida	0	0	0	0	0	0	0	0	2.5	0.7	0	0
Larvae (unid.)	0.9	1.9	0	0	0	0	0	0	0	0	0	0
Unid. remains	50.8	9.9	48	8.8	8.3	1.5	30.8	3	22.5	5.8	7.9	1.5

Frequency of occurrence (f_i) mean percentage of stomach contents of all predators that had each prey type (p_i). taxa in bold live amongst *A. nodosum* fronds *or* holdfast.


Control

Harvest

Figure 6. Trophic linkages of fishes and their most represented prey from Breiðafjörður, in the control (top) and harvested (bottom) areas. The width of linking lines correspond to the contribution by percentage (p_i; mean percentage of stomach contents that had each prey type) of each food item to fish diets, based on Table 1. Abbreviations for food types: Gastropoda unidentified (gastr.), Nudibranchia (nud.), Hyas araneus (H.A.), Polychaeta (poly.), Digested/unidentified fish (D.F.), Amphipoda (amp.), Idotea granulosa (I.G.), Unidentified remains (U.R.), Littorina obtusata (L.O.), Annelida unidentified (ann.), Ammodytidae (amm.), Nemertea (nemt.) And items in bold live amongst A. nodosum fronds or holdfast.

Amphipoda (32% contribution), *I. granulosa* (15% contribution), and 'Unidentified remains' (10% contribution) as the main contributors. Across all three species, Amphipoda consistently accounted for the greatest proportion of differences between treatments, being more abundant in fish stomachs in control areas (Supplementary Table S4).

Discussion

Our study provides an assessment of the transient and resident fish species found in the *A. nodosum*-dominated rocky intertidal zone of the sub-Arctic, focusing on the tide-in fish assemblages and their dietary preferences. The multi-mesh gill net proved to be an effective method in capturing a range of species and sizes over the course of the sampling period. The data revealed a varied assemblage of species using *A. nodosum* beds, either as place of permanent residence (*M. scorpius, P. gunnellus*, and *G. aculeatus*), or as juvenile nursery grounds, including commercially important gadoids *P. virens* and *G. morhua* and the flatfish *L. limanda, P. flesus*, and *P. platessa*. Our findings emphasise the role of *A. nodosum* beds in supporting fish communities, aligning with earlier studies that highlight the importance of nearshore macrophyte-dominated areas for fish in the Northern Atlantic Ocean (Schmidt *et al*., 2011; Vercaemer *et al*., 2018).

The fish assemblage underwent seasonal changes in composition and abundance. Abundance peaked during the summer with lower numbers for spring, aligning with previous findings and likely driven by lower water temperatures and available food (Faria and Almada, 2006; Gibson, 1972; Milton, 1983; Pihl and Wennhage, 2002). A large shoaling event significantly increased the number of individuals caught, contributing to observed abundance patterns. These were predominantly small *P. virens* in the 0+ age group. The decline in size during late summer suggests that larger fish may have migrated to other areas. By the following year, evidence of growth in *P. virens* was observed, indicating cohort progression.

The use of the rocky intertidal by juvenile *P. virens* has been previously recorded in Canada (Rangeley and Kramer, 1995a, 1995b), where they were seen to move in large groups from the subtidal to the intertidal zone with the rising tides, using the intertidal zone as a refuge and as foraging areas (Rangeley and Kramer, 1998). Juvenile *G. morhua* have also been the focus of research both in the Eastern (Pihl, 1993) and Western (Hanson, 1996; Rangeley and Kramer, 1998) Atlantic Ocean, including Iceland (Jónasson *et al.*, 2009; Pálsson, 1976, 1980). Abundances in shallow waters are highest in the summer and then decrease as fish migrate to deeper waters in the winter (Methven and Bajdik, 1994; Pálsson, 1980). Intertidal use by these juvenile fishes usually follows tidal movements, with a migration to shallower waters most probably as feeding excursions (Keats, 1990). In our study, both cod and saithe were in the +0- and +1-year classes, which again suggests the use of the rocky intertidal as nursery grounds. Juvenile use of the intertidal zone is supported by previous studies that have shown the importance of the rocky intertidal at high tide for juvenile fish (Faria and Almada, 2006; Schmidt *et al.*, 2011; Seitz *et al.*, 2014; Studebaker, 2006). Even when the adult stock declined, studies in Canada for saithe and cod confirmed the persistence of juvenile fish in coastal habitats, aiding stock recovery by supplying recruits to the adult stocks (McCain *et al.*, 2016), which in turn highlights the importance of proper management and monitoring of these areas.

A. nodosum harvesting and its impact on intertidal communities have been the subject of several studies in the North Atlantic (Black and Miller, 1991; Fegley, 2001; Rangeley, 1994), yet the effects of harvest on transient and resident fishes and crustaceans remain understudied, particularly at high latitudes (Magnússon *et al.*, 2024). Diversity and evenness were higher in the control areas, while richness and density were higher in harvested areas. However, there were no statistically significant differences on fish community composition between treatments. This suggests that while abundance distribution might vary slightly, species identity remains consistent, possibly reflecting behavioural responses to habitat structure changes. When examining species individually, *P. virens* seemed to show a preference for harvested areas, possibly reflecting the species' pelagic and shoaling behaviour. This could make it more susceptible to capture in structurally altered habitats, such as the shorter and less dense algal canopies after harvesting. *M. scorpius* length distribution did not show any effects of harvesting, probably because it is a resident benthic fish that feeds and stays close to the bottom (Landry *et al.*, 2018), so a wider range of sizes and ages are expected to be present throughout the year and would be less affected by harvesting. Only median length of *G. morhua* was significantly less in the harvested plots, but as the total number was less than 30, and fish were infrequently caught, no strong conclusions can be made.

Stomach content analysis showed some differences in prey selection and in the frequency of occurrence of prey items between treatments. There were also differences amongst the three main species, indicating niche differentiation. The prevalence of amphipods, isopods, and annelids in rocky intertidal fish stomachs as a key dietary component aligns with previous studies that emphasise their importance in intertidal ecosystems (Compaire *et al.*, 2016; Norton and Cook, 1999; Velasco *et al.*, 2010) particularly in areas with dense macroalgal cover under, on and amongst which they live (Gollety *et al.*, 2011; Larsen, 2012; Pavia *et al.*, 1999). Similarly, the importance of fish and fish remains in examined stomachs implies that it may be a significant component of the fishes diet (Norton and Cook, 1999).

While some differences between treatments were found in the relative contribution of prey items (e.g. amphipods), dietary composition did not differ significantly between treatments. This suggests that, despite some dietary differences in frequency of occurrence or abundance, the overall trophic structure remains similar. Stomachs from fish caught in harvested plots exhibited significantly greater prey richness, although prey diversity did not differ significantly between treatments, which suggests that individuals in harvested areas are consuming a broader range of prey types, but not necessarily with greater dietary complexity. Gastropods for example, were more frequently recorded in fish diets in harvested areas, which could suggest that harvesting creates disturbed foraging environment and provide less refuge from predation than full canopy areas. The most common prey items found, amphipods, isopods (i.e. *I. granulosa*) along with *L. obtusata* and *L. vincta* live on and amongst *A. nodosum* canopy, in most cases feeding on it (Pavia *et al.*, 1999; Pavia and Toth, 2000), emphasising their key role in intertidal food webs. *M. scorpius*, as a resident species feed mostly on *I. granulosa, H. araneus* and *L. obtusata*. Both *I. granulosa* and *L. obtusata* feed on *A. nodosum* or its epiphytes (Naylor, 1955; Williams, 1990); thus, *M. scorpius* is part of a tightly linked food web, directly utilising primary production from *A. nodosum*. Harvesting can alter diversity of prey available to fish visitors or resident in the intertidal zone through changes in plant biomass and complexity as well as habitat patchiness (Sharp *et al.*, 2006) although previous studies have found small or temporary impact of harvesting on seaweed-associated communities (Lauzon-Guay *et al.*, 2023; Trott and Larsen, 2010). Conversely, variety of available prey may increase due to fewer refuges; thus, harvesting could have subtle effects on trophic dynamics, including decreasing availability of some taxa that feed on *A. nodosum* to predators (e.g. *L. obtusata* is found in more stomachs in the control areas) or provide better access to benthic species. Amphipods on the other hand, which primarily live on or amongst *A. nodosum* and are clearly a crucial part of the food web, were not significantly different between treatments. Current harvesting practices may not entirely disrupt trophic interactions, but could be altering prey composition, warranting further study to explore long-term ecological impacts. The observed high variability in stomach content data suggests that larger sample sizes may be required to adequately describe fish diet composition in Breiðafjörður.

Our study did not detect strong effects of *A. nodosum* harvesting on intertidal fish communities, which aligns with previous studies in the North Atlantic (Lauzon-Guay *et al.*, 2023; Phillippi *et al.*, 2014; Sharp and Pringle, 1990; Trott and Larsen, 2010). Nonetheless, the relatively small sample size and sampling dates may have hindered our ability to detect subtle differences between treatments. Sites were selected to minimise variation of abiotic factors, but unmeasured differences in physicochemical parameters could have also influenced fish distributions. Nevertheless, given the proximity between plots (50–100 m) and the homogeneous nature of the study area, we assumed minimal variation in abiotic conditions between treatments. Additionally, differences in habitat complexity (i.e. substrate variation or canopy density and structure) could have also influenced fish distribution and behaviour.

While harvesting reduced *A. nodosum* cover in treatment sites, potentially altering prey accessibility, shelter availability and habitat complexity, our results suggest that these did not lead to major changes, likely due to the localised and small-scale nature of the disturbance and their resistance to perturbation (Phillippi *et al.*, 2014; Sharp and Pringle, 1990). Finally, while our experimental harvesting was done following local practices, precise biomass measurements were not collected, limiting our ability to fully quantify the harvesting intensity. Different levels of biomass removal (e.g. 30% vs. 60%) could lead to different ecological effects. Despite these limitations, our study provides insights into high-latitude fish assemblages in *A. nodosum*-dominated intertidal habitats and their seasonality, highlighting the ecological significance of these areas as nursery grounds for commercially important species that rely on them before migrating offshore.

Conclusion

Our study demonstrated the occupancy and use of the rocky intertidal zone by several fish species for feeding, living, and as nursery grounds. We also highlighted the significance of *A. nodosum* beds as feeding grounds for transient fish and the subtle impacts of harvesting on food web linkages.

No significant effects of *A. nodosum* harvesting were detected on fish assemblages and populations of common species. Nevertheless, a precautionary approach should be implemented when harvesting, as juvenile fish are susceptible to nursery habitat degradation which could affect the adult stocks of commercially important gadoids. Future research should focus on long-term monitoring to assess long-term trends in recovery rates, harvesting impacts, and diet composition of fish populations in commercially harvested areas.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315425100301.

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