

1 to stay within fjords varies annually and relates to capelin availability. Despite the
2 demonstrated capacity to alter diet and habitat use to changing environmental conditions,
3 notable declines in effective population size were associated with the regime shift of the 1990s
4 in the northwest Atlantic. Collectively, these results demonstrate that behavioral plasticity of
5 Arctic Charr may be insufficient to deal with the large environmental perturbations expected to
6 arise from a changing climate.

7 **KEYWORDS:** diet, telemetry, effective population size, long-term monitoring, Labrador,
8 Nunatsiavut

9 **1. INTRODUCTION**

10 Arctic Charr (*Salvelinus alpinus*) are an iconic Arctic species native to a wide latitudinal gradient
11 (Johnson 1980) that extends from the Arctic to north temperate regions (Reist et al. 2013).
12 Across this range this species exhibits a variety of adaptations (Dallaire et al. 2021) including
13 remarkable phenotypic diversity within both freshwater resident and anadromous life histories
14 (Klemetsen et al. 2003). In all but the southern extents of their range, anadromy is a common
15 life history trait (Klemetsen et al. 2003) that allows Charr to quickly increase somatic reserves in
16 productive coastal environments before returning to freshwater to reproduce and overwinter
17 (Klemetsen et al. 2003).

18 Behavioral plasticity is also common within anadromous populations of Charr. For example, at
19 sea Charr occupy habitats that range from sheltered estuaries to coastal headlands, show
20 variation in marine residency times (Dempson & Kristofferson 1987, Spares et al. 2015, Moore
21 et al. 2016, Gulseth & Nilssen 2000, Klemetsen et al. 2003, Harris et al. 2020), occupy a variety

1 of thermal habitats (Rikardsen et al. 2007a Spares et al. 2012, Harris et al. 2020, Mulder et al.
2 2020), and consume diverse prey often dominated by pelagic fish and plankton (e.g.
3 amphipods), but also items such as insects, and benthic organisms (Dempson et al. 2002,
4 Klemetsen et al. 2003, Rikardsen et al. 2007b, Spares et al. 2012, Davidsen et al. 2020).

5 Despite this plasticity, marine habitat use within populations can remain stable across years
6 even during changing environmental conditions (Harris et al. 2020).

7 While researchers have documented phenotypic variation over wide geographic scales, less is
8 known on how behavioral variation and plasticity are manifested over extended temporal and
9 smaller spatial scales (but see Dempson & Kristofferson 1987, Dempson et al. 2002, Davidsen et
10 al. 2020), particularly across latitudinal gradients over which climate responses are likely to
11 occur in the near future. Such information is important to detect and interpret the responses
12 of Arctic Charr to the rapidly changing Arctic (Reist et al. 2006, Power et al. 2012, Layton et al.
13 in 2021, Dallaire et al. 2021).

14 The challenges to understanding variability and plasticity in Arctic Charr behavior are twofold,
15 1) there is a scarcity of data sets of appropriate spatial and temporal scales and 2) there is a lack
16 of data associating behavior with biotic environmental variables such as prey availability.

17 Though considerable research is available on the marine movements of Arctic Charr (e.g.
18 Bégout-Anras 1999, Spares et al. 2015, Moore et al. 2016, Harris et al. 2020), it is difficult to
19 sustain these projects over extended temporal periods across a latitudinal gradient while
20 concurrently monitoring biotic/abiotic variables of interest. One area where extensive
21 behavioral data exist is in Nunatsiavut, northern Labrador, Canada, where conventional mark-

1 recapture tagging studies were conducted over several decades and supported by diet and
2 morphometric studies (Dempson & Kristofferson 1987, Power et al. 2000, Dempson et al. 2002,
3 Dempson et al. 2008). These studies provide a baseline that, when coupled with contemporary
4 telemetry and genomic methods, can be used to explore spatial and temporal variation in Arctic
5 Charr marine movement behavior and links to marine-phase diets.

6 Evaluating threats to southern sub-Arctic anadromous populations to further climate shifts and
7 predicting changes to more northerly populations will depend on understanding the
8 adaptability of local populations and their capacity to deal with ecosystem shifts. Past
9 environmental disruptions can inform our understanding of the capacity of fauna to
10 accommodate ecological change. For example, a regime shift coinciding with unusually cold
11 ocean temperatures and lower productivity occurred in the northwest Atlantic in the 1990s
12 (Pedersen et al. 2017). This time period was also associated with changes in species
13 distributions and abundance (Colbourne 2004; Rose 2005a, Carscadden et al. 2013) as well as
14 the decline of many important commercial fishery populations (Bundy et al. 2009, Mills et al.
15 2013, Pedersen et al. 2017). During this period the abundance of capelin (*Mallotus villosus*)
16 declined in coastal areas of Newfoundland and Labrador (Buren et al. 2019), affecting the diets
17 of a variety of fish, bird, and marine mammal species (Taggart et al. 1994, Lawson & Stenson
18 1995, Montevecchi & Myers 1997, Bryant et al. 1999, Rowe et al. 2000, Dempson et al. 2002)
19 including Arctic Charr (Dempson et al. 2002). As climate change progresses, other broad
20 redistributions of species (Perry et al. 2005, Rose 2005b) and productivity are expected (Moore
21 et al. 2018), which could have important repercussions on species like Arctic Charr.

1 In this study, we 1) apply acoustic telemetry data to evaluate spatial differences in marine
2 habitat use by Arctic Charr from two regions of northern Labrador (Saglek Fjord and Nain Bay);
3 2) evaluate if observed patterns in habitat use are stable over time as inferred by historical diet
4 and catch data from Nain Bay; and 3) use existing hindcasted indices of effective population size
5 to assess whether population-specific responses in diet and habitat use were sufficient to
6 safeguard Nain Bay populations during times of strong environmental change.

7 **2. MATERIALS AND METHODS**

8 2.1 Study Area

9 Our study was conducted in the coastal waters of the Nunatsiavut region of Labrador, Canada;
10 a land claim area established for the Labrador Inuit. The orientation of the northern Labrador
11 coastline lends itself well to studying potential climate change responses, since conditions in
12 southern areas may foreshadow expected changes further north and therefore help to predict
13 future effects of climate change (Layton et al. 2021). The coastal waters of this area extend 20
14 km offshore and encompass 48 690 km². Labrador Inuit are a critical part of this ecosystem,
15 relying on species such as Arctic Charr for subsistence and economic opportunities.

16 2.2 Acoustic Telemetry

17 Movements of Arctic Charr were followed in two coastal regions of Nunatsiavut separated by
18 approximately 200 km (Figure 1). Saglek Fjord is 65 km in length, 14 km at its widest point, and
19 is bathymetrically characterized by seven underwater basins (80-256 m) separated by sills
20 (Brown et al. 2012, Simo-Matchim et al. 2017). The second region, hereafter referred to as
21 Nain, is occupied by Charr of the Nain stock complex (Dempson et al. 2002; Figure 1), and is

1 more geographically complex due to presence of islands that extend outside of Anaktalak Bay,
2 Nain Bay, Tikkoatokak Bay, and Webb Bay. The Nain region is approximately 50 km wide with
3 maximum depths reaching at least 110 m (Nutt 1953), though its bathymetry remains largely
4 unmapped. Sea ice is common to both regions, occurring typically from November to mid-June
5 or early July (McCarney et al. in press).

6 We used an array of Vemco acoustic receivers (VR2W and VR2ARs, Innovasea, Halifax, Canada)
7 to monitor the marine movements of Arctic Charr from the summer of 2018 to autumn of 2019.
8 Receivers were positioned to monitor habitat use and the timing of migration events to and
9 from the marine environment of tagged animals through the course of their marine residency
10 period. Consequently, we placed receivers in river estuaries, gateways within, and at the
11 seaward extent of fjords to track exits to the coastal headlands. The more complex nature and
12 variety of migratory pathways off Nain required more receivers for coverage. In total, we
13 deployed forty-three receivers between our two study sites. Twenty-five were deployed off
14 Nain and eighteen receivers in Saglek Fjord (Figure 1). Of the forty-three receivers deployed,
15 twenty-three (15 in Nain and 8 in Saglek) were VR2-ARs that were recovered with acoustic
16 releases. The remaining receivers were VR2Ws and recovered with ground lines.

17 We tagged Charr in 2018 in Saglek Fjord (Jul 25-26, 2018) at Torr Cove, Branigan's Island, and
18 Jens Haven Island, and in Nain (Aug 2-4, 2018) at Webb's Bay, Tikkoatokak Bay, Nain Bay, and
19 Anaktalak Bay (Figure 1, Table S1). We also tagged Charr in Nain in Webb Bay (July 31) and
20 Tikkoatokak Bay (August 1) in 2019. Fish were collected using either barbless, single hook
21 fishing lines or 4½ inch (11.5cm) gillnets. Tagged fish in Saglek ranged from 45.7 to 64.0 cm
22 (mean=53.7 cm), whereas those from Nain ranged from 41.5 to 63.5 cm (mean=50.4 cm)(Table

1 S1). Based on fish length, we estimated ages to range from to 7-14 years (Dempson et al.
2 2008). Once captured, we measured length, and took a small clip of tissue (~1 cm²) from the
3 caudal fin to genetically assign a subset of fish to their natal river (see below). Prior to release,
4 tagged Charr were allowed to recover in a plastic tub equipped with air pumps and flowing sea
5 water. In total, 95 fish (40 in Saglek, 44 in Nain in 2018, and 11 in Nain in 2019) had uniquely
6 coded Vemco V13 (36mm [l] x 13mm [d], 9.2 g in air, tag life: 602 d) or V13T (46mm [l] x 13mm
7 [d], 9.7 g in water, tag life: 498 d) transmitters surgically implanted in their abdominal cavities.
8 Transmitters emitted pulses at random intervals between 60-120s to minimize signal collisions
9 that might occur if multiple tags were in close proximity.

10 We filtered our data of suspected mortality or tag shedding events (i.e. removing individuals that
11 consistently remained in the vicinity of a receiver beyond normal migration periods), grouping
12 the remaining data into individual detection events at specific receivers using the R package
13 GLATOS (<https://gitlab.oceantrack.org/GreatLakes/glatos>). Occupancy was measured in three
14 different habitat types using detections on receivers located in estuarine (immediate proximity
15 of a freshwater input), fjord, and coastal (headlands outside of fjords) habitats (Figure 1).

16 2.3 Genetic Assignment to River of Origin

17 Populations of Arctic Charr on the Labrador Coast mix in the marine environment (Dempson &
18 Kristofferson 1987, Layton et al. 2020). We used tissue samples from 72 of the 84 fish tagged in 2018
19 (40 in Saglek and 32 in Nain; Table S1) to extract DNA and genotype 111 genome-wide microsatellite
20 loci following Layton et al. (2020). Individual fish were assigned to river or region of origin (reporting
21 group) using a Bayesian mixed stock fishery analysis in the R package *rubias* (Anderson 2017, Moran &

1 Anderson 2018), as described in Layton et al. (2020). Only assignments with a probability of >0.80 were
2 reported. Previous work suggests assignment accuracy using these loci and baseline is approximately
3 90%.

4 2.4 Diet Analysis

5 We examined temporal and spatial variation in Charr diet using long-term monitoring data
6 collected from 5680 individuals harvested in the northern Labrador Charr fishery (1982-2008).
7 This dataset, was a temporally extended version of that explored by Dempson (1995) and
8 Dempson et al. (2002) and was reanalyzed within a multivariate framework to focus on prey
9 community differences among stock complexes and fishing areas (Figure 1). Samples were
10 collected in all 27 years from inshore areas of Nain (1982-2008) but only subsets of years were
11 collected for other stocks, which ranged from 6 (Okak) to 22 (Offshore Nain) years of data
12 (Table S2).

13 Prey from Charr stomachs were identified according to fish and invertebrate taxa and
14 categorized by abundance and biomass metrics as described in Dempson et al.
15 (2002). Additionally, for the years 1988-2008, quartiles of stomach fullness (i.e. 0 = empty and
16 4 = full) were recorded for each fish and converted to percent fullness. To reduce
17 autocorrelation of samples, we averaged stomach content biomass by sampling day and Charr
18 fishing area (Figure 1). We used the Bray–Curtis Index (Bray & Curtis 1957) to analyze
19 community similarity and dissimilarity in biomass. We identified prey taxa that typified (i.e.,
20 contributed most to within-group similarity values) stocks and months, and discriminated (i.e.,
21 contributed most to dissimilarity values) among groups using SIMPER (PRIMER 7). Differences in
22 prey communities across stocks, years, and months were evaluated through PERMANOVA

1 (PERMANOVA+1.0.3; 9999 permutations), a permutation-based multivariate analog of ANOVA
2 (Anderson 2001). Since the full model had a significant interaction between year and month,
3 we analyzed three more simple models: 1) a model applied to the entire diet dataset with fixed
4 terms for stock and month, and a stock * month interaction; 2) for Saglek data, a model with
5 fixed terms for year, month, and a year * month interaction term; and 3) for Nain, a model that
6 included the capture area (Inshore / Offshore) along with month, year, and all interaction
7 terms. We presented these data using multi-dimensional scaling (MDS) of centroids. Centroids
8 (representations of multivariate central tendency) were derived from Principal Coordinates
9 Analysis (PCoA) (Gower 1966) and used to simplify visual representations of biomass data. We
10 also evaluated the consistency of interannual seriation in diets from Charr caught in inshore
11 and offshore areas of Nain by comparing stock-specific annual centroid similarity matrices using
12 a permutation test of Spearman rank-correlation coefficients (RELATE algorithm in PRIMER
13 version 7; 999 permutations).

14 We further examined temporal data of stomach fullness for Nain Charr to evaluate whether
15 food availability explained patterns in marine migration to offshore areas. Stomach fullness
16 patterns across years for July and August for inshore and offshore stocks were visualized with
17 Generalized Additive Models (shrinkage cubic regression spline, mgcv package (v. 1.8-31, Wood
18 2019) in R (v. 3.6.3, R Core Team 2020). We also applied a linear model to evaluate if there was
19 a negative relationship between stomach fullness of the inshore stock and the proportion of
20 Charr captured offshore in Nain's commercial fishery. Such a relationship would provide
21 support for the hypothesis that Nain area Charr are more likely to undertake more extensive
22 marine migrations in years where food availability was low in inshore areas.

1 2.5 Effective Population Size

2 We evaluated responses of Charr populations to shifts in diet using effective population size
3 (N_e) data derived from Layton et al. (2021). Briefly, Layton et al. (2021) used LinkNe (Hollenbeck
4 et al. 2016); a method that combines estimates of recombination rate with linkage
5 disequilibrium, to estimate N_e from 1900-2013 with 968 single nucleotide polymorphisms
6 (SNPs) from an 87k SNP array (Nugent et al. 2019) that had corresponding linkage map
7 information (Nugent et al. 2017). LinkNe was run with bins of 0.05 Morgans and including only
8 SNPs with minor allele frequency exceeding 0.05. We binned estimates by generation and
9 approximate years were calculated assuming a generation time of four years. Here, we
10 extracted N_e data for eight populations from the Nain region from 1990-2013.

11 **3. RESULTS**

12 3.1 Genetic assignments of tagged fish

13 Bayesian mixed stock fishery analysis assigned 72 tagged fish to a river but only 55 (75%)
14 surpassed the 80% assignment certainty threshold (Table S1). These analyses indicated the fish
15 tagged in Saglek Fjord originated from within Saglek (Southwest Arm River [$n = 13$], Kiyuktok
16 Brook [$n = 7$], Pangertok Brook [$n = 1$], Ugjuktok River [$n = 2$]), or neighboring waterbodies
17 within 50 km such as Hebron Fjord (Ikarut River [$n = 11$]) and Ramah Bay (Stecker River [$n = 2$])
18 (Figure 1). Fish tagged in the Nain stock complex originated from Nain Bay (Fraser River [$n = 1$],
19 Kamanatsuk Brook [$n = 7$], Kingurutik River [$n = 8$]), southern Anaktalak Bay (Ikadlavik Brook [n
20 = 7]), and Webb Bay (Ikinet Brook [$n = 1$]) (Figure 1). Tagged fish from Saglek (mean length =

1 53.7 cm) were significantly longer ($t = 3.22$, $P = 0.002$) than those from Nain (mean length =
2 50.4 cm).

3 3.2 Movement

4 We acquired telemetry data for 75 Charr; 29 from Saglek and 46 from Nain (38 tagged in 2018
5 and 8 tagged in 2019). From our initial group of tagged fish, we were unable to detect 19 after
6 tagging occurred, and assumed they left our array, had a malfunctioning transmitter or died
7 beyond detection of our receivers. We excluded an additional individual due to suspected
8 mortality or tag shedding (e.g. Lacroix et al. 2004). Data for this fish consisted of a continuous
9 string of detections on one receiver extending from roughly the date of tagging through winter
10 months and no detections on other receivers in the subsequent year. Among the remaining
11 fish, one individual appeared to die or shed a tag after previous, distinct movements and
12 therefore post-mortality data for this fish were also excluded. Three other individuals were
13 detected only once (all in estuaries), which was insufficient to make a detection event within
14 the GLATOS package and thus they were also excluded from further analysis.

15 We last detected the majority of tagged Charr in both Saglek (23 of 29) and Nain (24 of 44) in
16 2018 in estuaries of the study area. It was assumed that the remainder overwintered in rivers
17 outside the respective study areas. Moreover, we only detected a subset of the fish tagged in
18 2018 (45%, $n = 13$ in Saglek and 34%, $n = 15$ in Nain) the following year. Migration timing into
19 freshwater in 2018 ($t_{29} = 1.55$, $p = 0.131$) and to the ocean in 2019 ($t_{12} = -0.58$, $p = 0.58$) did not
20 differ across study locations. The mean date of migration into rivers was August 9 for Nain fish
21 and August 16 for Saglek fish. Mean dates of migration back to the marine environment were

1 June 6 and June 4 for Nain and Saglek respectively (Figure 2A). We did not detect tagged
2 individuals in more than one study region.

3 Seventy-two individuals generated marine habitat occupancy information over the 2018 and
4 2019 monitoring period. We recorded 345 occupancy events for 27 fish in Saglek, and 232
5 events from 45 fish in Nain (37 tagged in 2018 and 8 tagged in 2019). Of these fish, we
6 observed 93% occupying estuarine environments in both Saglek and Nain during the marine
7 residency period but with a greater proportion of Saglek Charr utilizing fjord or coastal
8 environments (78% and 63% respectively) compared to Nain (27% and 16% respectively)(Figure
9 2B). Moreover, in Nain the use of fjords and coastal habitats only occurred in 2019 even for fish
10 detected in both study years (Figure 2A). Tagged fish did not use coastal headland areas until
11 June and their occupancy only became relatively high in July and August for Saglek and peaked
12 in August for Nain. We detected only a small percentage of individuals at coastal receivers in
13 September and we detected no fish in these areas by October.

14 3.3 Diet & changes to effective population size

15 Charr diets along the north coast of Labrador revealed considerable variation at spatial scales
16 within and among study regions ($P < 0.001$; Figure 3A), and at temporal scales of months to
17 decades (Figure 3B). At the largest spatial scales, the Northern stock was most unique with a
18 diet that included a higher proportion of non-fish prey such as amphipods (Table 1). In
19 contrast, diets of Charr captured in inshore areas of Nain largely comprised of bait fish such as
20 capelin and sand lance *Ammodytes* spp. (Table 1). Charr in offshore areas of Nain maintained
21 an intermediate level of piscivory relative to Nain Inshore and to the Northern Charr (Figure 3A;

1 Table 1). Diets of Charr from other areas (e.g. Okak and Voiseys) were more similar to Nain
2 Inshore (Figure 3A). With the exception of Cottid sculpins and *Parathemisto* amphipods (Nain
3 Inshore only), biomass of all prey taxa was lower in Charr from the Northern area.

4 The degree of variability explained by temporal scales varied by area. The model for Nain Charr
5 had a significant year * month interaction term so we examined month-specific differences
6 separately. We observed diet differences for captured fish among areas (inshore and offshore)
7 and years in Nain for both July ($P < 0.001$ for both area and year) and August ($P = 0.001$ for
8 area; $P = 0.03$ for year), whereas we only detected differences in the Northern stock across
9 years ($P = 0.002$) and not months ($P=0.48$). For Nain Inshore stocks, capelin tended to be
10 abundant in Charr stomachs in July (but also present in August). Decadal patterns were also
11 evident (Figure 3B), with samples from the 1980s grouping very differently than those in the
12 early 1990s and an intermediate state observed in the 2000s. While not a planned statistical
13 comparison, we assessed decadal groupings within a PERMANOVA framework for Nain Inshore
14 and Nain-Offshore areas. The full model that included decade and area as fixed effects had a
15 significant interaction. When each area was run separately, pairwise comparisons showed that
16 all decades were significantly different from one another in both areas but that the difference
17 between 1990s and 2000s in the Nain-Offshore area was weaker and only marginally significant
18 ($P=0.046$ compared to $P<0.001$ for the others). Interestingly, this decadal pattern was shared
19 across the Nain areas (inshore and offshore) as the correlation in interannual patterns was
20 significant across the years when data was available for both locations ($Rho=0.351$; $P=0.004$).

21 Capelin appeared to be a key driver of the observed temporal patterns in Nain, especially
22 compared to other fish prey such as sand lance (Figure 4). Effective population size of Charr in

1 inshore Nain also showed interannual patterns with a mean decline of 34.3% (range 32.9-
2 36.8%) between the first (1990) and second (2001) time point that corresponds to declines in
3 capelin in their diets (Figure 4). All populations recovered by the third time point to a mean of
4 95.9% (range 83.0-109.6%) of their original population size.

5 Charr sampled from offshore areas for diet analyses were generally larger in most years than
6 those captured within the fjords of Nain (Figure 5A). Moreover, mean sizes of fish sampled
7 from the offshore areas did not vary across years to the same degree as those captured from
8 inshore areas of Nain (Figure 5A). Stomach fullness data also revealed differences between the
9 two areas over the time series (Figure 5B). In the offshore area, stomach fullness was more
10 consistent (typically averaging in the 50-60% range), with notable exceptions in 1994 and 2001.
11 In contrast, inshore stomach fullness was consistently lower than offshore throughout the late
12 1980s and 1990s before exceeding offshore values in the early 2000s and peaking in 2005.
13 Across all years, there was a tendency for more Charr to be captured in commercial fisheries
14 offshore of Nain when stomach fullness of Nain Inshore Charr was low ($F_{1,20}=12.51$, $P=0.002$,
15 $R^2=0.385$; Figure 5C). Such a pattern was also found when using CPUE as response variable
16 ($F_{1,20}=6.60$; $P=0.018$, $R^2=0.248$).

17 **4. DISCUSSION**

18 Arctic Charr demonstrated the capacity to buffer the effects of broad environmental change
19 through shifts in habitat use and diet. While behavioral plasticity is an important trait for
20 dealing with a variable environment, it was insufficient to fully safeguard populations from the
21 broad ecosystem changes experienced in the 1990s, even in areas that were under less

1 harvesting pressure (Layton et al. in 2021). It is likely however, that behavioral plasticity has
2 played a key role in the observed recovery in effective population size of Charr in our study area
3 and other parts of the Labrador Coast (Layton et al. 2021) despite only a partial recovery of
4 capelin in their diets.

5 Charr are generalist feeders utilizing a variety of fish and invertebrate taxa (Klemetsen et al.
6 2003), which enhances their capacity to endure fluctuating prey bases. In addition to varying
7 across stocks, diet composition changed across months during the marine phase and also
8 shifted over decadal scales, presumably in response to prey availability. In southern portions of
9 our study area, where piscivory on capelin was most prominent (Dempson et al. 2002,
10 Dempson et al. 2008), we observed year to year diet variation. Capelin abundance and
11 distribution in the north Atlantic is dynamic (Carscadden et al. 2013) and low capelin
12 abundance was a characteristic of the regime shift documented in the 1990s (Pedersen et al.
13 2017, Buren et al. 2019) that was captured in diet studies of Atlantic cod (Taggart et al. 1994),
14 Harp seals *Phoca groenlandica* (Lawson & Stenson 1995), and murrelets *Uria* spp. (Bryant et al.
15 1999). For example, capelin in the diet of Atlantic cod on the coast of Labrador was “virtually
16 absent” in 1991 and 1992 (Taggart et al. 1994). On the Gannet Islands of Labrador, feeding on
17 capelin by murrelets dropped by up to 75% in the early 1990s and shifted to Daubed Shannies
18 *Lumpenus maculatus* (Bryant et al. 1999), whereas Harp seals shifted to a diet dominated by
19 Arctic cod in the late 1980s and early 1990s (Lawson & Stenson 1995). The timing and nature of
20 these diet shifts correspond to those observed in Charr in Nain, which became more similar to
21 those observed from Northern fjords (i.e. dominated by invertebrates and sculpins).

1 Associated with diet shifts away from capelin was a tendency for Nain Charr to be captured at
2 the coastal headlands in commercial fisheries. The combination of the absence of capelin and
3 the low stomach fullness of Charr remaining in inshore areas suggest that Charr in Nain will
4 adjust foraging behavior, leaving to search for capelin or other prey when it is not available
5 closer to natal rivers. Tagged individuals in Nain also showed the capacity to change foraging
6 habitats; altering their use of fjord and coastal habitats from one year to the next. Based on
7 specimens obtained for diet analyses, Charr caught in the Nain Offshore area were frequently
8 larger than those from inshore areas. This pattern was noted previously where commercial
9 fishery samples of Charr from inshore bays were generally smaller beginning in the early 1990s
10 by comparison with those caught offshore (Dempson 1995, Dempson et al. 2004). While part
11 of this could have been associated with temporal differences either in the timing of migrations
12 back to freshwater or timing when sampling was carried out (Dempson 1995), it is also likely
13 that offshore areas provided enhanced feeding opportunities as evidenced from higher
14 stomach fullness data.

15 In comparison to some other anadromous species (e.g. Atlantic and Pacific salmon), Charr do
16 not range far from natal rivers during the marine phase (Dempson & Kristofferson 1987, Spares
17 et al. 2015, Moore et al. 2016, Layton et al. 2021; in this study <50km) and accordingly are
18 constrained to foraging on local prey assemblages. However, our results suggest that within
19 this range, Charr can adjust foraging habitats depending on local conditions. Other studies
20 have documented plasticity in foraging over diel (Spares et al. 2012, Mulder et al. 2020) and
21 seasonal timeframes (Harris et al. 2020) during the marine phase of Charr. For example, Harris
22 et al. (2020) observed that foraging patterns (i.e. diving behavior) shifted to deeper waters as

1 the summer season progressed. Unlike this study, however, these authors did not observe
2 foraging patterns to change across years, despite different environmental conditions. Certainly,
3 there is an expectation that foraging plasticity of Arctic Charr has limits when dealing with
4 environmental change. A genomic study across several regions of northern Canada (including
5 Labrador) showed region-specific adaptations to marine conditions; specifically to summer sea
6 surface temperature, salinity, tides, turbidity, and air temperature (Dallaire et al. 2021).
7 Furthermore, population level impacts have coincided with extreme environmental conditions
8 (Layton et al. 2021), including the populations tracked in this study.

9 Charr migrate to marine habitats to increase growth (Gross et al 1988). They do this by
10 occupying physiologically advantageous habitats (temperature and salinity) and seeking out rich
11 feeding areas. Estuaries appear to meet these conditions (Harris et al. 2020). However, the
12 observation that Charr undertake potentially costly migrations to coastal headlands when
13 capelin are in low abundance indicates the importance of this prey species to Nain Charr
14 populations. Where available, capelin provide a comparably rich food source for Charr (Lawson
15 1998, Fall & Fiksen 2020) and perhaps, in addition to earlier maturation and frequent spawning
16 (Dempson 1995, Power et al. 2005), explains why commercial harvests from the Nain stock
17 complex were sustained at high levels (averaged 70.5 tons annually; 2116 tonnes total from
18 1977-1989) despite harvest rates averaging 42% of the exploitable stock (Dempson 1995).

19 Over time, diet studies of Nain Charr reflect three ecosystem states, beginning with abundant
20 capelin in the 1980s, followed by very low capelin abundance in the 1990s, and intermediate
21 abundance in the early 2000s. Since that time, local knowledge holders have yet to observe
22 capelin to rebound to the levels observed in the 1980s (J. Angnatok pers. comm.). These trends

1 are generally mirrored in capelin bycatch off northern Labrador (Carscadden et al. 2013). In
2 contrast, capelin were more consistently at low biomass in Charr stomachs of Northern fjords
3 (Saglek, Hebron, and Ramah) compared to Nain and Okak (Andrews & Lear 1956, this study).
4 Unfortunately, we have no contemporary surveys to establish the current state of the prey base
5 on the Labrador Coast. Temperate species like capelin are expected to become increasingly
6 common in the north as the climate warms (Reist et al. 2006, Carscadden et al. 2013, Tai et al.
7 2019), and could provide an expanded prey base for more northern fish populations. Indeed,
8 researchers have already reported capelin in Charr diets of Arctic populations in recent years
9 (Spares et al. 2012, McNicholl et al. 2017, Harris et al. 2020).

10 Predicting responses of Charr to climate change remains challenging. Northward expansion of
11 key prey like capelin could provide an important food source for the low productivity coastal
12 ecosystems found along the north coast of Labrador (Murdoch et al. 2015). Comparisons of
13 Ungava and Labrador showed that slightly elevated temperatures coupled with higher local
14 productivity were associated with notably better growth of Ungava Charr (Murdoch et al.
15 2015). Conversely, the concomitant ecosystem changes that facilitate the northward expansion
16 of prey may have negative effects on Charr. For example, growth is dependent on interactions
17 between water temperature, prey availability, and seasonal phenologies (Power et al. 2012,
18 Murdoch et al. 2015). Charr growth is most efficient at lower temperatures when food is
19 limiting (Larsson & Berglund 2005). Therefore it is possible that increases in prey availability
20 may not overcome the reduced growth efficiency associated with warmer water. Positive
21 benefits to Charr are further limited by the potential for increased competition from temperate
22 salmonids (Power et al. 2012) and existing population adaptations that make it difficult for

1 anadromous Charr to thrive in warmer conditions (Layton et al. 2021). Such factors might drive
2 populations with partial migration (i.e. exhibit both anadromous and resident life histories) to
3 shift to resident life histories as the benefits of anadromy fade (Davidsen et al. 2020; Layton et
4 al. 2021). In Nain, despite recovering effective population sizes of local populations and
5 improving capelin abundance in Charr diets, local harvesters have reported Charr are smaller
6 and in lower abundance (Dempson et al. 2008, J. Angnatok pers. comm.); an indication that the
7 fishery, although greatly reduced from earlier times, is becoming less sustainable. Whether
8 these trends are caused by more concentrated fishing effort near communities or deteriorating
9 environmental conditions is not known.

10 Telemetry data provide insights that can be difficult to obtain using conventional mark-
11 recapture techniques. For example timing of migration to and from marine habitats (Dempson
12 & Green 1985, Dempson & Kristofferson 1987, Bégout Anras et al. 1999, Gulseth & Nilssen
13 2000, Jensen & Rikardsen 2012, Moore et al. 2016), occupancy patterns of different marine
14 habitats (Dempson & Kristofferson 1987, Spares et al. 2015, Moore et al. 2016), and foraging
15 behavior (inferred from by diving data; Spares et al. 2012, Mulder et al. 2020, Harris et al. 2020)
16 are more difficult to quantify with conventional techniques. Estuaries were a key marine
17 habitat to Charr in both study areas, with Charr spending considerable time in these areas early
18 in summer. Similar observations were found in Frobisher Bay (Spares et al. 2015) and
19 Cambridge Bay (Moore et al. 2016, Harris et al. 2020) in Arctic regions of Canada. Estuaries are
20 important habitats that provide favorable thermal environments and access to food resources
21 (Spares et al. 2015), and possibly refuges from higher salinity waters (Harris et al. 2020). The
22 mechanism driving heightened use of other marine habitats in Saglek remains unknown. It may

1 be driven by differences in productivity between the two regions, but the productivity patterns
2 of coastal habitats off Labrador remain poorly understood (McCarney et al. in press). An
3 alternate explanation is that estuaries of both areas have comparable productivity but that
4 Nain estuaries may be more attractive in years when they experience influx of migratory prey
5 like capelin. Certainly, tagged Charr in Nain illustrated that motivation to incorporate other
6 non-estuarine habitats can vary from year to year.

7 There are few (but see Dempson & Kristofferson 1987, Dempson et al. 2002, Spares et al. 2012)
8 studies that link observations of marine behavior of Charr to spatial and temporal variation in
9 diet. Complementary data streams such as these (i.e. diet and commercial harvests) provide a
10 more robust and holistic picture of Charr behavior while in the ocean and illustrate the
11 importance of long-term datasets. Even in this circumstance where historical diet and
12 commercial catch data did not temporally overlap with contemporary telemetry data, our
13 confidence in the likelihood that marine behavioral differences observed across Saglek and Nain
14 Charr populations persist over time is bolstered by the consistency of diet differences among
15 fjords over decadal scales. The complexity of dynamic prey fields and small scale spatial
16 variation in marine behavior, super-imposed upon a changing climate, is a challenge to
17 predicting and managing responses of Charr to commercial and food fisheries. Understanding
18 how productivity cycles fluctuate in conjunction with changing environmental conditions will
19 help to predict subsequent impacts on the marine behavior of local Charr populations. While
20 our study shows Charr are capable of surviving regime shifts in part by altering habitat use, prey
21 community shifts expected with climate change (Perry et al. 2005, Rose 2005b) will add to
22 other climate-related stressors that are expected to have widespread impacts on anadromous

1 Charr populations (Layton et al. 2021). With this in mind, recent concerns about the health of
2 Charr populations near Nain suggest renewed monitoring efforts of Charr and the coastal
3 ecosystem are needed to support sustainable management of this critical cultural (Berkes 2018)
4 and commercial (Power & Reist 2018) resource.

5 **5. ACKNOWLEDGEMENTS**

6 The extensive datasets used in this study were reliant on the dedication and innovation of many
7 residents of Nunatsiavut (Food Skills and Environmental Research Program), technicians and
8 biologists from DFO (J. Seiden, D. Lancaster, M. Shears, M. Bloom, S. Duffy), the Nunatsiavut
9 Government (P. McCarney, C. Andersen, L. Pijogge), Oceans North (S. Pain), and of the captains
10 and crew of the What's Happening and the Safe Passage. Suggestions by three anonymous
11 reviewers also greatly improved the manuscript. Funding for this research was provided in part
12 by ArcticNet and DFO Oceans.

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1 **Tables**

2 **Table 1:** Prey items differentiating diet among Arctic Charr captured in Northern stocks

3 (including Saglek Fjord, see Figure 1) and in inshore and offshore areas of Nain. Dissimilarity

4 scores are derived using the Bray Curtis Index.

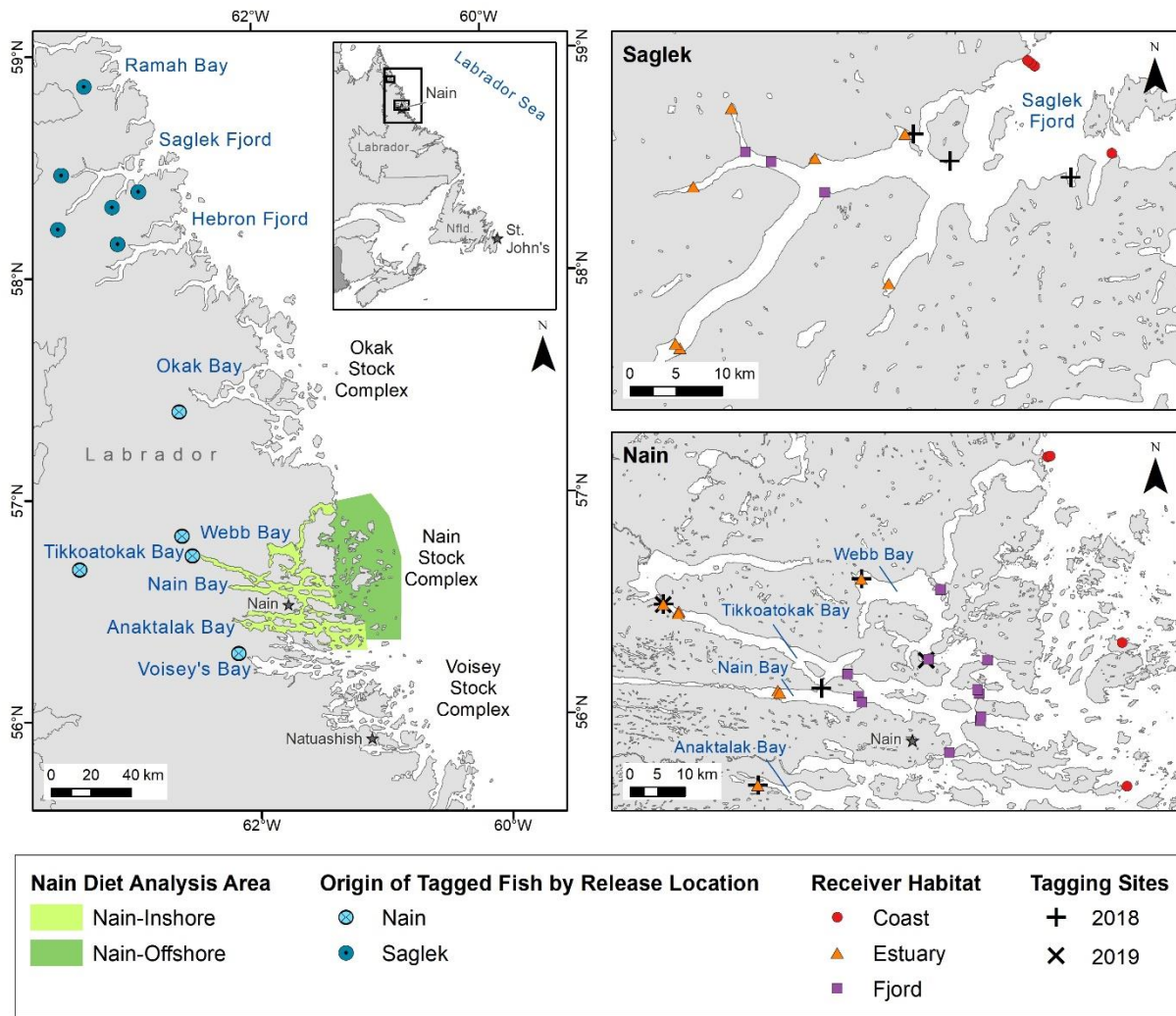
Nain Inshore vs. Nain Offshore				
Taxa	Nain Inshore average diet biomass (g)	Nain Offshore average diet biomass (g)	Dissimilarity Contribution (%)	Cumulative Dissimilarity (%)
Capelin	11.9	5.9	21.4	21.4
Sculpins (Cottid)	3.2	6.8	12.4	33.8
Sand lance	5.0	4.8	10.9	44.8
Amphipod (<i>Parathemisto</i> spp.)	1.7	4.8	9.1	53.9
Sculpin (<i>Myoxocephalus</i>)	1.7	4.5	8.8	62.7
Amphipod (Hyperid)	1.6	3.4	7.4	70.1
Nain Inshore vs. Northern				

Taxa	Nain Inshore average diet biomass (g)	Northern average diet biomass (g)	Dissimilarity Contribution (%)	Cumulative Dissimilarity (%)
Capelin	11.9	2.5	21.7	21.7
Sculpins (Cottid)	3.2	6.3	14.4	36.0
Amphipod (<i>Parathemisto</i> spp.)	1.7	6.9	13.3	49.3
Sand lance	5.0	0.8	11.8	61.1
Fish (unidentified)	3.9	1.0	7.7	68.7
Sculpin (<i>Myoxocephalus</i>)	1.7	0.8	5.0	73.7
Nain Offshore vs. Northern				
Taxa	Nain Offshore average diet biomass (g)	Northern average diet biomass (g)	Dissimilarity Contribution (%)	Cumulative Dissimilarity (%)
Sculpins (Cottid)	6.8	6.3	16.0	16.0

Amphipod <i>(Parathemisto</i> spp.)	4.6	6.9	14.9	30.9
Capelin	5.9	2.5	11.9	42.8
Sand lance	4.8	0.8	8.8	51.6
Sculpin <i>(Myoxocephalus)</i>	4.5	0.8	8.6	60.2
Amphipod (Hyperid)	3.4	1.1	7.0	67.1
Pteropods	2.0	0.3	4.8	71.9

1

1 **Figures**



2

3 **Figure 1:** Stock complexes of Arctic Charr in northern Labrador, Canada as defined by (Dempson
 4 & Kristofferson 1987). Ramah Bay, Saglek Fjord and Hebron Fjord comprise the areas of the
 5 Northern stock. River origin of fish tagged in marine environments of Nain and Saglek are
 6 shown at the point where rivers empty/drain into the ocean. One fish tagged in Nain originated
 7 from the Okak stock complex. Right panels indicate receiver locations and tagging areas within

- 1 the two study systems (Saglek Fjord and Nain). Different habitat types are denoted by receiver
- 2 color and shape.



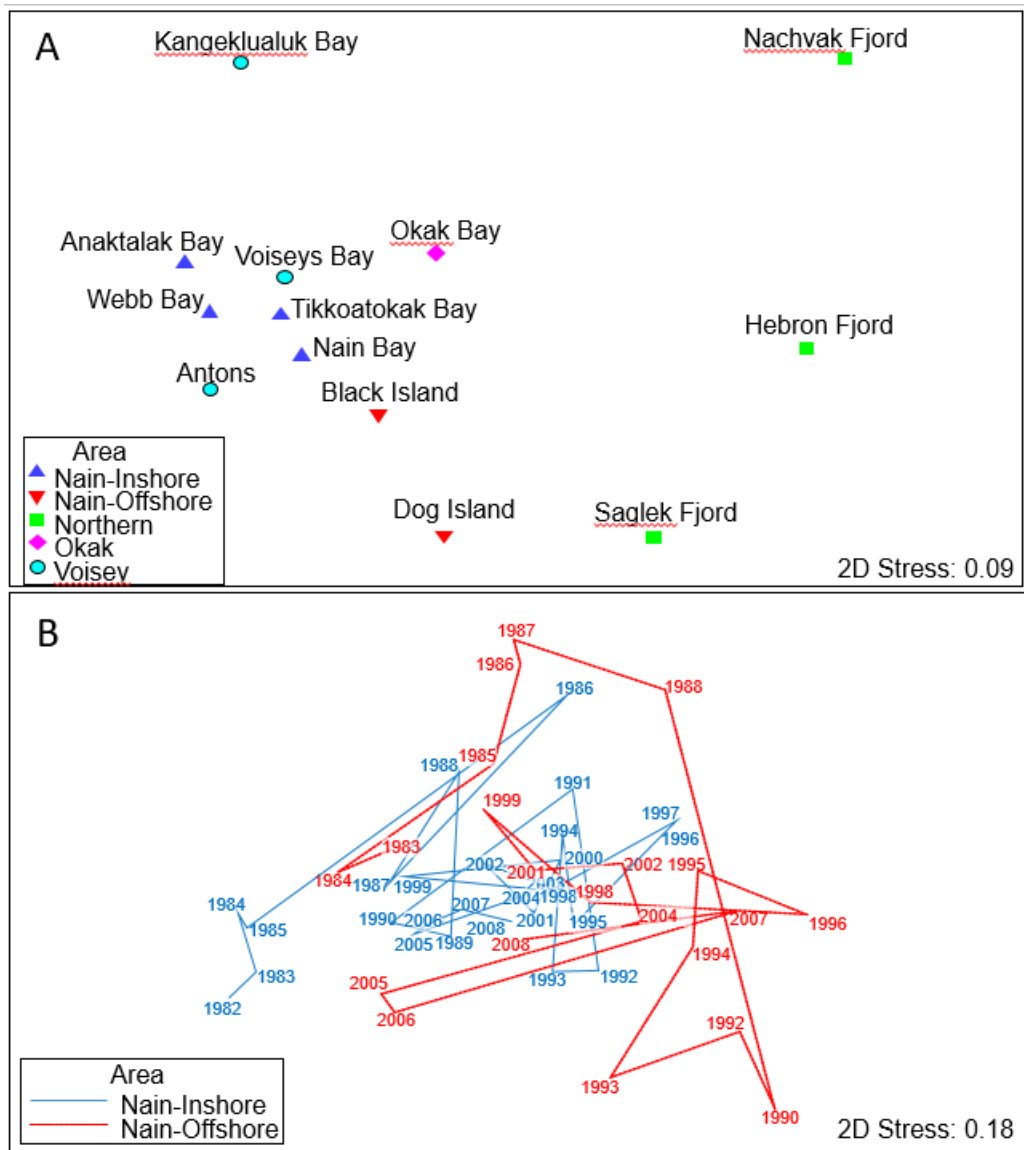
1

2 **Figure 2:** A: Detections (represented by dots) of Arctic Charr in different habitats (Estuary, Fjord

3 and Coast) across 2018 (left panel) and 2019 (right panel) in Nain and Saglek. Rows of

4 detections represent multiple records of individual fish. B: Number of Arctic Charr detected by

- 1 receivers in estuarine, fjord and coastal habitats by month during 2018 and 2019 in waters off
- 2 Nain (n=45) and Saglek (n=27).



1

2 **Figure 3:** A: Spatial patterns of Arctic Charr diets for fish captured at commercial fishing

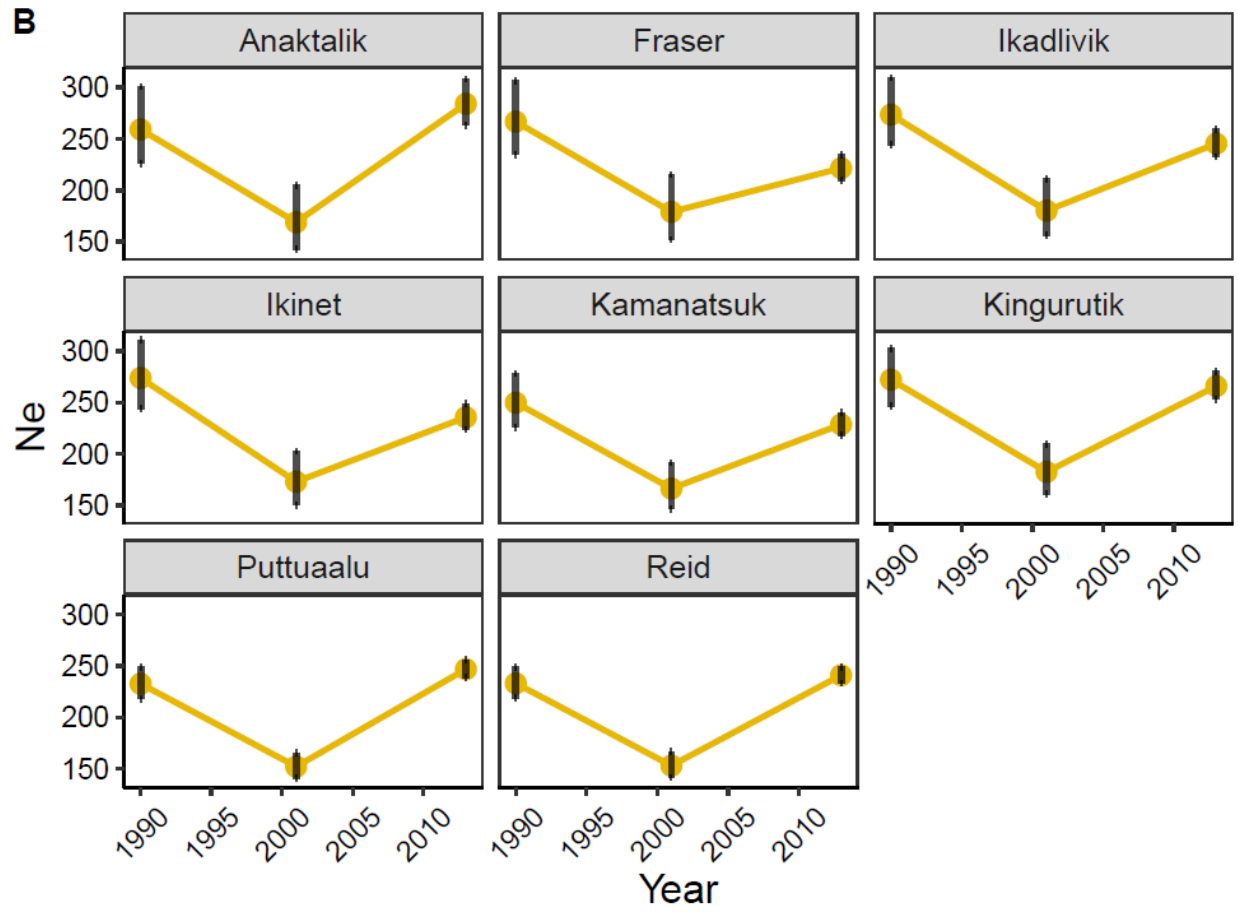
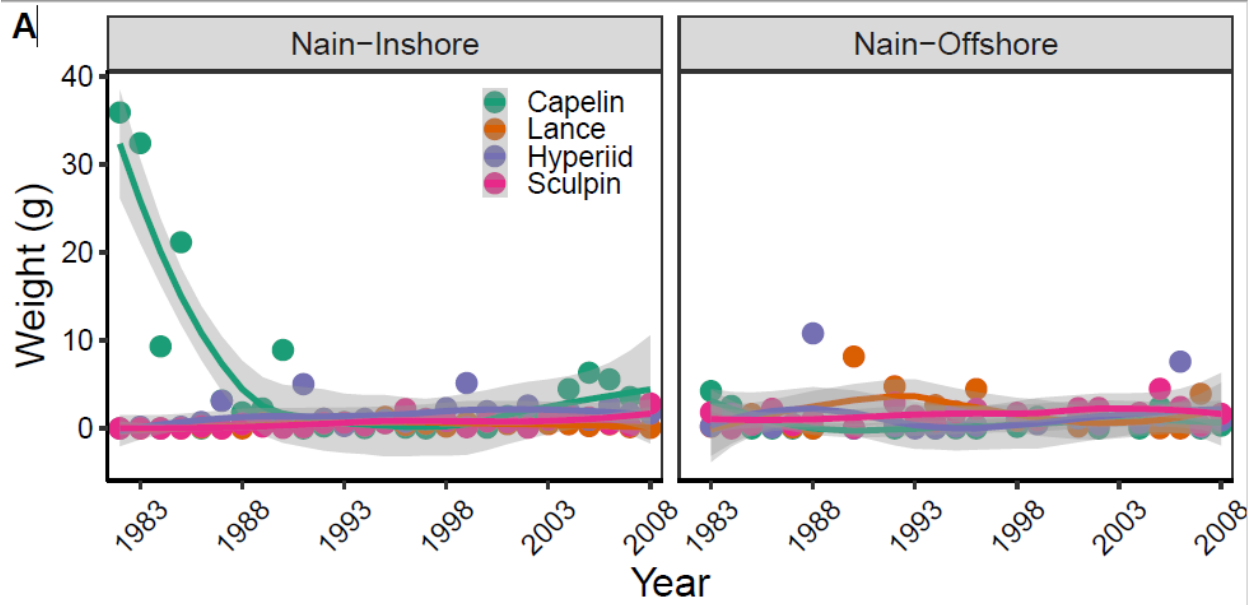
3 locations of the northern Labrador Coast (see Figure 1 for locations). B: Patterns of Arctic

4 Charr diets across years for Charr caught in Nain Inshore and Nain Offshore. Lines indicate the

5 time series progression for each area. Proximity of points in these non-metric multidimensional

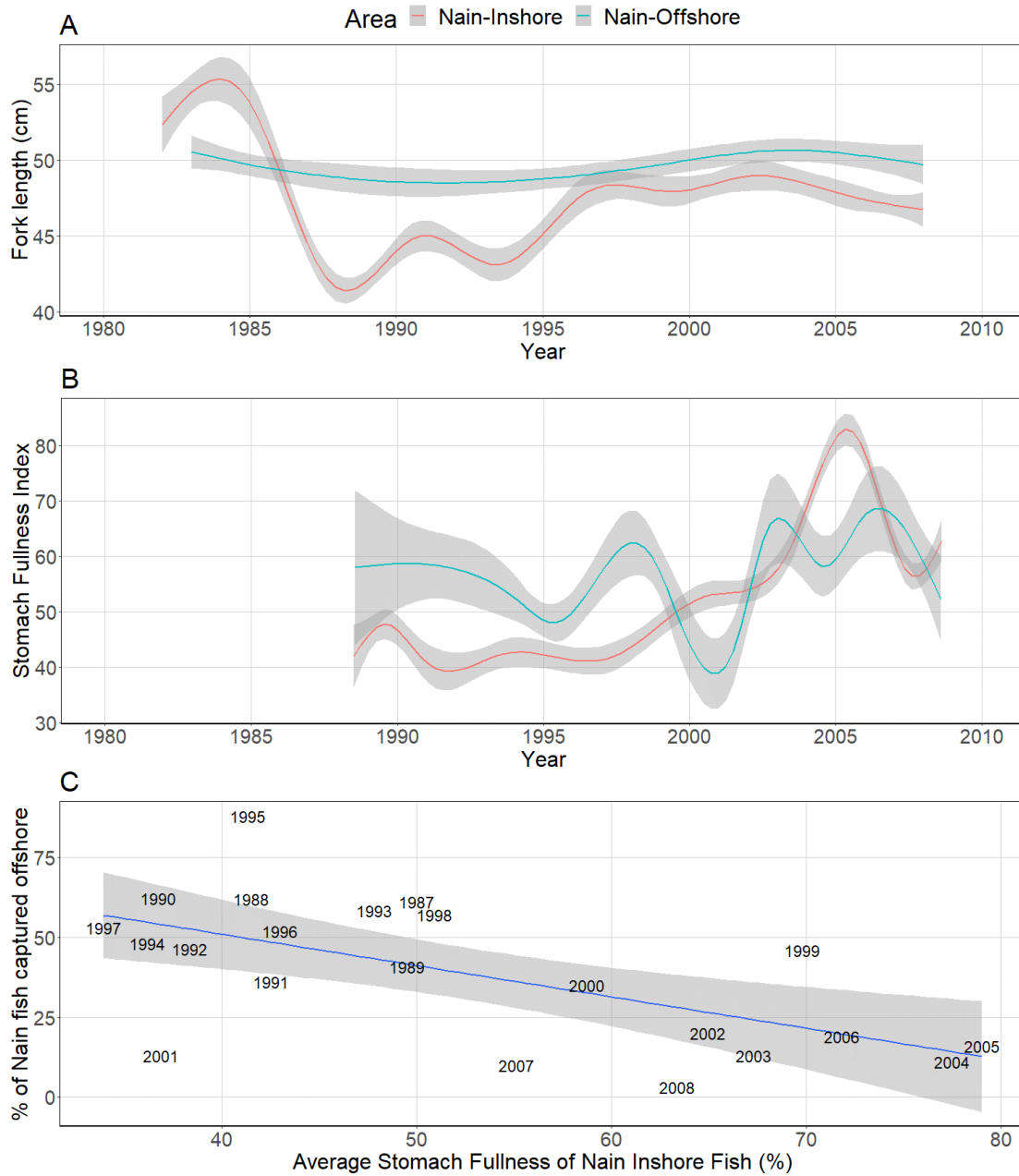
6 scaling plots reflect diet similarity (Bray-Curtis) of PCO-derived centroids.

1



2

1 **Figure 4:** A) Average weight of prey items in diets of individual Charr (solid lines) from Nain
2 Inshore and Nain Offshore from 1986-2008 and B) corresponding estimates of effective
3 population size (N_e) (number of individuals) in rivers associated with Nain Bay from 1990-2013
4 that were derived from Layton et al. (2021). Error bars represent 95% confidence intervals.



1

2 **Figure 5:** Changes to average fork length (A) and stomach fullness (B) of Arctic Charr sampled

3 for diet analyses from inshore and offshore areas of Nain. C: Catch of Arctic Charr captured in

4 Nain Offshore compared to stomach fullness of Charr captured in Nain Inshore. Trend lines in A

5 and B represent GAM cubic regression smoothers with 95% confidence intervals. Trend line in C

6 indicates the linear model and shaded area represents 95% confidence intervals.