



Using movement, diet, and genetic analyses to understand Arctic charr responses to ecosystem change

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ABSTRACT: Arctic charr *Salvelinus alpinus* are a commercially and culturally valued species for northern Indigenous peoples. Climate shifts could have important implications for charr and those that rely on them, but studies that evaluate responses to ecosystem change and the spatial scales at which they occur are rare. We compare marine-phase habitat use, long-term diet patterns, and trends in effective population size of Arctic charr from 2 areas (Nain and Saglek) of Nunatsiavut, Labrador, Canada. Tagged charr in both areas frequently occupied estuaries but some also used other habitats that extended to the headland environments outside of their natal fjords. Despite the relatively small distances separating these study areas (<200 km), we observed differences in habitat use and diet. Northern stocks (including Saglek) were more reliant on invertebrates than southern stocks (e.g. Nain), for which capelin and sand lance were important prey. The use of coastal headlands also varied, with Saglek charr occupying these environments more frequently than those from Nain, which only used these habitats in 1 year of the study. Long-term commercial catches also indicate that the tendency for Nain charr to stay within fjords varies annually and relates to capelin availability. Despite the demonstrated capacity to alter diet and habitat use to changing environmental conditions, notable declines in effective population size were associated with the regime shift of the 1990s in the northwest Atlantic. Collectively, these results demonstrate that behavioral plasticity of Arctic charr may be insufficient to deal with the large environmental perturbations expected to arise from a changing climate.

KEY WORDS: Diet · Telemetry · Effective population size · Long-term monitoring · Labrador · Nunatsiavut

1. INTRODUCTION

Arctic charr *Salvelinus alpinus* are an iconic Arctic species native to a wide latitudinal gradient (Johnson 1980) that extends from the Arctic to north temperate regions (Reist et al. 2013). Across this range, this species exhibits a variety of adaptations (Dallaire et al. 2021) including remarkable phenotypic diversity within both freshwater resident and anadromous life histories (Klemetsen et al. 2003). In all but the south-

ern extents of their range, anadromy is a common life history trait (Klemetsen et al. 2003) that allows charr to quickly increase somatic reserves in productive coastal environments before returning to freshwater to reproduce and overwinter (Klemetsen et al. 2003).

Behavioral plasticity is also common within anadromous populations of charr. At sea, for example, charr occupy habitats that range from sheltered estuaries to coastal headlands, show variation in marine residency times (Dempson & Kristofferson 1987, Gulseth

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& Nilssen 2000, Klemetsen et al. 2003, Spares et al. 2015, Moore et al. 2016, Harris et al. 2020), occupy a variety of thermal habitats (Rikardsen et al. 2007a, Spares et al. 2012, Harris et al. 2020, Mulder et al. 2020), and consume diverse prey often dominated by pelagic fish and plankton (e.g. amphipods), but also items such as insects and benthic organisms (Dempson et al. 2002, Klemetsen et al. 2003, Rikardsen et al. 2007b, Spares et al. 2012, Davidsen et al. 2020). Despite this plasticity, marine habitat use within populations can remain stable across years, even during changing environmental conditions (Harris et al. 2020).

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

The challenges to understanding variability and plasticity in Arctic charr behavior are two-fold: (1) there is a scarcity of data sets of appropriate spatial and temporal scales and (2) there is a lack of data associating behavior with biotic environmental variables such as prey availability. Though considerable research is available on the marine movements of Arctic charr (e.g. Bégout Anras et al. 1999, Spares et al. 2015, Moore et al. 2016, Harris et al. 2020), it is difficult to sustain these projects over extended temporal periods across a latitudinal gradient while concurrently monitoring biotic/abiotic variables of interest. One area where extensive behavioral data exist is in Nunatsiavut, northern Labrador, Canada, where conventional mark-recapture tagging studies have been conducted over several decades and supported by diet and morphometric studies (Dempson & Kristofferson 1987, Power et al. 2000, Dempson et al. 2002, 2008). These studies provide a baseline that, when coupled with contemporary telemetry and genomic methods, can be used to explore spatial and temporal variation in Arctic charr marine movement behavior and links to marine-phase diets.

Evaluating threats to southern sub-Arctic anadromous populations from further climate shifts and predicting changes to more northerly populations will depend on understanding the adaptability of local populations and their capacity to deal with ecosystem shifts. Past environmental disruptions can inform

our understanding of the capacity of fauna to accommodate ecological change. For example, a regime shift coinciding with unusually cold ocean temperatures and lower productivity occurred in the northwest Atlantic in the 1990s (Pedersen et al. 2017). This time period was also associated with changes in species distributions and abundance (Colbourne 2004, Rose 2005a, Carscadden et al. 2013), as well as the decline of many important commercial fishery populations (Bundy et al. 2009, Mills et al. 2013, Pedersen et al. 2017). During this period the abundance of capelin *Mallotus villosus* declined in coastal areas of Newfoundland and Labrador (Buren et al. 2019), affecting the diets of a variety of fish, bird, and marine mammal species (Taggart et al. 1994, Lawson & Stenson 1995, Montevecchi & Myers 1997, Bryant et al. 1999, Rowe et al. 2000, Dempson et al. 2002) including Arctic charr (Dempson et al. 2002). As climate change progresses, other broad redistributions of species (Perry et al. 2005, Rose 2005b) and productivity are expected (Moore et al. 2018), which could have important repercussions on species like Arctic charr.

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

2. MATERIALS AND METHODS

2.1. Study area

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

2.2. Acoustic telemetry

Movements of Arctic charr were followed in 2 coastal regions of Nunatsiavut separated by approximately 200 km (Fig. 1). Saglek Fjord is 65 km in length, 14 km at its widest point, and is bathymetrically characterized by 7 underwater basins (80 to 256 m) separated by sills (Brown et al. 2012, Simo-Matchim et al. 2017). The second region, hereafter referred to as Nain, is occupied by charr of the Nain stock complex (Dempson et al. 2002; our Fig. 1), and is more geographically complex due to the presence of islands that extend outside of Anaktalak Bay, Nain Bay, Tikkoatokak Bay, and Webb Bay. The Nain region is approximately 50 km wide with maximum depths reaching at least 110 m (Nutt 1953), though its bathymetry remains largely unmapped. Sea ice is common to both regions, occurring typically from November to mid-June or early July (McCarney et al. in press).

We used an array of Vemco acoustic receivers (VR2W and VR2ARs, Innovasea) to monitor the marine movements of Arctic charr from the summer of 2018 to autumn of 2019. Receivers were positioned to monitor habitat use and the timing of migration events to and from the marine environment of tagged animals through the course of their marine residency period. Consequently, we placed receivers in river estuaries, gateways within, and at the seaward extent of fjords to track exits to the coastal headlands. The more complex nature and variety of migratory pathways off Nain required more receivers for coverage. In total, we deployed 43 receivers between our 2 study sites: 25 were deployed off Nain and 18 in Saglek Fjord (Fig. 1). Of the 43 receivers deployed, 23 (15 in Nain and 8 in Saglek) were VR2-ARs that were recovered with acoustic releases. The remaining receivers were VR2Ws and recovered with ground lines.

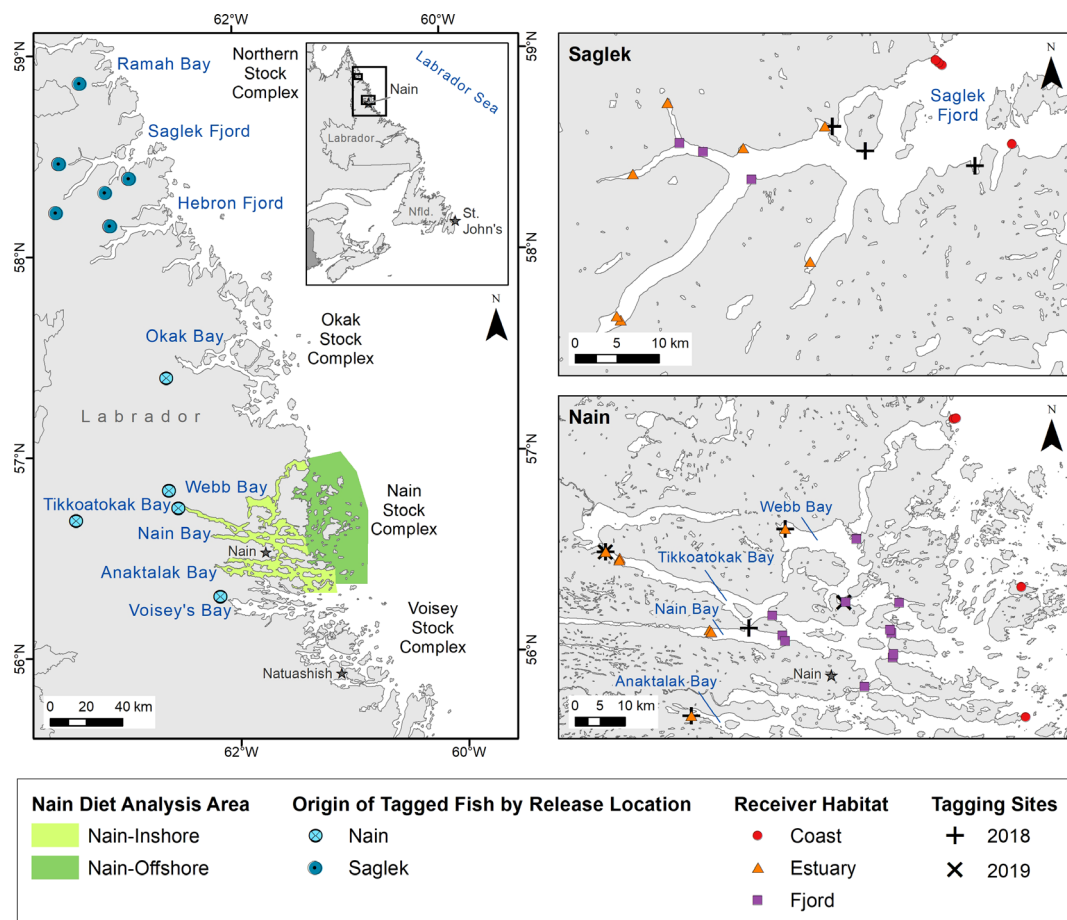


Fig. 1. Stock complexes of Arctic charr in northern Labrador, Canada as defined by Dempson & Kristofferson (1987). Ramah Bay, Saglek Fjord, and Hebron Fjord comprise the areas of the northern stock. River origin of fish tagged in marine environments of Nain and Saglek are shown at the point where rivers empty/drain into the ocean. One fish tagged in Nain originated from the Okak stock complex. Right panels indicate receiver locations and tagging areas within the 2 study systems (Saglek Fjord and Nain). Different habitat types are denoted by receiver color and shape

We tagged charr in 2018 in Saglek Fjord (July 25–26, 2018) at Torr Bay, Branagin Island, and Jens Haven Island, and in Nain (August 2–4, 2018) at Webb Bay, Tikkoatokak Bay, Nain Bay, and Anaktalak Bay (Fig. 1, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m673p135_supp.pdf). We also tagged charr in Nain in Webb Bay (July 31) and Tikkoatokak Bay (August 1) in 2019. Fish were collected using either barbless, single hook fishing lines or 4½ inch (11.5 cm) gillnets. Tagged fish in Saglek ranged from 45.7 to 64.0 cm (mean 53.7 cm), whereas those from Nain ranged from 41.5 to 63.5 cm (mean 50.4 cm) (Table S1). Based on fish length, we estimated ages to range from 7 to 14 yr (Dempson et al. 2008). Once captured, we measured length, and took a small clip of tissue (~1 cm²) from the caudal fin to genetically assign a subset of fish to their natal river (see Section 2.3). Prior to release, tagged charr were allowed to recover in a plastic tub equipped with air pumps and flowing sea water. In total, 95 fish (40 in Saglek, 44 in Nain in 2018, and 11 in Nain in 2019) had uniquely coded Vemco V13 (36 [length] × 13 mm [diam.], 9.2 g in air, tag life: 602 d) or V13T (46 × 13 mm, 9.7 g in water, tag life: 498 d) transmitters surgically implanted in their abdominal cavities. Transmitters emitted pulses at random intervals between 60 and 120 s to minimize signal collisions that might occur if multiple tags were in close proximity.

We filtered our data of suspected mortality or tag-shedding events (i.e. removing individuals that consistently remained in the vicinity of a receiver beyond normal migration periods), grouping the remaining data into individual detection events at specific receivers using the R package GLATOS (<https://gitlab.oceantrack.org/GreatLakes/glatos>). Occupancy was measured in 3 different habitat types using detections on receivers located in estuarine (immediate proximity of a freshwater input), fjord, and coastal (headlands outside of fjords) habitats (Fig. 1).

2.3. Genetic assignment to river of origin

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

son 2019), as described by Layton et al. (2020). Only assignments with a probability of >0.80 were reported. Previous work suggests assignment accuracy using these loci and baseline is approximately 90%.

2.4. Diet analysis

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

Prey from charr stomachs were identified according to fish and invertebrate taxa and categorized by abundance and biomass metrics as described in Dempson et al. (2002). Additionally, for the years 1988–2008, quartiles of stomach fullness (i.e. 0 = empty and 4 = full) were recorded for each fish and converted to percent fullness. To reduce autocorrelation of samples, we averaged stomach content biomass by sampling day and charr fishing area (Fig. 1). We used the Bray-Curtis Index (Bray & Curtis 1957) to analyze community similarity and dissimilarity in biomass. We identified prey taxa that typified (i.e. contributed most to within-group similarity values) stocks and months, and discriminated (i.e. contributed most to dissimilarity values) among groups using SIMPER (PRIMER 7). Differences in prey communities across stocks, years, and months were evaluated through PERMANOVA (PERMANOVA+1.0.3; 9999 permutations), a permutation-based multivariate analog of ANOVA (Anderson 2001). Since the full model had a significant interaction between year and month, we analyzed 3 more simple models: (1) a model applied to the entire diet dataset with fixed terms for stock and month, and a stock × month interaction; (2) for Saglek data, a model with fixed terms for year, month, and a year × month interaction term; and (3) for Nain, a model that included the capture area (Inshore/Offshore) along with month, year, and all interaction terms. We presented these data using multi-dimensional scaling (MDS) of centroids. Centroids (representations of multivariate central tendency) were derived from Principal Coordinates Analysis (PCO)

(Gower 1966) and used to simplify visual representations of biomass data. We also evaluated the consistency of interannual seriation in diets from charr caught in inshore and offshore areas of Nain by comparing stock-specific annual centroid similarity matrices using a permutation test of Spearman's rank correlation coefficients (RELATE algorithm in PRIMER version 7; 999 permutations).

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

2.5. Effective population size

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

3. RESULTS

3.1. Genetic assignments of tagged fish

Bayesian mixed stock fishery analysis assigned 72 tagged fish to a river but only 55 (75%) surpassed the 80% assignment certainty threshold (Table S1). These

analyses indicated that the fish tagged in Saglek Fjord originated from within Saglek (Southwest Arm River [n = 13], Kiyuktok Brook [n = 7], Pangertok Brook [n = 1], Uggjuktok River [n = 2]), or neighboring waterbodies within 50 km such as Hebron Fjord (Ikarut River [n = 11]) and Ramah Bay (Stecker River [n = 2]) (Fig. 1). Fish tagged in the Nain stock complex originated from Nain Bay (Fraser River [n = 1], Kamanatsuk Brook [n = 7], Kingurutik River [n = 8]), southern Anaktalak Bay (Ikadlavik Brook [n = 7]), and Webb Bay (Ikinet Brook [n = 1]) (Fig. 1). Tagged fish from Saglek (mean length 53.7 cm) were significantly longer ($t = 3.22$, $p = 0.002$) than those from Nain (mean length 50.4 cm).

3.2. Movement

We acquired telemetry data for 75 charr: 29 from Saglek and 46 from Nain (38 tagged in 2018 and 8 tagged in 2019). From our initial group of tagged fish, we were unable to detect 19 after tagging occurred, and assumed they left our array, had a malfunctioning transmitter or died beyond detection of our receivers. We excluded an additional individual due to suspected mortality or tag shedding (e.g. Lacroix et al. 2004). Data for this fish consisted of a continuous string of detections on 1 receiver extending from roughly the date of tagging through winter months and no detections on other receivers in the subsequent year. Among the remaining fish, 1 individual appeared to die or shed a tag after previous, distinct movements and therefore post-mortality data for this fish were also excluded. Three other individuals were detected only once (all in estuaries), which was insufficient to make a detection event within the GLATOS package and thus they were also excluded from further analysis.

We last detected the majority of tagged charr in both Saglek (23 of 29) and Nain (24 of 44) in 2018 in estuaries of the study area. It was assumed that the remainder overwintered in rivers outside the respective study areas. Moreover, we only detected a subset of the fish tagged in 2018 (45%, $n = 13$ in Saglek and 34%, $n = 15$ in Nain) the following year. Migration timing into 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 differ across study locations. The mean date of migration into rivers was August 9 for Nain fish and August 16 for Saglek fish. Mean dates of migration back to the marine environment were June 6 and June 4 for Nain and Saglek respectively (Fig. 2A). We did not detect tagged individuals in more than 1 study region.

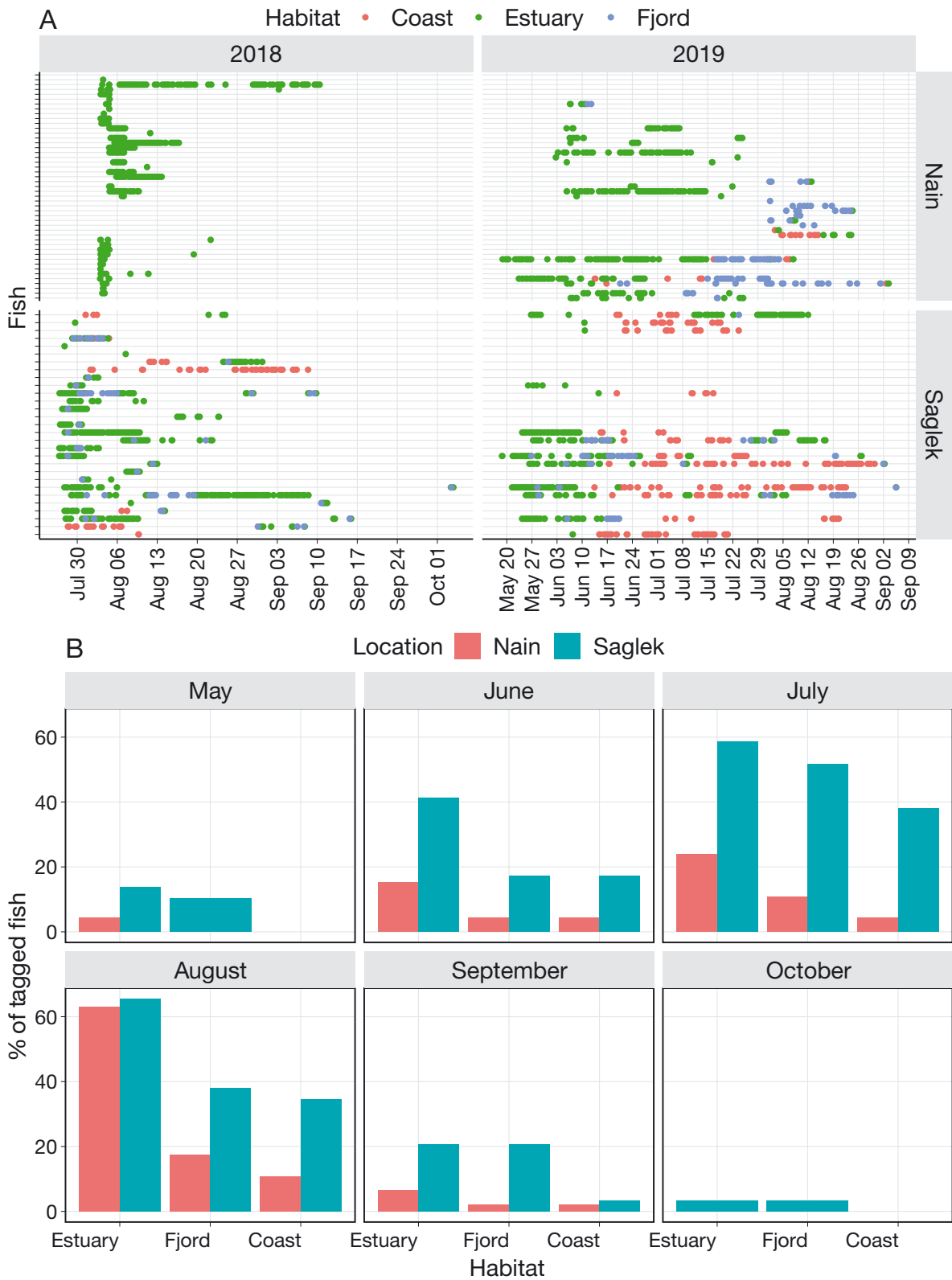


Fig. 2. (A) Detections (●) of Arctic charr in different habitats (estuary, fjord, and coast) across 2018 (left panel) and 2019 (right panel) in Nain and Saglek. Rows of detections represent multiple records of individual fish. (B) Number of Arctic charr detected by receivers in estuarine, fjord and coastal habitats by month during 2018 and 2019 in waters off Nain (n = 45) and Saglek (n = 27)

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

3.3. Diet and changes to effective population size

Charr diets along the north coast of Labrador revealed considerable variation at spatial scales within and among study regions ($p < 0.001$; Fig. 3A), and at temporal scales of months to decades (Fig. 3B). At the largest spatial scales, the Northern stock was most unique with a diet that included a higher proportion of non-fish prey such as amphipods (Table 1). In contrast, diets of charr captured in Nain Inshore largely comprised fish such as capelin and sand lance *Ammodytes* spp. (Table 1). Charr in Nain Offshore maintained an intermediate level of piscivory relative to Nain Inshore and Northern charr (Fig. 3A, Table 1). Diets of charr from other areas (e.g. Okak and Voiseys) were more similar to Nain Inshore (Fig. 3A). With the exception of Cottid sculpins and *Parathemisto* amphipods (Nain Inshore only), biomass of all prey taxa was lower in charr from the Northern area.

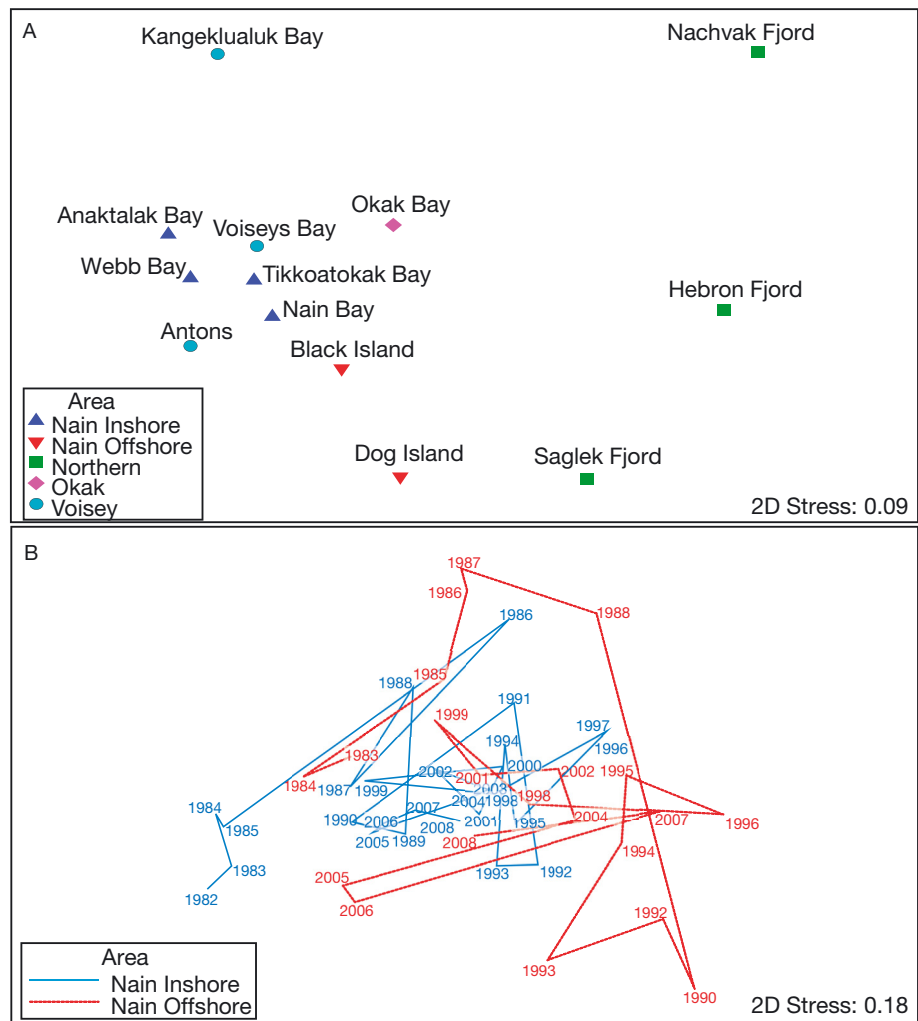


Fig. 3. (A) Spatial patterns of Arctic charr diets for fish captured at commercial fishing locations of the northern Labrador Coast (see Fig. 1 for locations). (B) Patterns of Arctic charr diets across years for charr caught in Nain Inshore and Nain Offshore. Lines indicate the time series progression for each area. Proximity of points in these non-metric multidimensional scaling plots reflect diet similarity (Bray-Curtis) of PCO-derived centroids

Table 1. Prey items differentiating diet among Arctic charr captured in northern stocks (including Saglek Fjord, see Fig. 1) and in inshore and offshore areas of Nain. Dissimilarity 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

The degree of variability explained by temporal scales varied by area. The model for Nain charr had a significant year \times month interaction term so we examined month-specific differences separately. We observed diet differences for captured fish among areas (Inshore and Offshore) and years in Nain for both July ($p < 0.001$ for both area and year) and August ($p = 0.001$ for area; $p = 0.03$ for year), whereas we only detected differences in the Northern stock across years ($p = 0.002$) and not months ($p = 0.48$). For Nain Inshore stocks, capelin tended to be abundant in charr stomachs in July (but also present in August). Decadal patterns were also evident (Fig. 3B), with samples from the 1980s grouping very differently from those in the early 1990s and an intermediate state observed in the 2000s. While not a planned statistical comparison, we assessed decadal groupings within a PERMANOVA framework for Nain Inshore and Nain Offshore areas. The full model that included decade and area as fixed effects had a significant interaction. When each area was run separately, pairwise comparisons showed that all decades were significantly different from one another in both

areas but that the difference between the 1990s and 2000s in the Nain Offshore area was weaker and only marginally significant ($p = 0.046$ compared to $p < 0.001$ for the others). Interestingly, this decadal pattern was shared across the Nain areas (Inshore and Offshore) as the correlation in interannual patterns was significant across the years when data was available for both locations ($\rho = 0.351$, $p = 0.004$). Capelin appeared to be a key driver of the observed temporal patterns in Nain, especially compared to other fish prey such as sand lance (Fig. 4). Effective population size of charr in Nain Inshore also showed interannual patterns with a mean decline of 34.3% (range 32.9–36.8%) between the first (1990) and second (2001) time point that corresponds to declines in capelin in their diets (Fig. 4). All populations recovered by the third time point to a mean of 95.9% (range 83.0–109.6%) of their original population size.

Charr sampled from Nain Offshore for diet analyses were generally larger in most years than those captured within the fjords of Nain (Fig. 5A). Moreover, mean sizes of fish sampled from Nain Offshore

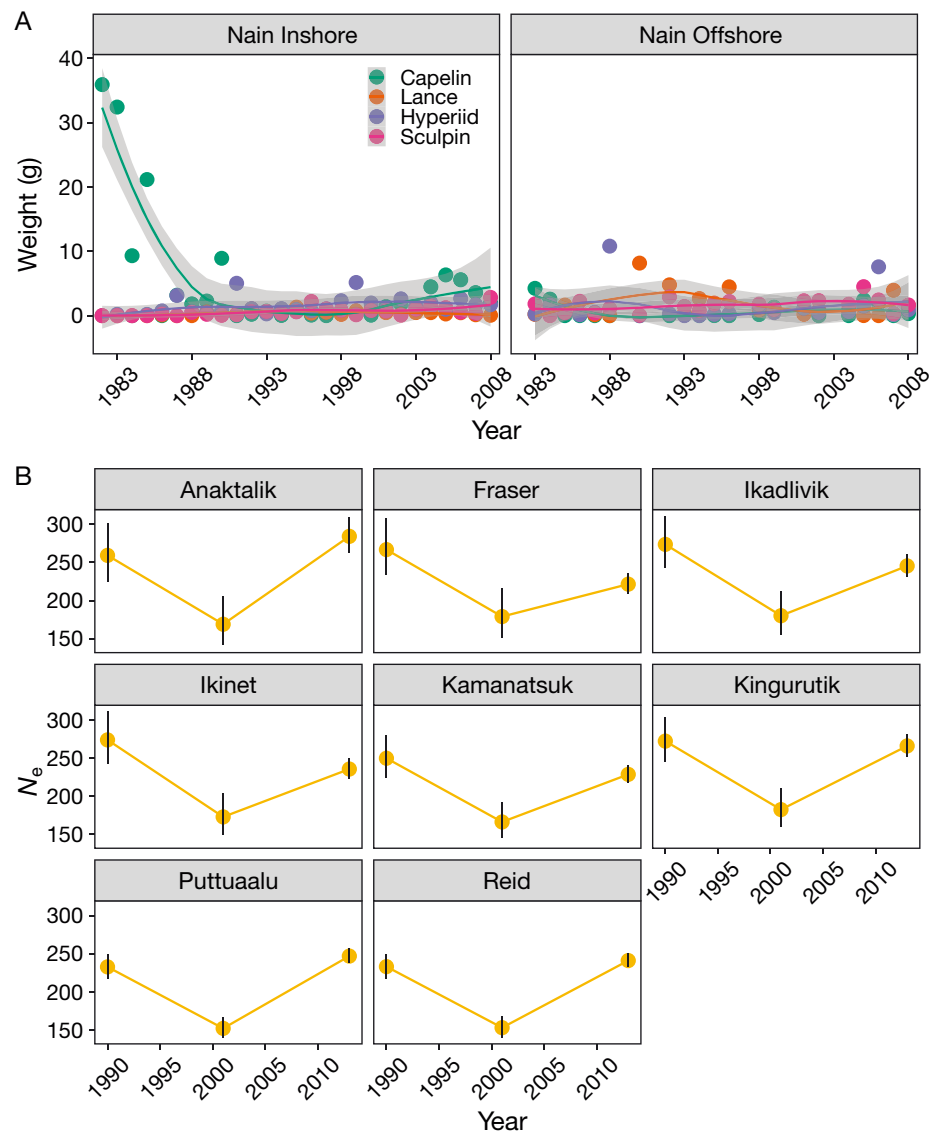


Fig. 4. (A) Average weight of prey items in diets of individual charr (solid lines; grey shaded areas represent 95% CIs of the GAM smoothing function) from Nain Inshore and Nain Offshore from 1986–2008 and (B) corresponding estimates of effective population size (N_e) (number of individuals) in rivers associated with Nain Bay from 1990–2013 that were derived from Layton et al. (2021). Error bars represent 95% confidence intervals

did not vary across years to the same degree as those captured from Nain Inshore (Fig. 5A). Stomach fullness data also revealed differences between the 2 areas over the time series (Fig. 5B). In Nain Offshore, stomach fullness was more consistent (typically averaging in the 50–60% range), with notable exceptions in 1996 and 2001. In contrast, Nain Inshore stomach fullness was consistently lower than Offshore throughout the late 1980s and 1990s before exceeding Offshore values in the early 2000s and peaking in 2005. Across all years, there was a tendency for more charr to be captured in commercial fisheries offshore of Nain when stomach fullness of Nain Inshore charr was low ($F_{1,20} = 12.51$, $p = 0.002$, $R^2 = 0.385$; Fig. 5C). Such a pattern was also found when using catch per unit effort (CPUE) as response variable ($F_{1,20} = 6.60$; $p = 0.018$, $R^2 = 0.248$).

4. DISCUSSION

Arctic charr demonstrated the capacity to buffer the effects of broad environmental change through shifts in habitat use and diet. While behavioral plasticity is an important trait for dealing with a variable environment, it was insufficient to fully safeguard populations from the broad ecosystem changes experienced in the 1990s, even in areas that were under less harvesting pressure (Layton et al. 2021). It is likely, however, that behavioral plasticity has played a key role in the observed recovery in effective population size of charr in our study area and other parts of the Labrador Coast (Layton et al. 2021) despite only a partial recovery of capelin in their diets.

Charr are generalist feeders utilizing a variety of fish and invertebrate taxa (Klemetsen et al. 2003),

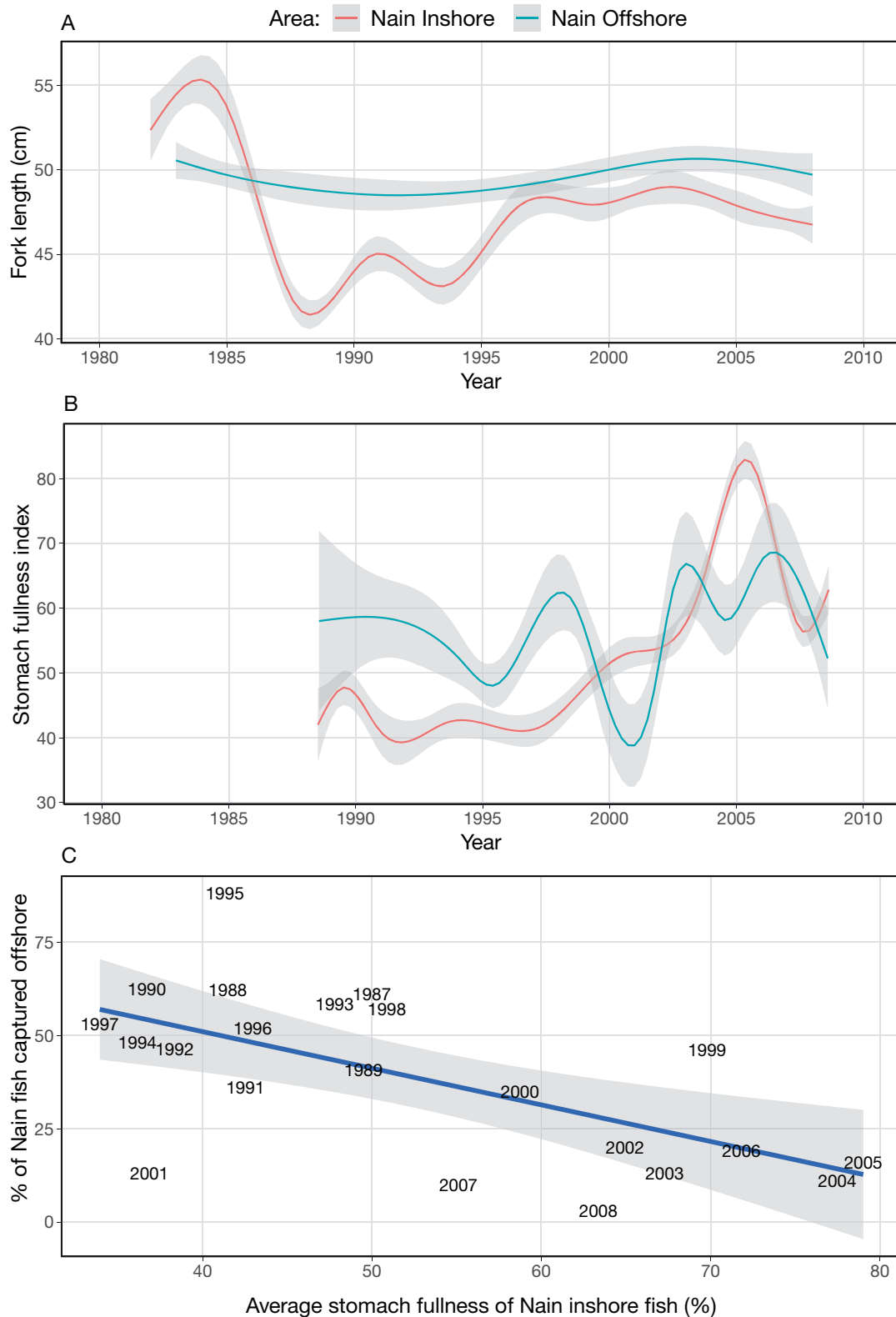


Fig. 5. Changes to average (A) fork length and (B) stomach fullness of Arctic charr sampled for diet analyses from Nain Inshore and Nain Offshore. (C) Catch of Arctic charr captured in Nain Offshore compared to stomach fullness of charr captured in Nain Inshore. Trend lines in (A) and (B) represent GAM cubic regression smoothers with 95% confidence intervals. Trend line in (C) indicates the linear model and shaded area represents 95% confidence intervals

which enhances their capacity to endure fluctuating prey bases. In addition to varying across stocks, diet composition changed across months during the marine phase and also shifted over decadal scales, presumably in response to prey availability. In southern portions of our study area, where piscivory on capelin was most prominent (Dempson et al. 2002, 2008), we observed year to year diet variation. Capelin abundance and distribution in the north Atlantic is dynamic (Carscadden et al. 2013) and low capelin abundance was a characteristic of the regime shift documented in the 1990s (Pedersen et al. 2017, Buren et al. 2019) that was captured in diet studies of Atlantic cod (Taggart et al. 1994), harp seals *Phoca groenlandica* (Lawson & Stenson 1995), and murre *Uria* spp. (Bryant et al. 1999). For example, capelin was 'virtually absent' in the diet of Atlantic cod on the coast of Labrador in 1991 and 1992 (Taggart et al. 1994). On the Gannet Islands of Labrador, feeding on capelin by murre dropped by up to 75% in the early 1990s and shifted to daubed shannies *Lumpenus maculatus* (Bryant et al. 1999), whereas harp seals shifted to a diet dominated by Arctic cod in the late 1980s and early 1990s (Lawson & Stenson 1995). The timing and nature of these diet shifts correspond to those observed in charr in Nain, which became more similar to those observed from Northern fjords (i.e. dominated by invertebrates and sculpins).

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

In comparison to some other anadromous species (e.g. Atlantic and Pacific salmon), charr do not range far from natal rivers during the marine phase (Dempson & Kristofferson 1987, Spares et al. 2015, Moore et al. 2016, Layton et al. 2021; in this study <50 km) and accordingly, are constrained to foraging on local prey assemblages. However, our results suggest that within this range, charr can adjust foraging habitats depending on local conditions. Other studies have documented plasticity in foraging over diel (Spares et al. 2012, Mulder et al. 2020) and seasonal timeframes (Harris et al. 2020) during the marine phase of charr. For example, Harris et al. (2020) observed that foraging patterns (i.e. diving behavior) shifted to deeper waters as the summer season progressed. Unlike this study, however, these authors did not observe foraging patterns to change across years, despite different environmental conditions. Certainly, there is an expectation that foraging plasticity of Arctic charr has limits when dealing with environmental change. A genomic study across several regions of northern Canada (including Labrador) showed region-specific adaptations to marine conditions, specifically to summer sea surface temperature, salinity, tides, turbidity, and air temperature (Dallaire et al. 2021). Furthermore, population level impacts have coincided with extreme environmental conditions (Layton et al. 2021), including the populations tracked in this study.

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

Over time, diet studies of Nain charr reflect 3 ecosystem states, beginning with abundant capelin in the 1980s, followed by very low capelin abundance in the 1990s, and intermediate abundance in the early 2000s. Since that time, local knowledge holders have yet to observe capelin rebound to the levels observed

in the 1980s (J. Angnatok pers. obs.). These trends are generally mirrored in capelin bycatch off northern Labrador (Carscadden et al. 2013). In contrast, capelin were more consistently at low biomass in charr stomachs from northern fjords (Saglek, Hebron, and Ramah) compared to Nain and Okak (Andrews & Lear 1956, present study). Unfortunately, we have no contemporary surveys to establish the current state of the prey base on the Labrador Coast. Temperate species like capelin are expected to become increasingly common in the north as the climate warms (Reist et al. 2006, Carscadden et al. 2013, Tai et al. 2019), and could provide an expanded prey base for more northern fish populations. Indeed, researchers have already reported capelin in charr diets of Arctic populations in recent years (Spares et al. 2012, McNicholl et al. 2017, Harris et al. 2020).

Predicting responses of charr to climate change remains challenging. Northward expansion of key prey like capelin could provide an important food source for the low productivity coastal ecosystems found along the north coast of Labrador (Murdoch et al. 2015). Comparisons of Ungava and Labrador showed that slightly elevated temperatures coupled with higher local productivity were associated with notably better growth of Ungava charr (Murdoch et al. 2015). Conversely, the concomitant ecosystem changes that facilitate the northward expansion of prey may have negative effects on charr. For example, growth is dependent on interactions between water temperature, prey availability, and seasonal phenologies (Power et al. 2012, Murdoch et al. 2015). Charr growth is most efficient at lower temperatures when food is limited (Larsson & Berglund 2005). Therefore, it is possible that increases in prey availability may not overcome the reduced growth efficiency associated with warmer water. Positive benefits to charr are further limited by the potential for increased competition from temperate salmonids (Power et al. 2012) and existing population adaptations that make it difficult for anadromous charr to thrive in warmer conditions (Layton et al. 2021). Such factors might drive populations with partial migration (i.e. exhibit both anadromous and resident life histories) to shift to resident life histories as the benefits of anadromy fade (Davidsen et al. 2020, Layton et al. 2021). In Nain, despite recovering effective population sizes of local populations and improving capelin abundance in charr diets, local harvesters have reported charr to be smaller and in lower abundance (Dempson et al. 2008, J. Angnatok pers. obs.); an indication that the fishery, although greatly reduced from earlier times, is becoming less sustain-

able. Whether these trends are caused by more concentrated fishing effort near communities or deteriorating environmental conditions is not known.

Telemetry data provide insights that can be difficult to obtain using conventional mark-recapture techniques. For example, timing of migration to and from marine habitats (Dempson & Green 1985, Dempson & Kristofferson 1987, Bégout Anras et al. 1999, Gulseth & Nilssen 2000, Jensen & Rikardsen 2012, Moore et al. 2016), occupancy patterns of different marine habitats (Dempson & Kristofferson 1987, Spares et al. 2015, Moore et al. 2016), and foraging behavior (inferred from diving data; Spares et al. 2012, Harris et al. 2020, Mulder et al. 2020) are more difficult to quantify with conventional techniques. Estuaries were a key marine habitat to charr in both study areas, with charr spending considerable time in these areas early in summer. Similar observations were found in Frobisher Bay (Spares et al. 2015) and Cambridge Bay (Moore et al. 2016, Harris et al. 2020) in Arctic regions of Canada. Estuaries are important habitats that provide favorable thermal environments and access to food resources (Spares et al. 2015), and possibly refuges from higher salinity waters (Harris et al. 2020). The mechanism driving heightened use of other marine habitats in Saglek remains unknown. It may be driven by differences in productivity between the 2 regions, but the productivity patterns of coastal habitats off Labrador remain poorly understood (McCarney et al. in press). An alternate explanation is that estuaries of both areas have comparable productivity but that Nain estuaries may be more attractive in years when they experience influx of migratory prey like capelin. Certainly, tagged charr in Nain illustrated that motivation to incorporate other non-estuarine habitats can vary from year to year.

There are few studies (but see Dempson & Kristofferson 1987, Dempson et al. 2002, Spares et al. 2012) that link observations of marine behavior of charr to spatial and temporal variation in diet. Complementary data streams such as these (i.e. diet and commercial harvests) provide a more robust and holistic picture of charr behavior while in the ocean and illustrate the importance of long-term datasets. Even in this circumstance, where historical diet and commercial catch data did not temporally overlap with contemporary telemetry data, our confidence in the likelihood that marine behavioral differences observed across Saglek and Nain charr populations persist over time is bolstered by the consistency of diet differences among fjords over decadal scales. The complexity of dynamic prey fields and small-scale spatial

variation in marine behavior, super-imposed upon a changing climate, is a challenge to predicting and managing responses of charr to commercial and food fisheries. Understanding how productivity cycles fluctuate in conjunction with changing environmental conditions will help to predict subsequent impacts on the marine behavior of local charr populations. While our study shows charr are capable of surviving regime shifts in part by altering habitat use, prey community shifts expected with climate change (Perry et al. 2005, Rose 2005b) will add to other climate-related stressors that are expected to have widespread impacts on anadromous charr populations (Layton et al. 2021). With this in mind, recent concerns about the health of charr populations near Nain suggest renewed monitoring efforts of charr and the coastal ecosystem are needed to support sustainable management of this critical cultural (Berkes 2018) and commercial (Power & Reist 2018) resource.

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