Morphology of Arctic cod (*Boreogadus saida*) assessed according to habitat preference and age in the Beaufort Sea

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Abstract

The Arctic cod (*Boreogadus saida* (Lepechin, 1774)) represents the most widespread and abundant fish in the Arctic and is a critical trophic link in its ecosystems. Like many species endemic to the region, it has lost essential habitat as the extent and thickness of sea ice have declined substantially in recent decades. Extreme warming induced by climate change continues to deteriorate polar marine environments. Thus, understanding how Arctic cod use and partition their habitat/environment is central to their conservation. We assessed Arctic cod functional morphology using traditional (including gill rakers) and geometric morphometrics and explored whether these differed among primarily depth-based habitats and age classes using multivariate techniques. While distinct ecotypes have been proposed, these were not detected in our analyses. Rather, results show similar patterns in external morphology of Arctic cod across habitats and age classes in the Beaufort Sea. However, analysis of gill rakers revealed concurrent habitat- and age-specific changes likely associated with dietary preferences. Findings indicate that although Arctic cod do not specialise in external morphological features in any habitat, important aspects of their internal feeding morphology shift as they grow, likely underpinning important distributional shifts and its critical role in transferring energy in Arctic marine ecosystems.

Key words: arctic marine ecosystem, functional morphology, geometric morphometrics, gill rakers, benthic–pelagic coupling, ontogeny

Introduction

The Arctic cod (*Boreogadus saida* (Lepechin, 1774)) is the most abundant fish spanning the Arctic Ocean (Lowry and Frost 1981; Craig et al. 1982; Parker-Stetter et al. 2011; Hop and Gjøsæter 2013; Aune et al. 2021; Pettitt-Wade et al. 2021). While most Arctic fishes are either benthic or demersal, juvenile Arctic cod (≤age class 1; Hop et al. 1997*b*) act as forage specialists in the near surface pelagic zone (Walkusz et al. 2011; Majewski et al. 2016; Bouchard and Fortier 2020). There, they also provide forage for many other fishes, marine mammals, and seabirds (Bradstreet et al. 1986; Welch et al. 1992; Crawford and Jorgenson 1996) and transfer a significant portion of primary production to these higher trophic levels (Christiansen et al. 2012; Hop and Gjøsæter 2013; Benoit et al. 2014; Karamushko et al. 2021). Owing to their circumpolar distribution, abundance, and unique role, the Arctic cod is considered a central species in Arctic marine ecosystems (Welch et al. 1992; Christiansen et al. 2014).

The effects of climate change are increasingly evident in the Arctic where warming occurs at up to four times the global average (Rantanen et al. 2022). Among the most important consequences is the loss of sea ice (Wassmann et al. 2011; Christiansen et al. 2014) where the extent, thickness, and duration have declined considerably, with further reductions expected as temperatures rise (Hoegh-Guldberg and Bruno 2010; Comiso 2012; Box et al. 2019). The continued loss of sea ice and heightened pressure induced by incoming sub-Arctic non-native fishes create an alarming future for Arctic cod (Wassmann et al. 2011; Fossheim et al. 2015). Florko et al. (2021) project substantial declines in Arctic cod abundance, biomass, and mean body weight in response to warming ocean conditions. If their numbers or range were to shrink, Arctic cod consumers would be forced to shift to lower-quality prey (Florko et al. 2021), possibly triggering trophic cascades and significantly altering energy transfers and community dynamics throughout Arctic marine ecosystems (McNicholl et al. 2016; Florko et al. 2021). Yet, for all their importance, many critical aspects of Arctic cod ecology and evolution remain poorly understood (Majewski et al. 2016).

Previous findings have described a shift in habitat and diet related to the species' ontogeny (Renaud et al. 2012; Walkusz et al. 2013; Benoit et al. 2014; Geoffroy et al. 2016; Majewski et al. 2016; McNicholl et al. 2016; Kessel et al. 2021). Once spawned, larval/juvenile Arctic cod remain in near surface pelagic areas, feeding on small copepods and their eggs, and copepod nauplii (Walkusz et al. 2011; Bouchard and Fortier 2020). They exploit this niche for as long as possible (Benoit et al. 2014), before shifting their distributions to greater depths where they broaden their diet to include larger calanoid copepods and hyperiid amphipods (Renaud et al. 2012; Gray et al. 2016; McNicholl et al. 2016). While occurrence of shifts has not yet been associated with a single specific mechanism, several hypotheses have been proposed, e.g., complex interaction of factors related to size/age, prey availability and competition, and thermal tolerance (Benoit et al. 2010; Benoit et al. 2014; Christiansen et al. 2012; Majewski et al. 2016). However, specific hypotheses related to ontogenetic morphological shifts have not been explored.

Many species show morphological adaptations to different food items available in different habitats. Typically, pelagic ecotypes have more streamlined fusiform body shapes with either upturned or terminal mouths optimised for capturing pelagic prey (e.g., zooplankton), while benthic/littoral types have deeper (more rounded) bodies with subterminal mouths, facilitating substrate feeding (Helfman et al. 2009; Harrod et al. 2010; Lucek et al. 2013; Skoglund et al. 2015; Friedman et al. 2020). It is also well-established that a greater density of gill rakers allows individuals to sieve out and capture smaller prey, especially as these relate to zooplanktivores (Friedland et al. 2006; Tanaka et al. 2006; Harrod et al. 2010; Costalago et al. 2012; Rösch et al. 2013). Ontogenetic shifts, whereby juveniles are more densely rakered than older larger individuals, have also been observed in many species (Mummert and Drenner 1986; MacNeill and Brandt 1990; Freidland et al. 2006; Tanaka et al. 2006). Such patterns in feeding morphology have also been shown in sympatric species whereby different ecotypes occupying the same region can partition resources. In many cases, more densely rakered species are capable of filtering smaller food items and typically exploit pelagic habitats, while more sparsely rakered ones exploit larger more benthic associated prey in deeper habitats (Malmquist 1992; Amundsen et al. 2004; Harrod et al. 2010; Costolago et al. 2012; Alsafy et al. 2023). While several studies have assessed Arctic cod habitat use based on biomass, size, and age (Benoit et al. 2014; Geoffroy et al. 2016; Kessel et al. 2021), functional morphological assessments of Arctic cod occupying different habitats have not been performed. Similarly, despite notable dietary shifts reported (Christiansen et al. 2012; Renaud et al. 2012; Walkusz et al. 2013; Benoit et al. 2014; Majewski et al. 2016; McNicholl et al. 2016), no evidence linking this shift to functional morphology has been provided.

In this study, we assess Arctic cod morphology based on the habitat in which they were collected. The shapes, morphometric traits, and gill raker densities of fish collected from four habitats in the Beaufort Sea were compared to test the hypothesis that Arctic cod have varying morphologies related to habitat preference and age. If the species segregates in the water column according to habitat and age classes, and we assess the shape and traits of these aggregations, then we should observe differences across habitats and age classes. Further, if fish occupying more shallow pelagic environments exhibit a different diet than those in progressively deeper, more benthic areas, then they should display associated shifts in feeding morphology. We predict that Arctic cod found in shallower, more surface-associated pelagic waters will have more streamlined body shapes with more terminal or supraterminal mouths, with higher gill raker densities than those residing in progressively deeper more benthic areas. We also predict that fish found at greater depths will have deeper body shapes (more rounded) with more subterminal mouths and have lower gill raker densities. These predictions are borne out of previous studies showing fish shapes and morphology adapted to different habitats and feeding strategies along a pelagic—benthic gradient (Helfman et al. 2009; Harrod et al. 2010; Lucek et al. 2013; Skoglund et al. 2015; Friedman et al. 2020). This analysis aims to better understand the morphology of this key species and potentially identify important morphological traits related to specific habitats or life-history stage.

Materials and methods

Arctic cod were sampled during Canadian Beaufort Sea Marine Ecosystem Assessment (CBSMEA) expeditions in August and September of 2018 and 2019 at 18 stations along transects defined by Fisheries and Oceans Canada (Fig. 1). Stations ranged from 25 to 640 m in depth and from 2.4 to 192.6 km from shore. Arctic cod were captured primarily in the Franklin and Darnley embayments, the Amundsen Gulf, and Minto Inlet using a modified Atlantic Western IIa otter trawl and benthic beam trawl. A sub-sample of fish were selected from each catch to represent the range of size classes present, while also ensuring enough muscle tissue was available for concurrent studies. Fork lengths were measured and both the right and left sides were photographed. Post-sampling, all Arctic cod ($n = 320$) were assigned into four habitats based largely on capture depth along collection transects following classifications proposed by Majewski et al. (2017) (Table 1). These habitats were delineated based on the composition and abundance of aquatic species, their spatial distribution in the water column and across the Beaufort Sea Shelf and slope, as well as other environmental variables (e.g., salinity, temperature, and dissolved oxygen) (Majewski et al. 2017). The four habitats are hereafter referred by their depths and their proximity to shore as: nearshore-shelf (NS): 0–50 m, offshore-shelf (OS): 51–200 m, upper-slope (US): 201–500 m, and lower-slope (LS): +501 m. It is important to note that, while there may be more pelagic and more benthic regions within each defined habitat, the habitats themselves nevertheless represent broad categories along ecological gradients within the Beaufort Sea ecosystem. These gradients include not only the proximities to the surface (pelagic) versus bottom (benthic), but also the near versus offshore, and continental shelf versus continental slope areas. These habitats, however, are also well described by depths in relation to the samples used (Majewski et al. 2017). Some individu-

Fig. 1. The 18 CBSMEA stations located in the Beaufort Sea from which Arctic cod were collected in 2018 and 2019. Depth contours are represented in meters. Stations are coloured by habitat aggregation according to the legend in the top right corner. Fish were captured primarily near the Mackenzie Delta outlet, in Minto Inlet, across the Amundsen Gulf, and in Franklin and Darnley Bays. Station colours correspond to habitat groups as defined in the text; nearshore-shelf (NS), offshore-shelf (OS), upper-slope (US), and lower-slope (LS). Stations coordinates provided by Fisheries and Oceans Canada (DFO) and bathymetry and base map by the National Oceanic and Atmospheric Administration (NOAA–NCEI 2020*a*, NCEI 2020*b*).
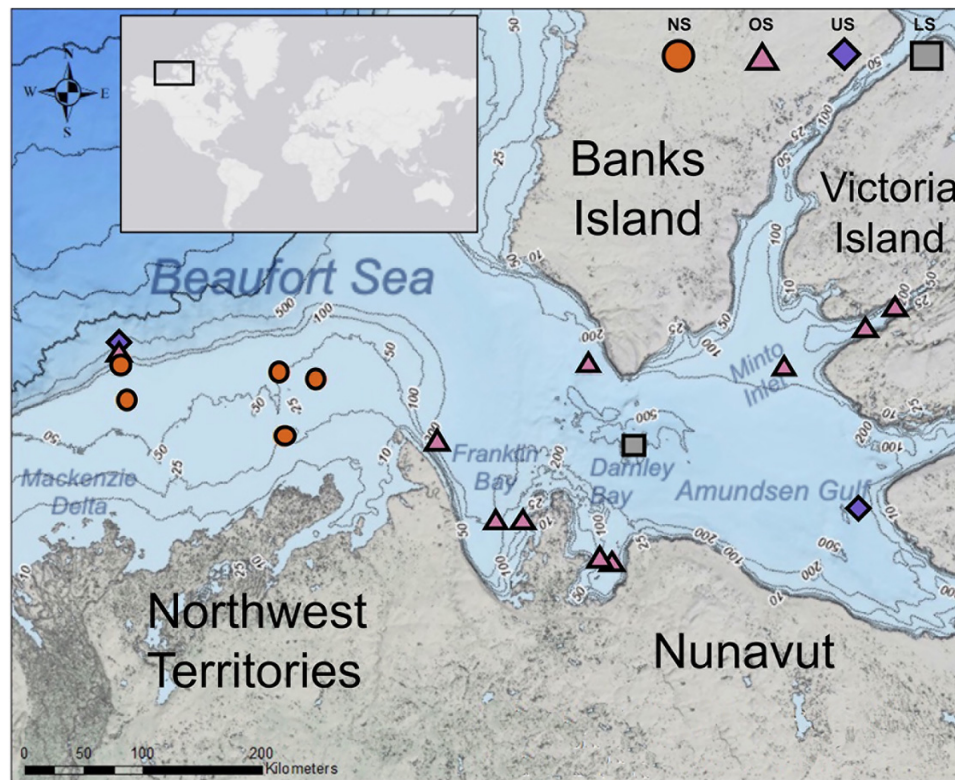
Table 1. Number of Arctic cod captured and photographed in 2018–2019 from the nearshore-shelf (NS), offshore-shelf (OS), upper-slope (US), and lower-slope (LS) habitats of the Beaufort Sea.

Habitat aggregation	n (GM/TM)	Fork length (mm)	n (GR)	Number of gill rakers	Length of gill arch (mm)	Gill raker density
NS	10	90.2 (7.3)	8	32.5 (1.4)	14.6 (1.1)	2.3 (0.2)
OS	77	98.1 (2.3)	11	33.2 (2.1)	21.7 (2.2)	1.6 (0.1)
US	62	125.5 (2.6)	11	37.2 (1.5)	26.3 (1.6)	1.5 (0.1)
LS	7	144.0 (3.5)	7	40.0 (1.2)	28.2 (1.4)	1.4 (0.1)
Age class						
0	0	36.0 (5.3)	0	NA	NA	NA
1	66	77.8 (1.0)	11	30.0 (1.1)	13.7 (0.5)	2.2 (0.1)
2	58	118.1 (1.0)	11	35.6 (1.8)	22.1 (0.9)	1.6 (0.1)
3	23	147.8 (1.3)	11	39.6 (0.6)	28.1 (0.8)	1.4 (0.0)
4	6	171.9 (3.7)	4	39.3 (2.4)	32.3 (2.1)	1.2 (0.1)
5	0	197.8 (5.3)	0	NA	NA	NA

Note: Mean (with standard error) of fork lengths for all photographed Arctic cod, and the number of specimens from each habitat/age class used in geometric morphometric (*GM*), traditional morphometric (*TM*), and gill raker (*GR*) analyses. Means for the age classes were calculated after individual ages were estimated from fork length with von Bertalanffy Growth Function (VBGF).

als were excluded from geometric morphometric (GM) and linear morphometric analyses due to extreme arching of the body and/or difficulty in recovering landmarks in the photographs. However, excluded individuals were still assessed for length.

Ages of individual fish were not available for collected samples. However, as fish grow continuously and at a predictable rate in specific areas, size can serve as a reliable index and predictor of age class (Kozłowski 1996; Katsanevakis and Maravelias 2008; Matić-Skoko et al. 2011). Here, Arctic cod

Fig. 2. The 22 landmarks applied to Arctic cod photos for geometric morphometric analyses and the wireframe shape outlines they generated. The dashed grey lines on the wireframe represent the 11 interlandmark measurements used in the analysis of linear morphometric traits. Descriptions of the position of the landmarks and the traits measured are available in Fig. S1.
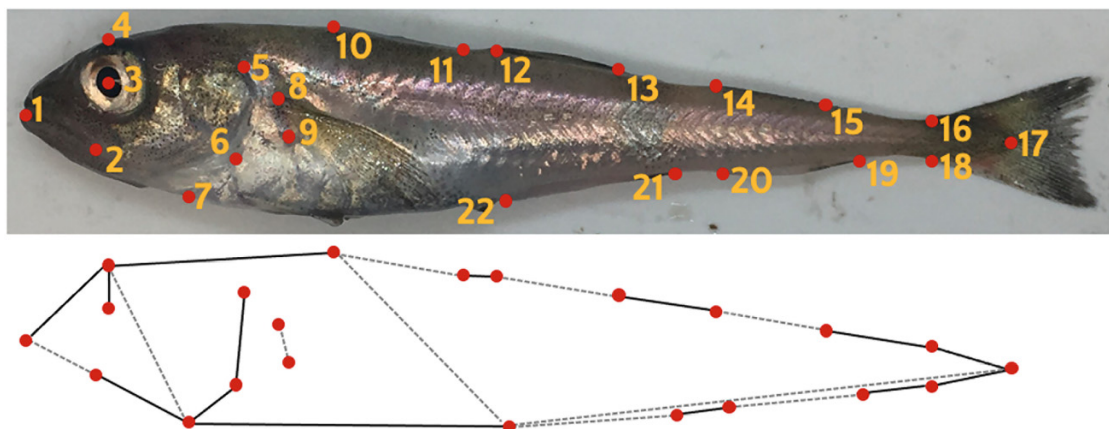
age was estimated using the von Bertalanffy Growth Function (VBGF).

$$(1) \qquad L = L_\infty \left(1 - e^{-k(t-t_0)} \right)$$

The equation is typically used to calculate length from a known age (von Bertalanffy 1938), but rearranging terms allows it to approximate age from length:

$$(2) \qquad t = \frac{\ln \left(1 - \frac{L}{L_\infty} \right)}{-k} + t_0$$

where L represents the fish's current length, L_∞ is the maximum length the species can achieve, k is the species' growth rate, t is the fish's current age, and t_0 is the theoretical age when its length would have been zero (Siegfried and Sansó 2006). All parameters for the function (2) were obtained from Forster et al. (2020) who derived these for Arctic cod sampled in the Beaufort Sea. Ages estimated from the VBGF were rounded to the nearest integer to assign fish to discrete age classes.

Geometric morphometrics

We applied 22 landmarks (Fig. 2 and Fig. S1) on each Arctic cod digital image using tpsUtil64 and tpsDIG2w64 software (Rohlf 2015). A General Procrustes Analysis (GPA) was performed on landmark data to generate a set of Procrustes coordinates. A GPA superimposes the original landmark configurations of each specimen using their centroids, rotating these to eliminate differences in orientation, location, and scale of individual samples so that only shape variation remains expressed in multiple shape variables (Adams et al. 2004; Slice 2007; Zelditch et al. 2012). Here our application of 22 landmarks generated 44 shape variables suitable for further analyses using multivariate techniques (Klingenberg 2010; Zelditch et al. 2012). Because size is known to impact the shape of many species through allometric relationships, we assessed the possibility of such a relationship in our data.

Because significant differences in fish sizes were observed among habitats ($F_{3, 304} = 28.8$, $p < 0.000$, $\eta^2 = 0.21$) and age classes ($F_{3, 304} = 546.8$, $p < 0.000$, $\eta^2 = 0.90$), we performed a size correction on the shape variables to remove its effect. This prevents observing contrasts in morphology stemming solely from differences in size, rather than true differences in shape (Zelditch et al. 2012; Klingenberg 2016). For this, a multivariate regression of the landmark coordinates and log-transformed fork lengths was conducted and the residuals from this model were retained as size-corrected shape variables (hereafter shape variables) in remaining analyses.

To assess variation in Arctic cod shape derived from GMs, a Principal Components Analysis (PCA) was performed on shape variables to reorganise these into those that accounted for most of the shape variation and whether habitats and/or age classes were associated with this shape variation (Klingenberg 2010; Zelditch, et al. 2012; Adams et al. 2021). Age classes 0 and 5 were excluded due to low sample sizes. A Multivariate Analysis of Covariance (MANCOVA) was performed on the first four principal components, which together explained 53.8% of shape variance in the data. The model tested whether there were significant differences in body shape among explanatory factors (habitat and age class) and whether there were some interactions between them. Statistical analyses were performed in R (R Core Development Team 2021), with the generation of shape variables implemented with functions available in the "geomorph" package (Adams et al. 2021). Wireframe outlines of the consensus configuration for each habitat and age class were generated to visualise morphological differences.

Linear morphometric measurements

Eleven traditional morphometric measurements were also considered (Fig. 2 and Fig. S1). The distance between landmarks was measured digitally and scaled to each individual picture, eliminating discrepancies in specimen focal distance. The interlandmark distances were also size-corrected and allometrically aligned following the procedure described in Skoglund et al. (2015). A PCA was also used to visualise the

Fig. 3. Frequency distribution of Arctic cod used in the morphological analysis. Age classes were estimated from the VBGF for the nearshore-shelf (NS), offshore-shelf (OS), upper-slope (US), and lower-slope (LS) habitats of the Beaufort Sea.
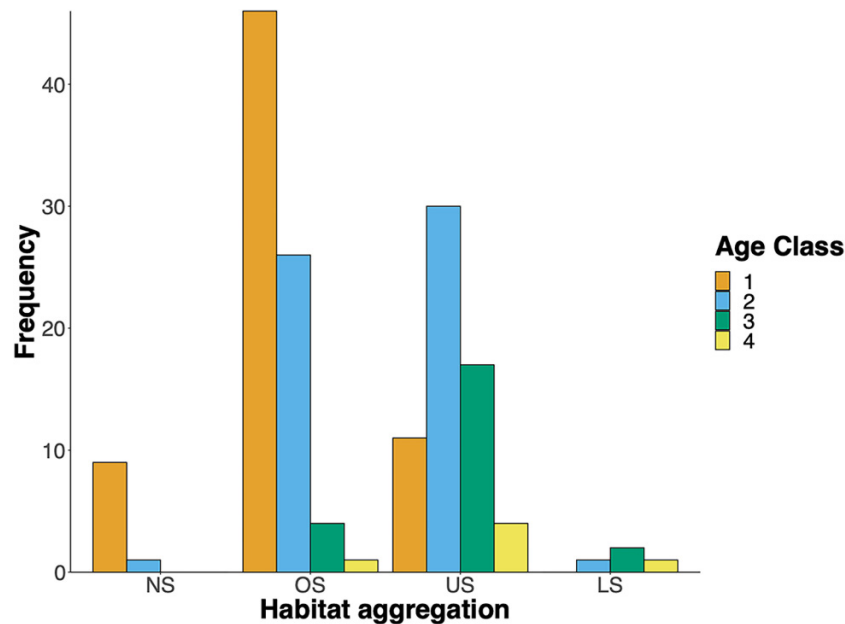
data along the most important axes of linear trait variation and how the data are partitioned along these axes among habitat and/or age classes. As with shape variables, linear traits were also analysed using a MANCOVA, post PCA, to test if differences in morphology existed among habitat, age classes, and their interactions.

Gill rakers

Finally, individuals were selected from amongst those included in the GM analysis based on the quality of specimen remains. For groupings that comprised a large number of fish (i.e., OS and US habitats and age classes 1–3), individuals were randomly selected until each group was composed of at least 10 individuals. The first gill arch on the right side of each specimen was extracted and photographed, and gill rakers were counted (as a meristic trait, gill rakers are not subject to allometry; Helfman et al. 2009). The gill arch was then measured digitally using the software ImageJ (Schneider et al. 2012). The ratio of gill raker number over the length of the gill arch was calculated (hereafter gill raker density) standardising the gill raker data per individual (Kahilainen and Ostbye 2006; Vonlanthen et al. 2012; Lucek et al. 2013). Gill raker number, gill arch length, and gill raker density were tested for normality (using the Shapiro–Wilks test). Differences in gill raker variables among habitat and age classes were assessed using a linear model coupled with the anova() function as performed in the base package of R, which accounts for unequal sample sizes (Whitlock and Schluter 2020). Differences among groups were assessed with post-hoc Tukey's HSD tests. Because each age class did not occur in every habitat and given limited samples, we could not test for an interaction between habitat and age class in relation to gill raker metrics, and therefore performed separate linear models for each.

Results

Age-class estimates

The VBGF estimates for Arctic cod yielded six age classes (Table 1). As with the habitat aggregations, some individuals were not retained for GM analysis if they did not have proper photos available. Ninety-five percent of the fish ($n = 302$) were assigned to the age classes 1, 2, or 3 (38%, 37%, and 20%, respectively), while the remaining age classes (0, 4, and 5) were each composed of less than 10 individuals (Table 1).

Few fish ($n = 17$) were captured in the NS habitat (Table 1), which made it difficult to survey its age structure. It was composed of primarily age 1 fish (69%), with some age 2 fish (Fig. 3). Most Arctic cod were caught in OS and US areas which allowed for more complete examination of their age class distributions. The OS ($n = 165$) was dominated by age 1 (50%) and 2 (36%) cod, but this shifted to mainly age 2 (40%) and 3 (31%) in the US ($n = 126$) (Fig. 3). The LS also had a small sample ($n = 13$), represented by mainly age class 3 (60%), followed by a single age 2 and age 4 fish (Fig. 3). However, here too it was difficult to examine its age structure extensively due to limited numbers captured in this habitat.

Geometric morphometrics

Arctic cod from each habitat aggregation and age class expressed similar body shapes. This was reflected in the PCA, where 95% confidence ellipses for habitat aggregations and age classes overlapped considerably (Figs. 4a, 4b). PC1-3 accounted for 46.6% of the overall shape variation (Table S1), with the remaining axes each explained less than 10%. The loadings of the shape PC axes were explored to determine which landmarks contributed most to the variance along

Fig. 4. Top: PCA plots for size-corrected Arctic cod shape data. Bottom: PCA plots for linear morphometric traits. Individuals are coloured according to habitat aggregations (*a* and *c*) and VBGF-estimated age classes (*b* and *d*). Ellipses indicate 95% confidence. Colours represent habitats nearshore-shelf (NS), offshore-shelf (OS), upper-slope (US), and lower-slope (LS) defined in the Beaufort Sea. Age classes 1–4 are defined in the main text.
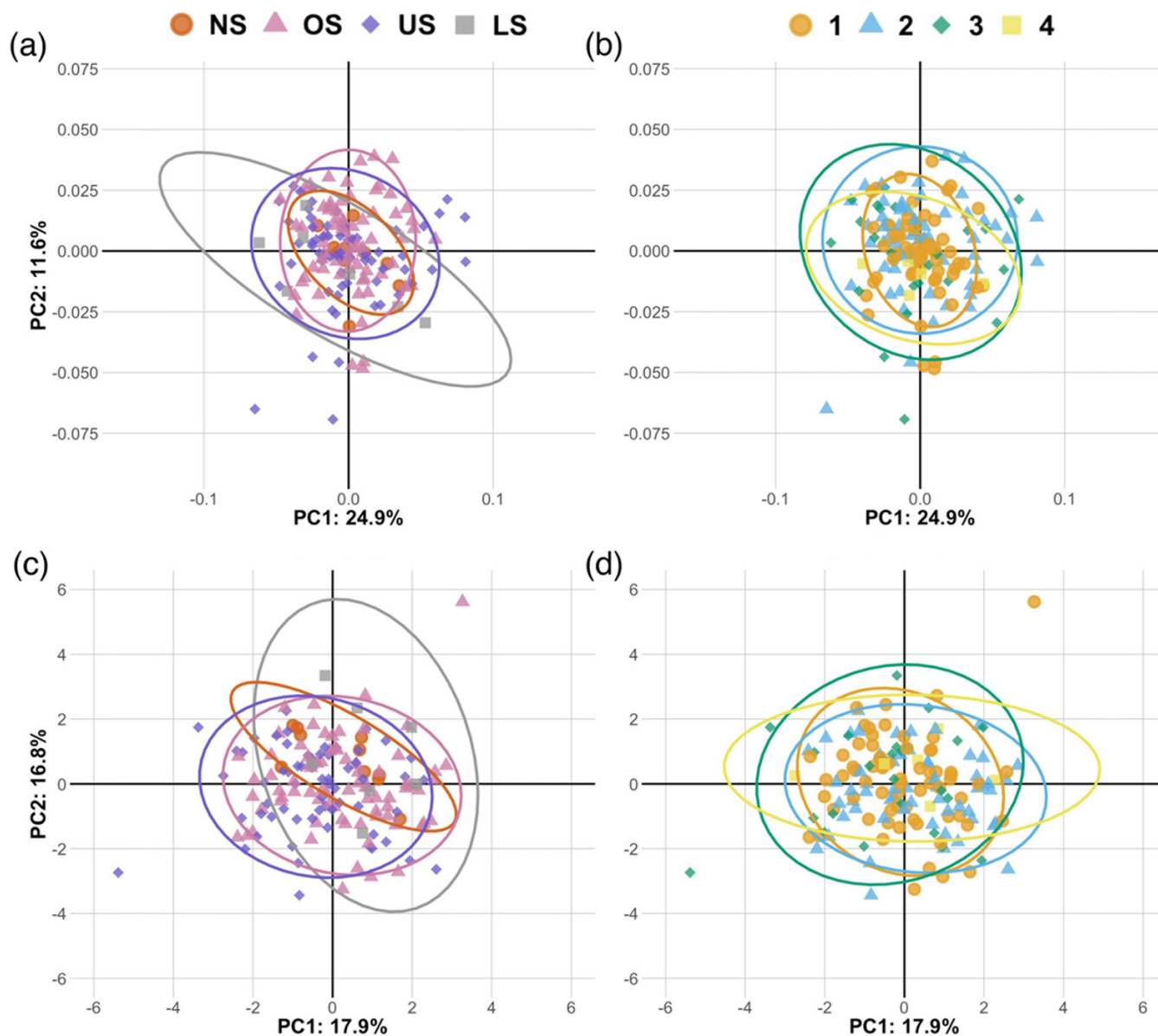
the first four axes. While some landmarks contributed more than others (e.g., landmark 1 – PC1; Table S1), their ability to differentiate among habitats and age classes was not obvious. This was reflected in the substantial overlapping distributions of all groups (habitat and age classes) along PC1 and 2 (Figs. 4*a*, 4*b*), and in the similarity in body shape among them as seen in the wireframe outlines (Fig. S2). Although the LS habitat aggregation exhibited more variation along PC1 than the others, this was based on only seven individuals. Similarly, and although age classes tended to be more centralised along PC1, substantial overlap in shape was also observed along PC1 and 2 among all age classes. The MANCOVA confirmed that the body shape of Arctic cod does not vary across these habitats and/or age classes. No

significant differences in body shape between habitats or age classes were observed with each explanatory variable reporting a small effect size (Table 2). Moreover, the model did not detect an interaction between the two explanatory variables.

Linear morphometric measurements

None of the 11 morphometric traits measured were found to be correlated with fork length after size correction. The PCA of size-corrected linear traits did not identify any group-related structuring among either habitat aggregations or age classes (Figs. 4*c*, 4*d*). PC 1–3 accounted for just over 40% of the overall trait variation, with all other PCs explaining less than 10% (Table S2). In this case, several traits had a relatively high

Table 2. MANCOVA results of the first four PC axes (accounting for 53.8% of overall shape variation) of size-corrected shape data and 11 size-corrected linear morphometric traits for the four Beaufort Sea habitats and VBGF-estimated age classes of Arctic cod.

Source	df	Pillai	F	p	η^2
Shape					
Habitats	3	0.09	1.11	0.352	0.03
Age class	3	0.06	0.76	0.694	0.02
Habitat × Age class	6	0.12	0.78	0.760	0.03
Traits					
Habitats	3	0.31	1.40	0.076	0.10
Age class	3	0.20	0.85	0.703	0.07
Habitat × Age class	6	0.45	1.03	0.418	0.08

loading onto PC1-3, but none contributed more than 33% of the variation along each (Table S2). Few differences were observed in habitat aggregations or age classes in linear trait morphology as assessed by PCA (Figs. 4c and 4d). As with the GM analysis above, the LS aggregation seemed to have a larger and more-shifted score along PC1 and 2, but this could be driven by low samples sizes (Fig. 4c). Similarly, the 95% confidence ellipse of the age class 1 seemed more constrained around the origin than did the other age classes (Fig. 4d). The MANCOVA model of linear traits also confirmed the lack of differences among habitat aggregations or age classes and did not find any interaction between the two explanatory factors (Table 2).

Gill rakers

Significant differences were observed in the number of gill rakers, the length of the gill arch, and the density of gill rakers in sampled Arctic cod in relation to habitat (Figs. 5a–5c; Table 3). NS and OS fish tended to have lower numbers of gill rakers than the LS fish, but not the US ones. The gill arch of NS fish was significantly smaller than the other aggregations, and, while it increased gradually in the OS, US, and LS habitats, none of these three were found to be significantly different from each other. The gill raker density was significantly higher in the NS relative to the other habitats (Figs. 5a–5c; see also Table 3). Patterns in gill raker analyses among age classes were also clear and significant (Figs. 5d–5f; see also Table 3). Age class 1 had significantly lower numbers of gill rakers, smaller gill arch lengths, and a higher density of gill rakers than did the other age classes. All age classes differed with respect to gill arch length (likely reflecting changes incurred during growth), but age classes 2–4 did not differ in either gill raker numbers, or in gill raker density (Figs. 5d–5f; Table 3). Pattern similarity in gill raker analyses among habitats and age classes likely reflects that some age classes dominate in some habitats, e.g., age class 1 in NS (Fig. S3). However, we could not test for an interaction age–habitat due to unequal distribution between age and habitat. The patterns observed in the data, however, suggest a strong effect of age class considering the F-ratios calculated (Table 3).

Discussion

Arctic cod do not exhibit differences in external morphology based on habitat preference or age class in the Beaufort Sea. GM analysis showed that fish that inhabit NS, OS, US, and LS areas all share similar body shapes. Similarly, when morphology was assessed using traditional linear approaches, no differences were observed. The similarity in body shape and linear morphology among age classes also indicates that the external structures of this species remain seemingly consistent throughout a large portion of its life cycle. While these findings do not support any adjustments in the external morphology of Arctic cod based on their habitat or developmental stage, analysis of internal feeding structures identified concurrent habitat- and age-specific adaptations that likely correspond with dietary shifts. We see important changes in gill raker densities associated with size/age and habitat preference that could explain how Arctic cod exploit a range of depths and thus, how the species figures as a central component of energetic transfers in Arctic marine food webs. Below, we address these results and put them in the context of what is known about the species.

Habitat

The difference in habitats occupied by Arctic cod was expected to relate with some aspect of its morphology. The species is well known to have a circumpolar distribution and occupy diverse habitats at a range of depths (Lowry and Frost 1981; Craig et al. 1982; Parker-Stetter et al. 2011; Hop and Gjøsæter 2013; Nelson et al. 2020; Aune et al. 2021; Pettitt-Wade et al. 2021). This entails living in areas with varied temperatures, salinity levels, currents, oxygen content, and other features, both biotic and abiotic (Majewski et al. 2016). The habitat delineations used here were established from such environmental features, and from the species assemblages within them, specifically determined in the Beaufort Sea (Majewski et al. 2017). It has been suggested that these environmental variations might be related to morphological specialisations in Arctic cod, which may have developed these as adaptations to their varied habitat preferences (Moskalenko 1964; Quintela et al. 2021). Chernova (2018) reported several morphological "forms" of Arctic cod in the Barents, Laptev, and Chukchi Seas. Morphological differences were attributed to habitat preference within several regions, as well as the depth at which the fish were collected; though, this was not tested formally. Our analysis, however, does not support morphological adaptations among depth-based habitats and that fish from the NS, OS, US, and LS habitats of the Beaufort Sea express similar external morphologies. Fish surveyed in our study likely originate from a single genetic group as described by Nelson et al. (2020), and thus the area may represent a too small spatial scale to reflect morphological adaptations that occur over a broader circumpolar scale. Genetic analyses of Arctic cod from the western Beaufort Sea north of Alaska using mitochondrial DNA and microsatellite markers failed to detect significant population or other genetic clustering (Wilson et al. 2019), which is consistent with our phenotypic assessments. However, another recent microsatellite-based investigation performed using a circumpolar distribu-

Fig. 5. The number of gill rakers, length of the gill arch, and gill raker density of Arctic cod. The left panels (*a,c,e*) are coloured according to habitat aggregation (nearshore-shelf (NS), offshore-shelf (OS), upper-slope (US), and lower-slope (LS)), and the right (*b,d,f*) are coloured according to age class (as defined in the main text). Squares and tails show mean and 95% confidence interval for each group. W-X-Y-Z indicate different groupings based on results of post-hoc Tukey's HSD tests (*p* < 0.05) following testing with linear model-based anova() as performed in R for each metric. Linear model results are in Table 3.
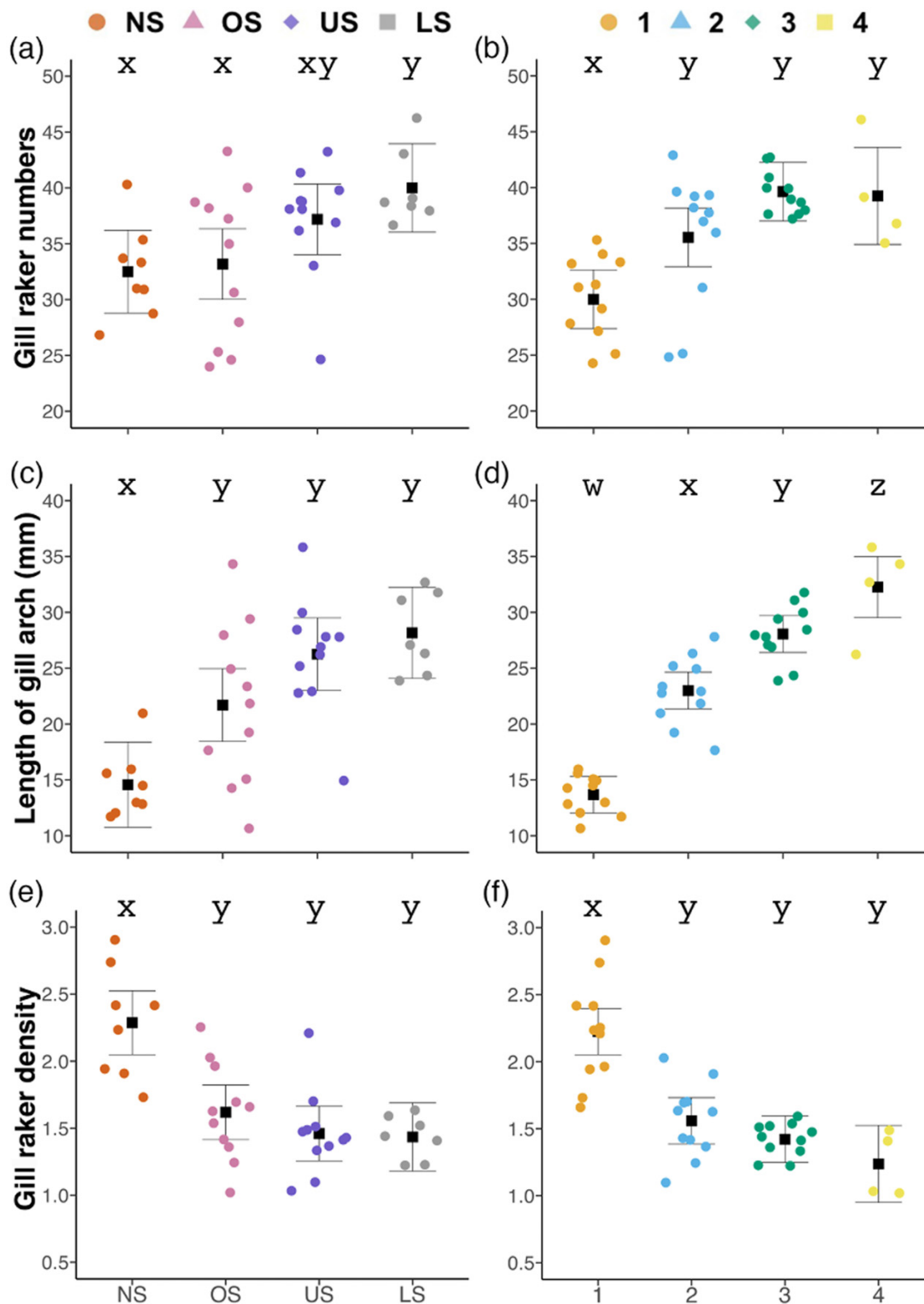
Table 3. ANOVA results for the number of gill rakers, length of the gill arch, and gill raker density for Arctic cod from four habitat aggregations in the Beaufort Sea and their VBGF-estimated age classes.

Source	Number of gill rakers			Length of gill arch			Gill raker density		
	$F_{3,\,33}$	p	η^2	$F_{3,\,33}$	p	η^2	$F_{3,\,33}$	p	η^2
Habitat	3.82	0.019	0.26	10.54	< 0.001	0.49	11.95	< 0.001	0.52
Age class	10.60	< 0.001	0.49	73.08	< 0.001	0.87	20.75	< 0.001	0.65

tion of samples identified four genetically distinguishable, geographic subgroups of Arctic cod (Nelson et al. 2020). It remains unknown whether genetic variability among large-scale regions translates into noticeable morphological differences, and if they do, which structures that might be involved in local adaptations (Maes et al. 2021; Quintela et al. 2021). Future analyses could benefit from an expanded approach that includes samples from a broader distribution and that integrates molecular and morphological techniques to help differentiate individuals.

Size and age

Size and age have been intimately linked to habitat preference in Arctic cod. Research conducted in the Beaufort Sea has consistently reported that Arctic cod size increases as a function of depth (Geoffroy et al. 2011, 2016; Majewski et al. 2016, 2017). Consistent with these findings, younger cod are also predominantly found in the surface layers of the water column (Ponomarenko 2000; Benoit et al. 2014; Geoffroy et al. 2016). Therefore, it was initially expected that fish would exhibit distinguishable morphologies related to life history stage and that these would also be reflected when the four depth-based habitats were compared. However, neither shapes nor linear traits were found to differ among age classes, even after correcting the data for size differences. These results demonstrate that this species exhibits nearly equivalent external morphologies throughout their lives and through different habitats investigated.

Although our analyses determined that Arctic cod developmental stages through ages 1 to 4 are isometric, as size/age has little impact on their external morphology, it was limited by the number of young fish sampled. It has been suggested that the species undergoes an important shape transition from larval to sub-adult, juvenile form at approximately 30 mm in length (Ponomarenko 2000). However, because our samples did not include fish less than 30 mm, we could not assess this morphological transition. Thus, a critical portion of Arctic cod demographics, which may represent an important morphological transition, was not assessed here. Nevertheless, further insights into Arctic cod morphological variation could be gained by surveying more individuals less than 1 year old that may represent an important transitioning phase in this species.

The lack of clear shape or linear morphological differences among assessed year classes could partially result from how age was approximated with the deterministic VBGF model. Like many fishes, Arctic cod grow rapidly during early stages (Forster et al. 2020; Karamushko et al. 2021), but this slows as they approach their lifespan and asymptotic size (typically

5–7 years; Hop et al. 1997b; Geoffroy et al. 2016). Rounding of individual age estimates derived from the VBGF to the nearest age class may have influenced the inclusion of individuals within age classes. However, the logistic nature of this relationship is more likely to impact older, larger fish rather than younger ones (Fig. S4; Sainsbury 1980). While this allowed us to assign fish into distinct age classes, it may have also truncated possible variations in growth rates among individuals (the denominator in our VBGF equation; see Sainsbury 1980; Katsanevakis and Maravelias 2008, for discussion). Nevertheless, and short of having verified age estimates from hard structures such as otoliths, values obtained from the VBGF, implemented with recent region- and species-specific parameters (Forster et al. 2020), likely serve as strong proxies for age (Chen et al. 1992; Katsanevakis and Maravelias 2008; Matić-Skoko et al. 2011).

Possible links to diet

Despite the similarity in shape and morphometric traits displayed by Arctic cod, internal feeding structures varied among both habitats and age classes that were also likely related. Analyses of gill rakers revealed that the species exhibits different gill raker densities according to age which corresponds with their transition from pelagic to benthic habitats. It has been consistently reported that Arctic cod change their diet as a function of depth and life stage (Renaud et al. 2012; Benoit et al. 2014; McNicholl et al. 2016), and this has led some to speculate that the species undergoes an important ontogenetic niche shift (e.g., Kessel et al. 2021). And, while some hypotheses have been borne out of previous studies as to why this happens (Benoit et al. 2010; Christiansen et al. 2012; Benoit et al. 2014; Majewski et al. 2016), specifically which mechanisms contribute to it have been seldom tested.

Here we show that age 1 fish, and hence those predominant in NS habitats (65%, $n = 17$), had significantly higher gill raker densities than older fish located in deeper waters and in more slope-associated habitats. Higher density gill rakers would allow juvenile Arctic cod to sieve smaller pelagic prey more efficiently through filtering. As the species grows and the gill raker density becomes sparser, exploiting small prey becomes less efficient and the fish shifts to deeper habitats containing larger prey (Renaud et al. 2012; Walkusz et al. 2013; Benoit et al. 2014; Geoffroy et al. 2016; Majewski et al. 2016; McNicholl et al. 2016; Kessel et al. 2021), more effectively retained by sparser, less dense gill rakers (MacNeill and Brandt 1990; Freidland et al. 2006; Tanaka et al. 2006; Costalago et al. 2012). Thus, gill raker density and the ability to efficiently filter different sized prey may be an important aspect related to Arctic cod's habitat transition with age/size. This is consis-

tent with previous work demonstrating that younger/smaller Arctic cod tend to feed on smaller copepods and their eggs in shallow habitats, whereas their diet shifts to larger calanoid copepod and hyperiid amphipod prey as they grow and move to deeper, more slope-associated areas (Lowry and Frost 1981; Craig et al. 1982; Bradstreet et al. 1986; Benoit et al. 2010; Geoffroy et al. 2011; Benoit et al. 2014; Geoffroy et al. 2016; Majewski et al. 2016; Majewski et al. 2017; Kessel et al. 2021). This may also contribute to their ability to couple the pelagic and benthic habitats in Arctic marine ecosystems, and thus why they play such a central role in energy transfers in these systems (Bradstreet et al. 1986; Welch et al. 1992; Hop et al. 1997a; Christiansen et al. 2012). More importantly, and especially if the biomass of important Arctic cod prey species is expected to decline as Arctic waters warm (Aarflot et al. 2018), rising temperatures will likely have important negative impacts on essential habitat for juvenile Arctic cod. This could lead to abundance and distribution shifts that have cascading impacts through the Arctic marine ecosystem in terms of supporting the maintenance and growth of other Arctic species (Wassmann et al. 2011; Christiansen et al. 2014; Fossheim et al. 2015; McNicholl et al. 2016; Florko et al. 2021).

Conclusions

This study characterised and quantified the external morphology of Arctic cod with GM and traditional linear techniques, as well as identified a critical aspect of the species' ontogeny related to its internal feeding structures. The species varies little in external morphologies in the habitats assessed and through age classes in the Beaufort Sea; however, Arctic cod do show important differences in gill raker densities, which are associated with a shift in habitat as they get larger/older. Although habitat and dietary changes experienced during its development have been demonstrated in previous work (Ponomarenko 2000; Benoit et al. 2014; Geoffroy et al. 2016; Gray et al. 2016; Kessel et al. 2021), future efforts should confirm whether species and size distribution of items in Arctic cod diet exist with different gill raker densities. This finding clarifies how Arctic cod may thus be able to exploit multiple habitats through its life history and may be a possible contributing mechanism underlying this species' benthic–pelagic coupling of energy transfers in Arctic marine ecosystems (Hop et al. 1997a). Further research could assess whether the observed gill raker pattern is manifested in other portions of the species' range or whether this is more typical of fish in the Beaufort Sea. Our analysis remains rooted in a larger project aiming to describe the population structure of Arctic cod using genomics. The ability to corroborate discoveries based on molecular techniques with those of phenotypic observations can contribute to a more comprehensive understanding of this key Arctic species, especially as its environment undergoes unprecedented changes.

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Article information

History dates

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Data availability

The raw data supporting the findings in this work are available on Dryad at https://doi.org/-10.5061/dryad.5dv41nsbh. Annotated scripts used for data formatting, manipulation, and analyses are also available on GitHub at https://github.com/denisroy1/Arctic-cod-Morphology.

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