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Environmental drivers of benthic fish distribution in and around Barrow Canyon in the northeastern Chukchi Sea and western Beaufort Sea



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ABSTRACT

We investigate the relationships between Arctic fish and their environment with the goal of illustrating mechanisms of climate change impacts. A multidisciplinary research survey was conducted to characterize fish distribution and oceanographic processes in and around Barrow Canyon in the northeastern Chukchi Sea in summer 2013. Benthic fish were sampled with standard bottom trawl survey methods. Oceanographic data were collected at each trawl station. The density of Arctic cod (*Boreogadus saida*), the most abundant species, was related to bottom depth, salinity and temperature. Arctic cod were more abundant in deep, cold and highly saline water in Barrow Canyon, which was likely advected from the Chukchi Shelf or from the Arctic Basin. We hypothesize that Arctic cod occupied Barrow Canyon to take advantage of energy-rich copepods transported in these water masses. Arctic cod were similarly more abundant in deep, cold and high salinity water in the Beaufort Sea, documented by a comparable multidisciplinary survey conducted in 2008. These linkages between oceanographic variables and benthic fish distribution and abundance suggest that advection, sea-ice dynamics and pelagic-benthic coupling are important for the ecology of benthic Arctic fishes. These processes have been and will likely continue to be impacted by climate change. Our results improve the understanding of the mechanistic linkages between climate change and benthic Arctic fish ecology.

1. Introduction

Arctic marine ecosystems are thought to be particularly impacted by climate change. Potential stressors include ocean warming (Overland et al., 2014), loss of sea ice (Frey et al., 2014) and ocean acidification (Mathis et al., 2014). An elementary prediction is that the range of mobile Arctic marine taxa will shift northwards with rising ocean temperatures (Cheung et al., 2009). However, spatial and temporal dynamics of seasonal ocean production, the complexities of ocean current systems and the relationships between ocean dynamics and organisms' ecology indicate that such predictions may not apply to all taxa (Hollowed et al., 2013). Our overall goal is to relate spatial variability in the distribution and abundance of Arctic marine fauna to oceanographic variables that are potentially affected by climate change. In this way, we aim to illustrate potential mechanisms linking climate change to Arctic marine communities.

The Chukchi Sea is a shallow continental shelf covered by sea ice for 5–7 months a year. Bering Strait defines the southern boundary of the Chukchi Sea and is the passageway for Pacific Water to enter the Arctic (Moore and Stabeno, 2015; Woodgate et al., 2015). Transport in the

eastern Chukchi Sea during the summer occurs in two pathways: the Alaskan Coastal Current, which flows north along the Alaska Coast, and a Central Channel Current, which flows north through the Central Channel and around Hanna Shoal (Fig. 1). The two currents separate at Point Hope and then merge again in Barrow Canyon, a focal area for advection of Pacific water towards the open Arctic (Pickart et al., 2005). These two currents are known as the “Bering to Barrow Current System” (Gong and Pickart, 2015). Primary production begins annually in a spring bloom once sufficient light reaches the photic zone of nutrient-rich Pacific waters (Carmack, 2006), which can occur with ice retreat and beneath first-year ice (Arrigo et al., 2012). Zooplankton grazing pressure is relatively low, such that much of the organic carbon is exported to the seafloor where it supports a rich benthic community (Grebmeier et al., 2006a).

High benthic productivity on Pacific Arctic shelves supports predators such as Pacific walrus (*Odobenus rosmarus divergens*), gray whales (*Eschrichtius robustus*), bearded seals (*Erignathus barbatus*) and spectacled eiders (*Somateria fischeri*). Arctic cod (*Boreogadus saida*) occupy benthic and pelagic habitats and are the dominant fish in much of the Pacific Arctic (Logerwell et al., 2015). Arctic cod is a key prey item for

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ship's bottom sounder indicated rough bottom ahead of the net in which case the net was retrieved early to avoid damage. Net height and width during trawling operations were measured with Marport Deep Sea Technologies acoustic net mensuration equipment (Lauth and Nichol, 2013). A bottom contact sensor (inclinometer/accelerometer) provided data used to assess the bottom tending performance of the net and to determine when the footrope was in contact with the seafloor. Bottom contact data were used to estimate distance fished.

The entire catch for each trawl was weighed on a Marel motion-compensated marine scale. All fish caught were sorted, identified to the lowest possible taxonomic level, counted and weighed. Specimens of all fish taxa were collected for confirmation of field identification in the AFSC's taxonomic laboratory (J. Orr and D. Stevenson, AFSC, pers. comm.). All specimens were photographed with the trawl number for proper assignment when species identification was verified or changed. Specimens were counted, weighed and preserved in a 10% formalin and sea-water solution buffered with sodium bicarbonate. Length frequency data were collected for all fish species caught. Lengths were recorded by millimeter interval and measured from the tip of the snout to the end of the middle rays of the caudal fin for fish that have a forked tail (fork length), to the tip of the tail for fish that do not (total length). Individual fish were frozen for measurement of individual weight and removal of otoliths for ageing.

Net width and distance fished were used to calculate area swept, which was then used to calculate catch per unit effort (CPUE) for each fish species. CPUE (kg/km^2) was calculated at each station from the catch weight of each species divided by the area swept.

2.2. Oceanographic sampling

A Seabird FastCAT conductivity-temperature-depth (CTD) instrument was deployed at each bottom trawl station, immediately before or after the bottom trawl was deployed. Data were processed using a combination of the manufacturer's software (Seabird Electronics, 2012) and custom Matlab software (version 14a, 2014, Mathworks) designed for visual inspection and despiking of the profile data. Raw data were binned to 1 decibar pressure levels (approximately 1 m depth intervals).

2.3. Bottom hardness

Acoustic measurements for substrate classification were collected using a Simrad ES60 echosounder operating at 38 kHz (12° beam angle between half power points). The echosounder was calibrated prior to the survey following Foote (1983). Water column and seabed backscatter (i.e. reflected echoes) were recorded continuously along survey transects, sampling at a rate of 1 Hz. Backscatter data were averaged in 100 m horizontal bins. Bottom types were quantified using a hardness (E2) metric (values 1 – 10) by integrating the first and second bottom reflections in Echoview software (v6.1). The entire second bottom echo is integrated for the E2 hardness metric based on the acoustic impedance mismatch between the seabed and the water column (Chivers et al., 1990). Values of acoustically-determined bottom hardness were assigned to each bottom trawl station by taking the average of all acoustic data points that fell within the start and stop locations of the trawl.

2.4. Mapping and statistics

The distribution of fish CPUE was mapped using ArcMap (version 10.3, 2014, ESRI, Inc.). Fish CPUE was mapped as kg/ha because the 2008 Beaufort Sea catch data were presented in kg/ha . Statistical analyses of the 2013 Chukchi Sea catch data were conducted on CPUE in kg/km^2 .

Ten variables were selected for statistical analysis of the relationships between fish CPUE and the environment: distance from shore (km), depth (m), bottom hardness, surface temperature ($^\circ\text{C}$; "surface" is

the mean temperature within the surface mixed layer), surface salinity, surface density (kg/m^3), bottom temperature ($^\circ\text{C}$), bottom salinity, bottom density (kg/m^3) and water column density difference (bottom density minus surface density, kg/m^3). The density difference is an integrated indicator of the amount of water column stratification due to temperature and salinity variations, whereby greater differences indicate greater stratification. Correlations between environmental variables were examined.

The high degree of collinearity among the environmental variables could lead to problems conducting multivariate statistical analyses. Elevated values of variance estimates, a known result of multicollinearity, would make it difficult to identify relationships between environmental variables and CPUE. Thus we chose a variable reduction strategy that would generate a set of variables that did not exhibit collinearity. Principal Components Analysis (PCA) of the environmental variables was used to reduce the dimensionality of the data, and the first two principal components were rotated using the varimax method (Dunteman, 1989). The resulting components were then used in statistical models to test the effects of the principal components, each representing a suite of environmental variables, on fish CPUE.

Generalized Linear Models were formulated for saddled eelpout (*Lycodes mucosus*), warty sculpin (*Myoxocephalus verrucosus*) and variegated snailfish (*Liparis gibbus*) because of the relatively high proportion of stations with zero catch (20 for saddled eelpout, 19 for warty sculpin, and 17 for variegated snailfish; out of 29 total stations). GLMs were fitted with a binomial distribution using a logit link function, where each fish species occurrence (0 = absent, 1 = present) was modeled as a function of the first two principal components. For Arctic cod, which were present at every station, fish density was analyzed with a Generalized Additive Model (GAM) using a Gaussian distribution and a cubic regression spline smoother with 4 knots. GAM was chosen over a linear model because plots of Arctic cod CPUE versus principal components indicated non-linear relationships. For kelp snailfish (*Liparis tunicatus*), which were present at 22 of the 29 stations, linear models were used to test the relationship between CPUE and principal components because binary plots indicated linear relationships. Examination of the Arctic cod and kelp snailfish catch data indicated increasing variance with increasing means, so CPUE data were log transformed. Residual and QQ plots (plots of the quantiles of the first data set against the quantiles of the second data set) from all models were checked to ensure that the data were consistent with model assumptions.

All modeling was conducted in R (version 2.13.1, The R Foundation for Statistical Computing, 2011). The 'psych' package was used for principal components varimax rotation (Revelle, 2015). The 'mcgv' package was used for GAM fitting (Wood, 2006).

2.5. Comparison with the Beaufort Sea 2008 survey

We graphically compared the results from this survey in the northeast Chukchi Sea to published survey results from the western Beaufort Sea (Logerwell et al., 2011) using GIS maps. GIS maps of Arctic cod weight and age data from the Beaufort Sea are presented in this paper for the first time. The bottom trawl gear and deployment methods were the same for the two surveys, except for some stations in the Beaufort Sea survey that were sampled with a net augmented with a 3.8-cm mesh liner on the entire net. Fish CPUE was higher in the lined net catches than the unlined net catches (Rand and Logerwell, 2011), so statistical comparison of the Chukchi Sea and Beaufort Sea survey data was not appropriate.

3. Results

3.1. Chukchi Sea 2013 survey

Arctic cod dominated the catch (Table 1), making up 81.7% of the

Table 1
Total fish catch by weight and number.

Scientific name	Common name	Total catch	
		Weight (kg)	Number
<i>Boreogadus saida</i>	Arctic cod	60.513	4470
<i>Myoxocephalus verrucosus</i>	warty sculpin	3.188	57
<i>Lycodes mucosus</i>	saddled eelpout	2.364	16
<i>Liparis gibbus</i>	variegated snailfish	2.198	28
<i>Liparis tunicatus</i>	kelp snailfish	2.136	213
<i>Triglops pingeli</i>	ribbed sculpin	0.426	45
<i>Gymnancanthus tricuspis</i>	Arctic staghorn sculpin	0.419	37
<i>Hippoglossoides robustus</i>	Bering flounder	0.408	11
<i>Liparis marmoratus</i>	festive snailfish	0.338	33
<i>Lycodes raridens</i>	marbled eelpout	0.306	7
<i>Mallotus villosus</i>	capelin	0.242	27
<i>Gadus chalcogrammus</i>	walleye pollock	0.192	32
<i>Pleuronectes quadrituberculatus</i>	Alaska plaice	0.154	1
<i>Gymnelus viridis</i>	fish doctor	0.146	7
<i>Icelus spatula</i>	spatulate sculpin	0.143	29
<i>Lycodes polaris</i>	Canadian eelpout	0.136	4
<i>Liparis fabricii</i>	gelatinous seasnail	0.132	14
<i>Eumesogrammus praecisus</i>	fourline snakeblenny	0.112	5
<i>Hemilepidotus papilio</i>	butterfly sculpin	0.100	2
<i>Lumpenus fabricii</i>	slender eelblenny	0.100	28
<i>Lycodes palearis</i>	wattled eelpout	0.096	1
<i>Limanda sakhalinensis</i>	Sakhalin sole	0.072	8
<i>Eumicrotremus derjugini</i>	leatherfin lump sucker	0.032	2
<i>Ulcina olrikii</i>	Arctic alligatorfish	0.029	22
<i>Enophrys dicerca</i>	antlered sculpin	0.028	1
<i>Nautichthys pribilovius</i>	eyeshade sculpin	0.018	4
<i>Liparis</i>	snailfish unid.	0.012	2
<i>Lumpenus medius</i>	stout eelblenny	0.010	3
<i>Arctediellus scaber</i>	hamecon	0.010	1
<i>Podothecus veternus</i>	veteran poacher	0.006	1
<i>Aspidophoroides bartoni</i>	alligatorfish	0.002	1

total survey catch by weight and 87.4% of the catch by number. Arctic cod ranged in length from 28–232 mm and age from 0–4 years (although age-0 fish were only caught at one station). The next most abundant species, by weight, was the warty sculpin, followed by saddled eelpout and two species of snailfish, variegated snailfish and kelp snailfish. Catches of other species were less than 1% of the total catch by weight and number.

Arctic cod were caught at every station and CPUE by biomass and number was greatest at the deeper stations in the center of Barrow canyon, around 100 m and deeper (Fig. 3). Saddled eelpout had high CPUE both in the deeper waters of the canyon and in shallow waters inshore of the canyon. They were not caught offshore of the canyon (Fig. 4a). Warty sculpin were similarly not caught at the outermost stations (Fig. 4b). Variegated snailfish were caught in the canyon and just offshore of the canyon (Fig. 4c). Kelp snailfish abundance decreased with distance from shore. Catches were zero or very low for eelpout, sculpin and snailfish in the northeast part of the study area (offshore of the canyon on transects 5 and 6).

Cold (< 1 °C) and high salinity (> 32.5) water was found at depth in Barrow Canyon, as shown by the vertical sections of transects 1 – 6 (Fig. 5). Nearshore waters (depths < 40 m), inshore of the canyon were generally unstratified. Surface waters tended to be warmer (2–6 °C) and less saline (< 30) over the canyon and offshore. Surface waters had particularly low salinity in the northeastern portion of the study area (offshore of the canyon on transects 5 and 6), resulting in strong stratification. Bottom hardness was relatively high at depths less than 150 m in Barrow Canyon and inshore. Bottom hardness decreased from the midline of Barrow Canyon to offshore of the canyon where it was lowest (Fig. 6). Previous studies of benthic habitat in the Chukchi Sea showed that sediments ranged from mud, clay, silt, sand to gravel (in order of increasing hardness) (Feder et al., 1994).

Many of the environmental variables were correlated with each other (Table 2). Salinity and density were nearly perfectly correlated

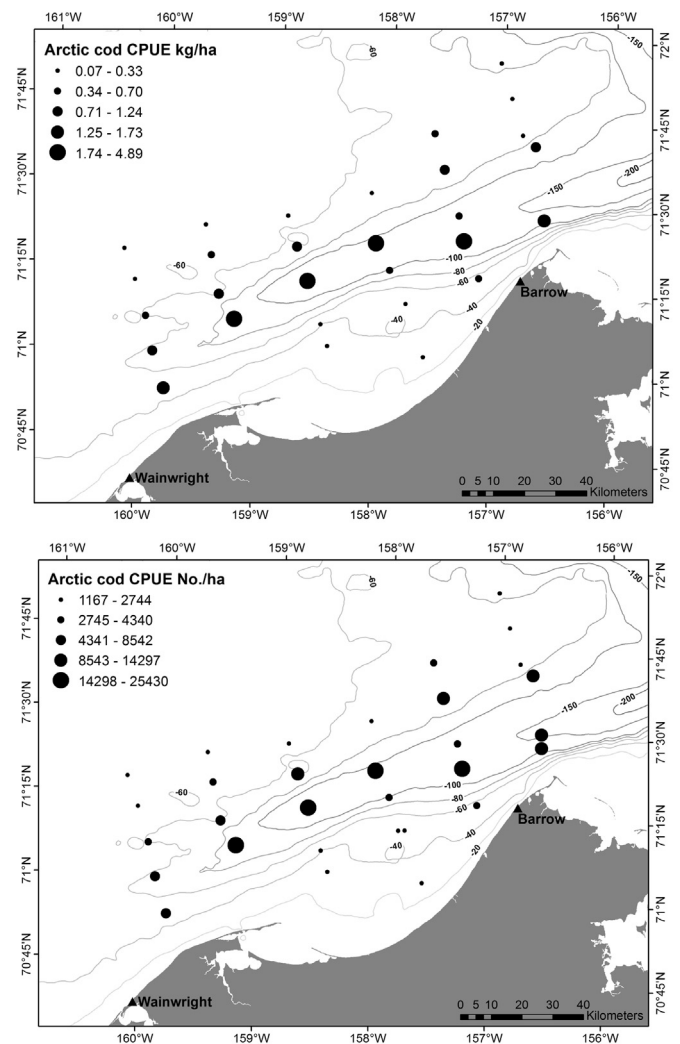


Fig. 3. Catch-per-unit-effort (CPUE) by biomass (kg/ha) and number (No./ha) for the most abundant fish species, Arctic cod. Depth contours in meters.

($r = 0.997$), so salinity was used in subsequent PCA analyses but density difference was used as a measure of stratification. Surface salinity and bottom temperature were negatively correlated with distance from shore, indicating that surface waters had lower salinity and bottom waters were generally colder offshore. The vertical density difference was positively correlated with distance from shore, indicating greater stratification offshore. Bottom temperature was negatively correlated and bottom salinity was positively correlated with water depth, consistent with cold and high salinity water in the bottom of Barrow Canyon. Surface salinity and density difference (stratification) were strongly negatively correlated, indicating that low surface salinity (e.g. ice melt) was associated with stronger stratification. Similarly, bottom temperature (–) and bottom salinity (+) were correlated with the density difference, indicating that cold, high salinity waters at depth also contributed to stratification. Bottom hardness was negatively correlated with distance from shore, i.e. softer bottom was found farther from shore. Bottom hardness was negatively correlated with the density difference. The mechanistic link here may be due to current velocity: stronger currents will tend to scour the bottom more readily, while slower currents will allow organic matter to settle to the seafloor. Stronger currents may also be associated with greater turbulence and mixing, which tend to erode stratification.

The eigenvalues for the first two principal components of the PCA were 3.91 and 1.77. The eigenvalues for the remaining principal components were all less than 1, so only the first two principal

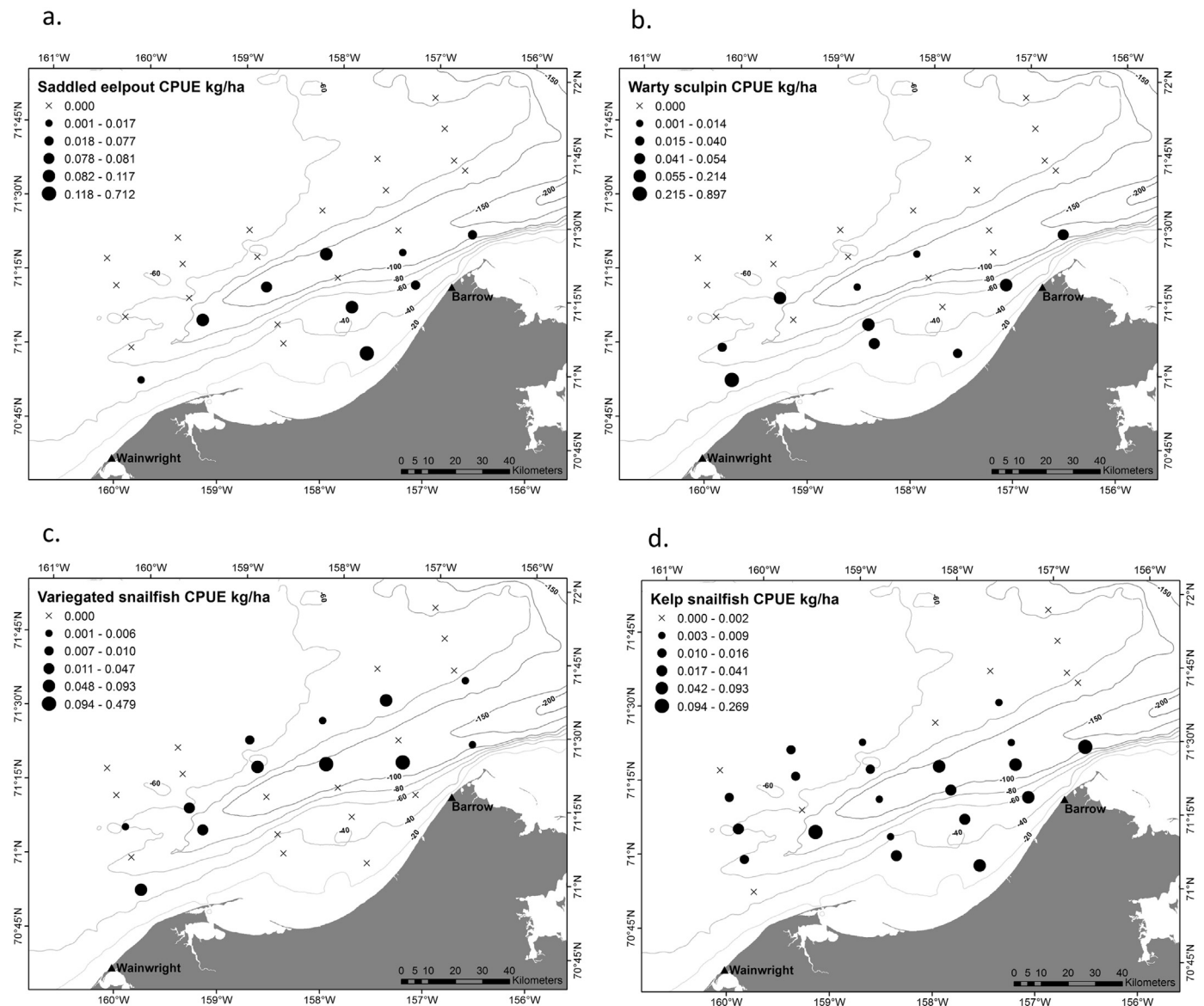


Fig. 4. Catch-per-unit-effort (CPUE, kg/ha) of the most abundant fish taxa, following Arctic cod. Depth contours in meters. a. Saddled eelpout, b. Warty sculpin, c. Variegated snailfish, d. Kelp snailfish. Depth contours in meters.

components were retained for further analysis (Dunteman, 1989). The rotated principal component 1 (PC1) accounted for 41% of the variance and the rotated PC2 accounted for 30% of the variance, for a cumulative 71% of the variance in the environmental variables explained by these two principal components. The variable loadings show that bottom hardness, surface temperature, surface salinity, density difference and distance from shore were relatively strongly correlated with PC1 (loadings > 0.5 or < -0.5) (Table 3). Depth, bottom temperature and bottom salinity were strongly correlated with PC2 (Table 3).

The GLM showed that PC1 was significantly related to saddled eelpout and warty sculpin, with positive coefficients (Table 4). This is consistent with a greater likelihood of these species occurring on hard bottom close to shore. They were also less likely to occur where the water column had relatively low surface temperature, low surface salinity and high density difference, which was characteristic of the northeast portion of the study area. The linear model for kelp snailfish similarly showed that PC1 was a significant factor (Table 5). Kelp snailfish CPUE increased with PC1 scores (Fig. 7). PC1 was not a significant factor for variegated snailfish, and PC2 was only marginally significant (Table 4).

The GAM for Arctic cod showed that PC2 was a significant factor (Table 6). Arctic cod CPUE increased with PC2 scores (Fig. 8), consistent with Arctic cod being more abundant at greater depths and in waters with low bottom temperature and high bottom salinity.

3.2. Comparison between Chukchi Sea 2013 survey and Beaufort Sea 2008 survey

During both surveys, Arctic cod CPUE was highest at greater depths (around 80 m and deeper). High CPUEs occurred in Barrow Canyon in the Chukchi Sea and on the outer shelf and slope in the Beaufort Sea (Fig. 9), where bottom waters were cold and highly saline. Linear regressions of the Beaufort Sea fish and environmental data indicated that Arctic cod CPUE increased significantly with decreasing bottom temperature (Logerwell et al., 2011). As described above, Chukchi Sea Arctic cod were similarly associated with cold bottom temperatures and high salinity. Thus, results from both surveys are consistent with Arctic cod being associated with cold, high salinity waters.

In the Beaufort Sea, Arctic cod were larger (by weight) and older at depths greater than 100 m (Fig. 10). There was some indication of a similar pattern in the Chukchi Sea, but not as strong. In addition, age-4

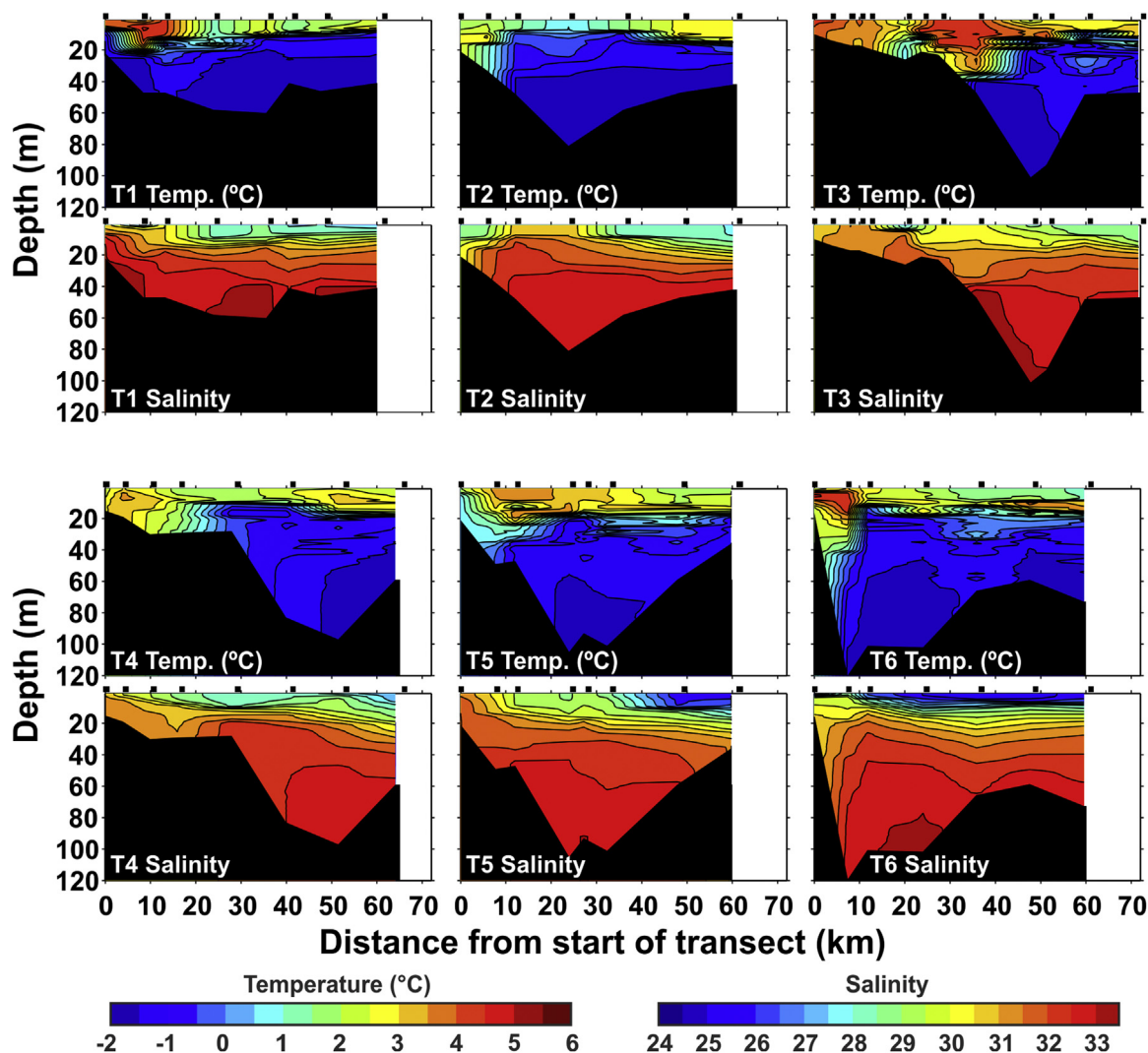


Fig. 5. Vertical sections of temperature (°C) and salinity along each of the six transects (from west to east). Distance (km) is from the nearshore start of each transect.

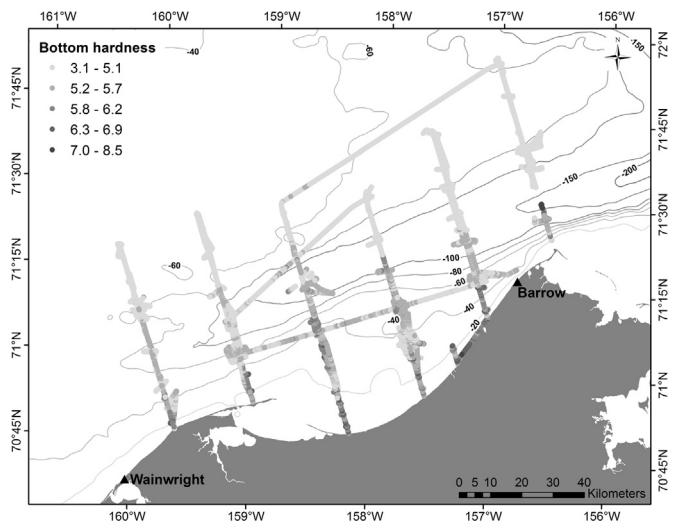


Fig. 6. Acoustically-determined bottom hardness. Possible scale range is 0–10, increasing hardness with increasing values.

fish were much less common in the Beaufort Sea.

Beaufort Sea eelpout catch was dominated by marbled eelpout (*Lycodes ravidus*) and Canadian eelpout (*Lycodes polaris*), with saddled eelpout making up a small portion of the catch (Rand and Logerwell,

2011). During both surveys, eelpout CPUE was high in the deeper water of the canyon and slope, but there were also high CPUEs in the shallower water closer to shore (Fig. 9b). Linear regression of the Beaufort Sea data indicated that eelpout CPUE (all species combined) was significantly negatively correlated with bottom temperature (Logerwell et al., 2011). In the Chukchi Sea, other environmental factors, bottom hardness and water column stratification, were significantly associated with saddled eelpout (presence/absence).

Warty sculpin were one of the most abundant sculpin species caught during the Beaufort Sea survey, along with ribbed sculpin (*Triglops pingeli*), Arctic staghorn sculpin (*Gymnoanthus tricuspis*), and hamecon (*Artiedellus scaber*) (Rand and Logerwell, 2011). Sculpin in the Beaufort Sea (all species combined) were found almost exclusively at depths less than 100 m. Except for one station, catches of sculpin were zero offshore of 100 m (Fig. 9c). Warty sculpin from the Chukchi Sea survey were similarly more abundant close to shore. A GLM (binomial distribution) of Beaufort Sea sculpin data indicated that bottom depth, bottom salinity and density difference were significant factors, consistent with sculpin being associated with low salinity and less stratified water on the shelf (Logerwell et al., 2011). Density difference and distance from the shore were similarly significant factors for Chukchi Sea warty sculpin.

The two most abundant snailfish caught during the Beaufort Sea survey were variegated snailfish and the gelatinous seasnail (*Liparis fabricii*) (Rand and Logerwell, 2011). However, snailfish density

Table 2
Correlation matrix of environmental variables measured at each station. Bold, italic numbers are significant Pearson's product moment correlations ($P < 0.05$, $N = 29$).

	Distance from shore (km)	Depth (m)	Bottom hardness	Surface temperature (°C)	Surface salinity	Surface density (kg/m ³)	Bottom temperature (°C)	Bottom salinity	Bottom density (kg/m ³)	Density difference (kg/m ³)
Distance from shore (km)										
Depth (m)	-0.21									
Bottom hardness	-0.66	0.09								
Surface temperature (°C)	-0.33	-0.04	0.37							
Surface salinity	-0.49	-0.11	0.59	0.37						
Surface density (kg/m ³)	-0.47	-0.10	0.58	0.30	0.997					
Bottom temperature (°C)	-0.44	-0.45	0.49	0.29	0.31	0.29				
Bottom salinity	0.22	0.59	-0.31	-0.21	-0.18	-0.17	-0.87			
Bottom density (kg/m ³)	0.25	0.58	-0.33	-0.22	-0.20	-0.19	-0.90	0.998		
Density difference (kg/m ³)	0.50	0.32	-0.62	-0.34	-0.92	-0.92	-0.60	0.54	0.55	

Table 3
Variable loadings on first two principal components after varimax rotation.

Variable	PC1	PC2
Bottom hardness	0.82	-0.09
Depth	0.18	0.86
Surface temperature	0.55	-0.10
Surface salinity	0.82	-0.14
Bottom temperature	0.45	-0.78
Bottom salinity	-0.23	0.90
Density difference	-0.78	0.47
Distance from shore	-0.82	-0.04

Table 4
Results of GLM (binomial distribution) between environmental principal components and fish presence/absence. Deviance explained, bold and italic values are significant at $P < 0.05$ ($N = 29$), positive (+) and negative (-) coefficients are indicated in parentheses. * $P < 0.10$.

	PC1	PC2
Saddled eelpout (null deviance = 35.924)	38.0% (+)	2.7%
Warty sculpin (null deviance = 37.363)	33.7% (+)	1.5%
Variegated snailfish (null deviance = 39.336)	0.3%	11.1% (+)*

Table 5
Results of the linear model of environmental principal components and kelp snailfish CPUE (kg/km²). R^2 and P values are shown. Significant P values and the corresponding R^2 are in bold, positive (+) or negative (-) relationship.

	PC1	PC2
Kelp snailfish (n = 29)		
R^2	0.32 (+)	0.009
P	< 0.001	0.62

patterns were not analyzed in Logerwell et al. (2011), so comparisons of snailfish distribution in the Beaufort and Chukchi seas were not made for this paper. Bottom hardness data were not collected during the Beaufort Sea survey and distance from shore was not calculated.

4. Discussion

Understanding the mechanisms driving the distribution and abun-

dance of demersal fauna is needed to forecast the impacts of climate change on Arctic ecosystems. Our work provides baseline information on the distribution and abundance of benthic fish in the northeast Chukchi Sea around Barrow Canyon. Our results also provide insight into the oceanographic processes and habitat characteristics that affect benthic fish distribution and potentially their feeding, growth and survival. A similar approach to understanding the habitat of pelagic fish in the Chukchi Sea showed that water mass characteristics were important for the distribution of zooplankton and the juvenile fish that prey on them (Eisner et al., 2013).

Arctic cod were the most abundant demersal fish in the study area, followed by warty sculpin, saddled eelpout and variegated snailfish and kelp snailfish. This species composition was expected based on past surveys in the Chukchi Sea (Logerwell et al., 2015).

Although not caught in large numbers or biomass, walleye pollock (*Gadus chalcogrammus*) were present. The range in pollock length was 65–168 mm, with an average of 101.6 mm ($n = 32$). These fish were likely age-1 to age-2 (Hinckley, 1984; Brown et al., 2001) and thus were not commercially valuable (walleye pollock recruit to the Bering Sea fishery at age-3 or-4 (Ianneli et al., 2014)). Walleye pollock of similar size (60–160 mm) have been observed in low numbers in other recent surveys of benthic fish in the Chukchi Sea (Logerwell et al., 2015).

Another Bering Sea commercial fishery species caught during this survey was a single Alaska plaice (*Pleuronectes quadrituberculatus*). The one specimen was measured and otoliths collected for ageing; it measured 237 mm and was age 11, although it was smaller than an age 11 fish caught in the Bering Sea (~310–360 mm). Alaska plaice fishery selectivity is estimated at 50% selected for females at 9–10 years old (~350 mm) and 10 years for males (~300 mm). They are 82% and 69% selected for males and females, respectively, at age 11 (Wilderbuer et al., 2014).

4.1. Water mass characteristics

The cold and high salinity characteristics of water in Barrow Canyon were consistent with winter-transformed Bering Sea water advected through Bering Strait, across the Chukchi Shelf and then northward through Barrow Canyon in spring and summer (Gong and Pickart, 2015; Pickart et al., 2005). A regression of the wind field versus along-canyon flow as recorded by current meters suggests that the canyon experienced both up-canyon and down-canyon flows during the period of the survey (Danielson et al., 2014; Ladd et al., 2016). As a result of this current flow, zooplankton may have been advected into the canyon from the Chukchi Sea shelf and/or the Beaufort Sea. Furthermore, high zooplankton biomass may occur in Barrow Canyon because of up-

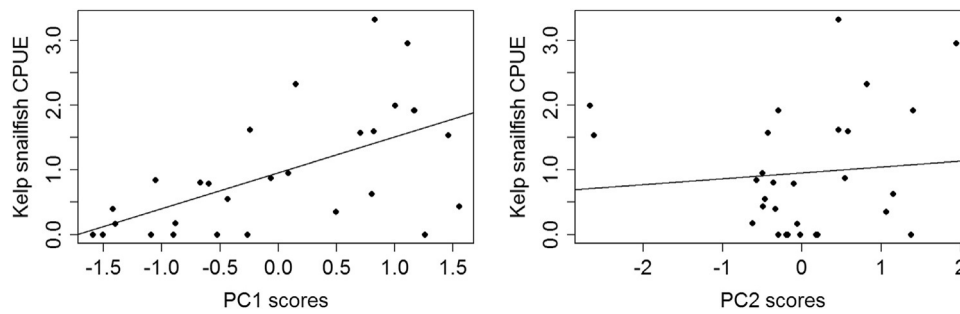


Fig. 7. Univariate linear regression plots showing the relationship between environmental principal components (PC) scores and kelp snailfish CPUE.

Table 6

Results of Generalized Additive Models (GAM) between environmental principal components and Arctic cod CPUE (kg/km²). Deviance explained and significance of smooth term. Bold, italic text indicates statistically significant smooth terms.

	PC1	PC2
Arctic cod (n = 29)	11.1% p = 0.128	48.1% <i>p < 0.001</i>

canyon flow coupled with the ontogenetic migration of large lipid-rich *Calanus hyperboreus*, which populate the Arctic Basin, to the upper 200 m in the summer (Kosobokova and Hirche, 2000; Kosobokova, 1982; Minoda, 1967). In addition, euphausiids (“krill”, mainly *Thysanoessa* spp.) may aggregate in deep waters in the canyon due to their diel vertical migration behavior. Zooplankton samples collected during this survey confirmed that *Calanus hyperboreus* were more abundant in Barrow Canyon than in nearshore waters and that *Thysanoessa raschii* were distributed in the canyon and its vicinity (Pinchuk and Sousa, unpubl. data/in press).

In the northeast portion of the study area, surface waters had high temperature and low salinity and were highly stratified. These waters were likely derived from ice-melt water from the Beaufort Sea or the typically later seasonal melt of ice on Hanna Shoal in the Chukchi Sea (Spall, 2007). Export of pelagic production to the benthos is an important process on Arctic shelves. Extremely high seasonal pelagic primary production is not limited by zooplankton grazing pressure such that large amounts of organic carbon settle to the seafloor, supporting a rich benthic food web (Grebmeier et al., 2006a). The area of stratification in the northeast of our study area could have been an area of relatively low pelagic input to the benthos if the stratification prevented vertical mixing into the euphotic zone such that the area became nutrient-limited after the initial spring bloom (Sakshaug, 2004). On the other hand, a sub-surface chlorophyll maximum has been observed under melt water in the Chukchi Sea (Martini et al., 2016). Further sampling is needed to determine whether this area of stratification, should it occur year after year, positively or negatively impacts pelagic-benthic coupling or is so limited that advection from other areas

swamps the local effect.

Oceanographic conditions in 2008 and 2013 were similar. In August of both years, the coarse-scale flow pattern north of Bering Strait was characterized by suppressed flow of the Alaska Coastal Current (Bond and Stabeno, 2018). Winds over the Chukchi Shelf in August 2008 and 2013 were atypically northeasterly. This resulted in reversals of currents from northwards to southwards (Weingartner et al., 2013; 2014). The northeasterly winds also likely retarded the northward flow of warm Bering Sea water into the NE Chukchi and Beaufort Seas. In addition, sea ice was relatively heavy and persistent in both years, particularly over Hanna Shoal. This resulted in extensive cold and low salinity melt waters at the surface and strong stratification in both years (Weingartner et al., 2013; 2014). At the local scale of Barrow Canyon and the western Beaufort Sea shelf, water mass properties in both years indicated the presence of cold, high salinity water formed on the Chukchi Sea shelf in the previous winter (Logerwell et al., 2011). There was also evidence in both years of episodic wind-driven upwelling and reversed, up-canyon, flow (Danielson et al., 2014; Logerwell et al., 2011).

4.2. Arctic cod

Arctic cod were more abundant in the deep, cold and high salinity waters in Barrow Canyon. We hypothesize that Arctic cod occupied Barrow Canyon to take advantage of energy-rich prey, potentially resulting in improved condition and survival. GAM analysis of environmental principal component scores confirmed that Arctic cod biomass density was associated with bottom depth, salinity and temperature. Younger, pelagic Arctic cod (age-0) have similarly been shown to be associated with colder water in the Chukchi Sea (de Robertis et al., 2016).

Calanus hyperboreus and *Thysanoessa raschii* were present in Arctic cod stomachs collected in this study and were the dominant component of the diet by weight (Sousa, North Slope Borough, pers. comm.; Pinchuk, University of Alaska Fairbanks, pers. comm.). Arctic cod sampled in other studies in the Chukchi Sea similarly showed that they consumed calanoid copepods and euphausiids (Gray et al., 2015;

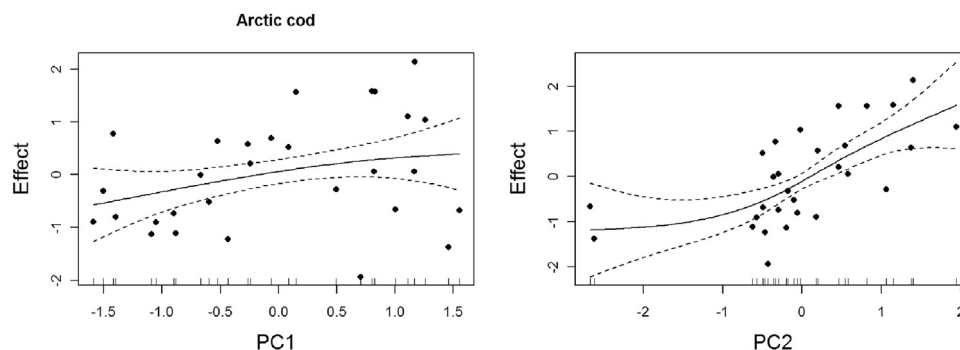


Fig. 8. Smoothed response plots of univariate GAM showing the effects of environmental principal components (PC) scores on Arctic cod CPUE. The y-axis is the effect of the PC scores on Arctic cod CPUE, the tick marks along the x-axis show the distribution of x-values and the dotted lines represent 95% confidence intervals.

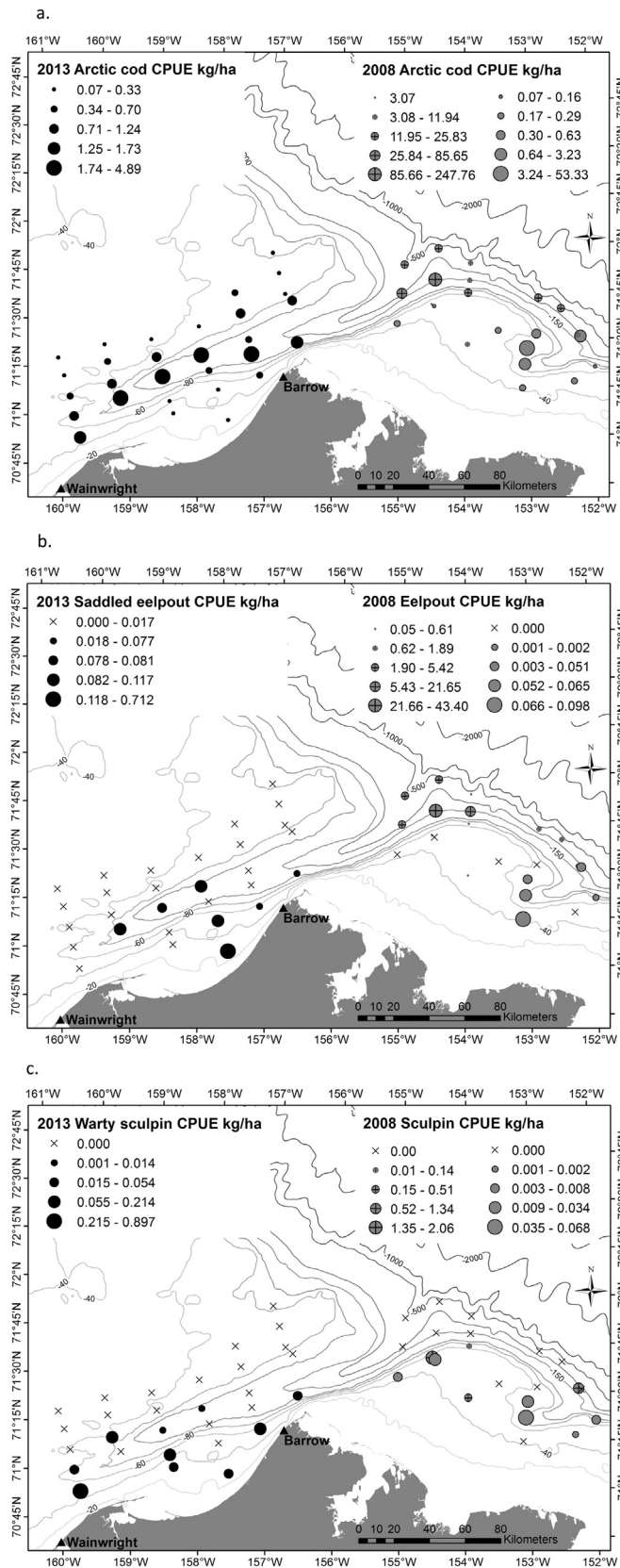


Fig. 9. Catch-per-unit-effort (CPUE, kg/ha) of fish taxa from the 2013 Chukchi Sea survey and the 2008 Beaufort Sea survey (Logerwell et al. 2011). Symbols for the 2008 Beaufort Sea survey with crosses indicate catches with the lined bottom trawl, plain symbols for both surveys indicate the unlined bottom trawl. Depth contours in meters. a. Arctic cod, b. Saddled eelpout (2013) and eelpout, all species combined (2008), c. Warty sculpin (2013) and sculpin, all species combined (2008).

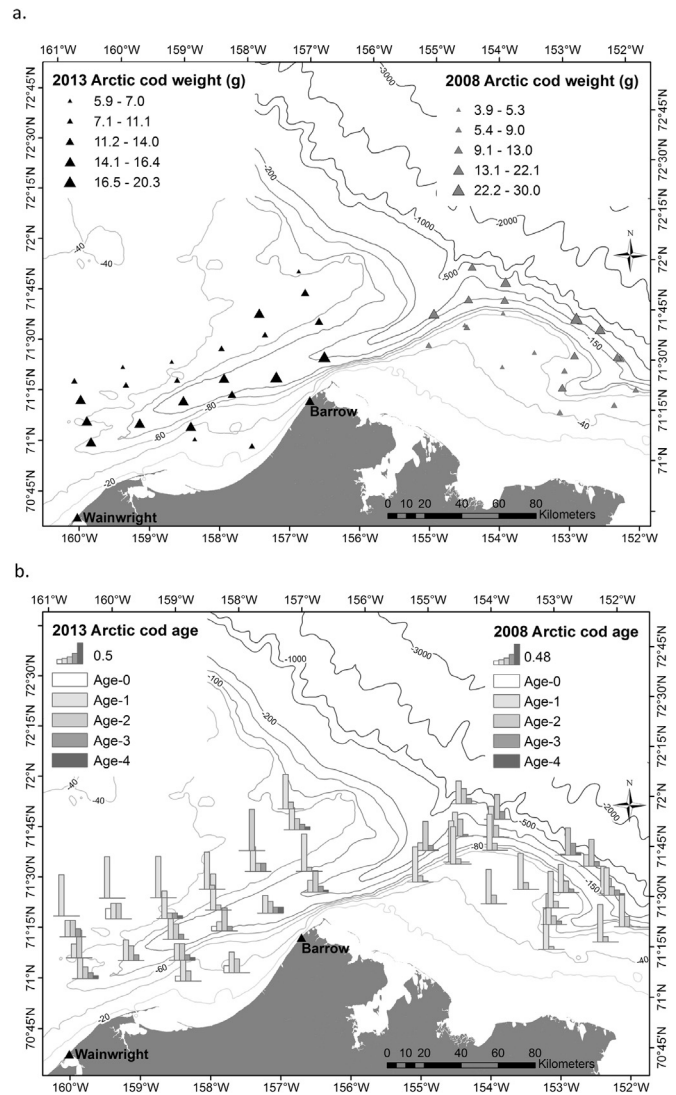


Fig. 10. Arctic cod weight and age from the 2013 Chukchi Sea survey and the 2008 Beaufort Sea survey (Logerwell et al. 2011). a. Mean individual weight of fish (g), b. Age distribution of fish, proportion.

Whitehouse et al., 2016). Arctic cod fatty acid signatures, also assessed during the Chukchi Sea survey, were consistent with feeding on these high-energy zooplankton (Copeman, Oregon State University, pers. comm.). Fish condition is highly correlated with the proportion in fish tissue of the long chain monounsaturated fatty acids characteristic of zooplankton such as *Calanus hyperboreus* (Copeman, pers. comm.). Laboratory studies support the hypothesis that colder waters are good habitat for Arctic cod. Age-0 Arctic cod had better growth and condition at colder temperatures than other juvenile gadids, such as saffron cod (*Eleginus gracilis*), Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Gadus chalcogrammus*) (Laurel et al., 2015).

A similar habitat selection may have occurred in the Beaufort Sea, documented by the 2008 survey (Logerwell et al., 2011). Arctic cod density was greater in deep, cold and high salinity waters downstream of Barrow Canyon in the western Beaufort Sea. Fish also were larger, by weight, and older in the deeper water. Similar to the Chukchi Sea, copepods and euphausiids were common diet items of Arctic cod in the Beaufort Sea (Rand et al., 2013).

Other Arctic taxa use Barrow Canyon for foraging. Surface and subsurface feeding seabirds (black-legged kittiwakes (*Rissa tridactyla*), thick-billed murres and shearwaters (Procellariidae)) are found in high densities at the mouth of Barrow Canyon (Kuletz et al., 2015). Barrow

Canyon and waters around Point Barrow have similarly been shown to be an area of aggregation of foraging bowhead whales in late summer. Whale aggregations have been documented with aerial surveys and diet composition assessed from whale stomachs sampled during subsistence harvests. Whales in Barrow Canyon foraged on copepods (Citta et al., 2015; Moore et al., 2010). Whales at Point Barrow and to the east foraged on euphausiids that were transported onto the shelf and aggregated by local wind-driven current patterns (Ashjian et al., 2010; Citta et al., 2015). Our results indicate that Arctic cod similarly may be foraging on these aggregations of copepods and euphausiids driven by local oceanographic processes. The importance of Barrow Canyon to foraging beluga whales, which are predators on Arctic cod (Frost and Lowry, 1984) has been documented by both aerial and acoustic surveys (Moore et al., 2000; Stafford et al., 2013).

Epibenthic invertebrate density, taxonomic composition and functional trait distribution are similarly influenced by physical processes in and around Barrow Canyon (Rand et al., 2018). In the Chukchi Sea invertebrate biomass density was highest in the Canyon and towards shore, where flow is on average greater and the bottom type was harder and made of coarser sediments. This increase in biomass was driven by an increase in the catch of large-bodied basket stars (*Gorgonocephalus* spp.) and a prominence of filter/suspension feeders which could take advantage of the coarse sediments and high flow. In the Beaufort Sea, invertebrate density was highest in the mouth of Barrow Canyon and in the deep water off the shelf break where waters were cold and high salinity. There was a concomitant shift in taxonomic composition from sea cucumbers (*Psolus peronii*), mussels (*Musculus* spp.) and mudstars (*Ctenodiscus crispatus*) on the shelf to brittle stars (*Ophiura* spp.) and snow crabs (*Chionoecetes opilio*) on the slope. Deposit feeding was the dominant functional trait in the deeper slope waters where flow generally slows and sediments are finer grained.

There are two ocean-climate processes that could be expected to impact Arctic cod prey abundance in and around Barrow Canyon: advection and the timing of seasonal sea-ice retreat. Advection through Bering Strait brings nutrients and plankton-rich Pacific water into the Chukchi Sea, across the shelf and through Barrow Canyon (Pickart et al., 2005; Woodgate et al., 2015). The seasonal sea-ice zone provides ice algae and early stabilization of the water column by melting ice, which initiates a spring bloom. Both of these features, sea-ice retreat and advection, have been shown to be impacted by global climate change. Ocean warming has resulted in reduction in seasonal sea-ice extent and earlier sea-ice retreat (Grebmeier et al., 2006b; Frey et al., 2014). This change in timing of ice break up means that although ice melt still stabilizes the water column, sunlight is not sufficient to initiate an intense spring bloom (Clement, 2004), suggesting a lowering of overall primary production and less export to the benthos where Arctic cod feed. Alternatively, earlier sea-ice breakup could result in increased primary production due to a longer growing season, as has been observed in the Arctic Ocean (Arrigo et al., 2008). The second process of interest here, advection through Bering Strait, has increased by almost 50% from 2001 to the present (Woodgate et al., 2015). A larger-scale analysis of flow patterns from 1979 to 2014 shows, in contrast, that there was slightly less poleward advection across the Chukchi Sea shelf since the turn of the century (Bond and Stabeno, 2018). Changes in transport and flow patterns are important to fishes such as Arctic cod because they could result in changes in nutrients and plankton being delivered to the Chukchi Sea shelf into Barrow Canyon as well as changes in heat transport and the loss rate of sea ice (Woodgate et al., 2010). Although the present study from two years' surveys suggests some potential mechanisms, further research over multiple years and over a broader study area is needed to confirm how the dynamics of advection and sea-ice retreat impact the foraging habitat of Arctic cod.

4.3. Other species: eelpout, sculpin and snailfish

The first environmental principal component (PC1) was an important factor in the presence/absence models for saddled eelpout and warty sculpin and for the linear model for kelp snailfish. Distance from shore was one of the environmental variables correlated with PC1, and can thus be considered one of the drivers of the distribution of these species. Very few fish, if any, were caught in the outermost stations on all transects. A broad-scale survey of the entire Chukchi Sea shelf, conducted in 2012 with the same bottom trawl gear as this study likewise showed that eelpout, sculpin and snailfish were only caught inshore of Barrow Canyon (Godard et al., 2014). The distributions of these fishes extended farther offshore only south of latitude 70°N. The relationship between fish density and distance from shore could reflect the use of nearshore areas as nursery grounds. In a synthesis of catch and size data from fish surveys in the Chukchi Sea across habitats from the beach to the shelf, Logerwell et al. (2015) found that age-0 sculpins were present in the beach and nearshore benthic habitats, and fish were larger and older offshore. Similarly, eelpout and snailfish increased in size from the beach through the nearshore and to the offshore habitat. Logerwell et al. (2015) hypothesized that nearshore habitats function as nursery areas and fish migrate offshore as they age. However, this does not fully explain why eelpout, sculpin and snailfish were not found in greater densities further offshore in the northeast Chukchi Sea during this survey. More data on their ontogenetic migrations is needed to fully flesh out this hypothesis. The effect of distance from shore on Beaufort Sea fish was not evaluated for the 2008 survey.

Surface salinity, surface temperature and the water column density difference were also correlated with PC1. Fish were less likely to be present or were found in lower densities in this ice melt water (where surface waters had low temperature and low salinity and the water column was highly stratified). We hypothesize above that ice-melt water in the northeast portion of the study area was relatively low in pelagic production because the high stratification would have limited mixing of nutrients into the photic zone; and thus less production would be available to be exported to the benthos.

Bottom hardness, as measured by the acoustic return signal, was also correlated with PC1. This indicates that fish were more likely to be present or were found in greater densities on harder bottom. Harder bottom may have been more favorable for the distribution of their benthic prey: shrimp, polychaetes, and crab (T. Buckley, AFSC, unpubl. data). Some mobile benthic species such as crab may choose harder substrates because the structural complexity provides shelter for larvae and early juveniles (Tapella et al., 2009). However, polychaetes are typically found in fine sediments where they burrow into the substrate for food and protection from predators (Hutchings, 1998). The mechanisms linking the distribution of these fish species to bottom hardness require further investigation.

4.4. Conclusion

We demonstrate linkages between oceanographic variables and benthic fish distribution and abundance that suggest advection, sea-ice dynamics and pelagic-benthic coupling are important for the ecology of Arctic cod and other benthic fishes of the Chukchi Sea marine ecosystem. These ocean processes have been and will likely continue to be impacted by climate change (Frey et al., 2014; Grebmeier et al., 2006b; Woodgate et al., 2015). Our results improve the understanding of the mechanistic linkages between climate change and benthic fish ecology, which is needed to make better predictions of the effects of climate change on Arctic fish communities beyond relatively simplistic predictions of northward range shifts. Because benthic fish such as Arctic cod are important prey for apex predators, many of which are exploited for subsistence use, our work contributes to understanding the impacts of climate change on human communities of the Pacific Arctic.

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