



Original Article

Seasonal, interannual, and spatial patterns of community composition over the eastern Bering Sea shelf in cold years. Part II: ichthyoplankton and juvenile fish

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Climate-mediated oceanographic changes have led to protracted periods of above- or below-average water temperatures over the eastern Bering Sea shelf since the early 2000s. Ecosystem components, from phytoplankton to marine birds, have shown dichotomous responses to these temperature stanzas. Understanding within-stanza responses is fundamental to modelling efforts that project ecosystem responses under future climate scenarios. This study describes fish communities associated with Walleye Pollock during the age-0 period and also examines within-stanza homogeneity of assemblages. Spatial patterns of assemblage structure are compared with pre-defined ecoregions and environmental indices are assessed to determine potential mechanisms that delineate species assemblages. Walleye Pollock, rockfishes, Sand Lance, and Northern Rock Sole contributed to spring assemblages in every year. Assemblages were delineated by across-shelf gradients in 2008 and 2010 while 2009 assemblages showed less spatial structure. In summer, the diversity of fish assemblages increased across years but early-stage juvenile Walleye Pollock represented a small portion of the total abundance in 2009. Environmental gradients were related to fish assemblages, but patterns were along-shelf in 2008 and across-shelf in 2010. In fall, late-stage juvenile Walleye Pollock dominated the catch in 2008, but did not typify any assemblage in 2009. Overall, patterns of assemblage structure were not consistent with pre-defined ecoregions. Assemblage structure in 2009 was unique and indicates that within-stanza variability may complicate modelling projections based on ecosystem-level responses to climate changes.

Keywords: community structure, eastern Bering Sea, ichthyoplankton, spatiotemporal shifts, Walleye Pollock (*Gadus chalcogrammus*).

Introduction

Species-specific responses to oceanographic conditions, such as shifts in distributions, have been observed in the North Atlantic (Brander *et al.*, 2003), the North Sea (Perry *et al.*, 2005), and on the Bering Sea shelf (Mueter *et al.*, 2007; Mueter and Litzow, 2008; Spencer, 2008). Shifts in species' ranges may lead to atypical

species interactions as northern species are displaced by more southern species (Overland and Stabeno, 2004). In the Bering Sea, several studies have described the response of key commercial fishery species (Walleye Pollock, *Gadus chalcogrammus*, hereafter 'Pollock'; Pacific Cod, *G. macrocephalus*) to climate-mediated ecosystem stanzas (Mueter *et al.*, 2011; Hurst *et al.*,

2012; Siddon *et al.*, 2013; Farley *et al.*, 2016), but fewer studies have examined changes in these species' distribution or abundance as part of a broader fish assemblage (but see Eisner *et al.*, 2015).

Pollock are an important component of the eastern Bering Sea (EBS) ecosystem, as a predator of zooplankton and fish (Buckley *et al.*, 2016) and as a prey resource for other fish (Sigler *et al.*, 2016), seabirds (Hunt *et al.*, 1996), and marine mammals (Nordstrom *et al.*, 2013). Pollock also support the largest single-species commercial fishery in the United States. Research focused on the mechanistic linkages driving recruitment dynamics of Pollock in the EBS is spatially and temporally comprehensive and exceeds any such efforts elsewhere in the world.

Understanding dynamics in the community composition with which Pollock co-occur provides information on potential competitors and predators and may help forecast recruitment variability (Duffy-Anderson *et al.*, 2016) and inform ecosystem assessments. Studies that have examined shifts in fish assemblages in the Bering Sea have largely focused on interannual variability within a single season (Duffy-Anderson *et al.*, 2006; Siddon *et al.*, 2011; Busby *et al.*, 2014). Previous assemblage analyses in the southeastern Bering Sea during spring identified spatial gradients in species composition including across-shelf delineation, an influence of Alaska Coastal Current waters through Unimak Pass, and from nearshore to offshore habitats (Siddon *et al.*, 2011). Fall assemblage analyses showed the outer shelf community varied less than inner or middle shelf communities between warm and cold periods, suggesting the outer shelf may be less impacted by climate variability (Eisner *et al.*, 2015).

Oscillations of 3–5-year stanzas of above average (warm year) or below average (cold year) conditions have occurred in the EBS since the early 2000s (Stabeno *et al.*, 2012a; see Figure 4B within). A substantial body of work has investigated how various components of the ecosystem respond to these protracted climate stanzas by comparing ecosystem changes observed between warm year and cold year phases, including studies of phytoplankton (Eisner *et al.*, 2016), zooplankton (Coyle *et al.*, 2011; Eisner *et al.*, 2014), ichthyoplankton (Busby *et al.*, 2014), marine fish (Moss *et al.*, 2009; Smart *et al.*, 2013; Andrews *et al.*, 2016), marine mammals (Zerbini *et al.*, 2015), and seabirds (Kuletz *et al.*, 2014; Renner *et al.*, 2014). The perspective of most of these works is that the climate and oceanographic factors forcing the system are similar through the stanza, resulting in a consistent ecosystem response. The acceptance of this paradigm has perpetuated assurance that ecosystem response to climate stanzas can be reliably forecast. However, there has been little work to date to examine whether within-stanza responses of the ecosystem substantiate these assumptions. For example, 2007 was the first cold year in a cold stanza that continued until 2011. Juvenile Pollock are typically in better condition (i.e., higher in energy density) during cold years, fuelled by lipid-rich prey sources (Heintz *et al.*, 2013), leading to improved survival and recruitment success (Siddon *et al.*, 2013). Yet, in 2007, juvenile Pollock were in poor condition, possibly due to a weak spring bloom and low surface nutrient enrichment during summer (Gann *et al.*, 2016), highlighting within-stanza variability in ecosystem response.

A broad-scale integrated ecosystem project, Bering Sea Project (Wiese *et al.*, 2012), resulted in substantial understanding of Bering Sea shelf dynamics, both physically and biologically. Marine ecoregions were delineated based on bathymetry, oceanography, and faunal distributions as well as established ecological domains (e.g. Pribilof Islands). In general, the across-shelf

boundaries were based on bathymetry (0–50 m [inner domain], 50–100 m [middle domain], 100–200 m [outer domain]) (Coachman, 1986), while along-shelf breaks were set by water mass and/or faunal characteristics. The underlying structure compiled multiple data sources and proposed 16 ecoregions to describe the current knowledge of mesoscale processes on the Bering Sea shelf (Ortiz *et al.*, 2012). Building on this scheme, Baker and Hollowed (2014) utilized statistical approaches to determine ecological break-points along environmental gradients. Based on functional guilds and integrating physical and biological information, ecologically significant boundaries were identified. Six distinct biogeographical domains (ecoregions) link environmental and biological data from a standardized bottom trawl survey targeting adult life-stage fishes. Lower-trophic level dynamics are likely more influenced by oceanographic forcing, therefore analyses of zooplankton (Eisner *et al.*, this issue) and larval and juvenile fish (this paper) utilize the Ortiz *et al.* (2012) ecoregion scheme.

In this article, we report on seasonal changes in larval and juvenile fish assemblages within three cold years (2008–2010) over the EBS shelf. The objectives of this study were to (1) describe the community composition that Pollock are associated with seasonally (spring–fall) during the age-0 period, (2) examine fish communities during a cold stanza to determine interannual homogeneity of response, (3) test the hypothesis that community composition is similar within spatial ecoregions of the EBS shelf (Ortiz *et al.*, 2012), and (4) relate the assemblages to environmental gradients to identify variables affecting community composition. Within-season analyses are compared qualitatively among years and seasonal patterns are addressed in the Discussion. Comparisons of patterns are made to those reported by Eisner *et al.* (this issue) that look at the seasonal changes of zooplankton community composition (i.e. prey field) in similar regions over the same time period.

Material and methods

Biological sampling

Samples were collected from a series of oceanographic surveys conducted over the EBS shelf during the multi-disciplinary Bering Sea Project (Wiese *et al.*, 2012) and by the Alaska Fisheries Science Center Bering Arctic Subarctic Integrated Survey (BASIS) (Supplementary Table S1). The spatial extent of samples covered the shelf from inshore of the 50 m isobath westward to the shelf break, and from the Alaska Peninsula northward to 62.8°N (northern boundary of Ecoregions 10 and 11; Figure 1). The spatial coverage of spring samples focused on waters north of the Alaska Peninsula, which includes known spawning and nursery areas for a variety of ecologically and economically important species (Lanksbury *et al.*, 2007; Bachelet *et al.*, 2010), while summer and fall sampling was more extensive. Gear type, mesh size, and sampling depth also varied across cruises to target the life stages occurring at the time of sampling (Supplementary Table S1; Shima and Bailey, 1994). In spring, larvae were collected with Bongo plankton sampling nets; in summer, early-stage juveniles were collected with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS); in fall, late-stage juveniles and adult fish were collected with a midwater rope trawl. Over the seasons, ontogenetic changes (i.e. growth and development) influence fish's vulnerability or the ability to avoid sampling gear. In addition, the depth and geographic distribution of many species changes during transformation from the larval to juvenile

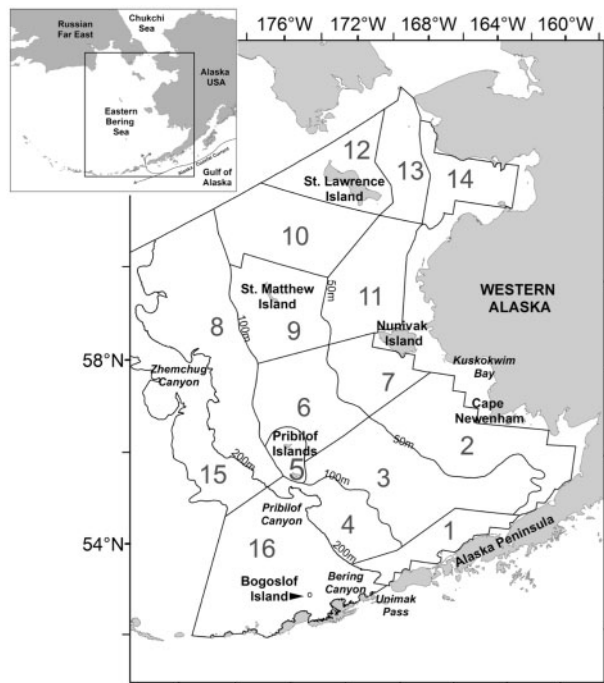


Figure 1. Map of the EBS study area. Ecoregions are indicated by solid lines and numbers. The inner domain (<50 m) is designated by Ecoregions 2, 7, and 11; the middle domain (50–100 m) by Ecoregions 3, 6, 9, and 10; the outer domain (100–200 m) by Ecoregions 4 and 8; shelf break regions (>200 m) by Ecoregions 15 and 16; Pribilof Islands by Ecoregion 5; and Alaska Peninsula by Ecoregion 1. Note that the inner and middle domain demarcation is at ~40 m north of 60°N.

stages, so both the gear used and the spatial extent of sampling were adapted. Therefore, across-season comparisons are purely qualitative.

Spring survey

Larval fish were collected in May using 60-cm Bongo nets fitted with 335- or 505- μm mesh; prior work showed the quantitative catch of larvae is similar between the two mesh sizes in species-level analyses (Shima and Bailey, 1994; Boeing and Duffy-Anderson, 2008). Quantitative oblique tows to a maximum depth of 300 m (or to within 10 m off-bottom) provided vertically integrated estimates of larval fish abundance. The nets were equipped with a calibrated flowmeter and catch rates were standardized to catch per unit effort (CPUE; #10 m^{-2}). Sampling occurred 24 h a day, and it was assumed that vertically integrated abundance estimates were not affected by diel vertical migrations. Samples were preserved at sea in 5% buffered formalin seawater solution. Fish larvae were sorted, identified to the lowest possible taxonomic level, measured (mm standard length, SL), and enumerated at the Plankton Sorting and Identification Center in Szczecin, Poland. Identifications were verified at the Alaska Fisheries Science Center, NOAA (National Oceanic and Atmospheric Administration) in Seattle, WA, USA.

Summer survey

Early-stage juveniles were collected during June and July using a 1- m^2 MOCNESS fitted with 505- μm mesh and equipped with a

flowmeter (Supplementary Table S1). Data from depth-stratified samples was combined, thereby providing vertically integrated estimates of abundance to a maximum depth of 100 m (or to within 10 m of the seafloor) (CPUE; #10 m^{-2}). MOCNESS sampling occurred 24 h a day, therefore it was assumed that vertically integrated sampling was not affected by diel vertical migrations of larvae. The samples were preserved in a 10% formalin seawater solution for later analysis. Larvae were sorted, identified to the lowest possible taxonomic level, measured (mm SL), and enumerated at the University of Alaska Fairbanks. Identifications were verified at the Alaska Fisheries Science Center, NOAA in Seattle, WA, USA.

Fall survey

Late-stage juvenile and adult fish were collected during August and September using a 198-m long midwater rope trawl configured to sample the upper 15–20 m of the water column (Farley *et al.*, 2005, 2007). The net had hexagonal mesh wings and a 1.2-cm mesh codend liner. The mouth opening was ~55-m horizontal by 20-m vertical. The net was towed at speeds of 3.5–5.0 knots for 30 min. Sampling was conducted during daytime only and occurred above the pycnocline as determined by water column profiles (see below). The catch was sorted to species and counted to estimate abundance of each taxon (# km^{-2}). For large catches, a random sub-sample was sorted and counted, and results were extrapolated to estimate the total catch by taxa. Sampled fish were predominantly juvenile life stages; juvenile salmonids were less than ~300 mm fork length (FL). Small numbers of adult fish (and immature and maturing salmonids; greater than ~300 mm FL) were collected and included in the analyses as potential competitors and predators, however they did not have a large influence on analyses based on overall fish abundance.

Environmental indices

Oceanographic data were collected concurrently at every station with a Sea-Bird Electronics (SBE) model 19 (spring) or 911 plus (summer and fall) Conductivity–Temperature–Depth profiler (CTD). In spring and summer, the CTD was attached in-line to the Bongo or MOCNESS and provided real-time measurements of temperature, salinity (estimated from conductivity and temperature), and pressure over the oblique towed path. In fall, separate vertical CTD casts provided contemporaneous environmental data.

Environmental data were processed into 1-m vertical bins using Sea-Bird software. Station-specific indices were developed for comparison with the vertically integrated fish abundances to determine the water column properties delineating fish assemblages. Integrated measurements of water-column temperature and salinity were calculated as well as averages above and below the mixed layer depth (MLD) (Supplementary Figures S1–S4). The MLD was estimated as the depth where σ_t is 0.10 kg/m^3 higher than the value at 5 m (Danielson *et al.*, 2011). Maximum station depth was included as a covariate as bathymetry is known to delineate species assemblages (see Siddon *et al.*, 2011).

Data analyses

Station selection

Analyses were restricted to stations over the EBS shelf south of 62.8°N (Ecoregions 1 through 11, 15–16; Figure 1). The Ecoregion 1 boundary along the Alaska Peninsula is 'jagged', but

does not reflect a biological boundary. Therefore, stations along the peninsula but inshore of the ecoregion boundary were included in Ecoregion 1. Stations in or near Unimak Pass were removed from analyses because of the high degree of water flow and mixing as well as the influence of Gulf of Alaska water masses (i.e. Alaska Coastal Current) and species' ingress that would obscure our interpretations of species assemblages over the south-eastern shelf.

Diversity analyses

Using abundance information based on the complete assemblage (i.e. including rare species), Simpson's Index of Diversity ($1-D$) was calculated for each station. D equals

$$D = \sum \left(\frac{n}{N} \right)^2, \quad (1)$$

where n is the total number of organisms of a particular species and N is the total number of organisms of all species. A two-factor ANOVA was used to test for differences in assemblage diversity between seasons and years. All analyses were performed using R Statistical Software (R version 3.0.2; R Core Team, 2013).

Multivariate analyses

In order to study seasonal patterns, community structure was analysed quantitatively within each season, and then qualitatively among seasons due to seasonal differences in survey extents and gear used to target different ontogenetic life stages. Both ordination and classification techniques were used on zero-adjusted Bray Curtis dissimilarity coefficients calculated on abundance among stations for data exploration and cluster identification. This was followed by multivariate permutation tests, also using zero-adjusted Bray Curtis dissimilarity, to examine year and ecoregion effects as well as relationships with environmental variables (PRIMER-E, Anderson *et al.*, 2008; Clarke *et al.*, 2014). Rare species, occurring at <3% of stations within a season, were removed from the analyses because they are unlikely to significantly contribute to patterns of community composition. Before calculating the Bray Curtis dissimilarity, a fourth root transformation was applied to allow more even contribution of small and large relative abundances. The zero-adjusted Bray Curtis incorporates rare species into assemblages and samples with little or no species by adding a dummy species to the species by station matrix (Clarke *et al.*, 2006).

Nonmetric multidimensional scaling (nMDS) and cluster analysis (classification procedure) were used to determine species assemblages across all years combined. Assemblages were determined based on dendrograms from a hierarchical agglomerative cluster analysis using group average linkage, followed by similarity profile tests (SIMPROF; Clarke *et al.*, 2014). SIMPROF is a permutational analysis, which tests for randomness at each node of the dendrogram, beginning at the top. Tests used a significance level of 0.05. Clusters were then verified by nMDS by superimposing the groups on the ordination to check that the similarity level was sufficient to separate. Cluster groups were then mapped; for brevity, clusters with less than three stations are not shown. Similarity percentages routines were used to show the percent contribution to similarity within cluster groups.

In order to test for significant differences in community structure among years and ecoregions, a permutational multivariate

ANOVA (PERMANOVA) was applied to the biological distance matrix (zero-adjusted Bray Curtis dissimilarity) mentioned above. PERMANOVA uses distance-based measures (in this case, zero-adjusted Bray-Curtis dissimilarity of species abundance among stations) to test for significant factors (Year, Ecoregion, and Year \times Ecoregion interaction) by partitioning the total sum of squares as in a multivariate ANOVA. This was followed by pairwise tests of significance wherever significant differences were found as well as permutational tests of dispersion (PERMDISP), which is analogous to the Levine's univariate test for equality of variances. Components of variation from the PERMANOVA were used to determine the percent variability explained by each factor. When a significant interaction of Year \times Ecoregion occurred, further analyses were conducted within year.

Significant correlations with environmental variables were explored using a distance-based linear model (DistLM). The forward selection option using an adjusted R^2 criterion selected the most important variables in order of their significance. In addition, distance-based redundancy analysis (dbRDA), yielding constrained ordination plots of the fitted part of the model, was used to see how the community structure changed across environmental gradients. For highly correlated variables (<-0.95 or >0.95), only one variable was selected to use in the analyses to avoid problems with multicollinearity. To further examine the year and ecoregion effects after accounting for important environmental variables, selected environmental variables were entered as covariates into a second PERMANOVA in the order given by DistLM. Although the DistLM dropped some environmental variables according to forward selection, we also dropped any variables that had a P -value of >0.1 that did not increase the adjusted R^2 by more than 0.02. This second PERMANOVA partitioned the variability (components of variation) into that explained by environmental variables (temperature and salinity above and below the pycnocline), spatial variables (latitude, longitude, and bottom depth), Year and Ecoregion factors, and residual variability (Underwood and Petraitis, 1993, Anderson *et al.*, 2005). PERMANOVA with covariates is analogous to a univariate analysis of covariance (ANCOVA) to test the significance of factors after removing the effects of covariates. Wherever there was a significant interaction between Year and Ecoregion, pairwise tests were performed to test for an ecoregion effect within each year. Corresponding dbRDA plots were examined to see how community structure changed along environmental gradients within each year.

Results

Spring survey

Twenty-three species were retained in the analyses (Supplementary Table S2 shows those contributing to 95% of the total abundance by year). Four species consistently contributed to fish assemblages in spring: Pollock, rockfishes (*Sebastes* spp.), Sand Lance (*Ammodytes* spp.; Orr *et al.*, 2015), and Northern Rock Sole (*Lepidopsetta polyxystra*). Recent DNA and morphological investigations of sand lances (genus *Ammodytes*; Orr *et al.*, 2015) revealed two species; *A. hexapterus* (Arctic Sand Lance) and *A. personatus* (Pacific Sand Lance) occur sympatric in the eastern Bering Sea. Distinguishing larval stages of these two species is not possible at this time and collections and identifications of later stage individuals used in this study were accomplished before publication of the updated taxonomic and distribution work,

Table 1. Percent contribution of individual species to SIMPROF clusters for spring.

Species/taxa	Common name	a	b	c	d	e	f	g	h	i	k	l	m
<i>Ammodytes</i> spp.	Sand Lance								67.8	95.7	24.5		
<i>Atheresthes</i> spp.	Arrowtooth and Kamchatka Flounders			17.4									
<i>B. pacificus</i>	Pacific Blacksmelt			21									
<i>B. saida</i>	Arctic Cod	49.2										42.6	
<i>Gadus chalcogrammus</i>	Walleye Pollock			14.7		19.9	83.1	40.3	14.2				
<i>Gadus macrocephalus</i>	Pacific Cod										28.2	26.7	
<i>Hemilepidotus hemilepidotus</i>	Red Irish Lord	50.8											
<i>L. polyxystra</i>	Northern Rock Sole					15.4	13.7	16.1			36.3	30.7	100
<i>Podothecus</i> spp.	Poachers							27.5	15.8				
<i>P. rothrocki</i>	Whitebarred Prickleback		81.9										
<i>Sebastes</i> spp.	Rockfishes		16.4	35.8	91.2	49.5							
Other			1.7	11.1	8.8	15.2	3.2	16.1	2.2	4.3	11		

Additional species contributing <8% are grouped into "Other". A0 = age-0; A1+ = age-1+; J = juvenile

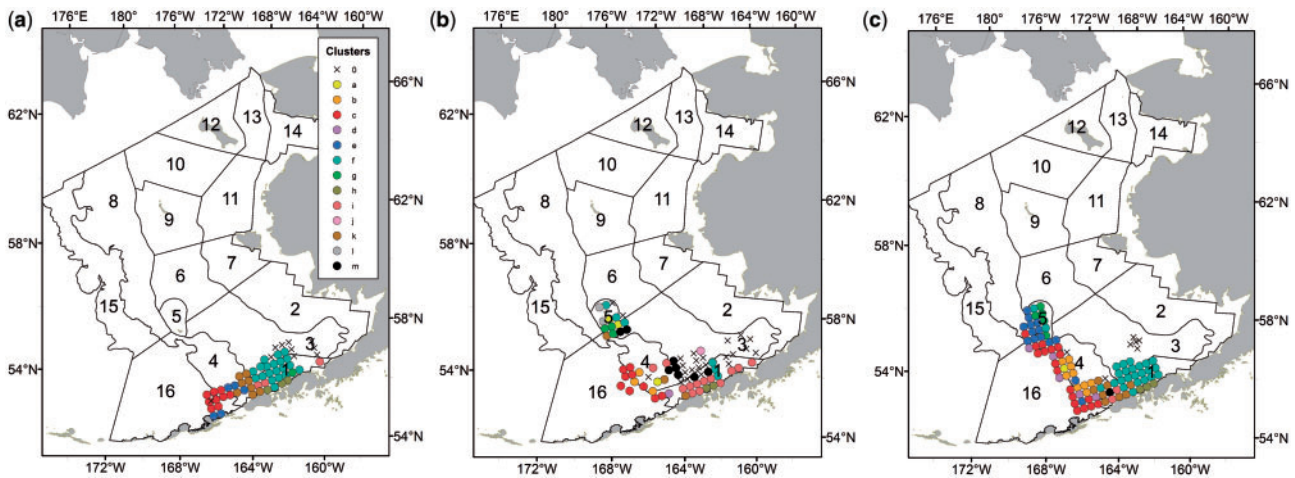


Figure 2. Maps of the spring clusters (stations based on similar species contributions) overlaid on the ecoregions for each Year (2008 [a], 2009 [b], 2010 [c]).

therefore we refer to sand lances as *Ammodytes* spp. throughout, and Northern Rock Sole (*Lepidopsetta polyxystra*). Pollock comprised 59.7, 10.8, and 27.8% of the total abundance by year, respectively.

Obj. 1: community composition associated with Pollock

SIMPROF was used to determine significant nodes in the dendrogram, resulting in 12 clusters (Table 1). Pollock co-occurred with Northern Rock Sole inshore along the Alaska Peninsula in 2008 and 2010, with sturgeon and veteran poachers (genus *Podothecus*, hereafter ‘poachers’) and Northern Rock Sole near the Pribilof Islands in 2009 and 2010, and with a diverse mix of deeper-water species such as Pacific Blacksmelt (*Bathylagus pacificus*) and *Atheresthes* spp. (Arrowtooth [*A. stomias*] and Kamchatka [*A. evermanni*] Flounders) along the slope in all years (Figure 2; Table 1).

Obj. 2: within-stanza homogeneity of response

Assemblage structure differed across the three cold years with 2009 having unique spatial patterns. In addition, although diversity was not significantly different across years, it was higher in 2008 (0.38), lower in 2009 (0.33), and intermediate in 2010 (0.35) (Supplementary Table S3). The greatest number of species

comprising 95% of total abundance occurred in 2009 although total diversity was lowest; the diversity analysis included rare species, which could help explain this result. Several species appeared in 2009 and continued through 2010, including *Atheresthes* spp., poachers, and ronquils (genus *Bathymaster*) (Supplementary Table S2).

Obj. 3: community composition within ecoregions

Spring clusters were overlaid on the ecoregions to estimate if community composition was similar within ecoregions of the EBS shelf (Figure 2; Table 1). In 2008, sampling occurred only along the Alaska Peninsula, which highlighted an across-shelf gradient in species assemblages. Assemblages shifted from an inshore cluster dominated by Pollock over the middle domain, to an assemblage of Northern Rock Sole, Pacific Cod, and Sand Lance along the 100 m isobath, to slope species (i.e. rockfishes, Pacific Blacksmelt, *Atheresthes* spp.) at the shelf break. Assemblages in 2009 showed less spatial structure within ecoregions, but Sand Lance occurred near-shore along the Alaska Peninsula while the slope species assemblage occurred along the shelf break. Across-shelf spatial patterns along the Alaska Peninsula in 2010 were similar to 2008. Sampling northward along the shelf break allowed identification of an outer

Table 2. Percent variance explained by variables included in the PERMANOVA models with and without covariates.

		All Years				
		Without covariates	With covariates	2008	2009	2010
SPRING	<i>n</i> =	193		51	53	89
Environmental			40.7	53.4	47.0	53.9
	Temperature above		7.4	0	6.1	11.1
	Salinity above		3.4	13.7	11.4	5.9
	Temperature below		15.1	22.2	12.3	22.2
	Salinity below		14.8	17.6	17.2	14.7
Spatial			8.4	25.1	6.2	11.1
	Latitude		2.5	14.1	6.2	4.8
	Longitude		1.8	11.0	0	3.1
	Depth		4.1	0	0	3.2
Year		7.7	6.4	–	–	–
Ecoregion		32.5	7.9	0	10.5	6.8
Year × Ecoregion		3.1	3.6	–	–	–
Residual		56.7	33.1	21.6	36.3	28.3
SUMMER	<i>n</i> =	155		38	63	54
Environmental			16.3	39.6	14.7	35.0
	Temperature above		2.3	10.0	0	7.1
	Salinity above		8.6	4.0	6.7	6.5
	Temperature below		1.9	2.6	8.0	11.9
	Salinity below		3.5	23.0	0	9.5
Spatial			4.0	23.0	3.0	9.0
	Latitude		4.0	17.8	0	4.5
	Longitude		0	2.6	3.0	4.5
	Depth		0	2.6	0	0
Year		5.2	4.8	–	–	–
Ecoregion		20.1	6.6	11.0	16.9	17.1
Year × Ecoregion		21.0	21.0	–	–	–
Residual		53.7	47.2	26.4	65.4	38.9
FALL	<i>n</i> =	219		31	77	111
Environmental			15.4	19.8	28.4	16.4
	Temperature above		3.1	6.5	4.9	3.0
	Salinity above		2.4	0	0	0
	Temperature below		4.8	13.3	12.8	7.8
	Salinity below		5.1	0	10.7	5.6
Spatial			21.2	13.0	11.1	23.6
	Latitude		9.0	4.8	4.1	12.1
	Longitude		9.5	8.2	7.0	5.7
	Depth		2.7	0	0	5.8
Year		7.7	6.2	–	–	–
		24.3	7.2	0	8.2	13.4
Year × Ecoregion		6.9	5.0	–	–	–
Residual		61.1	45.0	67.3	52.4	46.7

Environmental covariates included temperature and salinity above and below the pycnocline; spatial covariates included latitude, longitude, and depth. Within-year analyses do not include Year and Year × Ecoregion variables (–). Sample size (*n*) is shown for each model. The variable explaining the highest amount of variance for each model is shown in bold. Values shown in italics under the first model (All years; without covariates) indicate significance at the 5% level of the main effects and their interaction

domain assemblage including Whitebarred Prickleback (*Poroclinus rothrocki*) and rockfishes as well as a Pribilof Islands assemblage of Pollock, poachers, and Northern Rock Sole. The slope assemblage consistently occurred along the shelf break in the south and may be influenced by on-shelf transport through Bering Canyon. In 2009 and 2010, the sampling grid extended north to the Pribilof Islands (Ecoregion 5). In 2009, this Ecoregion contained a more distinct species assemblage, characterized by colder water temperatures

(Supplementary Figure S5), whereas in 2010 the species assemblages in Ecoregion 5 were more similar to other assemblages within the outer domain and slope region (Figure 2b–c).

Differences among Ecoregions varied by year (PERMANOVA without covariates, Year × Ecoregion: $P=0.006$, Table 2) and some of these differences were at least partially due to unequal dispersion, or variance (PERMDISP, Ecoregion: $P=0.002$). Specifically, Ecoregion 4 (in close proximity to Unimak Pass and

transport from the Gulf of Alaska) was the most dispersed (had the greatest variance; data not shown). Although 32.5% of the variability was explained by Ecoregion and 7.7% by Year, 56.7% of the variability was unaccounted for (residual) (PERMANOVA without covariates; Table 2).

Obj. 4: relate assemblages to environmental gradients

Across all years, environmental variables explained 40.7% of variability in species assemblages in spring; ~17.9% of variability was explained by factors (Year, Ecoregion, Year \times Ecoregion) while 33.1% remained unexplained by variables included in the model (PERMANOVA with covariates; Table 2). Within years, environmental gradients (temperature and salinity above and below the pycnocline) also explained a consistently large portion of variability in species assemblages (53.4, 47.0, and 53.9%, respectively). In 2008, environmental gradients combined with spatial variables (latitude, longitude, bottom depth) explained enough of the variability that the factor Ecoregion was no longer significant, indicating that the environmental and spatial variables explained much of the community structure defining Ecoregions and 78.6% of the total variability. For 2009 and 2010, Ecoregion was still significant, however environmental and spatial variables explained 53.3 and 65.0% of the total variability in community structure (Table 2).

The dbrDA, which explained 33.0% of the total variability in the first two components, indicated that differences in assemblage structure occurred over across-shelf and along-shelf gradients (Supplementary Figure S5). The first axis (x -axis), explaining 24.8% of total variation and 61.9% of fitted variation, was related to gradients of longitude and salinity (Supplementary Figures S2 and S4) and differentiated assemblages between off-shelf (Ecoregion 16), the outer domain (Ecoregions 4 and 8), and the middle domain (Ecoregions 1, 3, and 5). Variability of assemblage structure within Ecoregions 1, 3, and 5 was due to latitude and temperature gradients (Supplementary Figures S1 and S3) along the second axis (y -axis) explaining 8.2% of the total variation and 20.4% of the fitted variation.

Summer survey

Thirty species were retained in the analyses (Supplementary Table S2 shows those contributing to 95% of the total abundance by year). Pollock comprised 23.9 and 25.4% of the total abundance in 2008 and 2010, respectively. Pollock represented only 7.7% in 2009.

Obj. 1: community composition associated with Pollock

SIMPROF determined significant nodes in the dendrogram, resulting in 13 clusters (Table 3). Pollock dominated the species assemblage in the southern middle domain in 2008, near the Pribilof Islands in 2009, and again in the southern middle domain as well as the northern outer domain in 2010 (Figure 3; Table 3). Pollock co-occurred with rockfishes and ronquils near the Pribilof Islands and along the Alaska Peninsula in 2008, in the outer domain in 2009, and along the slope in 2010. Pollock co-occurred with a diverse assemblage near the Pribilof Islands in 2008 (cluster h) containing Northern Rock Sole, poachers, Rex Sole (*Glyptocephalus zachirus*), Alaska Plaice (*Pleuronectes quadrituberculatus*), sculpins (genus *Myoxocephalus*), and Variegated Snailfish (*Liparis gibbus*).

Obj. 2: within-stanza homogeneity of response

Assemblage structure differed across the three cold years with 2009 having unique spatial patterns (Figure 3). Alaska Plaice represented 49.4% of total abundance in 2008, but was not present in 2009 or 2010 (Supplementary Table S2). Rockfishes characterized a large proportion of the assemblage, especially in 2009 and 2010. The diversity of species contributing to the fish assemblages was not significantly different, but increased across the years from 0.43 (2008) to 0.49 (2009) to 0.55 (2010) (Supplementary Table S3). For example, *Atheresthes* spp. and Flathead Sole (*Hippoglossoides elassodon*) appeared in 2009 and 2010 while additional species (e.g. Northern Sculpin, *Icelinus borealis*) emerged only in 2010 (Supplementary Table S2). In terms of species assemblages over time, cluster h occurred near the Pribilof Islands in 2008 only. An assemblage containing poachers, *Liparis* spp., and Pollock phased out in 2009 while *Gymnocanthus* spp. and an assemblage containing Slender Eelblenny (*Lumpenus fabricii*) and Arctic Cod (*Boreogadus saida*) emerged in 2009 and persisted through 2010 (Figure 3; Table 3).

Obj. 3: community composition within Ecoregions

Summer clusters were overlaid on the ecoregions to determine whether community composition is similar within ecoregions (Figure 3). In 2008, assemblage structure showed a latitudinal gradient from Daubed Shanny (*Lumpenus maculatus*) in the north to Alaska Plaice between St. Matthew and Nunivak Islands, and rockfishes in the southern outer domain as well as ronquils, Flathead Sole, and Pollock along the Alaska Peninsula. Assemblages also followed longitudinal gradients from Pollock in the middle domain to rockfishes, ronquils, and Pollock near the Pribilof Islands, and rockfishes in the outer domain. Assemblage structure in 2009 was less structured by latitudinal or longitudinal gradients, although Slender Eelblenny and Daubed Shanny occurred in the north. In 2010, fish assemblages followed a stronger longitudinal gradient with Variegated Snailfish, Sand Lance, and sculpins inshore, Pollock in the middle domain over the southern shelf and outer domain farther north, and rockfishes, ronquils, and Pollock along the slope.

Differences among Ecoregions varied by year (PERMANOVA without covariates, Year \times Ecoregion: $P=0.001$, Table 2) and some of these differences were at least partially due to unequal dispersion, or variance (PERMDISP, Ecoregion: $P=0.004$, results not shown). In the PERMANOVA analysis, this interaction accounted for 21.0% of the variability in the model, although the main effect of Ecoregion (20.1%) explained more of the variability than Year (5.2%), similar to spring. However, the majority of the variability (53.7%) remained unexplained.

Obj. 4: relate assemblages to environmental gradients

Across all years, environmental variables explained only 16.3% of variability in species assemblages in summer; 32.4% was explained by factors, while 47.2% remained unexplained in the model (PERMANOVA with covariates; Table 2). Within years, environmental variables described a greater amount of the variability in species assemblages for 2008 (39.6%) and 2010 (35.0%) than for 2009 (14.7%). Ecoregion remained significant in all within-year models indicating it continued to account for a substantial amount of the variability in fish assemblages, even after removing the effects of covariates. Environmental and spatial

Table 3. Percent contribution of individual species to SIMPROF clusters for summer.

Species/Taxa	Common name	a	c	d	e	f	g	h	i	j	k	l	m	n
<i>Ammodytes</i> spp.	Sand Lance													35.5
<i>Atheresthes</i> spp.	Arrowtooth and Kamchatka Flounders	88.2												
<i>Bathymaster</i> spp.	Ronquils		16.8	26.2										
<i>B. saida</i>	Arctic Cod											100		
<i>Gadus chalcogrammus</i>	Walleye Pollock		12.9	14		97.5	10.1	16.4						
<i>G. zachirus</i>	Rex Sole							12						
<i>Gymnancanthus</i> spp.												96		
<i>H. elassodon</i>	Flathead Sole		13.8											
<i>L. polyxystra</i>	Northern Rock Sole		11.3					21.9						
<i>Leuroglossus schmidti</i>	Northern Smoothtongue	11.8												
<i>L. gibbus</i>	Variegated Snailfish							12		40				
<i>Liparis</i> spp.							35.6							
<i>L. fabricii</i>	Slender Eelblenny												89.5	
<i>L. maculatus</i>	Daubed Shanny													95.1
<i>Myoxocephalus</i> spp.	Sculpins							10.4		23.6				
<i>P. quadrituberculatus</i>	Alaska Plaice							10.4	94					
<i>Podothecus</i> spp.	Poachers						47.7	16.9						
<i>Sebastes</i> spp.	Rockfishes		19.2	48.8	91.2									
Other			26	11	8.8	2.5	6.6		6	0.9	4			4.9

Additional species contributing <8% are grouped into "Other". A0 = age-0; A1+ = age-1+; J = juvenile

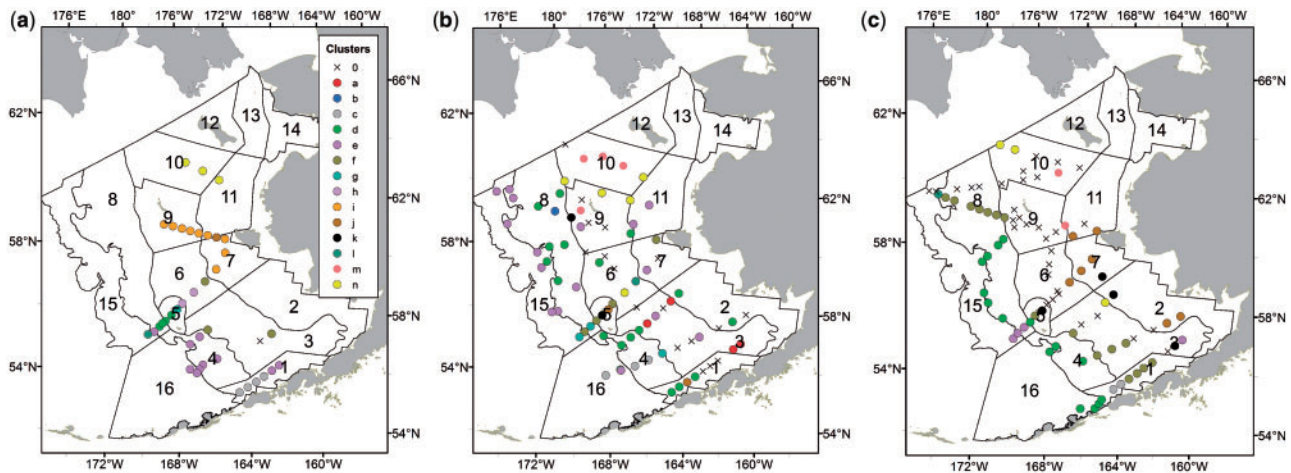


Figure 3. Maps of the summer clusters (stations based on similar species contributions) overlaid on the ecoregions for each Year (2008 [a], 2009 [b], 2010 [c]).

variables explained 62.6, 17.8, and 44.0% of the total variability for 2008, 2009, and 2010, respectively.

The dbRDA revealed that 18.4% of the total variability was explained in the first two components and differentiated along-shelf and across-shelf gradients of species composition (Supplementary Figure S6). The first axis, explaining 14.4% of total variation and 64.8% of variation in the fitted model, was related to gradients of latitude and bottom temperature (Supplementary Figure S1) that delineated ecoregions from south to north. Southern ecoregions (1–5, 16) were characterized by the warmest bottom temperatures, Ecoregions 6, 7, and 9 were intermediate, and Ecoregions 10 and 11 (farthest north) had the coolest bottom temperatures. Ecoregion 15 spans a large spatial range and showed greater variability along the vertical axis. The second (orthogonal) axis, explaining only 4.0% of the total variability and 18.0% of the variability in the fitted model, described an across-shelf gradient related to longitude, surface

temperature (Supplementary Figure S3), and bottom salinity (Supplementary Figure S2). For example, separation of species assemblages occurred among Ecoregions 2 (inner domain), 3 (middle domain), and 8 (outer domain).

Fall survey

Fifty-four species were retained in the analyses (Supplementary Table S2 shows those contributing to 95% of the total abundance by year). Juvenile Pollock represented the majority (91.8%) of catch in 2008. In 2009, that same cohort represented only 3.9% of the total abundance as age-1 fish and the 2009 cohort of juvenile Pollock did not substantially contribute to the fish assemblages over the shelf. By 2010, juvenile Pollock comprised ~7.9% of the assemblage.

Table 4. Percent contribution of individual species to SIMPROF clusters for fall.

Species/taxa	Common name	b	c	d	e	f	g	h	i
<i>C. pallasii</i>	Pacific Herring				50.5	19.3	37.1		25.7
<i>Eleginus gracilis</i> A0	Saffron Cod					9.8			
<i>Gadus chalcogrammus</i> A0	Walleye Pollock age-0	55.5	10.1	11.2		11.6		11.6	
<i>G. chalcogrammus</i> A1+	Walleye Pollock age-1+					21.3			
<i>G. macrocephalus</i> A0	Pacific Cod age-0	32							
<i>M. villosus</i>	Capelin					38	39.2	72.3	
<i>O. gorbuscha</i> J	Pink Salmon			19.3					15.5
<i>Oncorhynchus keta</i> J	Chum Salmon			8.1					27.8
<i>Oncorhynchus kisutch</i> J	Coho Salmon								12.2
<i>Oncorhynchus nerka</i> J	Sockeye Salmon		20.3						
<i>Oncorhynchus tshawytscha</i> J	Chinook Salmon						9.4		8.8
<i>Sebastes</i> spp.	Rockfishes			42.3					
<i>T. trichodon</i>	Pacific Sandfish		49.7						
Other		12.5	19.9	19.1	49.5		14.3	16.1	10

Additional species contributing <8% are grouped into "Other". A0 = age-0; A1+ = age-1+; J = juvenile

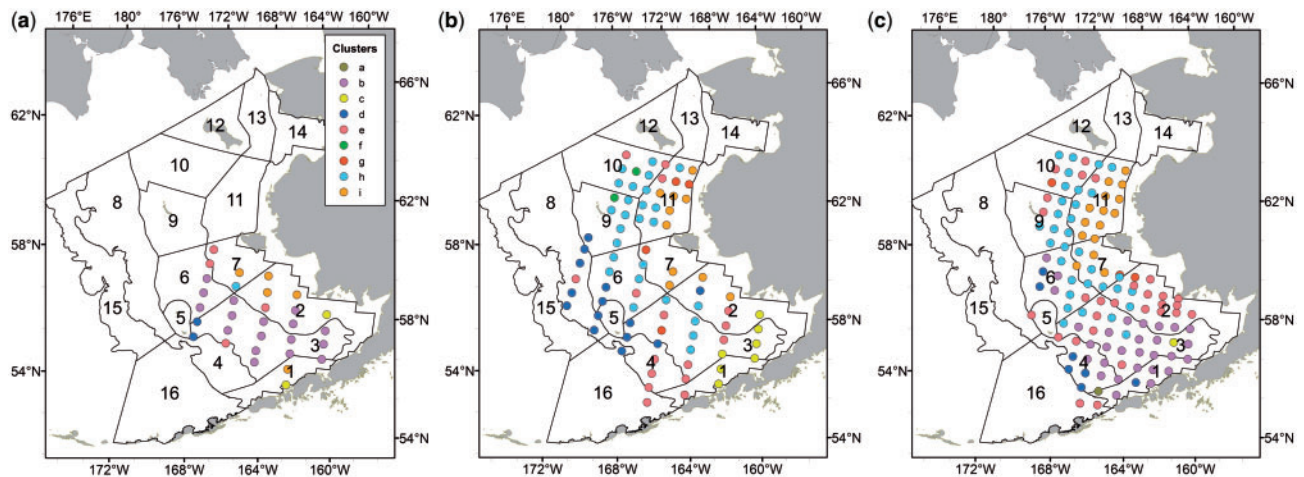


Figure 4. Maps of the fall clusters (stations based on similar species contributions) overlaid on the ecoregions for each Year (2008 [a], 2009 [b], 2010 [c]).

Obj. 1: community composition associated with Pollock

SIMPROF was used to determine significant nodes in the species dendrogram; nine clusters were identified (Table 4). Juvenile Pollock co-occurred with juvenile Pacific Cod over the southern middle domain in 2008 and 2010 (Figure 4; Table 4). Juvenile Pollock co-occurred with Capelin (*Mallotus villosus*) over the northern shelf in 2009 and 2010. Juvenile Pollock co-occurred with rockfishes, juvenile Pink Salmon (*Oncorhynchus gorbuscha*), and juvenile Chum Salmon (*O. keta*) in the outer domain, and with Pacific Sandfish (*Trichodon trichodon*) and juvenile Sockeye Salmon (*O. nerka*) inshore along the Alaska Peninsula in 2009 (Figure 4).

Obj. 2: within-stanza homogeneity of response

The spatial patterns of assemblage structure differed across the three years (Figure 4), although diversity was not significantly different with 2008 and 2009 showing comparable levels (0.31) and 2010 slightly higher (0.35) (Supplementary Table S3). In 2009, Capelin dominated the catch at 68.4% with other species contributing between 2.7 and 5.5%, including Pacific Herring (*Clupea*

pallasii), rockfishes, and juvenile salmonids (Supplementary Table S2). In 2010, Capelin continued to dominate the catch at 79.7%. Juvenile Pacific Cod were present in 2008 and 2010 at 1.6 and 5.3%, respectively.

Obj. 3: community composition within Ecoregions

Fall clusters were overlaid on the ecoregions to determine whether community composition is similar within ecoregions (Figure 4). In 2008, the survey was restricted to the southern shelf and juvenile Pollock and Pacific Cod were abundant across the middle domain (Figure 4; Table 4). A diverse shallow-water assemblage of Pacific Herring and juvenile Chum, Pink, Coho (*O. kisutch*), and Chinook (*O. tshawytscha*) Salmon occurred in the inner domain while deeper water stations were a mix of assemblages. In 2009, the cluster containing juvenile Pollock and Pacific Cod was absent and the patterns of species assemblages were more variable. Along the Alaska Peninsula and southern shelf, Pacific Sandfish, juvenile Sockeye Salmon, and juvenile Pollock occurred over the inner and middle domains with Pacific Herring over the outer domain. The shallow-water assemblage observed in 2008 continued along the inner domain north of

Cape Newenham; Capelin and juvenile Pollock followed the middle domain over much of the shelf and an assemblage comprised of juvenile Pink Salmon, juvenile Chum Salmon, rockfishes, and juvenile Pollock occurred near the Pribilof Islands and northern outer domain. In 2010, juvenile Pollock and Pacific Cod again dominated the southern shelf. Pacific Herring occurred by Cape Newenham and Kuskokwim Bay. In the northern portion of the study area, Capelin and juvenile Pollock occurred over the middle shelf with the shallow-water assemblage along the inner domain.

Differences among ecoregions varied by year (PERMANOVA without covariates, Year \times Ecoregion: $P=0.001$, Table 2) and some differences were at least partially due to unequal dispersion, or variance (PERMDISP, Year \times Ecoregion: $P=0.001$, results not shown). 24.3% of the variability was explained by Ecoregion, 7.7% by Year, and 61.1% of the variability was unaccounted for in the model (residual).

Obj. 4: relate assemblages to environmental gradients

Across all years, environmental variables explained only 15.4% of variability in species assemblages in fall; 18.4% of variability was explained by factors while 45.0% remained unexplained by variables included in the model (PERMANOVA with covariates; Table 2). Within years, environmental gradients explained a moderate portion of variability in species assemblages (19.8, 28.4, and 16.4% for 2008–2010, respectively). In 2008, similar to the spring model, the factor Ecoregion was no longer significant, suggesting that the environmental and spatial variables explained much of the community structure defining Ecoregions. However, those covariates only explained 32.8% of the total variability while 67.3% remained unexplained. For 2009 and 2010, Ecoregion remained significant while environmental and spatial variables explained ~40% of the total variability in community structure in each year, although 52.4 and 46.7% of variability remained unexplained in 2009 and 2010, respectively (Table 2).

Results of the dbrDA explained 23.0% of the total variability in the first two components and delineated species assemblages along latitudinal then longitudinal gradients (Supplementary Figure S7). The first axis explained 15.7% of total variation and 48.4% of variation in the fitted model and identified assemblages along gradients of latitude, surface temperature (Supplementary Figure S3), and salinity (Supplementary Figures S2 and S4). Northern Ecoregions (9–11) had cooler water temperatures and lower salinities as compared with southern Ecoregions (1 and 4). The second axis explained 7.3% of total variability and 22.5% of fitted variability in the model and described an across-shelf gradient related to longitude and bottom temperature (Supplementary Figure S1). This axis differentiated assemblages between the middle and outer domains (e.g. Ecoregion 3 vs. 4), and middle and inner domains (e.g. Ecoregion 9 vs. 7) with the middle domain ecoregions having cooler bottom temperatures than the outer or inner domain ecoregions.

Interannual variability

Fish assemblages showed heterogeneity in composition and variation in determinants of community composition during the recent cold stanza over the EBS shelf. However, during all seasons 2009 was unique relative to assemblage structure in 2008 and 2010. In spring, assemblage diversity was lowest in 2009 (though not significant) and spatial patterns of assemblages were unique in 2009 and more similar between 2008 and 2010 (Figure 2).

In summer, larval Pollock represented 25% of the total abundance in 2008 and 2010 and only 7.7% in 2009 (Supplementary Table S2). Assemblages were less structured by spatial gradients (latitude, longitude, or bottom depth) in summer 2009 than in 2008 and 2010 (Figure 3) and environmental variables described less than half the amount of variability in 2009 than 2008 and 2010 (Table 2). In fall, the assemblage composition remained unique in 2009 (Supplementary Table S2) and environmental variables accounted for a greater amount of the variability (Table 2).

Spatial patterns

The spatial patterns in fish assemblages generally followed broader across- and along-shelf gradients than those proposed by the 16 ecoregions (Figures 2–4). Larval distributions varied from inshore to offshore, particularly for assemblages in 2008 and 2010. Assemblages over the outer shelf were heterogeneous (Ecoregion 4; in close proximity to Unimak Pass and transport from the Gulf of Alaska) and may represent transitional assemblages between the shelf and slope communities. Sampling near the Pribilof Islands in 2009 and 2010 identified a unique assemblage in Ecoregion 5. In summer, spatial patterns were unique in each year, although differences in sampling locations confound the patterns. In 2008, communities varied along-shelf, from the southern region along the Alaska Peninsula northward to the Pribilof Islands and Ecoregions 7 and 9. Spatial patterns again showed less structure in 2009. In 2010, an across-shelf pattern was evident from an inner domain assemblage to middle domain and slope assemblages. By fall, communities were more closely aligned with bathymetric boundaries, especially in 2008 and 2010. The outer shelf communities were more variable within ecoregions in 2010 with patterns of species assemblages more consistent over the outer domain in 2009.

Discussion

This study draws on a unique comprehensive dataset of fish assemblages over the EBS shelf spanning seasonal and interannual changes. Incorporating a seasonal component enabled an understanding of ontogenetic shifts and subsequent ecological implications. Data from three cold years allowed within-stanza heterogeneity of assemblage patterns to be evaluated. Combined, this paper describes individual and community changes and the spatiotemporal drivers of assemblage structure. Seasonal changes in assemblage structure were correlated with broad-scale spatial (latitude, longitude) patterns and underlying gradients in temperature and salinity (especially for spring). By fall, much of the variability in assemblage structure remained unaccounted for indicating that communities are delineated by additional factors that were not included in the current study. Across the three cold years examined, broad similarities in how the ecosystem is structured were observed, but 2009 experienced several unique oceanographic features that affected community composition over the EBS shelf.

Seasonal patterns

The first goal of this article was to describe the community with which Pollock are associated with seasonally during the age-0 period. Co-occurrences during the larval period may indicate similar spawning distributions of the adult fish, as larvae are susceptible to drift trajectories. Ontogenetic shifts during the age-0

period include increased swimming ability as well as changes in prey opportunities, among others, such that co-occurrences in fall may indicate potential competitors or predators.

In spring, Pollock, rockfishes, Sand Lance, and Northern Rock Sole consistently contributed to fish assemblages. Pollock most commonly co-occurred in assemblages with Northern Rock Sole and poachers. In summer, Pollock co-occurred most consistently with ronquils, Rex Sole, rockfishes, and poachers. In fall, juvenile Pollock co-occurred with Capelin and Pacific Cod, while age-1 Pollock co-occurred with Capelin and Pacific Herring.

Previous assemblage work conducted in spring of both warm (2002–2005) and cold (2006–2008) years (Siddon *et al.*, 2011) found similarity in the common species contributing to the larval fish assemblages (i.e. Pollock, rockfishes, Sand Lance, and Northern Rock Sole). The persistence of these species in spring assemblages likely reflects input of larvae from late winter and early spring (February–May) spawning aggregations. Taken together, results from these two works indicate that spring larval fish assemblages over the EBS shelf are dominated by the presence of fewer than half a dozen key fish taxa irrespective of climate stanza.

Previous analyses on fish assemblages in fall across warm and cold years (2003–2010) found that while the individual species comprising assemblages were observed in all years, they occurred in unique assemblages in cold years (Eisner *et al.*, 2015). Latitudinal variations in communities were also more prominent in cold years. Species co-occurring with Pollock shifted over the time period, but independent of climate conditions. Pollock co-occurred with Pacific Herring and Sockeye Salmon from 2003–2008, then co-occurred with Capelin and Pacific Herring in 2009–2010, and Pacific Cod and Yellowfin Sole (*Limanda aspera*) in 2010.

While spring communities were comprised of a limited number of species, diversity was significantly greater in the summer (Supplementary Table S3) and fall communities had unique species occurrences. More clusters were dominated by a single species in summer than in spring or fall. For example, Alaska Plaice represented 49.4% of the total fish abundance in summer 2008. Alaska Plaice abundance could be an artefact of spatial sampling differences between years (sampling was limited to south of 60°N in 2008). Adult Alaska Plaice are collected from northern regions of the EBS and are considered a ‘cold water species’ (G. Hoff, NOAA/AFSC, pers. comm.). *Atheresthes* spp. were not observed in summer 2008, but appeared in 2009 and 2010. Capelin dominated the catches in fall 2009 (68.4%) and 2010 (79.7%); Capelin primarily occur north of 60°N (Andrews *et al.*, 2016) which was not sampled in 2008.

Interannual patterns

The second goal of this article was to examine fish communities during a cold stanza to determine interannual homogeneity of response. We show that the cold years of 2008–2010 should not be interpreted as ‘replicates’ by demonstrating differences in species assemblages within a cold year stanza. Across all seasons, assemblages in 2009 showed less spatial structure over the EBS shelf (Figures 2–4). In addition, the species composition of fish assemblages was unique in the summer and fall of 2009. In summer 2009, juvenile Pollock represented only 7.7% of the total abundance (Supplementary Table S2) and in fall 2009 juvenile Pollock were not represented in the top 95% of the assemblage. However,

larval phenology was not different in 2009. For example, estimated hatching dates were similar across 2008–2010 and mean standard lengths were not different between spring 2009 and 2010 (2008 data unavailable) (Gann *et al.*, 2016). In this study, sampling only occurred south of 60°N in 2008, an area of high juvenile Pollock abundance, therefore 2008 and 2010 may have had more similar abundance of juvenile Pollock over the southern shelf. Such within-stanza variability in juvenile Pollock abundance adds uncertainty to model predictions.

Oceanographic conditions transitioned from a warm to cold stanza during 2006 (Stabeno *et al.*, 2012a; see Figure 4B within); 2007 through 2012 were decisively cold years. The warm years of 2002–2005 had 67% lower average recruitment to age-1 relative to the cold years of 2007–2012, although variability among the cold years was quite high with an anonymously strong year class in 2008 followed by moderate recruitment in 2009 and 2010 (Ianelli *et al.*, 2015). In this study, larval and juvenile fish assemblage structure was more similar across seasons between 2008 and 2010 than in 2009. However, the 2008 cohort of Pollock produced an anonymously high recruitment that established models (i.e. FEAST) did not predict. Such variability will complicate modelling efforts to predict ecosystem-level responses to future climate scenarios.

Several factors may have contributed to within-stanza differences in assemblage structure, including water transport through Unimak Pass, current and wind trajectories over the shelf, the timing of sea ice retreat, and the extent of the cold pool (defined as waters <2°C; a footprint of winter ice extent—Hunt *et al.*, 2011; Stabeno *et al.*, 2012b). The onset and location of oceanographic fronts affect water current trajectories (Kachel *et al.*, 2002), larval transport pathways (Duffy-Anderson *et al.*, 2006; Petrik *et al.*, 2016), and subsequent community composition (Siddon *et al.*, 2011). Transport through Unimak Pass varies seasonally with weakest flow from May to September and greatest flow from fall to mid-spring (Stabeno *et al.*, 2016). Diverse clusters, such as cluster c in summer (rockfishes, ronquils, Flathead Sole, Pollock, and Northern Rock Sole; Table 3), may reflect both on-shelf transport via Bering Canyon and transport of Alaska Coastal Current waters through Unimak Pass (Figure 3). Gyres that circulate around the Pribilof Islands appear to retain species and create localized, unique assemblages (clusters f and g in spring 2009; Figure 2b).

Assemblage structure was unique in 2009 and could be due, in part, to unique transport strength and pathways. Transport through Unimak Pass was moderate in 2008, weak in 2009, and strong in 2010 (Stabeno *et al.*, in press). A greater volume of transport through Unimak Pass in 2010 may have contributed to increased diversity while weak transport in 2009 may have led to unique assemblage structure and weaker correlations with environmental variables.

Sea ice retreat over the southern shelf occurred later in 2009 than in 2008 or 2010 (Sigler *et al.*, 2014). The timing of ice retreat varies due to environmental conditions and affects the seasonal progression of physical oceanographic conditions (Stabeno *et al.*, 2012a). The cold pool was quite extensive in 2008–2010, extending to the Alaska Peninsula. Surface water temperatures were warmest in 2008, intermediate in 2009, and cooler in 2010 while bottom temperatures were similar across years (Zador and Siddon, 2016). Fish may have altered their distributions to avoid the cold pool, thereby affecting spawning locations and/or times. Lastly, the factors driving assemblage structure may be different

than those included in the current models (i.e. temperature, salinity) and may reflect differences in the input of larvae by adults.

Qualitative comparisons across seasons reflect available larval input (based on spawning location and timing) and species' vulnerability to sampling gear, ecological processes of competition and predation, as well as natural mortality over time. Environmental variables (e.g. temperature and salinity) were more important in spring and reveal larvae's susceptibility to their environment, as they are largely planktonic with limited swimming ability and associated with discrete water masses. In particular, below pycnocline temperature and salinity were strongly correlated with spring assemblages, possibly reflecting the influence of subsurface currents on larval distributions. Temperature and salinity remained important in summer 2008, but in 2009 and 2010 the majority of variability was unexplained by the models. In fall, assemblage structure more closely followed ecoregion boundaries while a large amount of variability remained unexplained by the variables included in the models. Species contributing to fish communities across seasons were more homogenous in 2008. In 2009 and 2010, broad similarities in species composition occurred between spring and summer, but by fall the juvenile fish assemblage was dominated by different taxa.

Spatial patterns

This article tested whether community composition was similar within ecoregions and then related assemblages to environmental gradients to identify factors affecting community composition. The results indicated that larval and juvenile fish assemblages were delineated by broader spatial and environmental gradients over the shelf with spatial heterogeneity within ecoregions (e.g. near Unimak Pass, along the shelf break) and temporal heterogeneity of unique assemblages (i.e. Pribilof Islands) by season. Limitations to the applicability of these ecoregions arise from such spatial and temporal heterogeneity. For example, Ecoregion 5 (Pribilof Islands) is defined by an anticyclonic gyre, but earlier work has shown biological processes near the Pribilof Islands occur at broader spatial scales (Ciannelli *et al.*, 2004). Delineations along the Alaska Peninsula (Ecoregion 1) and congruency with southern shelf ecoregions (2–4) vary temporally as the inner front sets up seasonally and affects species distributions (Petrik *et al.*, 2016).

By examining assemblage structure spatially over the shelf, different spawning populations can be identified and potentially infer contributions to the shelf population. Three main spawning locations have been described for Pollock (near Unimak Pass, Pribilof Islands, Bogoslof Island; Bacheiler *et al.*, 2010) and several locations for Northern Rock Sole (Pribilof Islands, wide swaths of the middle shelf, Gulf of Alaska/Unimak Pass; Cooper *et al.*, 2013; Wilderbuier and Nichol, 2015). Pacific Ocean Perch are known to spawn along the continental slope in the vicinity of Pribilof and Zhemchug Canyons (Rooper *et al.*, 2010). In spring, larval Pollock contributed significantly to clusters f (Pollock and Northern Rock Sole) and g (Pollock, poachers, and Northern Rock Sole). In 2008, these clusters occurred over the southern middle domain and likely reflect spawning activity near Unimak Pass. In 2009, they were found around the Pribilof Islands, potentially arising from spawning grounds nearby or advection from Pribilof Canyon. In 2010, cluster f occurred over the southern middle domain and cluster g occurred near the Pribilof Islands, likely reflecting contributions to the shelf populations from multiple spawning areas.

Table 5. Variability explained by PERMANOVA models for zooplankton (Zoo) and fish across seasons (spring, summer, fall) and years (2008–2010).

Variability explained	Spring		Summer		Fall	
	Zoo (%)	Fish (%)	Zoo (%)	Fish (%)	Zoo (%)	Fish (%)
Total						
2008	85	78	77	74	61	33
2009	67	64	72	35	58	48
2010	81	72	76	61	64	53
T and S						
2008	66	53	36	40	20	20
2009	47	47	52	15	30	28
2010	64	54	31	35	19	16

T = temperature; S = salinity

Congruency with zooplankton assemblage structure

Companion research (Eisner *et al.*, this issue) examined the seasonal progression of zooplankton community composition over the EBS shelf in 2008–2010. Similarities and differences between zooplankton and fish patterns can elucidate congruency across trophic levels within the ecosystem. In spring, summer, and fall, zooplankton assemblages followed comparably broad delineations based on bathymetry (i.e. inner, middle, outer domains) and north–south gradients in species composition. Similar uniqueness observed for 2009 spring ichthyoplankton was observed for spring zooplankton assemblages; the ice retreat occurred substantially later in 2009, which may have caused cascading effects throughout the zooplankton and fish communities. The delayed sea-ice retreat resulted in a later spring bloom and subsequent delays in zooplankton spawning and stage progression (Eisner *et al.*, this issue).

Results of both zooplankton and fish community analyses showed that environmental gradients of temperature and salinity explained more variability in assemblage structure in spring and summer, while spatial variables (latitude, longitude) were stronger factors in fall. More total variability in community composition was explained for zooplankton assemblages (69–77%) than fish assemblages (53–67%), although the variability explained was highest in spring for both zooplankton and fish communities. Models explained less variability in 2009 for zooplankton and fish communities across all seasons (except fall fish) (Table 5).

Taken together, seasonal community analyses of assemblage structure over the EBS shelf suggest revision to the ecoregion classifications. For example, we suggest an expansion of the Pribilof Islands ecoregion to better capture physical and biological processes affected by the island complex. Influx of Alaska Coastal Current waters through Unimak Pass affects transport and drift trajectories over the southeastern Bering Sea shelf (Siddon *et al.*, 2011); therefore, a unique ecoregion should be designated to account for this impact to shelf communities.

Conclusions

This study examined the seasonal progression of larval and juvenile fish assemblage structure over the EBS shelf across three cold years. Patterns of assemblage structure were assessed temporally as well as spatially to determine what drivers delineate communities. Results indicate interannual heterogeneity in assemblage response within the cold stanza, suggesting caution should be taken

when forecasting fisheries and ecosystem-level changes under future climate stanzas. In addition, fish assemblages followed longitudinal and latitudinal gradients and showed variable agreement with the pre-defined ecoregions. Community-level research integrates our current understanding of ecosystem function including multispecies variations, and broadens our ability to conduct ecosystem-based fisheries management as it can provide a causal relationship to explain ecosystem responses.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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