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Spatial and temporal variation of late summer ichthyoplankton assemblage structure in the eastern Chukchi Sea: 2010–2015

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Abstract

The survival of the planktonic stages of marine fishes is widely considered to be a bottleneck in recruitment success and is a period when fishes are highly sensitive to changes in their environment. In high latitude areas that are forecasted to experience warming temperatures, it is critical to determine a baseline of ichthyoplankton assemblages to detect how the ecosystem may change in response to shifting conditions. This study used ichthyoplankton data from the eastern Chukchi Sea in the summers of 2010–2015 to assess temporal and spatial variation in assemblage structure. Larval densities were examined in relation to oceanographic conditions at depth and corresponding water masses. Additionally, the standard lengths of polar cod (*Boreogadus saida*), a key trophic link in Arctic food webs, were assessed for size-at-catch relationships. In 2010 and 2011, years of widespread presence of warm, low salinity bottom water masses such as Alaska Coastal Water, yellowfin sole (*Limanda aspera*) and longhead dab (*Limanda proboscidea*) dominated the assemblages. In 2012 and 2013, the increased presence of colder, more saline Winter Water coincided with a shift to polar cod-dominated assemblages. In 2014 and 2015, water masses were less spatially defined and different assemblages, characterized by Arctic sand lance (*Ammodytes hexapterus*) and saffron cod (*Eleginus gracilis*), were detected than previous years. The greatest range in sizes of polar cod was observed in 2014, as well as the highest number of juveniles and age-1 individuals were collected. The biophysical patterns identified here support the strong connection between interannual oceanographic conditions and ichthyoplankton assemblages which reflect the importance of continuous, multi-year surveys to document assemblage changes in the Arctic.

Keywords Arctic · Polar cod · *Boreogadus saida* · Larval fish · Fisheries oceanography

Introduction

High latitude coastal seas have been identified as 'gateways' to the Arctic Ocean (Woodgate et al. 2005; Mecklenburg and Steinke 2015) which is characterized by an ocean basin 200–1700 m deep (Jakobsson 2002). Unlike other Arctic seas with deeper bathymetry more similar to the Arctic basin, the Chukchi Sea is a unique ecosystem characterized by a wide (800 km north to south), shallow shelf with over half of the area less than 50 m deep (Hunt et al. 2013; Logerwell et al. 2015). The Chukchi Sea extends across the continental shelf from Wrangel Island in the west to Point Barrow, Alaska in the east and constrained by the narrow Bering Strait to the south. This bathymetry creates a unique environment relative to other well-studied Arctic seas such as the Barents and Beaufort Seas averaging 198 and 1420 m, respectively (Jakobsson 2002).

Historically ice-covered and largely inaccessible much of the year, the region has posed a considerable challenge for the collection of biological data. Although adult fish and zooplankton sampling in the Chukchi Sea dates back to the mid-1900s (Alverson and Wilimovsky 1966; Ershova et al. 2015), the collection of ichthyoplankton did not begin until the late 1980s and the taxonomic resolution was coarse (Horner and Wencker 1980). Since that time, several other studies were conducted before the end of the century (Wyllie-Echeverria et al. 1997) but it was not until the early 2000s that the region became the focus of increased larval

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sampling. While previous studies described the abundance and distribution of larval fishes (Wyllie-Echeverria et al. 1997; Norcross et al. 2010; Busby et al. in prep.; 2014), an extended, continuous Arctic ichthyoplankton time series is needed to understand annual variations in the ecosystem and establish a baseline to detect future changes.

Remotely sensed sea ice extent from 2012 to 2017 had its lowest maximum extents observed in nearly four decades (Fetterer et al. 2017, NSIDC). As summer sea ice extent diminishes, this creates greater accessibility to the waterways north of Bering Strait for potential resource extraction, tourism, and trade as well as generates renewed interest in the development of Arctic fisheries (Datsky 2015). Changes in the timing of sea ice formation and retreat directly impact the ecosystem by affecting the location and timing of the spring phytoplankton bloom (Thedinga et al. 2013), and the temperature and salinity of the surrounding water (Wyllie-Echeverria 1995). Fish eggs and larvae are generally considered to be the bottleneck that determines recruitment success, but these life stages are particularly sensitive to changes in their environment. This sensitivity has resulted in ichthyoplankton being recognized as sentinels of climate change (Busby et al. 2014; Suzuki et al. 2015). Therefore, it is critical to understand how ichthyoplankton distribution and abundance respond to interannual climate fluctuations to determine how changing oceanographic conditions may affect these species.

One species dependent on the presence and timing of sea ice formation and breakup throughout all life stages is polar cod (*Boreogadus saida*) (Mueter et al. 2016; Gordeeva and Mishin 2019). Polar cod are thought to remain near or beneath the ice edge throughout early development and large aggregations of immature adults have been observed below the sea ice (Melnikov and Chernova 2013). As adults, polar cod are believed to spawn beneath sea ice at depth throughout the winter months (Benoit et al. 2008). Rich in lipids, polar cod is an essential prey resource for other fishes, seabirds, and marine mammals (Mueter et al. 2016) and is the primary linkage between the lower and upper trophic levels in the Chukchi Sea (Fortier et al. 2006; Whitehouse et al. 2014, 2017; Gordeeva and Mishin 2019). Although the distribution of polar cod is circumpolar, most spawning is believed to occur in the coastal seas over the continental shelves (David et al. 2016). This life history strategy makes the species particularly vulnerable to changes in reproductive success due to increased sub-Arctic temperatures and reduced sea ice (David et al. 2016). Warming sea surface temperatures may also prompt a range expansion of boreal species which may increase competition for prey (Falardeau et al. 2014) and/or a poleward range constriction of polar cod to maintain preferred colder temperatures (Mueter et al. 2016).

This study examines Arctic ichthyoplankton assemblages based on opportunistic sampling conducted in the eastern Chukchi Sea between 2010 and 2015. Objectives were threefold: (1) identify ichthyoplankton assemblages with a focus on temporal variation among years and spatial variation along a north to south gradient, (2) assess assemblage patterns in relation to oceanographic conditions, and (3) examine the length–frequency of larval and juvenile polar cod throughout the study. This study provides baseline data on ecosystem processes and biophysical linkages in the Chukchi Sea necessary to understand the impacts of climate change on summer ichthyoplankton assemblages as well as identify temporal and spatial variation in abundance and size structure of the ecologically important polar cod.

Materials and methods

Study site and oceanography

Along its eastern coastline, the Chukchi Sea extends north from Point Hope to Point Barrow (Fig. 1). The seafloor is comprised of coarse sediment with nearly half of the shelf area between 30 and 50 m deep (Barber et al. 1997; Hunt et al. 2013). The northern extent is defined by the deep gully of Barrow Canyon (> 300 m), a primary production hotspot of the region (Arrigo et al. 2014). The southern boundary is defined by the Bering Strait, which is a narrow passage roughly 50 m deep that funnels water from the Bering Sea into the Chukchi Sea and drives the structure of water masses over the shelf. Historically averaging 0.8 Sverdrups (1 Sverdrup = 10^6 m^3 s^{-1}) per year, the flow has increased by 50% from 2001 to 2011 (Woodgate et al. 2005, 2012), which can dramatically shift the distribution of water masses over time.

In the summer months, waters over the Chukchi Shelf stratify into a two-layer water mass system separated by the thermocline at approximately 10 m depth (Chu et al. 1999; Ershova et al. 2015). Primarily, two masses are advected through the Bering Strait influence the eastern Chukchi Sea: Alaska Coastal Water (ACW) and Bering Sea Summer Water (BSSW). ACW, present most commonly at the surface near the Alaskan coastline, is warm with low salinity and nutrients (Table 1). BSSW, present most often in the southern Chukchi Sea, either at depth inshore or at the surface offshore, is colder and high in salinity and nutrients. A hydrographic front often forms where ACW and BSSW mix between Icy Cape and Point Franklin, the peninsula just beyond Wainwright (Barber et al. 1997; Weingartner 1997). The other predominant water mass in the Chukchi Sea is Winter Water (WW), which persists at depth year-round. Cold and highly saline, WW is also nutrient-rich from mixing with the Siberian Coastal Current, which flows into the central Chukchi Sea from the Russian coastline during times of reduced advection through Bering Strait (Woodgate et al.
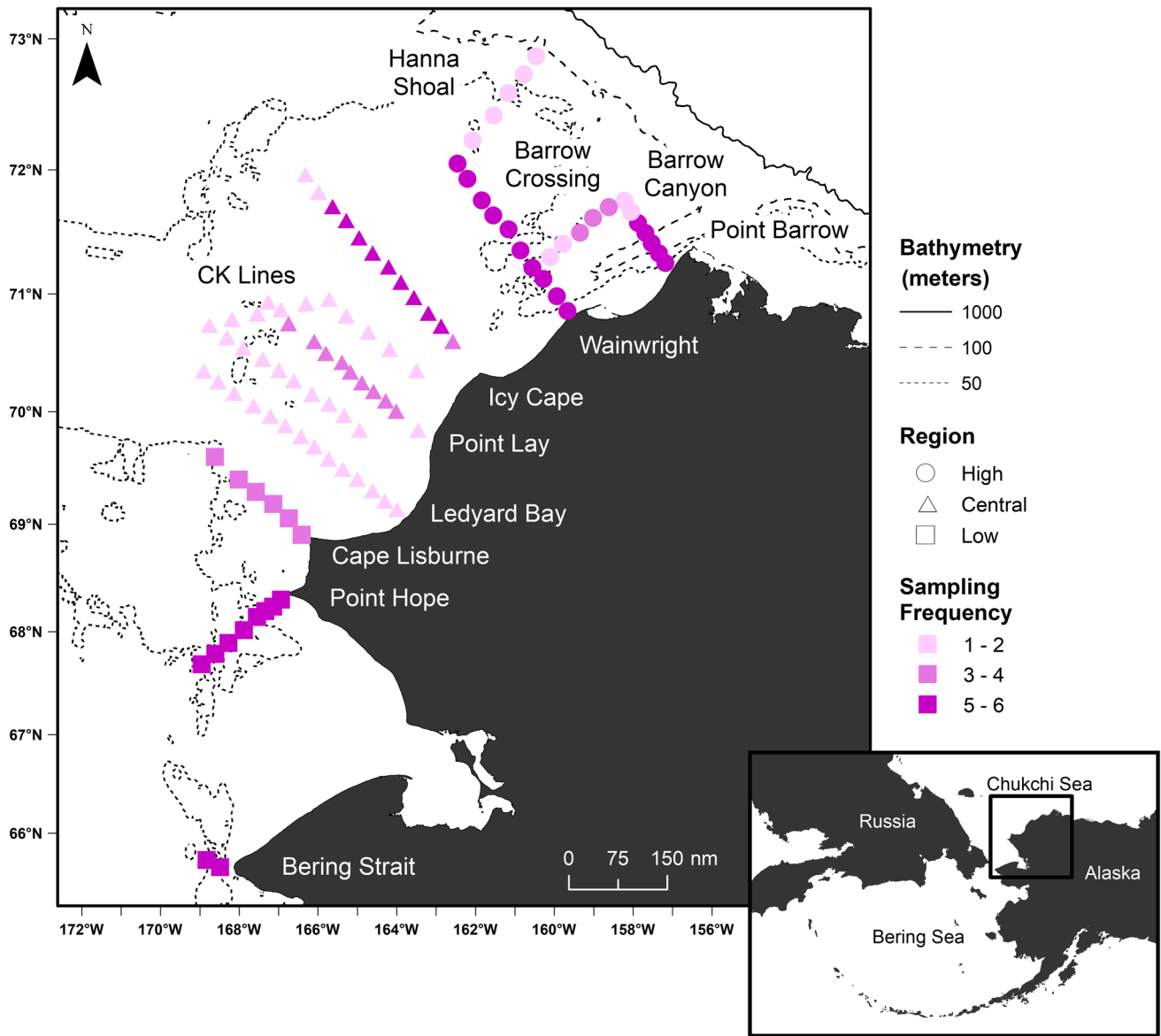
Fig. 1 Map of station transects in the northeastern Chukchi Sea. Low transects were defined as the start of the inshore-most station below 68.5°N (squares), Central transects originating between 68.5° and 70°N (triangles), and High transects (H) originating above 70°N (cir- cles). The color gradient reflects the number of times each site was sampled in the six years of study with darker colors indicating higher sampling frequency. (Color figure online)

Table 1 Characteristics of bottom water masses identified across survey years

Water mass	Code	Origin	Temperature (°C)	Salinity (psu)
Alaska Coastal Water	ACW	Alaska Coastal Current, through Bering Strait	7 to 12	28.0 to 33.0
Bering Sea Summer Water	BSSW	Bering Sea, through Bering Strait	0 to 8	30.0 to 33.5
Alaska Coastal Water/Bering Sea Summer Water Mix	ACW/BSSW	Coastal and Bering Sea, through Bering Strait	7 to 8	30.0 to 33.0
Winter Water	WW	Resident water, Chukchi basin	−2 to 0	30.0 to 33.5
Winter Water/Bering Sea Mix	WW/BSSW	Resident water mixed with Bering Sea	0 to 1	30.0 to 33.5

Stations with water masses that fit multiple temperature and salinity ranges are identified as mixed masses because it was not possible to defini- tively distinguish which mass is prevalent. Water mass distinctions follow Berchok et al. (2015)

2005; Berchok et al. 2015). Following periods of increased on-shelf mixing, such as storm events, it is often difficult to delineate one water mass from another by temperature and salinity, so these are referred to these as mixed water masses (ACW/BSSW, WW/BSSW).

Field collections

Stations were sampled using a 1 m^2 Tucker trawl affixed to a sled frame (hereby referred to as 'sled') with a messenger-based opening-closing net system (Sameoto and Jaroszynski 1976) and a General Oceanics flowmeter suspended in the center of the net. Unlike bongo nets traditionally used to sample ichthyoplankton, the Tucker trawl is designed to capture a wider range of life stages and, with the addition of the sled frame, slide over soft-bottomed areas of the seafloor to collect demersal, juvenile fishes (Davies and Barham 1969; Dougherty et al. 2010). A 333-µm mesh was used from 2010 to 2012 before switching to 505-µm mesh in 2013, but mesh sizes were treated as analogous based on gear comparisons by Colton et al. (1980) and Shima and Bailey (1994). Experiments by Colton et al. (1980) examined retention rates of larvae between the two mesh sizes (333 and 505 µm) and found no significant differences in either larval abundance or size bias. Similarly, Shima and Bailey (1994) evaluated differences in the catch of walleye pollock (*Gadus chalcogrammus*) between the two mesh sizes as well as between the 60 cm bongo and the 1 m^2 Tucker trawl but found no significant differences in larval density between the mesh or gear types.

At each station the sled was lowered to the seafloor following procedures of Dougherty et al. (2010), the net opened remotely, and the sled towed obliquely from the seafloor to the surface. There was minimal variation in depth across all sites sampled across the shelf (30–50 m) except stations in Barrow Canyon which ranged from 120 to 160 m. Mechanical difficulties in 2010 prevented the net from tripping properly, so the net remained open during descent to the seafloor at all stations. The nets also remained open during descent at all stations of the Barrow Canyon transect (all years) because the sled could not move along the seafloor due to the irregularity of the seafloor. Tows conducted in this manner were considered comparable to oblique tows because the net does not effectively fish as the sled descends to the seafloor due to the high deployment speed of 40 m/min, compared to the 20 m/min retrieval speed (Dougherty et al. 2010). Due to time constraints and sea ice conditions, the total number of stations sampled varied between years (Table 2).

A Seabird 911 plus conductivity-temperature-depth (CTD) profiler was typically lowered to within 5 m of the seafloor to collect temperature and salinity profiles. As this study focused on water mass at depth, temperature and salinity values were averaged from 5 to 10 m above the seafloor, rather than averaged throughout the water column because this may not accurately reflect the conditions of either the surface or bottom water mass properties. Of the two water mass layers, the bottom water is more stable and is likely a more effective measure of interannual variation between years by reflecting advection strength (how far the ACW and BSSW persists into the Chukchi Sea) and wind effects driving the mixing of the surface and bottom water masses (presence of ACW at depth). Additionally, the majority of the fish species in the region are benthic, so their distribution would be influenced predominantly by water masses at depth rather than at the surface.

Laboratory processing

Samples were preserved at sea in 5% formalin and buffered with sodium borate then processed at the Plankton Sorting and Identification Center in Szczecin, Poland. Ichthyoplankton were removed, sorted by life stage (egg, larva, or juvenile), and identified by morphology and pigmentation to the lowest possible taxonomic level. Standard lengths (SL) were measured for the first 50 individuals of each species per station to the nearest 0.1 mm. Identifications were verified at the Alaska Fisheries Science Center, following Matarese et al. (1989, 2013), Busby et al. (2017), and the

Table 2 Dates and stations sampled in each year of the study

Year	Dates	Sled tows	Avg. temp. (°C)	Avg. sal. (psu)	Climate
2010	Aug 27–Sept 14	45	3.97	31.99	Warm
2011	Aug 12–Sept 11	44	1.61	31.09	Transition
2012	Aug 17–27	49	1.73	30.57	Transition
2013	Aug 23–Sept 9	32	-1.40	29.62	Cold
2014	Sep 23–Oct 10	60	2.46	30.97	Transition
2015	Aug 1–29	40	1.92	31.01	Transition
	Total	270	2.01	31.62	

Average temperature and salinity at depth were calculated for the Icy Cape line, the transect sampled most consistently across all years. Climate was broadly assigned based on the conditions observed at Icy Cape with the coldest and warmest years noted, while other years were referred to as transition years

Ichthyoplankton Information System (https://access.afsc.noaa.gov/ichthyo/). Scientific and common names follow Mecklenburg et al. (2011) and Orr et al. (2015).

Statistical analysis

For analysis, catch per 1000 m^3 was calculated using volume filtered estimates derived from flowmeter rotations (Smith and Richardson 1977), standardized, and analyzed in PRIMER 7.0 software (Clarke et al. 2014). Although identified and enumerated, we omitted eggs from the analysis because their distribution is a result of drift via ocean currents and, at present, only pelagic eggs of the families Gadidae and Pleuronectidae can readily be identified to genus (Busby et al. 2017). Larvae and juveniles were grouped for analysis, with the exception of the polar cod length–frequency analysis which examined all individuals collected, and only species occurring in > 4% of the stations in a given year were included to eliminate bias from rarely occurring taxa. Depth was generally uniform across stations sampled on the Chukchi Shelf (between 30 and 50 m), which made it difficult to distinguish between inshore and offshore. The survey area was instead divided into three regions based on latitude to assess spatial patterns. Transect lines which began below 68.5°N were categorized as 'Low' while transects that originated between 68.5° and 70°N were categorized as 'Central' (Norcross et al. 2010; Eisner et al. 2013). Transects above 70°N were categorized as 'High' (Fig. 1).

A cluster analysis was used to address the first objective of describing the ichthyoplankton assemblages with respect to temporal and spatial variability. Larval densities were fourth-root transformed to reduce the influence of highly abundant species, give more weight to rare taxa, and to equalize variances among species. A Bray–Curtis similarity was then computed using all years pooled. Assemblages from the cluster analysis were defined at 18% similarity which preserved reasonable biological species groups based on life history strategies. The cluster groups were then mapped by year to show which stations had similar assemblages. To determine which species contributed most to the similarity within clusters, years, and regions, the Bray–Curtis similarity was broken down by species, and percent contribution was calculated.

To address the second objective of examining assemblages in relation to oceanographic conditions, a permutational multivariate analysis of variance (PERMANOVA) was used to determine the amount of variability explained by environmental variables. Each environmental variable was evaluated and independently transformed if distributions were skewed. Values were normalized and Euclidean distances among variables were calculated. Since the order matters in PERMANOVA, a forward selection, adjusted R^2 criteria distance-based linear model (DistLM) was used for variable selection and ordering environmental variables. A PERMANOVA with covariates, added in order of importance as given by DistLM, along with year and region, determined the percent variation explained by each variable and factor.

Polar cod length–frequency analysis

The catch of polar cod in all years was assessed to examine length–frequency relationships and to track age classes throughout the time series. The size at transformation from the larval to the juvenile stage for polar cod was approximated at 25.0 mm SL based on known lengths of sub-arctic species of the same family, Pacific cod (*Gadus macrocephalus*) and walleye pollock (Craig et al. 1982). Individuals at lengths from 25 to 60 mm SL were categorized as age-0 (Craig et al. 1982) and individuals between lengths of 60 and 100 mm SL as age-1 (Helser et al. 2017).

Results

A total of 1968 larval and juvenile fishes were collected representing 35 taxa from 10 families (Table 3). Greatest taxonomic richness was observed in 2015 with 27 species in 10 families present. The lowest richness was observed in 2013 with only 13 species in 7 families present, as well as the lowest catches of the study with < 350 individuals collected. Only polar cod and kelp snailfish (*Liparis tunicatus*) were collected during all years of study. Polar cod was also the most frequently occurring taxon, present at nearly a third of all stations occupied throughout the study. Other frequently occurring species included yellowfin sole (*Limanda aspera*) present at ~ 25% of stations as well as Arctic sand lance (*Ammodytes hexapterus*) and Bering flounder (*Hippoglossoides robustus*), both present at ~ 20% stations. Despite a high frequency of occurrence, polar cod and yellowfin sole together represented less than 15% of the total catch (based on standardized larval density). Collectively, Arctic shanny (*Stichaeus punctatus*), Bering flounder, and Arctic sand lance accounted for over half of the total catch across all years.

Intra- and interannual variability

The percent contribution of each species to the similarity within each year reflects strong interannual variation in species composition (Table 4). The high abundance of yellowfin sole in 2010 was represented in the total catch that year and contributed to nearly 75% of the similarity of the assemblage. Although the species contribution decreased in 2011, yellowfin sole continued to influence the assemblage structure strongly and contributed nearly 40% to the average similarity across stations. In both 2011 and 2012,

Table 3 Ichthyoplankton catch by year of survey organized by phylogeny, depicting presence-absence data

Common name	Scientific name	2010	2011	2012	2013	2014	2015
	Osmeridae						
Capelin	*Mallotus villosus*	X		X		X	X
	Gadidae						
Arctic cod	*Arctogadus glacialis*						X
Polar cod	*Boreogadus saida*	X	X	X	X	X	X
Walleye pollock	*Gadus chalcogrammus*	X	X	X		X	X
Saffron cod	*Eleginus gracilis*		X	X		X	X
	Hexagrammidae						
Masked greenling	*Hexagrammos octogrammus*	X					
Whitespotted greenling	*Hexagrammos stelleri*	X					X
	Cottidae						
Arctic staghorn sculpin	*Gymnocanthus tricuspis*		X	X	X	X	X
Butterfly sculpin	*Hemilepidotus papilio*	X		X			
Spatulate sculpin	*Icelus spatula*		X	X			
Shorthorn sculpin	*Myoxocephalus scorpius*						X
Eyeshade sculpin	*Nautichthys pribilovius*						X
	Agonidae						
Alligatorfish	*Aspidophoroides monopterygius*						X
Arctic alligatorfish	*Aspidophoroides olrikii*		X	X	X	X	X
Veteran poacher	*Podothecus veternus*			X			X
	Liparidae						
Gelatinous snailfish	*Liparis fabricii*				X		
Variegated snailfish	*Liparis gibbus*			X	X		X
Kelp snailfish	*Liparis tunicatus*	X	X	X	X	X	X
	Zoarcidae						
Wattled eelpout	*Lycodes palearis*						X
Polar eelpout	*Lycodes polaris*						X
	Stichaeidae						
Blackline prickleback	*Acantholumpenus mackayi*			X			
Stout eelblenny	*Anisarchus medius*	X		X	X	X	X
Fourline snakeblenny	*Eumesogrammus praecisus*	X		X	X		X
Daubed shanny	*Leptoclinus maculatus*		X	X	X	X	X
Slender eelblenny	*Lumpenus fabricii*	X		X		X	X
Arctic shanny	*Stichaeus punctatus*		X	X	X	X	X
	Ammodytidae						
Arctic sand lance	*Ammodytes hexapterus*	X	X	X	X		X
	Pleuronectidae						
Bering flounder	*Hippoglossoides robustus*	X	X	X	X		X
Northern rock sole	*Lepidopsetta polyxystra*						X
Yellowfin sole	*Limanda aspera*	X	X	X		X	X
Longhead dab	*Limanda proboscidea*	X	X	X		X	X
Sakhalin sole	*Limanda sakhalinensis*	X		X	X		
Starry flounder	*Platichthys stellatus*		X	X			
Alaska plaice	*Pleuronectes quadrituberculatus*		X	X			X
Greenland halibut	*Reinhardtius hippoglossoides*					X	
	Total	15	15	24	13	14	27

Bering flounder became more predominant and contributed most to observed similarity. The following two years, 2013 and 2014, polar cod became dominant and represented over 60% of the catch similarity. Assemblages in 2015 were the least defined and had the greatest number of species contributing to within-year similarity. Unlike previous

Table 4 Results of the similarity percentage calculation showing which species contributed most to the observed assemblages of a particular year (all regions) or region (all years)

Similarity within	Species	Contribution (%)
Year		
2010	Yellowfin sole	74.05
	Butterfly sculpin	11.67
	Longhead dab	7.43
2011	Bering flounder	37.59
	Yellowfin sole	36.44
	Slender eelblenny	10.47
2012	Bering flounder	31.43
	Polar cod	14.42
	Arctic sand lance	14.05
	Variegated snailfish	13.89
	Slender eelblenny	7.04
2013	Polar cod	60.33
	Arctic shanny	13.57
	Arctic sand lance	12.51
	Slender eelblenny	10.86
2014	Polar cod	63.58
	Yellowfin sole	17.78
	Daubed shanny	10.38
2015	Arctic sand lance	21.25
	Kelp snailfish	14.61
	Saffron cod	14.38
	Polar cod	13.39
	Arctic shanny	9.62
	Daubed shanny	8.15
Region		
Low	Bering flounder	30.43
	Yellowfin sole	26.59
	Butterfly sculpin	16.97
	Arctic sand lance	8.12
	Longhead dab	6.05
Central	Bering flounder	63.34
	Butterfly sculpin	7.83
	Yellowfin sole	6.98
High	Polar cod	55.7
	Slender eelblenny	12.95
	Arctic shanny	7.16
	Arctic sand lance	6.95
	Kelp snailfish	6.62

Only species contributing greater than 5% were included

Table 5 Percent contribution of each species to the Bray–Curtis similarity within clusters

Assemblage	Species	Contribution (%)
A	Walleye pollock	53.7
	Butterfly sculpin	46.4
B	Saffron cod	91.2
C	Arctic sand lance	52.4
	Saffron cod	15.0
	Arctic shanny	9.3
	Slender eelblenny	6.9
	Arctic staghorn sculpin	5.3
D	Yellowfin sole	85.4
	Longhead dab	7.5
E	Bering flounder	78.4
	Variegated snailfish	9.4
F	Stout eelblenny	100.0
G	Daubed shanny	97.1
H	Arctic alligatorfish	100.0
I	Kelp snailfish	93.8
J	Polar cod	80.3
	Arctic shanny	7.6
	Arctic sand lance	5.7

Species contributing less than 5% were omitted

years, in 2015 polar cod contributed only 14% to assemblage structure. Although Arctic sand lance contributed the most to observed similarity that year, it only contributed 21% while dominant species in other years contributed between 30–74%.

Cluster analysis of stations yielded 10 distinct assemblages across all years (Table 5). When cluster groups were mapped, Assemblage D, typified by yellowfin sole and longhead dab, was present at more than 75% of stations in 2010 (Fig. 2). In 2011, the stations with Assemblage D decreased to only a third of occupied stations and were present at less than 10% in 2012. Assemblage D was absent in both 2013 and 2015. Assemblage E was typified by Bering flounder and variegated snailfish (*Liparis gibbus*), which included only one station off Icy Cape in 2010 but represented roughly 25% of stations in both 2011 and 2012. The assemblages present in 2012 depict a clear shift away from the primarily yellowfin sole-dominated assemblage. Assemblage J, comprised primarily of polar cod, was present at more than 80% of stations in 2013. The groups present in 2014 reflect a mixture of both the 2010/2011 and 2012/2013 assemblages with both yellowfin sole and polar cod-dominated assemblages (Fig. 2). The greatest diversity of assemblages was observed in 2015 with several groups unique to that year, including Assemblage C, typified by Arctic sand lance, saffron cod (*Eleginus gracilis*), and Arctic shanny which was present at more than half of the stations. Outliers, defined as assemblages present at fewer than four stations, were combined into a single group, Assemblage I, of which only kelp snailfish contributed more than 5% to the group similarity.
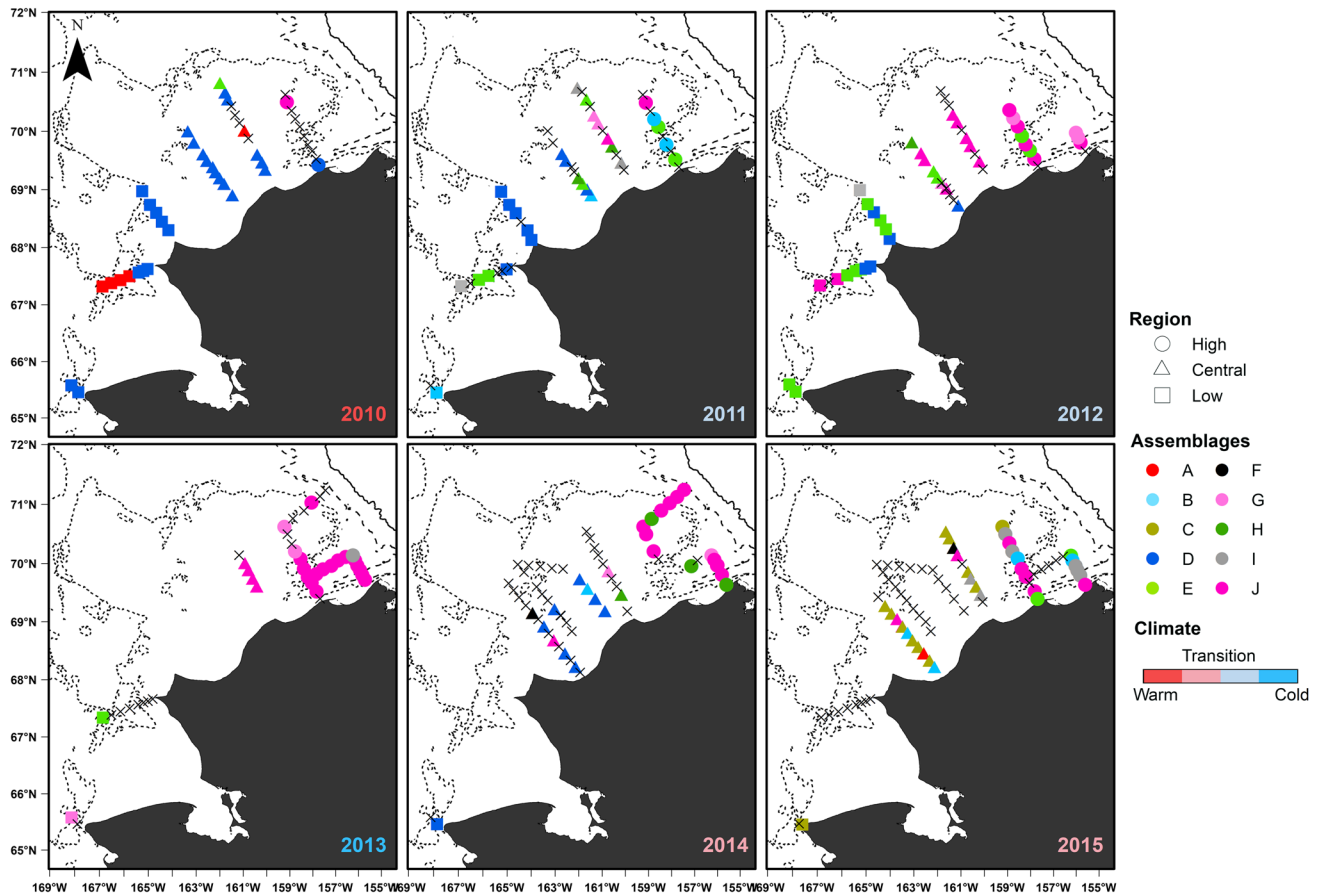
Fig. 2 Spatial arrangement of assemblages generated by cluster analysis based on similarity across all years with 'X' indicating stations of zero catch. (Color figure online)

Spatial variability

In the Low and Central regions, Bering flounder contributed most to similarities within the region at 30% and 63%, respectively (Table 4). In the Low region, yellowfin sole contributed only slightly less than Bering flounder at 27%. The Central region had the fewest number of contributing species with only two other species, butterfly sculpin (*Hemilepidotus papilio*) and yellowfin sole, both which contributed less than 10% to the observed assemblage structure. In the High region, polar cod contributed over 50% similarity to the assemblage, along with four other species which each contributed between ~ 6 and 13%.

When cluster groups across years were mapped, it is evident that there is spatial structure to the groupings. Assemblage A, of which walleye pollock is the highest contributing species, and D, dominated by yellowfin sole, were found almost exclusively in the Low and Central regions, and particularly prevalent along the inshore stations (Fig. 2). Assemblage E, dominated by Bering flounder, is found throughout all regions but most often occurred in the Central

region. Assemblage J, dominated by polar cod, is present throughout all years in the High region but is never present in the Low region. Unlike the other years, 2015 does not have the same, defined spatial structure and instead shows a dispersed assemblage pattern, although Assemblage J still appeared with relatively high frequency in the High region. Previously undetected, Assemblage C was also present throughout the Central region in 2015.

Oceanographic conditions

ACW was present almost exclusively in the Low and Central regions of Chukchi Sea except for one instance at the inshore-most station of the Wainwright line (Fig. 3). BSSW was closely associated with ACW, often as the mixed mass ACW/BSSW or at the stations nearest to ACW. WW was present in all years in the High region. Between 2012 and 2015, WW appeared to shift farther south into the Central and Low regions, usually as a mixed water mass, WW/BSSW. The warmest temperature was observed in 2010, followed by two years of intermediate temperatures, before
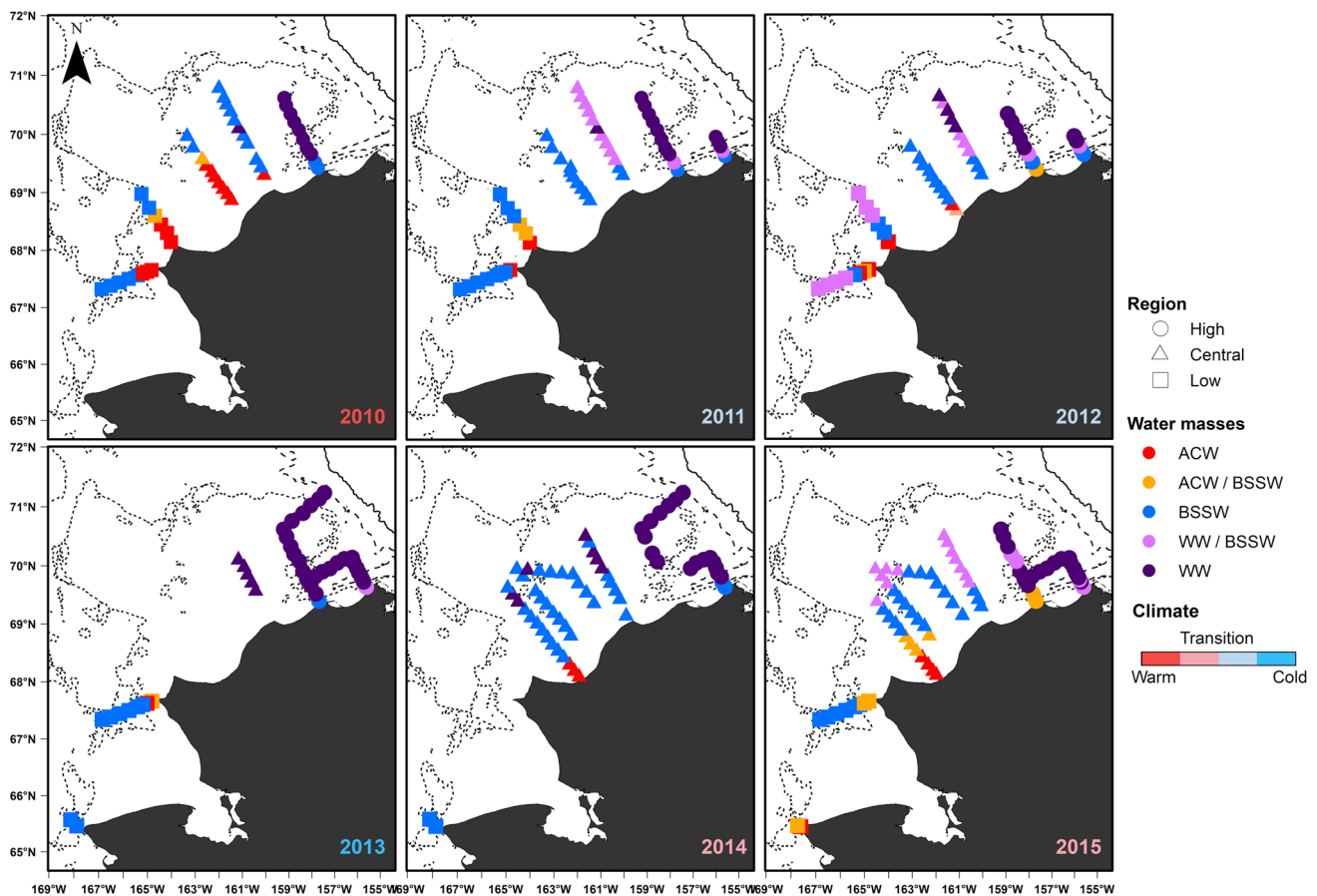
Fig. 3 Water mass designations assigned to each station based on temperature and salinity values averaged 5–10 m above the seafloor. Years were assigned a color based on the oceanographic conditions of the year, with red reflecting warm years and blue reflecting cold years. (Color figure online)

the coldest year of the series in 2013. 2011 and 2012 were identified as transition years between the warmest and coldest years of the surveys. Water temperatures began to rise again in 2014 and BSSW extended as far north as Barrow Canyon. By 2015, ACW was confined to the Central region, but the offshore-most stations remained much colder than in 2010, creating a water mass distribution unique to that year.

The warmest year in the series (2010) was characterized by a yellowfin sole-dominated assemblage with a distribution that mirrored the extent of ACW and ACW/BSSW mixed water masses (Fig. 3). From 2010 to 2012, the number of stations with assemblages dominated by yellowfin sole decreased from over 75% to 13% and were restricted to the south at only the most inshore stations where ACW was still present. The presence of colder WW in the north, beginning in 2012, coincides with the first occurrence of multiple stations represented by a polar cod-dominated assemblage. As the presence of WW persisted over the northern region in 2013, the presence of this assemblage increased to over 80% of the stations. Although the average temperatures at Icy Cape increased in 2014, WW was still present at nearly all

stations in the High region and several stations in the Central region and the presence of polar cod-dominated assemblages remained strong in 2014. The water masses of 2015 were uniquely distributed, marked by the return of ACW that was absent in 2013 and 2014. In addition to the ACW along the inshore stations, a cold WW and WW/BSSW mixed water mass was present in the north, reflecting the cold year pattern observed in 2013. Cluster groupings mirrored water mass distribution and a new assemblage dominated by Arctic sand lance and saffron cod was identified.

The distance-based forward selection linear model identified sea surface temperature, bottom water temperature, sea surface salinity, and bottom depth as significant variables influencing assemblages. When incorporated into a PERMANOVA, these environmental variables collectively explained approximately 15% of the observed variation (Table 6). The two factors used to examine temporal-spatial variation, Year and Region, explained 28% of the variation, leaving a residual value of 57% that could not be explained by the model. A significant interaction was found between Year and Region ($p = 0.001$) and required a pairwise test to

Table 6 Permutational multivariate analysis of variance (PER-MANOVA) test results in comparison with significant environmental variables and two factors, region and year, to assess effect of time and space on community assemblages, p (perm) reflects *p* value calculated from test permutations

Variables	p (perm)	Components of variation (%)
Environmental		
SST	0.001	7.5
BW temp	0.001	5.6
SS salinity	0.003	0.7
Bottom depth	0.001	1.3
Factors		
Year	0.001	13.8
Region	0.002	2.9
Year×Region	0.001	11.7
Residual		56.5

resolve significant differences within regions across years (Table 7). The least variation was observed in the Low region with the only significant differences found were between 2010 vs. 2012 and 2010 vs. 2013. In the Central region, 2012 was significantly different from both 2010 and 2011. The assemblages in 2015 were also significantly different from those observed in each of the first three years of

the study (2010-2012). No sampling was conducted in the Central region in 2013. The High region was the most variable of the regions with significant differences between nearly all years (Table 7).
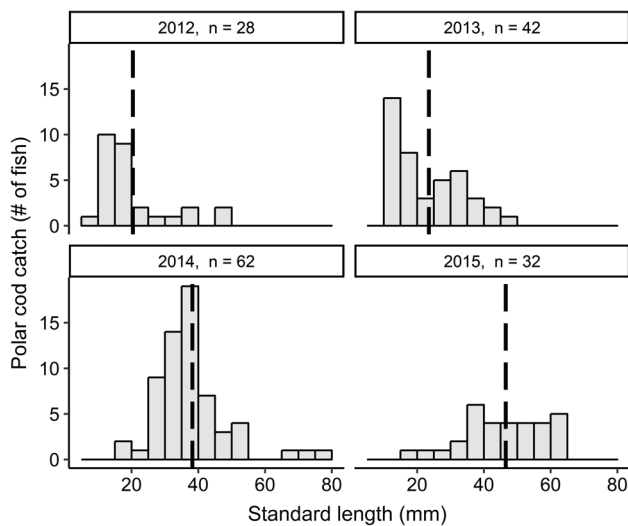
Polar cod analysis

Only four polar cod were collected between 2010 and 2011. Catches in subsequent years ranged from 28 to 62 individuals for a study total of 169, with the highest catch occurring in 2014. Standard lengths (SL) throughout the study ranged from 10.0 to 76.9 mm with averages ranging from 20.4 mm in 2012 to 46.5 mm in 2015 (Fig. 4). Although few polar cod were collected in the first two years of the study, the remaining four years provided a comparison of age classes (Fig. 4). A total of 10 age-1 individuals were collected between 2014 and 2015, representing 5% and 22% of the catch, respectively.

Discussion

Species composition and geographic distribution

Several species sampled in this study were among the first reported collections in the Chukchi Sea, enhancing

Table 7 Pairwise permutational multivariate analysis of variance (PERMANOVA) test to determine significant differences in observed assemblages between years of study with 'X' indicating years where no comparisons were possible and '–' indicates no significant difference was observed

	2010	2011	2012	2013	2014	2015
High						
2010						
2011	0.015					
2012	0.006	–				
2013	0.016	0.001	0.010			
2014	0.005	0.014	–	–		
2015	0.001	0.001	0.001	0.001	0.006	
Central						
2010						
2011	–					
2012	0.002	0.002				
2013	X	X	X			
2014	–	–	–	X		
2015	0.001	0.001	0.001	X	–	
Low						
2010						
2011	–					
2012	0.001	–				
2013	0.007	–	–			
2014	–	–	–	–		
2015	–	–	–	–	–	

Fig. 4 Length–frequency distribution for polar cod collected between 2012 and 2015 with the dashed line indicating average standard length. 2010 and 2011 were not included due to extremely low catches

geographic range estimates. In 2015, larvae of northern rock sole (*Lepidopsetta polyxystra)* were collected north of Bering Strait but were previously only recorded as far north as Cape Rodney in the northwestern Bering Sea (Mecklenburg et al. 2011). Similarly, the northern extent of masked greenling (*Hexagrammos octogrammus)* was thought to be St. Lawrence Island (Mecklenburg et al. 2011), but several specimens were collected in Bering Strait during the 2010 survey. This study also confirmed the presence of several species that were only recently reported in the Chukchi Sea. Among these were Sakhalin sole, first recorded in 1990, but absent again until the late 2000s (Mecklenburg et al. 2011). Mecklenburg and Steinke (2015) report similar findings, noting 11 species previously restricted to the Bering Sea (Andriashev 1954) are now commonly found in the Chukchi Sea. In this study, 3 of the 11 species were caught in multiple years including whitespotted greenling (*Hexagrammos stelleri*), fourline snakeblenny (*Eumesogrammus praecisus*), and Alaska plaice (*Pleuronectes quadrituberculatus*). Although there are reports of yellowfin sole collected as far as Kotzebue Sound (Andriashev 1954), individuals were collected farther north in five of six years of the survey and the taxon comprised over 20% of the total abundance.

Assemblage structure

Summer ichthyoplankton assemblages were found to vary significantly across years sampled and spatially across regions within the Chukchi Sea. Clear differences in species composition were observed between warm years, characterized by strong ACW flow and low sea ice extent, and cold years, characterized by weak ACW flow and greater sea ice extent. Two assemblages identified by cluster analysis, the yellowfin sole-dominated and polar cod-dominated, were present in nearly all years, though most prevalent in years of either extreme warm (2010) or cold year (2013), respectively. Assemblages in the transition years between these two extremes reflected a gradual decline of yellowfin sole-dominated stations, as temperatures and salinity declined, and an increase in stations of polar cod-dominated assemblages. As spatial structure became less defined starting in 2014 and water masses became increasingly mixed in 2015, new assemblages were identified, and variation increased within regions. The presence of a previously undetected assemblage, as well as a group composed of stations identified as outliers, highlights the dynamic nature of the Chukchi marine ecosystem. This observation is supported by evidence that at lower latitudes assemblages are influenced by temperature (Barber et al. 1997) and gradual shifts in assemblage structure may occur if changes, such as climate warming, persist over a long period (Mueter and Litzow 2008).

Although year effects better explained variation in observed assemblages, region effects were still significant. The presence and spatial extent of water masses varied across years but overall trends were similar to those previously reported (Eisner et al. 2013; Ershova et al. 2015; Pisareva et al. 2015). The southernmost region, Low, had the least observed variation across all years. Even in cold years, which resulted in the increased presence of BSSW and mixed WW/BSSW water masses, the Low region still experienced the mixing of ACW with BSSW, leading to reduced variation within the region. In the Central region, slightly more variation was observed, illustrating the contrast of assemblages between warm and cold years. The High region experienced the greatest degree of interannual variability among years, likely in part due to highly variable sea ice extent in the region. Between 2010 and 2015, the date which sea ice concentration between Wainwright and Barrow Canyon declined to 10% ranged from July 15th in 2011 to August 31st in 2013 (Spear et al. 2019). As the northernmost stations are most susceptible to interannual variability, the assemblages in this area may experience the most changes in a warming climate.

Polar cod analysis

Peak abundance of the assemblage dominated by polar cod was in 2013, coincided with the year of greatest sea ice extent in August over the study (S. Salo, Pacific Marine Environmental Lab, pers. comm., Spear et al. 2019). Spawning in the Chukchi Sea is believed to occur under the ice between January and March, but extremely cold temperatures (− 1.8 °C) may delay hatching until after the ice breakup later in the season (Mueter et al. 2016). In the

Beaufort Sea, it is well documented that the hatch season may extend into July (Bouchard et al. 2008; 2011), but this region has sea ice present much longer than the Chukchi Sea. It has been suggested that polar cod spawning may also occur in the Chukchi Sea based on the size of larvae caught in mid-July (Wyllie-Echeverria et al. 1997) but has yet to be confirmed. Ice retreat over the southern Chukchi Sea was one to two weeks later in 2012 and 2013 relative to the first two years of the study (Spear et al. 2019). Increased abundance of larval polar cod may be the result of more favorable environmental conditions such as increased retention or greater sea ice presence but may also be attributed to biological factors such as increased prey availability.

The greatest number of individuals was collected in 2014 as well as the first observations of age-1 individuals (Fig. 4). The high catch frequency of polar cod is consistent with recent acoustic evidence, which suggests that the species may be among the most numerically abundant in the region (De Robertis et al. 2017). The high abundance of polar cod in 2014 also coincided with low monthly transport estimates through the Bering Strait, relative to other years of the time series (Stabeno et al. 2018), which may decrease larval dispersal, resulting in increased retention and localized abundance. Historically, monthly heat influx through Bering Strait reached its maximum in August (Serreze et al. 2016) so the difference may have been even more pronounced at the time of sampling. Colder temperatures over the previous summer may have created optimized conditions for growth and development, resulting in higher overwinter survival of the individuals spawned in 2013 relative to other years. Alternatively, the larger catches of Age-1 polar cod collected in 2014 and 2015 may be late-hatching individuals from the previous summer that recruited in the ice during their first winter (Geoffroy et al. 2016), which may have been missed in the previous year's sampling. Greater standard lengths observed in 2014 may also have been an artifact of sampling several weeks later than other years of the survey.

With sea surface temperatures predicted to continue to rise over the coming decades, the thermal tolerances of polar cod may be tested. Lab rearing experiments conducted by Graham and Hop (1995) found that polar cod of the Canadian Arctic require temperatures colder than 3 °C to develop, with optimal conditions for embryonic growth in the range of 0–3 °C (Mueter et al. 2016). Recent work by Laurel et al. (2017) found that thermal sensitivity changes with ontogeny with age-0 individuals attaining a maximum growth rate at a warmer temperature than age-1 individuals. Laurel et al. (2018) also determined that higher temperatures negatively influenced hatch success and length-at-hatch of polar cod, with marked declines after temperatures exceeded 2 °C in rearing experiments. Under various warming scenarios, it has been suggested that polar cod may be extirpated from most of its current range as early as 2038 (Cheung et al.

2008). There are also concerns that warming may allow other prominent species such as saffron cod or Arctic sand lance to outcompete polar cod, and thus dramatically alter the Arctic food web (Falardeau et al. 2014; Mueter et al. 2017).

Results from this study show the dynamic biophysical connections between interannual water mass distribution and larval fish assemblages in the Chukchi Sea. Additional research is needed to collect and synthesize available oceanographic data to assess potential patterns in warm and cold year shifts and to understand how larval fish assemblages are influenced by water masses. This work contributes to establishing a baseline assemblage structure for Chukchi Sea fishes in the early stages of life and highlights the need for continued efforts to monitor fluctuations in ichthyoplankton assemblages in the changing Arctic climate.

Compliance with ethical standards

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