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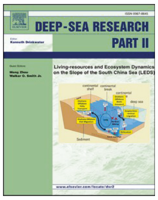

Pacific cod or tikhookeanskaya treska (*Gadus macrocephalus*) in the Chukchi Sea during recent warm years: Distribution by life stage and age-0 diet and condition

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ABSTRACT

Many fish species have moved poleward with ocean warming, and species distribution shifts can occur because of adult fish movement, or juveniles can recruit to new areas. In the Bering Sea, recent studies document a dramatic northward shift in the distribution of *Gadus macrocephalus* (Pacific cod in English and tikhookeanskaya treska in Russian) during a period of ocean warming, but it is unknown whether the current northward distribution shift continues into the Chukchi Sea. Here, we use catch data from multiple gear types to present larval, age-0, and older Pacific cod distributions from before (2010 and 2012) and during (2017, 2018, and 2019) recent Chukchi Sea warming events. We also report on the habitat, diet, and condition of age-0 Pacific cod, which were present in the eastern Chukchi Sea in recent warm years (2017 and 2019), but were absent in a cold year (2012). We hypothesize that age-0 recruitment to the eastern Chukchi Sea is associated with recent warm temperatures and increased northward transport through the Bering Strait in the spring. Age-0 fish were present in both benthic and pelagic habitats and diets reflected prey resources at these capture locations. Age-1 Pacific cod were observed in the western Chukchi Sea in 2018 and 2019, indicating possible overwinter survival of age-0 fish, although there was little evidence that they survive and/or remain in the Chukchi Sea to age-2. Observed low lipid accumulation in age-0 Pacific cod from the Chukchi Sea suggests juvenile overwinter mortality may be relatively high compared to more boreal regions (e.g. Gulf of Alaska). Adult Pacific cod were also observed in the Chukchi Sea during 2018 and 2019. Although densities in the western Chukchi Sea were very low compared to the Bering Sea, the adults are the first known (to us) records from the Chukchi Sea. The increased presence of multiple age-classes of Pacific cod in the Chukchi Sea suggests poleward shifts in both nursery areas and adult summer habitat beyond the Bering Sea, but the quantity and quality (e.g. summer productivity and overwintering potential) of these habitats will require continued surveys.

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Fig. 1. Map of the study area in the Chukchi and northern Bering Seas and the surrounding area.

1. Introduction

The ranges of many marine fish species have moved poleward in response to recent warming temperatures (Mueter and Litzow, 2008; Nye et al., 2009; Kotwicki and Lauth, 2013; Wildes et al., 2022), which is impacting fisheries and ecosystems (Mueter and Litzow, 2008; Figueira and Booth, 2010; Hollowed et al., 2013). Distribution shifts caused by temperature often vary by ontogenetic stage (Morley et al., 2017; Barbeaux and Hollowed, 2018), because species may expand their range by multiple mechanisms, including movement of subadults and adults (Nye et al., 2009; Hill et al., 2016), or juveniles recruiting to new areas and remaining there as they grow (Rindorf and Lewy, 2006; Nye et al., 2009; Figueira and Booth, 2010).

Currents on the eastern Bering Sea (EBS; Fig. 1) shelf generally move from the south to the north to the Bering Strait (Stabeno et al., 2016). Net flow though the Bering Strait is from the Bering Sea into the Chukchi Sea (Woodgate, 2018) and currents continue northwards through the Chukchi Sea (Stabeno et al., 2018). Summer temperatures in the Bering and Chukchi Seas have increased in recent years (Stabeno and Bell, 2019; Danielson et al., 2020; Woodgate and Peralta-Ferriz, 2021). In the EBS, sea-ice coverage during winter and spring causes an area of cold (<2 °C) bottom water known as the cold pool, which persists through the summer (Wyllie-Echeverria and Wooster, 1998; Stabeno et al., 2001). The annual spatial extent of the cold pool varies with annual sea-ice extent and can extend far into the southeastern Bering Sea in cold years, or be limited to areas of the northern Bering Sea (NBS) in warm years (Overland et al., 2012; Stabeno et al., 2012). In recent decades, the Bering Sea has alternated between multi-year periods of cold and warm summer ocean bottom temperatures (Overland et al., 2012; Stabeno et al., 2012; Baker et al., 2020a), including a cold period from 2007 through 2013, and a warm period which began in 2014 (Stabeno and Bell, 2019). Temperatures of the Bering Sea inflow entering the Chukchi Sea during the summer have increased in recent years (Woodgate and Peralta-Ferriz, 2021), and temperatures on the Chukchi Sea shelf were historically high from 2014 to 2018 (Danielson et al., 2020).

The summer distribution of *Gadus macrocephalus* (Pacific cod in English or tikhookeanskaya treska in Russian, hereafter referred to as “cod”) shifted northward in the EBS during the recent warm period (Thompson, 2018; Stevenson and Lauth, 2019; Baker, 2021), likely in response to the spatial reduction of the cold pool in the EBS, and warmer summer bottom temperatures in the NBS (Stevenson and Lauth, 2019). Sub-adult and adult cod abundance increased by more than 900% in the NBS between 2010 and 2017 (Stevenson and Lauth, 2019). The size range of cod inhabiting the NBS has also changed: in 2010, the surveyed population was comprised of juvenile fish from 10 to about 35 cm fork length (FL), and also larger adults >60 cm FL, with few fish in the intermediate size range. However, in 2017, there was a continuous length distribution of cod from juveniles through adults (Stevenson and Lauth,

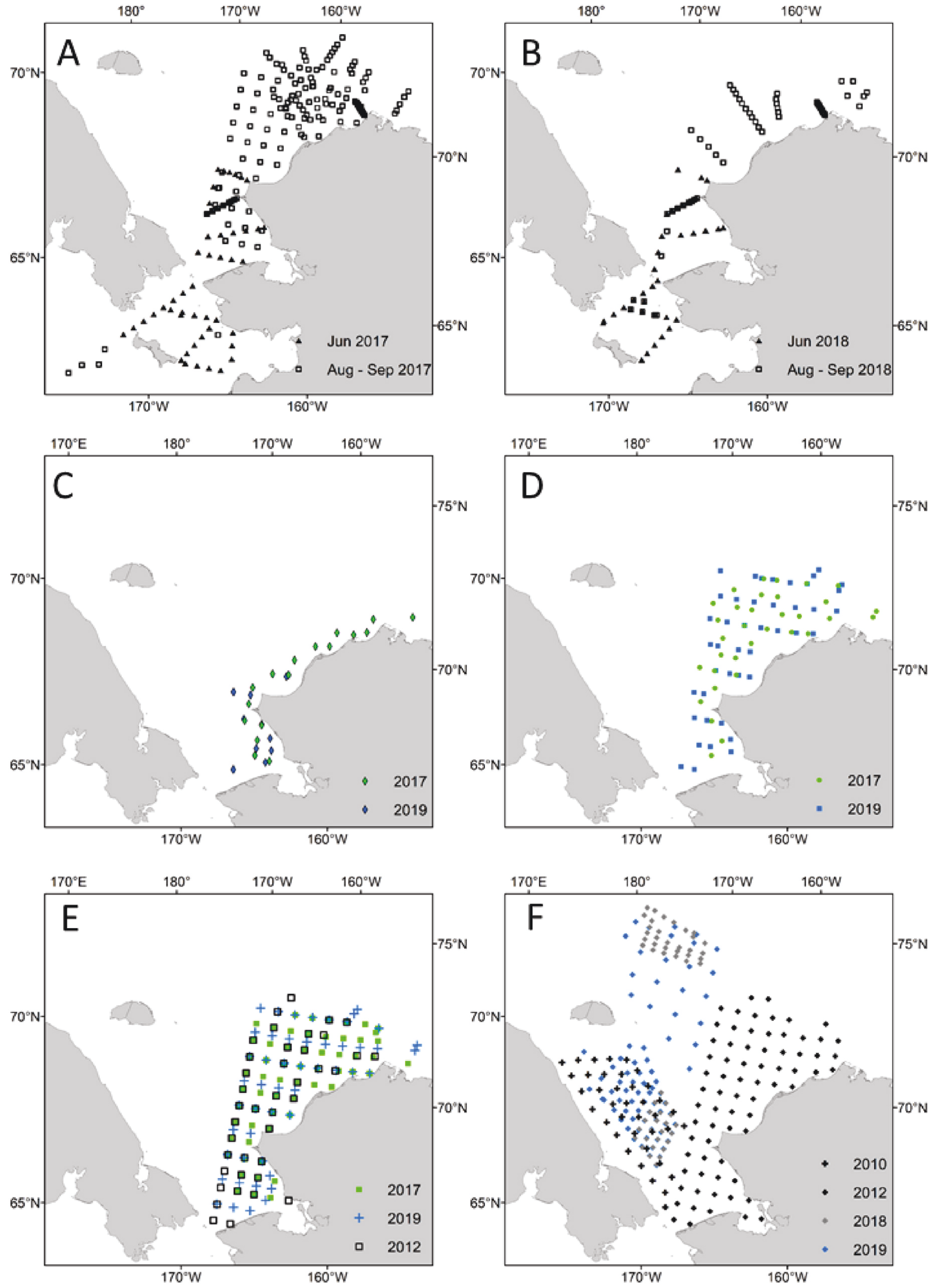

Fig. 2. Maps of sampling effort by gear type and year for A) larval nets in 2017, B) larval nets in 2018, C) surface trawl, D) midwater trawl, E) small-mesh benthic trawl, and F) large-mesh benthic trawls.

Table 1
Summary of trawling effort and number and presumed life stage of Pacific cod caught during each survey used in this study.

Year	Months	Trawl type	Mouth opening	Max. mesh (mm)	Min. mesh (mm)	No. stations	Chukchi Sea Region	Raw number (presumed age)
2010	Sep.	Large-mesh benthic	16.2 m horiz.	80	10	38	Western	0
2012	Aug.–Sep.	Large-mesh benthic	17.0 m horiz.	100	31	71	Eastern	4 (age-1)
2012	Aug.–Sep.	Small-mesh benthic	2.1 m horiz.	7	4	40	Eastern	0
2017	Aug.–Sep.	Surface	18 m horiz. X 24 m vert.	1620	12	17	Eastern	64 (age-0)
2017	Aug.–Sep.	Midwater	7.5 m horz. X 7.9 m vert.	64	30	33	Eastern	152 (age-0)
2017	Aug.–Sep.	Small-mesh benthic	2.1 m horiz.	7	4	60	Eastern	43 (age-0)
2018	Aug.–Sep.	Large-mesh benthic	16.2 m horiz.	80	10	54	Western	52 (age-1), 8 (adult)
2019	Aug.–Sep.	Surface	18 m horiz. X 24 m vert.	1620	12	10	Eastern	2 (age-0)
2019	Aug.–Sep.	Midwater	7.5 m horz. X 7.9 m vert.	64	30	42	Eastern	52 (age-0), 1 (adult)
2019	Aug.–Sep.	Small-mesh benthic	2.1 m horiz.	7	4	49	Eastern	7 (age-0)
2019	August	Large-mesh benthic	16.2 m horiz.	80	10	79	Western	51 (age-1), 4 (adult)

2019). In 2017, cod densities in the NBS were elevated near the Bering Strait (Stevenson and Lauth, 2019), which is at the southern border of the Chukchi Sea (Fig. 1), indicating that the population distribution may have continued into the unsampled southern Chukchi Sea. However, cod distribution and abundance have not been examined in the Chukchi Sea during the recent warm period, and the life stages and size distributions of any cod recently present in the Chukchi Sea are also unknown.

Juvenile cod have been documented in the Chukchi Sea (Barber et al., 1997; Mecklenburg et al., 2011, 2018; Logerwell et al., 2015) and Beaufort Sea (Andriashev, 1937; Rand and Logerwell, 2010), however, relatively few records exist and habitat of juvenile cod in the Chukchi Sea has not been examined (Mecklenburg et al., 2011). In the Chukchi Sea, the largest reported cod were 33 cm (Logerwell et al., 2015), 31 cm (Barber et al., 1997), and 17.6 and 8.7 cm total length (TL) (Mecklenburg et al., 2011), which are below the smallest known size of maturity for cod in the EBS or Gulf of Alaska (Stark, 2007). In the EBS, age-0 cod inhabit nearshore benthic habitat, or pelagic habitat in offshore deeper areas (Hurst et al., 2015). Because size and energetic storage are important factors contributing to the overwintering survival of juvenile marine fishes (Sogard, 1997; Hurst, 2007), it is unclear whether small boreal gadids such as cod can survive long periods of cold in low productivity habitats typical of the Chukchi Sea.

The juvenile cod observed in the Chukchi Sea may be sourced from larvae advected northward from the Bering Sea. Cod spawn in the EBS from March to mid-April as far north as the continental shelf break at about 60°N latitude (Neidetcher et al., 2014) and eggs likely remain at their spawned location because they are demersal (Thomson, 1963; Fadeev, 2005). Larvae become more buoyant at hatch (Laurel et al., 2010) and are typically in surface waters where they have been reported in the EBS from April through June (Matarese et al., 2003) and in the western Bering Sea (WBS) in June (Bulatov, 1986). Ocean currents during the larval period may carry larvae from the NBS to the Chukchi Sea through the Bering Strait. A mooring (A3) located just north of the Bering Strait (Fig. 1), provides hourly time series of ocean temperatures and currents from which estimates of the northward transport through the Bering Strait have been made (Woodgate, 2018).

The objectives of this study were to 1) investigate thermal and ocean transport conditions which could affect cod larvae transported between the NBS and Chukchi Sea; 2) describe cod distribution in the Chukchi Sea by life stage before (2010 and 2012) and during (2017, 2018, 2019) the recent period of warm summer ocean temperatures in the Chukchi Sea; and 3) understand the potential survival trajectories of age-0 cod in the Chukchi sea by comparing their habitat, size, diet and condition to juveniles collected farther south, in the Gulf of Alaska (GOA).

2. Methods

2.1. Bering Strait temperature and transport

Monthly averaged near-bottom temperatures in April through June from 1998 through 2019 measured at a subsurface mooring were used to investigate the thermal exposure of any cod larvae possibly in the Bering Strait during the larval period (Mooring A3 in Woodgate et al., 2015; Woodgate, 2018; Woodgate and Peralta-Ferriz, 2021). This mooring is located ~35 km north of the Bering Strait proper, at a point where water temperatures are considered to be a meaningful average of the water temperatures in the eastern and western sides of the Bering Strait (Woodgate, 2018). These measurements are made near bottom and represent the bottom layer (~30–40 m) of the water column. In April–June, sea surface temperatures are ~1–2 °C warmer than the near-bottom temperatures in the annual mean (Woodgate and Peralta-Ferriz, 2021; Woodgate, 2018, Fig. 1). Thus, depending on where they reside in the water column, larvae in April–June may be exposed to warmer (~1–2 °C) temperatures than considered here.

Estimates of water volume transport from the NBS to the Chukchi Sea during the larval period were obtained to investigate possible interannual differences in northward larval transport through the Bering Strait. Monthly-averaged northward transport estimates during April–June from 2000 to 2019 were calculated from the A3 mooring data (see Woodgate, 2018 for method), and an average transport value for April–June was calculated for each year.

2.2. Larval distributions

Larval Pacific cod were sampled in the Bering and Chukchi Seas during research cruises as part of the Arctic Shelf Growth, Advection, Respiration and Deposition (ASGARD) Rate Measurements Project, the Distributed Biological Observatory (DBO), and the Arctic Integrated Ecosytem Survey (AIES) funded by the North Pacific Research Board (NPRB) Arctic Integrated Ecosystem Research Program (AIERP; Baker et al., 2020b; 2023) in June 2017, June 2018, August–September 2017, and August–September 2018 (Fig. 2) using a paired 60-cm diameter bongo net (505-μm mesh) towed obliquely from the surface to 10 m off the bottom (see Deary et al., 2021 for a description of the sampling design for each survey). Samples were preserved at sea in 5% formalin buffered with sodium borate and seawater and identified to the lowest taxonomic level at the Plankton Sorting and Identification Center in Szczecin, Poland. Taxonomic verifications took place at the National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center in Seattle, WA, USA. Flowmeters (General Oceanics) attached to each net were used to calculate volume filtered for each net tow, enabling calculating catch per unit effort (CPUE) defined as (log[x+1]) where log is the natural log, and x is the number of individuals 10 m^{-2} (See Matarese et al., 2003). Hydrographic data were collected using a lowered conductivity-temperature-depth (CTD) profiler (SeaBird Electronics 911 plus) immediately prior to net deployments. Temperature (°C) measurements were averaged over the entire water column (deepest CTD cast was ~60 m) and nearest neighbor interpolated using the "gstat" package in R (version 4.1.2; R Core Team 2021).

2.3. *Juvenile and adult distributions*

Cod juveniles and adults were caught in several trawl types used for multi-species surveys in the eastern Chukchi Sea (ECS) and western Chukchi Sea (WCS) in cold years (2010 and 2012) and recent warm years (2017–2019; Table 1 and Fig. 2).

2.3.1. *Surface trawl*

A Nordic 264 Rope Trawl (NETS Systems) was deployed at nearshore stations during AIES surveys in the ECS in 2017 and 2019 (Table 1, Fig. 2). The rope trawl was 184 m long with non-uniform hexagonal mesh in the wings and body (maximum mesh size = 162 cm) and a 1.2 cm mesh liner in the codend. Tows were made at or near the surface for 30 min at 0.77–1.54 ms^{-1} (1.5–3 nautical miles $hour^{-1}$), and had typical trawl mouth openings of 20 m horizontally and 19 m vertically. All sampling was performed during daylight hours. CPUE was calculated as the number of fish divided by the surface area swept by the trawl. Surface area swept by the trawl was calculated as the width of the trawl opening multiplied by the distance fished. Distance fished was measured by Global Positioning System (GPS).

2.3.2. *Midwater trawl*

A modified-Marinovich midwater trawl (~34.5 m long, 12 m headrope, 6.4 to 1.8 cm mesh) with a 0.3 cm mesh codend liner was deployed during AIES surveys in 2017 and 2019 in the ECS to conduct targeted midwater hauls (Table 1, Fig. 2; De Robertis et al., 2017). Trawling location and depth were determined based on identification of strong scattering layers in shipboard acoustic data. CPUE of the midwater trawl was calculated as number of fish per trawl tow divided by the volume filtered by the trawl. Volume filtered was calculated as the trawl mouth opening multiplied by the distance fished. Distance fished was measured by GPS position. Net opening was measured using observation from a net sonar (Simrad FS70) placed on the headrope. For all hauls, the vertical net opening averaged 7.85 m (5.1–10.6 m range) and horizontal opening averaged 7.49 m (5–9.1 m range). Average headrope depth of midwater trawls was 32.1 m, ranging from 11.4 to 227.9 m, with an average ship speed during the tow of 1–1.5 m s^{-1}. Bottom depths of trawl locations ranged from 23 to 1130 m.

2.3.3. *Small-mesh benthic trawl*

A small-mesh benthic trawl was deployed in the ECS during the Arctic Ecosystem Integrated Survey (Arctic EIS) in 2012, and during AIES surveys in 2017, and 2019 (Table 1, Fig. 2). The trawl was a 3.05-m plumb staff beam trawl with a 7 mm mesh and 4 mm mesh codend liner (Gunderson and Ellis, 1986). In 2012, a tickler chain preceded the footrope (Gunderson and Ellis, 1986; Kotwicki et al., 2017). In 2017 and 2019, the tickler chain was removed, and the trawl was modified with a footrope of 10.2 cm rubber discs over a steel chain as in Abookire and Rose (2005). Mean trawl durations and ranges (minutes) were 2.9 (range = 2.8–7.4), 5.4 (range = 4.0–9.1), and 6.0 (range = 2.8–8.9) in 2012, 2017, and 2019, respectively. Targeted towing speed was 0.77 ms^{-1} (1.5 nautical miles $hour^{-1}$). CPUE was calculated as the number of cod in the trawl tow divided by the area swept by the trawl. Area swept by the trawl was the effective width of the trawl multiplied by the distance fished by the trawl. Effective trawl width of the trawl was assumed to be 2.26 m in 2012 (Gunderson and Ellis, 1986; Kotwicki et al., 2017), and 2.1 m in 2017 and 2019 (Abookire and Rose, 2005). Distance fished was measured as the distance between the locations that the trawl began and stopped contact with the bottom. Bottom contact was determined by HOBO G acceleration data logger (Onset Corp.) placed in a waterproof steel housing and hung from the footrope in a manner forcing the data logger to pivot when it contacted the bottom. Time stamps from the acceleration data logger were used to match the start and conclusion of trawl bottom contact with location from GPS data.

2.3.4. *Large-mesh benthic trawls*

A large-mesh benthic trawl (DT 27.1/24.4 bottom trawl; Zakharov et al., 2013) was deployed in the WCS in 2010, 2018, and 2019 (Table 1, Fig. 2). Trawl mesh was 8.0 cm in the wings and body, 6.0 cm in the intermediate, 3.0 cm in the codend, and the codend was equipped with a 10 mm mesh liner. Target trawl speed was ~1.5 ms^{-1} (3 nautical miles per hour) for a target duration of 30 min. CPUE was calculated as the number or weight of cod in the tow divided by the area swept by the trawl. Area swept by the trawl was calculated as the horizontal opening of the trawl (16.2 m) multiplied by the distance fished by the trawl. Distance fished was the distance between the locations that the trawl began and stopped contact with the bottom.

The large-mesh benthic trawl deployed in the ECS in 2012 (Table 1, Fig. 2) as part of the Arctic EIS survey was an 83–112 Eastern Trawl (Stauffer, 2004). Deployment of the trawl in 2012 is described by Kotwicki et al. (2017). The trawl horizontal opening was approximately 17 m. Stretched mesh size was 10.2 cm in the wings and body, 8.9 cm in the intermediate and codend, and the codend was equipped with a 3.2 cm mesh liner. Target trawl speed was ~1.5 ms^{-1} (3 nautical miles per hour) for a target duration of 15 min. CPUE was calculated as the number of cod divided by the area swept of the trawl. Area swept was calculated as the distance fished multiplied by the width of the trawl opening. Width of the trawl opening was measured with acoustic net mensuration sensors (Marport Deep Sea Technologies, Inc.). Distance fished was measured as the distance between the locations that the trawl began and stopped contact with the bottom.

2.3.5. *Gulf of Alaska small-mesh demersal seine*

Age-0 juvenile cod were collected in August of 2017 during the annual summer nearshore seine survey on Kodiak Island to compare condition to those collected in the ECS in 2017. The GOA survey uses a 36 m demersal bag seine with 1 m wide seine wings at the ends expanding to 2.25 m in the middle. The mesh size was 13 mm within the wings and 5 mm in the bag-end. The seine wings were attached to 25 m ropes for deployment using a small boat and was set parallel to shore at a distance of 25 m away and then retrieved by two people standing on the shore, effectively sampling ~900 m^2 of bottom habitat (see more details in Laurel et al., 2007).

2.4. *Trawl survey temperatures*

Bottom temperatures were recorded at each station for the small- and large-mesh benthic trawls in the ECS using an SBE-39 (Seabird Scientific, Inc.) temperature sensor attached to the trawl headrope. Bottom temperatures in the WCS were recorded with either an SBE-19 or SBE-25 temperature sensor from CTD cast conducted at the trawl location. Gear temperatures for the surface and midwater trawls were measured with CTD casts taken with an SBE 911 plus. Near surface temperatures were used for the surface trawl, and temperatures averaged over the depth range between the trawl headrope and footrope at the targeted trawl depth were used for the midwater trawl. CTD casts were co-located with surface trawl tows; however, midwater trawl tows were opportunistic and temperatures were obtained from the nearest CTD cast (the same sampling grid as for the small-mesh benthic trawl each year; Fig. 2).

2.5. Fish length and length-based age classification

In the surface, midwater, and small-mesh benthic trawls, cod were measured to the nearest millimeter at sea. In 2017, TL was measured, and in 2019, one large fish was measured to FL, and the smaller fish were measured to standard length (SL). For comparison with laboratory data and other studies of age-0 fish, lengths of juveniles were converted to SL. To compare sizes of the juvenile cod with larger cod caught with the large-mesh trawls, lengths of juvenile fish were converted to FL. Lengths of juvenile fish were converted between length types using length data provided by Oregon State University, the AFSC's Auke Bay Laboratories and RACE Division's Midwater Assessment and Conservation Engineering program for fish within the same size range as the observed fish. The conversion factors were SL = TL(0.902) + 1.284 (based on 120 samples up to 110 mm in length) and SL = FL(0.952) - 0.663 (based on 11 samples up to 78 mm in length). Cod caught in both large-mesh benthic trawls were measured at sea to the nearest cm FL.

The length mode (49–103 mm FL) of small juveniles caught in the ECS in the small-mesh benthic, midwater, and surface trawls was similar to reported lengths of age-0 fish in the EBS during the summer (Hurst et al., 2012a, 2015) and these fish will be referred to as age-0 for this study. The larger length mode of juveniles (100–230 mm FL) caught in the large-mesh benthic trawls in the ECS and WCS were smaller than age-1 fish in the Gulf of Alaska during the summer (150–250 mm TL; Laurel et al., 2016a); however, they are assumed to be age-1 based on length mode analysis (they were larger than the mode of age-0 fish), and will be referred to as age-1 fish for this study. There was an overlap in the size ranges of the age-0 and age-1 fish (100–103 mm FL); however, the size range contained only 3% of the fish in this study. Zero fish between 230 mm and 550 mm FL were caught in this study. The larger cod (550–780 mm FL) caught in this study are greater than the size of 50% maturity for cod from the EBS and GOA (Stark, 2007) and are referred to as adults for this study.

2.6. Age-0 diets

Diets of the age-0 cod caught in the ECS in 2017 were analyzed by capture trawl type (small-mesh benthic, midwater, and surface trawls) to investigate whether the age-0 cod captured in different parts of the water column used different prey resources. Sample sizes were 40 fish from 10 stations in the small-mesh benthic trawl, 28 fish from 6 stations in the midwater trawl, and 40 fish from 5 stations in the surface trawl. Fish were frozen at sea. Stomachs were dissected in the laboratory and stored in 10% formalin to fix stomach contents. Stomach contents were sorted to lowest practical taxonomic resolution and developmental stage (as appropriate) and weighed to the nearest 0.01 μg, and counted.

To determine prey importance in the age-0 cod diets in each type of trawl, we used the percentage of the prey-specific index of relative importance (%PSIRI) (Brown et al., 2012). %PSIRI is calculated using frequency of occurrence (FO), prey-specific count (%PN_i), and prey-specific weight (%PW_i), which were calculated using the following equations:

Frequency of occurrence (%FO):

$$\%FO_i = \frac{n_i}{n}$$

Prey-specific count (%PN):

$$\%PN_i = \sum_{j=1}^{n} \%N_{ij} / n_i$$

Prey-specific weight (%PW_i):

$$\%PW_i = \sum_{j=1}^{n} \%W_{ij} / n_i$$

where %N_{ij} is the proportional count (PN_i) and %W_{ij} is the proportional weight (PW_i)) of prey category i in stomach sample j; n_i is the number of stomachs containing prey i, and n is the total number of stomachs.

The %PSIRI was then calculated:

$$\%PSIRI_i = \frac{\%FO_i * (\%PN_i + \%PW_i)}{2}$$

%PSIRI was calculated for prey items at the lowest practical taxonomic resolution, and also for prey items grouped by the following prey habitat types: endobenthic, epibenthic, hyperbenthic, planktonic, or various (see Ferm et al., 2021 for a description, and a list of the habitat type for each prey taxon in the supplemental materials). Each prey item was assigned a prey habitat type based on a literature search.

The symmetric niche overlap coefficient (Pianka, 1973), was calculated to determine whether there was niche overlap among the diets of cod caught in the different trawl types using:

$$O_{kl} = \frac{\sum_{i}^{n} p_{il} p_{ik}}{\sqrt{\sum_{i}^{n} p_{il}^2 \sum_{i}^{n} p_{ik}^2}}$$

where O_{kl} is the resource overlap index between capture trawl type k and l, and p_{il} is the proportion of resource i that is used by capture trawl type l.

This resource overlap index produces values from 0 to 1, where 0 indicates that no resources are shared and 1 indicates complete shared resource utilization between the cod collected in different trawl types. To test whether the observed diet differences between pairs of trawl types were significantly different (null hypothesis was there was no difference), we used the niche overlap methods in the EcoSimR package. The package first created a matrix of prey weights (columns) by trawl type at each station (rows). This matrix of prey weights was randomly shuffled 2000 times by row using the RA3 (default) algorithm in the EcoSim R package. For each randomization, the O_{kl} value was calculated. The actual calculated O_{kl} values observed for each trawl pair were compared to the histogram of O_{kl} values from the 2000 randomized data sets, and the diet difference between the trawl types was considered statistically significant when the actual O_{kl} values were outside the 95% percentile of the histogram of O_{kl} values from the randomized data. All data analyses were conducted using R statistical analysis software (R Core Team, 2020).

2.7. Age-0 condition

One-hundred and seventeen age-0 cod collected in the ECS in 2017 and 30 age-0 fish from the annual August GOA beach seine survey in 2017 were saved for condition analyses. Fish from the four different gear types described above, small-mesh benthic (n = 45), midwater (n = 31), surface trawls (n = 41) and the GOA beach seines (n = 30) were frozen immediately at −20 °C and maintained at −80 °C at the land-based laboratory. Samples were frozen and shipped overnight from Alaska to the Marine Lipid Ecology Laboratory at Oregon State University's Center for Marine Ecosystem and Resources Studies facility at the Hatfield Marine Science Center in Newport, OR, USA. Samples were stored at −80 °C and dissected within 6 months of capture. At the laboratory, all fish were measured to SL (±0.1 mm) and wet weight (WWT; ±0.0001 g). All of the fish from the Chukchi Sea and 18 of the 30 fish from the GOA were used in the biochemical analysis. For these fish, intestinal tracts were removed and fish were washed with filtered seawater, blotted dry, and heads were removed for later otolith analysis. Fish were bisected along a dorsal ventral plane and half of the tissues were frozen

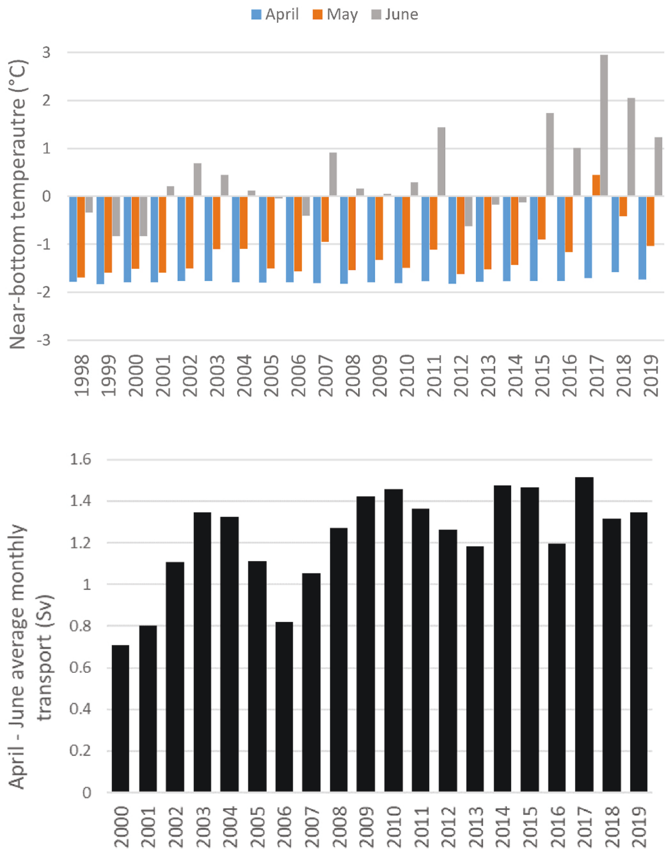

Fig. 3. Environmental measurements from the A3 mooring north of the Bering Strait. Monthly-averaged near bottom temperatures in April–June from 1998 through 2019 (Top panel) and mean of average monthly northward transport from April–June in 2000–2019 (Bottom panel).

for other analyses while half of the body tissues were placed in chloroform under nitrogen until extraction, within 1 month of sampling.

Cod tissues were homogenized in 2:1 chloroform:methanol according to Parrish (1987) using a modified Folch procedure (Folch et al., 1956). Lipid extracts were derivatized through acid trans-esterification using a Hilditch Reagent, H_2SO4 in MeOH as described in Budge et al. (2006). Fatty acid methyl esters (FAMEs) formed in the reaction were analyzed on an HP 7890 GC FID equipped with an auto-sampler and a DB wax + GC column (Agilent Technologies, Inc.). The column length was 30 m with an internal diameter of 0.25 mm and a film thickness of 0.25 μm. The column temperature profile was as follows: 65 °C for 0.5 min, hold at 195 °C for 15 min after ramping at 40 °C min^{-1}, and hold at 220 °C for 1 min after ramping at 2 °C min^{-1}. The carrier gas was hydrogen, flowing at a rate of 2 ml min^{-1}. Injector temperature was set at 250 °C and the detector temperature was constant at 250 °C. Peaks were identified using retention times based upon standards purchased from Supelco (BAME, PUFA 1, 37 component FAME, PUFA 3). Nu-Check Prep GLC 487 quantitative FA mixed standard was used to develop correction factors for individual FAs. Chromatograms were integrated using Chem Station (version A.01.02, Agilent). Total fatty acids were expressed in relation to fish WWT (g) to give an index of total acyl lipid storage.

Regressions between $\log_{10}$ (SL) and $\log_{10}$ (WWT) as well as $\log_{10}$ (SL) and fatty acid concentrations (mg/g) were run as indices of morphometric- and lipid-based condition, respectively. Residuals from these relationships were compared between the GOA and ECS using a two-sample *t*-test.

3. Results

3.1. Bering Strait temperature and transport

Monthly-averaged near-bottom water temperatures in the Bering Strait in April were consistently cold throughout the time series, ranging from −1.58 to −1.89 °C (Fig. 3). Both temperature and inter-annual temperature variability increased in May, although May near-bottom temperatures remained below 0 °C for all years except 2017 (Fig. 3). Inter-annual temperature variability increased in June, with monthly averaged temperatures ranging from −0.83 to 2.95 °C. Any larvae transported northward though the Bering Strait in June 2012 would have been exposed to temperatures of about 0.5–1.5 °C (near bottom temperature of −0.5 °C plus 1–2 °C warmer in the water column). June

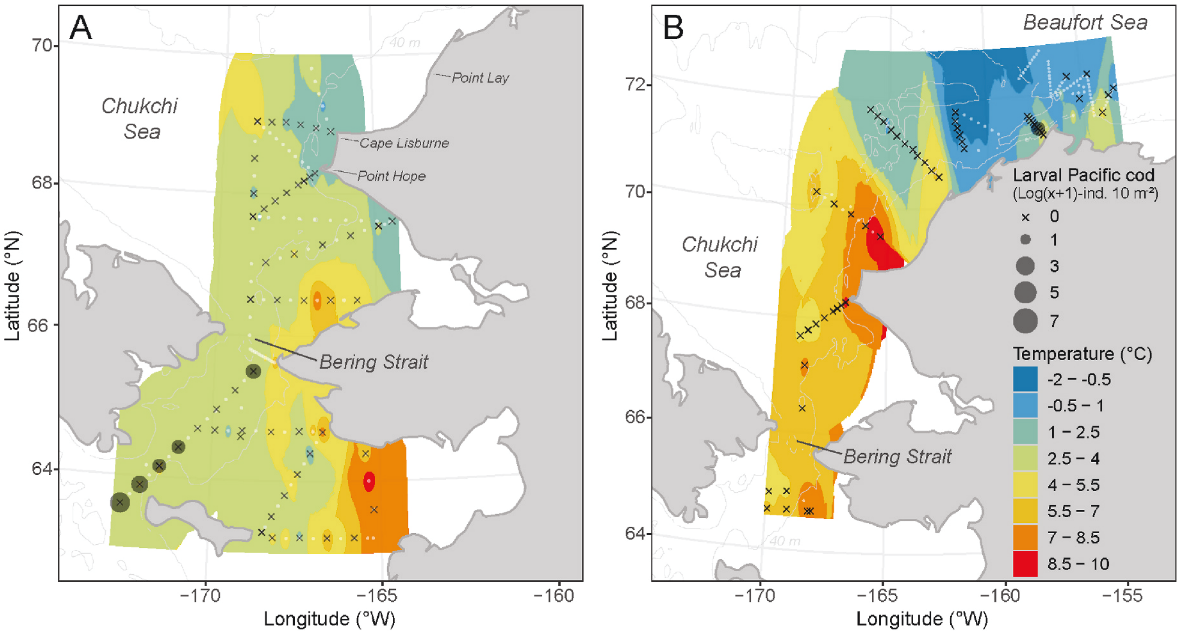

Fig. 4. Maps of larval Pacific cod CPUE and interpolated mean water column temperatures in A) June 2017 and B) August 2018. CPUE is in units of log[x+1], where x is the number of individuals per 10 m^{-2}, and shown with black circles. Black x's indicate zero catch and white circles indicate CTD station locations.

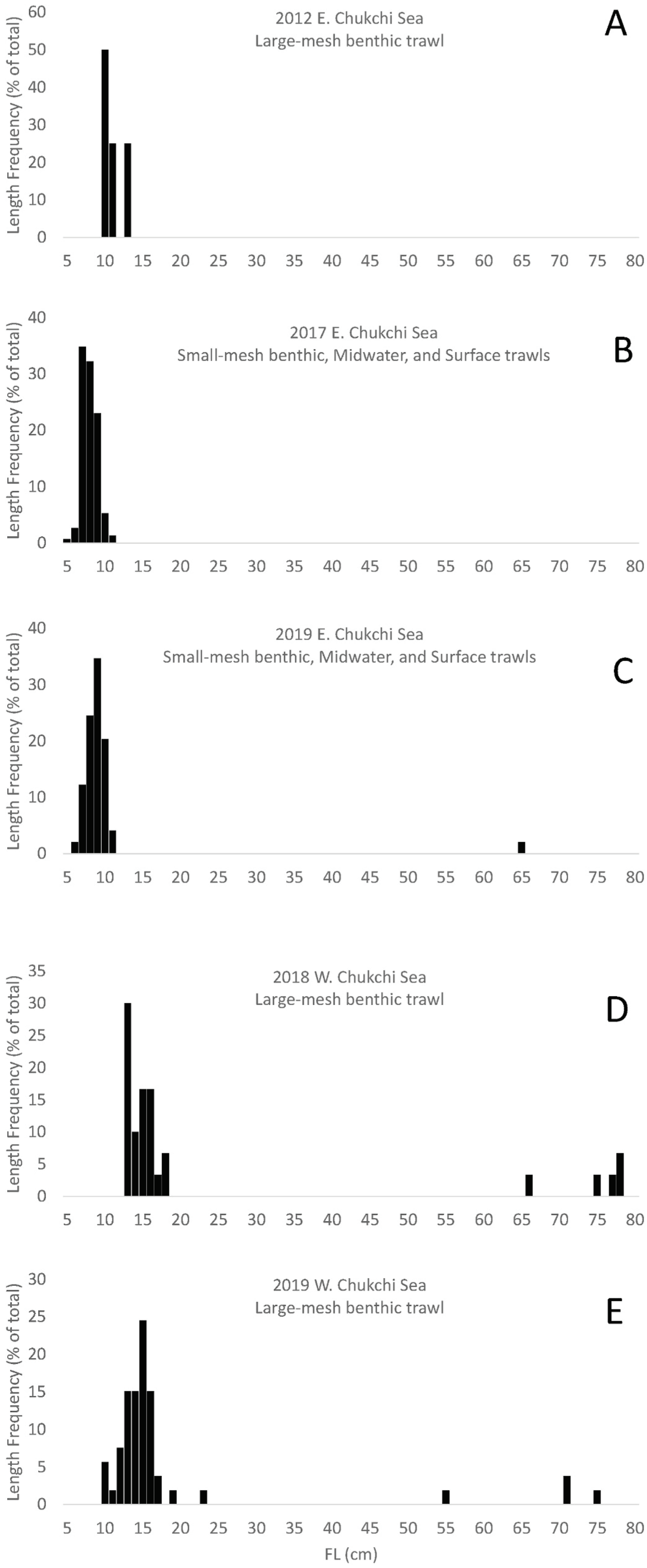

Fig. 5. Length frequency distributions for Pacific cod caught in the Chukchi Sea in: A) 2012 in a large-mesh trawl in the eastern Chukchi Sea, B) 2017 in three trawls (small-mesh benthic trawl, midwater trawl, and surface trawl) in the eastern Chukchi Sea, C) 2019 in three trawls (small-mesh benthic, midwater, and surface) in the eastern Chukchi Sea, D) 2018 in a large-mesh benthic trawl in the western Chukchi Sea, and E) 2019 in a large-mesh-benthic trawl in the western Chukchi Sea.

near-bottom temperatures from 2015 to 2019 were among the highest in the time series. Larvae in June would have been exposed to temperatures of ~4–5 °C in 2017 and ~2.3–3.3 °C in 2019.

Net northward transport from the NBS to the Chukchi Sea averaged over the larval period (April–June) increased over the past two decades from ~0.7 Sv (1Sv = $10^6 m^3 s^{-1}$) in 2000 to ~ 1.5 Sv in 2017, the record maximum (Fig. 3).

3.2. *Larval distributions and temperatures*

Pacific cod larvae were present in the NBS near the Bering Strait in June 2017 at sites where water temperatures ranged from 2.6 to 3.7 °C on average (Fig. 4A) and in the northeastern Chukchi Sea in August 2018 where temperatures ranged from 1.3 to 2.5 °C (Fig. 4B). Larvae were absent in August 2017 and June 2018. Larvae caught in June 2017 were 8–14 mm SL, and the single larva caught in the northeastern Chukchi Sea was 8 mm SL.

3.3. *Age-0 cod in the ECS*

3.3.1. *Distribution and temperature*

Age-0 cod ranging in length from 45 to 94 mm SL (49–103 mm FL) were caught in the surface, midwater, and small-mesh benthic trawls in 2017 and 2019 in the ECS (Fig. 5). Age-0 cod were absent from the ECS in 2012; however, the only trawl type deployed in 2012 capable of catching small juveniles was the small-mesh benthic trawl. Detailed results are reported by trawl type.

In 2017, age-0 cod were present in the surface trawl catch at one station near Point Lay, and at several stations from the vicinity of Cape Lisburne to the southern end of the survey area (Fig. 6A). In 2019, age-0 cod were caught only at the most northerly surface trawl station, between Point Lay and Cape Lisburne (Fig. 6B). Surface temperatures where age-0 cod were present in the surface trawl ranged from 5.0 to 6.2 °C in 2017, and surface temperature was 9.3 °C at the one station with age-0 presence in 2019. In both years, age-0 cod were present at stations near the median temperatures of all available surface trawl stations (Fig. 7). Bottom temperatures at stations where age-0 cod were caught in the surface trawl were slightly colder than surface temperatures (range = 4.1–5.6 °C) in 2017; however, bottom temperature was slightly warmer at the one station with age-0 presence in 2019 (Fig. 7).

In 2017, age-0 cod were present in the midwater trawl catch at stations from offshore of Point Lay south to the vicinity of Point Hope (Fig. 6C). In 2019, the observed distribution of age-0 cod shifted north, with absences near Point Hope and Cape Lisburne, and presences north of Point Lay (Fig. 6D). Age-0 cod were present in the midwater trawl catch at stations with gear temperatures ranging from 4.6 to 6.7 °C and 2.3–10.0 °C in 2017 and 2019, respectively. Age-0 cod were almost exclusively caught in the midwater trawl at locations warmer than the median temperature of all midwater trawls (Fig. 7). At stations with age-0 presence, bottom temperatures were colder than the midwater gear temperatures, however, generally by less than 1 °C (Fig. 7).

In 2012, age-0 cod were absent at all 40 stations sampled with the small-mesh benthic trawl (Fig. 8A). In 2017, age-0 cod were present at 11 of 59 sampled stations, from offshore of Point Lay south to the southern edge of the sampling grid, including at 7 stations which had been sampled in 2012 (Fig. 8B). CPUEs at stations with fish presence in 2017 ranged from about 1350 to 46,000 age-0s km^{-2}. In 2019, age-0 cod were present at 4 of 49 sampled stations, at CPUEs ranging from about 1700 to 7100 age-0s km^{-2} (Fig. 8C). Age-0 cod were present in bottom temperatures ranging from 2.5 to 5.9 °C and 4.4–9.5 °C in 2017 and 2019, respectively. Station bottom temperatures during the 2017 and 2019 surveys ranged from below 0 °C in the northern part of the survey area to near or exceeding 10 °C in the inshore and southern part of the survey grids each year (Figs. 7 and 8). In the mooring data, June temperatures in the Bering Strait were colder in 2012 than in 2017 and 2019 (Fig. 3), and summer bottom temperatures were colder in the northern

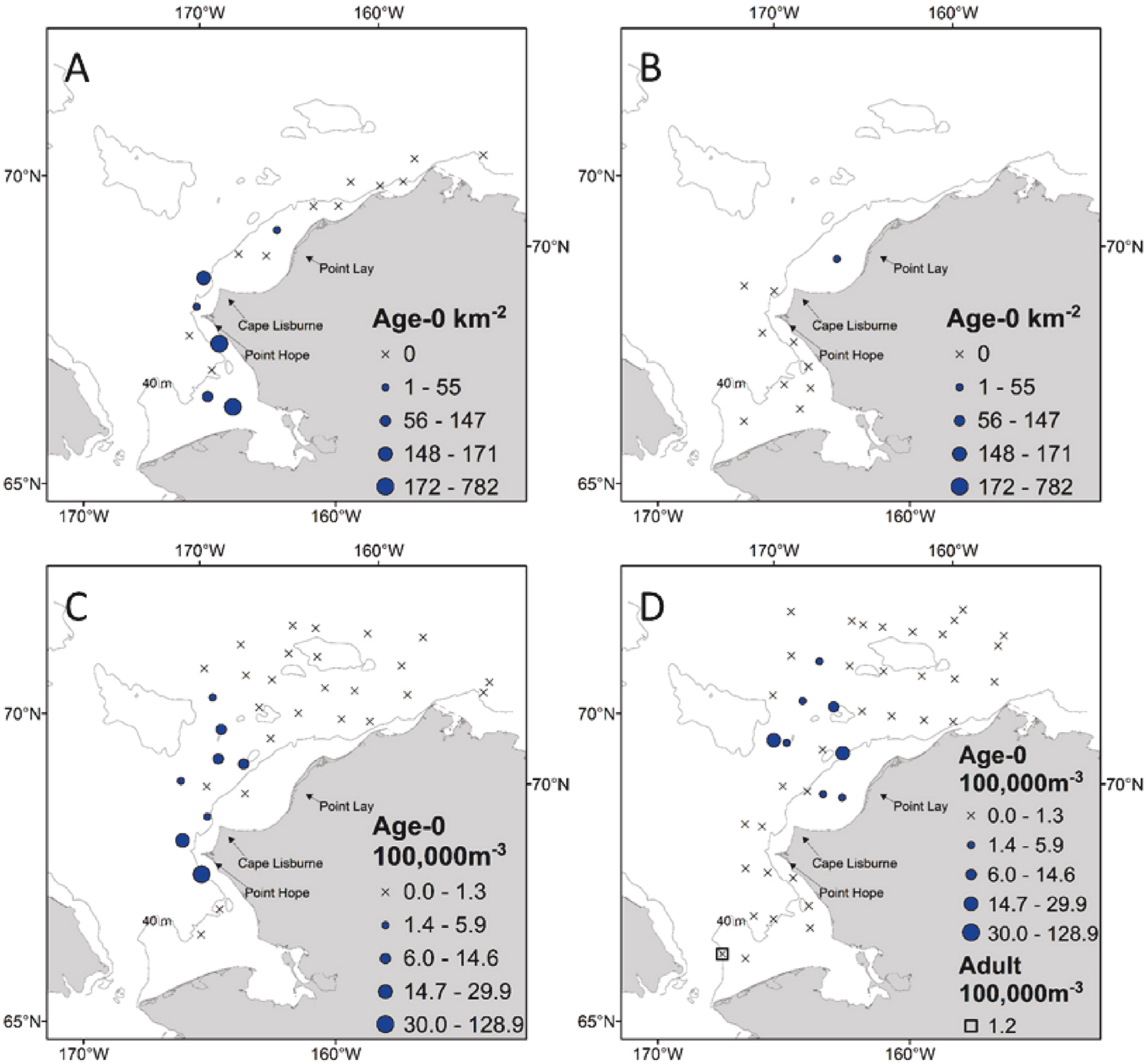

Fig. 6. Distribution and catch per unit effort of age-0 Pacific cod caught in: A) the surface trawl in 2017; B) the surface trawl in 2019; C) the midwater trawl in 2017; D) the midwater trawl in 2019.

and offshore stations in 2012 than in 2017 and 2019 (Fig. 8). However, bottom temperatures at the southern and nearshore stations with age-0 cod presence in 2017 were generally warmer in 2012 than in 2017 (Fig. 8), and the range of available bottom temperatures surveyed by the bottom trawl in 2012 included the temperature range where age-0 cod were present in 2012 and 2019 (Fig. 7).

3.3.2. Age-0 catch rates by depth

Catch rates of age-0 cod by bottom depth varied by gear type in a similar pattern each year (Fig. 9). The highest catch rates in the small-mesh benthic trawl were between 20 and 29 m and 30–39 m bottom depth in 2017 and 2019, respectively, and in both years, catch rates were lower at depths greater than 40 m. In contrast, the highest catch rates in the midwater trawl were at greater bottom depths; between 40 and 59 m in 2017, and between 40 and 49 m in 2019. Catch rates in the surface trawl were highest in the 20 – 29 m bottom depth range, however, the surface trawl was fished only at nearshore station and most surface trawls occurred over relatively shallow bottom depths.

3.3.3. Age-0 diet by gear type

Age-0 cod collected in all the surface, midwater, and small-mesh benthic trawls in 2017 consumed a variety of prey taxa (Table 2, Fig. 10). Copepods were the most important (importance measured by % PSIRI) prey taxa for fish collected in all three gears (Fig. 10), with benthic-caught fish primarily consuming the epibenthic calanoid copepod species *Eurytemora herdmandi* (PSIRI = 13.55%), while the surface- and midwater-caught fish primarily consumed various pelagic calanoid copepods (PSIRI = 70.54% and 26.40% for the surface and midwater trawls, respectively). The benthic-caught age-0 cod also consumed near equal percentages of a taxonomically-broad suite of prey items; including benthic prey taxa such as polychaetes, benthic amphipods, benthic decapods, and benthic cnidarians (anemones). The most important prey taxa for the pelagic-caught fish, after calanoid copepods, were decapods for the surface trawl-caught fish, and fish (unidentified Gadidae) and decapods for the midwater trawl-caught fish. The niche overlap indices for diets of age-0 cod caught in the benthic and pelagic trawls were low (benthic and midwater = 0.01, benthic and surface = 0.08), indicating little overlap in diets, although only the difference between the benthic and midwater values was statistically significant (P = 0.0175), and there was somewhat higher overlap for the diets of the two pelagic trawls (surface and midwater = 0.2). Grouped by general habitat classifications, prey of the pelagic-caught fish were almost entirely pelagic or unknown, while the benthic-caught fish also consumed endo-, epi-, and hyper-benthic prey (Fig. 10).

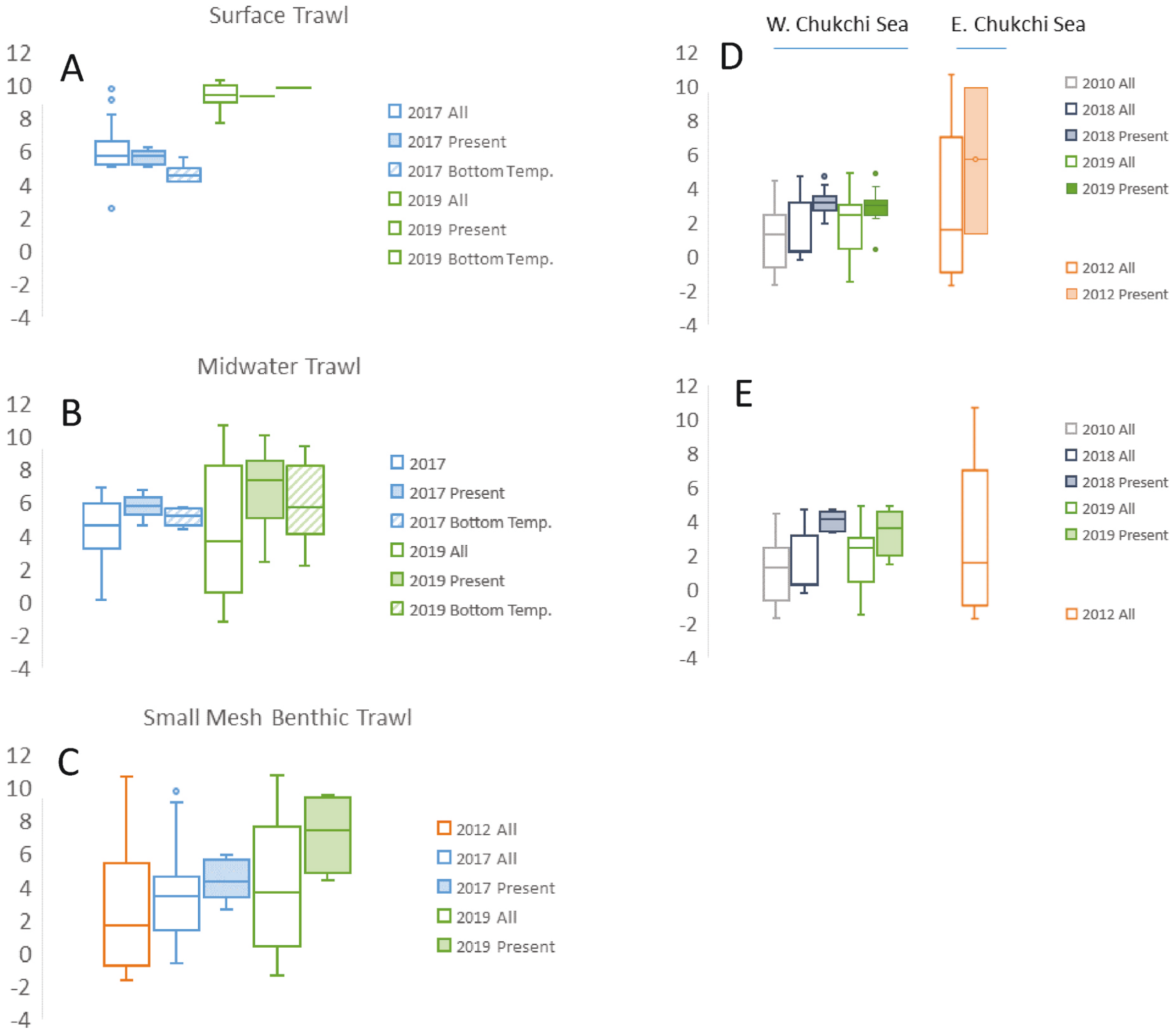

Fig. 7. Boxplots of water temperatures at trawl stations in the Chukchi Sea by trawl type and year: A) surface trawl for age-0 Pacific cod sampling, B) midwater trawl for age-0 Pacific cod sampling, C) small-mesh benthic trawl for age-0 Pacific cod sampling, D) Large-mesh benthic trawl for age-1 Pacific cod sampling and E) Large-mesh benthic trawl for adult Pacific cod sampling. Open boxplots represent gear temperatures at all sampled stations. Filled boxplots represent gear temperatures at stations with Pacific cod presence. Striped boxplots represent bottom temperatures at stations where Pacific cod were present in pelagic (surface and mid-water) trawls.

3.3.4. Age-0 condition: ECS versus Goa

Two measures of condition, length-weight residuals and total fatty acid concentration, were compared between age-0 cod from the ECS and the nearshore GOA (Fig. 11). Age-0 cod from the GOA were longer and heavier than age-0 cod from the ECS even though they were collected in August compared to fish collected in September in the ECS. Fish from the GOA in August averaged ~80 mm SL and weighed 5 g while fish from the ECS were ~67 mm SL and 3 g. The residuals from the log-length and log-weight relationship demonstrated that fish from the GOA were heavier at a given length than fish from the ECS. Total fatty acids per WWT did not increase with length ($r^2 = 0.02$). The residuals from the length to total fatty acids relationship showed that fish from the GOA had a higher concentration of fatty acids per WWT at a given length than fish from the ECS ($p < 0.001$). Both morphometric condition and that based on length-lipid concentration showed that fish from the GOA were in better condition at the end of the summer/fall than fish from the ECS.

3.4. Age-1 and adults

3.4.1. WCS distributions and temperatures

Cod were absent from the trawl sampling in the WCS in 2010 (Fig. 12). Both age-1 juveniles and adults were present in the WCS in 2018 and 2019 (Fig. 12). In both years, there was a length mode of juveniles (assumed to be age-1), from 130 to 180 and 100–230 mm FL in 2018 and 2019, respectively, and larger adult-sized fish, from 660 to 780 and 550–750 mm FL in 2018 and 2019, respectively (Fig. 5). Although there were two juveniles larger than 180 mm FL in 2019, there was little evidence of a new length mode of fish greater than 180 mm FL in 2019, and these two fish are also assumed to be age-1. CPUEs of age-1 cod at stations where they were present ranged from 23 to 133 and 9–95 fish km^{-2} in 2018 and 2019, respectively. A total of five adult cod were caught in 2018 and four in 2019. Estimated densities of adult-sized fish, where they were present, ranged from 12 to 24 and 10–22 fish km^{-2} in 2018 and 2019, respectively. CPUEs by weight for the age-1 and adults combined at stations where they were present, and in units for comparison with previous reports in the Bering Sea were 0.004–1.54 and 0.0018–1.073 kg/ha in 2018 and 2019, respectively.

Bottom temperatures where cod were present ranged from 1.9 to 4.7 °C and 3.3–4.7 °C for age-1s and adults, respectively in 2018 (Fig. 7), and from 1.4 to 4.9 °C and 0.4–4.9 °C for age-1s and adults, respectively in 2019 (Fig. 7). Although 2010 was a year with cold temperatures in the Bering Strait in June (Fig. 3), much of the sampled area in the southwestern Chukchi Sea in 2010 was within the bottom temperature range that contained cod in 2018 and 2019 (Figs. 7 and 12).

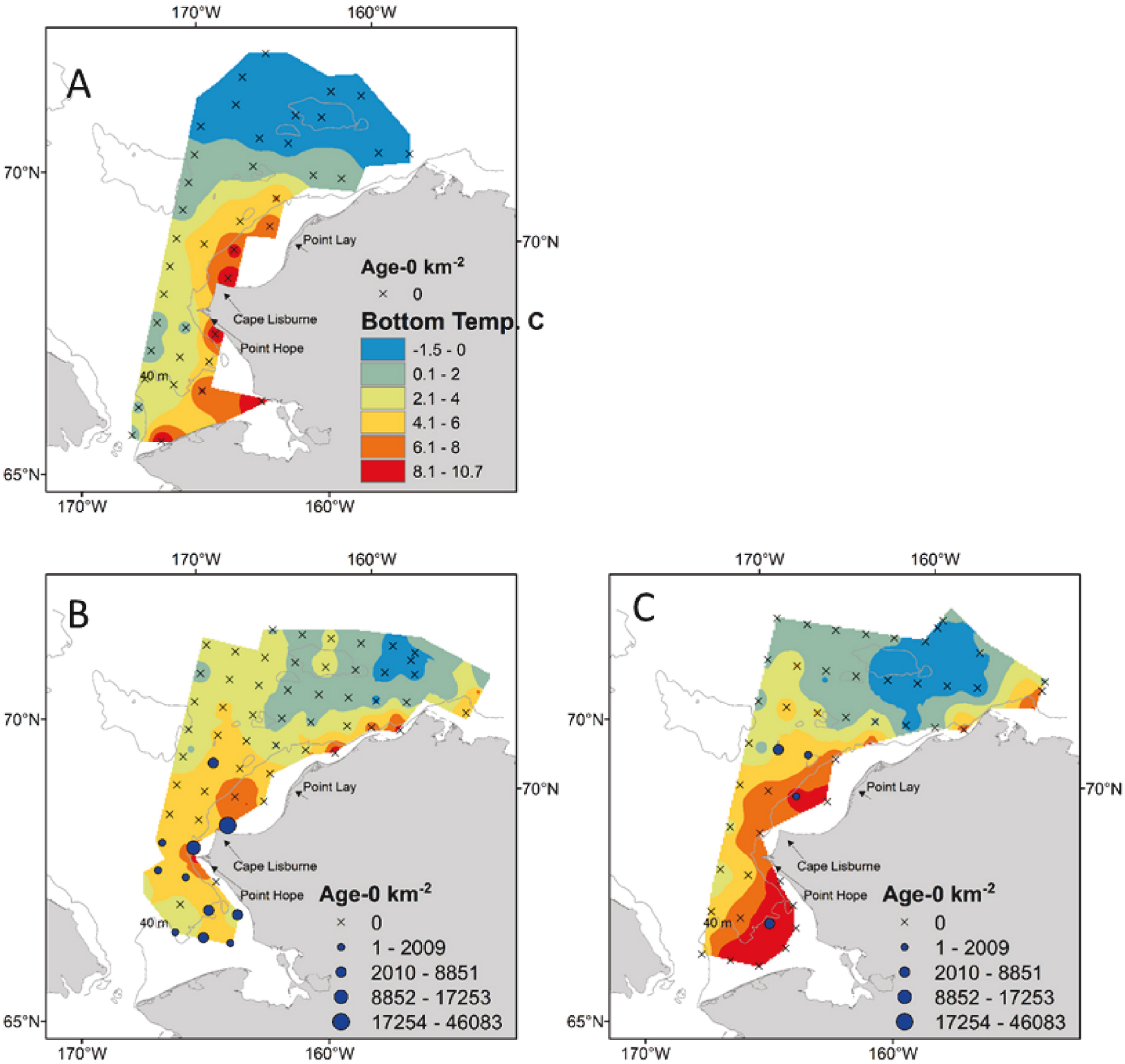

Fig. 8. Maps of catch per unit effort of age-0 Pacific cod caught in the small-mesh benthic trawl and interpolated bottom temperatures for three survey years: A) 2012; B) 2017; and C) 2019. Note the colors representing interpolated bottom temperatures are the same for all three plots.

3.4.2. ECS distributions and temperatures

Age-1 cod were present at three stations in 2012 in the large-mesh benthic trawl in the ECS (Fig. 12). These age-1s ranged in size from 100 to 130 mm FL (Fig. 5), and CPUE from 44 to 106 fish km^{-2}. Adults were absent at all stations in the ECS in 2012.

Bottom temperatures where age-1 cod were present in 2012 in the large-mesh benthic trawl sampling ranged from 1.3 to 9.9 °C (Fig. 7). Similar to 2010 in the WCS, 2012 was a year with cold June water temperature in the Bering Strait, (Fig. 3); however, much of the sampled area in the shallow southeastern Chukchi Sea in 2012 was as warm as or warmer than areas with age-1 and adult presence in the WCS in 2018 and 2019 (Figs. 7 and 12).

In addition to the age-0 cod caught in the midwater trawl (section 3.3.1), one much larger (64.7 cm FL) adult was caught using the midwater trawl during a tow that fished near the benthos at the southern end of the survey area in 2019 (Fig. 6).

4. Discussion

Age-0 cod were absent from the Chukchi Sea in a cold year (2012) and present in recent warm years (2017 and 2019) of this study. Increased temperatures could explain the age-0 cod presence in the Chukchi Sea though several mechanisms, including increased temperature-dependent larval growth and survival near the Bering Strait, increased springtime transport through the Bering Strait, and/or more larvae arriving at the Bering Strait due to changes in the EBS.

Warmer springtime temperatures in the NBS possibly led to age-0 cod presence in the Chukchi Sea in recent warm years. In 2012, a cold year, larvae near the Bering Strait in June would have been exposed to cold (estimated ~0.5–1.5 °C) water. The growth of cod larvae is highly temperature-dependent and survival in the laboratory is reduced at 2 °C (Hurst et al., 2010). Unfed yolksac larvae can survive lower temperatures (e.g., 0 °C), but growth and development rates are very slow (Laurel et al., 2008) and hatch success is poor (Laurel and Rogers, 2020). It is therefore unlikely that eggs and larvae have historically occupied these Arctic regions where juveniles have recently been observed. We note that larvae were observed near the Bering Strait in June in a warm year (2017), which would have likely contributed to better larval survival and increased presence of age-0 fish in the Chukchi Sea in 2017 and 2019. Warm June temperatures at the Bering Strait also occurred in a previous year (2007) when age-0-sized cod were observed in the Chukchi Sea (Mecklenburg et al., 2011).

The observed higher springtime transport in recent warm years could also contribute to age-0 presence in the Chukchi Sea. Larvae were

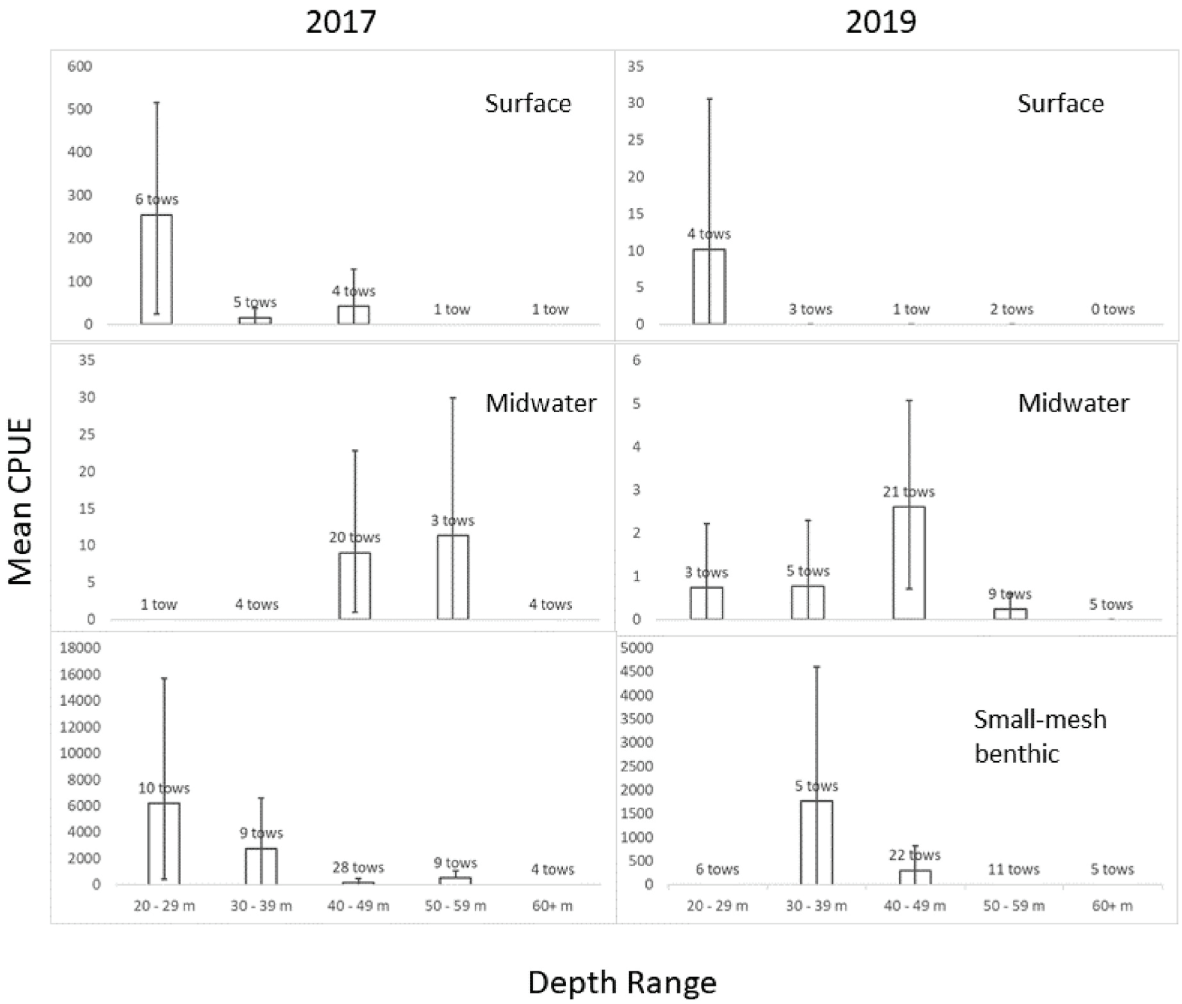

Fig. 9. Mean catch per unit effort (CPUE) of age-0 fish by bottom depth range for each gear type in 2017 and 2019. CPUE units are number of fish per km^2 for the surface and small-mesh benthic trawls, and number of fish per 100,000 m^3 for the midwater trawl. Error bars represent 95% confidence intervals as determined by the 2.5 and 97.5 percentile values from 2000 bootstrap replicates.

present in the NBS in June 2017, and the observed increased northward springtime transport in 2017 and other recent years could have advected them into the Chukchi Sea. Walleye pollock (*Gadus chalcogrammus*), a pelagic boreal species has also been observed in the Chukchi Sea in recent years of high transport (Orlov et al., 2019, 2020, 2021; Levine et al.,; Maznikova et al., 2023; Emelianova et al., 2022). Similar trends have also been noted in pelagic forage fishes in the same years (Baker et al., 2022).

Age-0 cod presence in the Chukchi Sea could also be due to a supply of larvae from the Bering Sea reaching the Bering Strait in recent years. Pacific cod spawning in the EBS occurred from March through April in 2005 and 2006 as far north as the shelf break east of St. Matthew Island (Neidetcher et al., 2014). Larvae originating from this location could be transported by the Bering Slope Current (Stabeno et al., 2016), and could reach the north side of St. Lawrence Island in about 4 months (Fig. 12 in Stabeno et al., 2016). Given size at hatch of about 5 mm (Laurel et al., 2008), growth rates of about 0.5–0.1 mm/day for pre-flexion larvae estimated from laboratory experiments at temperatures of 1–6 °C (Hurst et al., 2010), and four months of larval transport, these larvae may have reached north of St. Lawrence Island at a size range of about 11–17 mm, which is similar to the observed larval size of about 8–14 mm in this area in June 2017. However, even if the larvae were spawned in March and traveled as fast as historical currents, with an estimated 20–30 day egg incubation period (Laurel et al., 2008) and four months in the Bering Slope Current, they would not arrive until August. It seems likely that if the larvae observed near the Bering Strait were from the Bering Sea, they either spawned earlier than previous reports, were spawned north of previous reports, or were transported by increased current speeds. Another possibility is that changes due to warmer temperatures in the EBS or NBS caused successful larval delivery to the Chukchi Sea by other mechanisms (or a combination of mechanisms), such as improving egg survival (Laurel and Rogers, 2020), or improving larval prey fields (Laurel et al., 2021). It seems especially unlikely that the 8 mm SL larvae observed in the northeastern Chukchi Sea in August 2018 was spawned as far south as the known spawning areas in the EBS, implying spawning must occur north of previously documented spawning areas.

Age-0 fish from other temperate areas have expanded their nursery habitat in recent years in response to increased larval transport or warmer temperatures. Age-0 nursery areas for Atlantic cod, *Gadus morhua*, shifted northward in the North Sea during years with increased northward winds during the larval period and warm ocean temperatures (Rindorf and Lewy, 2006). In the Barents Sea, age-0 fish from several species including Atlantic cod expanded their geographical habitat in an unusually warm year, and were also larger than the long-term average (Eriksen et al., 2020).

Recent adult cod presence in the Chukchi Sea in 2018, and 2019, and absence in 2010 and 2012 may also be related to warmer temperatures in the NBS and Bering Strait in the spring. Adult cod avoid the cold pool in the EBS (Kotwicki and Lauth, 2013), and the movement of adult cod

Table 2
Prey-specific relative index of importance (PSIRI) for prey taxa by trawl type for Pacific cod small juveniles collected in the eastern Chukchi Sea in 2017. Only prey items with PSIRI greater than 3 are listed.

Trawl Type	Prey Taxa	Prey Group	PSIRI
Small-mesh benthic	Polychaeta	Annelid worm	13.57
Small-mesh benthic	Eurytemora herdmandi	Calanoid copepods, <2.5 mm Total length	13.55
Small-mesh benthic	Nematoda parasite	Unidentified	10.55
Small-mesh benthic	Euphausiidae juv/adult	Euphausiids, j+a	10.00
Small-mesh benthic	Decapoda	Decapoda	8.83
Small-mesh benthic	Cistenides spp.	Annelid worm	5.59
Small-mesh benthic	Margarites spp.	Gastropod	4.41
Small-mesh benthic	Argis spp.	Carideans	3.21
Small-mesh benthic	Paguridae juv/adult	Anomuran crab	3.06
Midwater	Calanoida (<2.5 mm)	Calanoid copepods, <2.5 mm Total length	17.68
Midwater	Actinopterygii	Fish	17.48
Midwater	Caridea	Carideans	17.01
Midwater	Gadiformes	Fish	12.89
Midwater	Cirripedia cypris	Barnacle	8.72
Midwater	Centropages abdominalis	Calanoid copepods, >2.5 mm Total length	8.09
Midwater	Brachyura megalopa	Brachyuran crab	6.80
Midwater	Paguridae zoea	Anomuran crab	6.04
Surface	Centropages abdominalis	Calanoid copepods, >2.5 mm Total length	31.41
Surface	Calanoida (<2.5 mm)	Calanoid copepods, <2.5 mm Total length	31.28
Surface	Decapoda	Decapoda	13.45
Surface	Crustacea	Crustacean	8.33
Surface	Pseudocalanus spp.	Calanoid copepods, <2.5 mm Total length	7.34
Surface	Brachyura megalopa	Brachyuran crab	5.73

into the NBS between 2010 and 2017 coincides with a reduction in the cold pool in the NBS (Stevenson and Lauth, 2019; Baker, 2021). Preliminary tagging data suggests that adult cod move from the EBS into the NBS after sea ice has retreated northward in the spring and summer (J. Nielsen, Kingfisher Marine Research, and S. McDermott, AFSC, personal communication, February 23, 2021). Based on these tagging data, it is possible that the early ice retreat in both 2018 and 2019 (Stabeno and Bell, 2019; Siddon et al., 2020) allowed the fish to reach the Bering Strait early enough in the year to continue northward into the Chukchi Sea by August.

Increased temperatures on the Chukchi Sea shelf in the summer are less likely to be the cause of the increased cod presence in recent years than temperatures in the spring in the NBS and Bering Strait. Annual summer water temperatures on the ECS shelf have increased since 2014 (Danielson et al., 2020); however, even in the earlier and colder years of this study (2010 and 2012), when age-0 and adult cod were absent, some of the sampled habitat was warm enough (based on observed presence in 2017 and 2019) to support cod. The entire water column of the relatively shallow southeastern Chukchi Sea warms in the summer due to both advection and wind mixing (Grebmeier et al., 2015; Woodgate et al., 2015), and the nearshore areas are in the Alaska Coastal Current, which is typically warmer than the rest of the shelf from June to at least October (Woodgate et al., 2010; Woodgate, 2018). Even in the cold years of this study, the Chukchi Sea appeared warm enough during the summer for age-0 and adult cod to be present.

Age-0 cod in the Chukchi Sea use both pelagic and demersal habitats, which is similar to their habitat use in the EBS (Hurst et al., 2015). Diet differences between age-0 fish in pelagic and benthic habitats imply that age-0 cod remain at a habitat type for, at minimum, a daily feeding cycle. It should be noted that the age-0 fish from the benthic and midwater trawls that had significantly different diets were from different geographic areas, and prey field differences could be responsible for the observed diet differences. Nevertheless, the benthic-caught fish ate predominately benthic prey items, and the midwater-caught fish ate predominately pelagic prey items. In the EBS, age-0 cod are pelagic over deeper water and benthic in nearshore shallower areas, which is possibly related to temperature; the juveniles occupy demersal habitat in inshore areas with relatively warm bottom temperatures, and occupy warmer pelagic habitat when they are over deep water with cold benthic habitat (Hurst et al., 2015). Age-0 habitat use in the Chukchi Sea fits the same general pattern, with the addition that some fish use the pelagic nearshore habitat. This may mean that, in addition to temperature, fish in nearshore areas may select their depth in the water column based on some other factor, such as localized prey fields, or salinity.

The absence of a length mode of juveniles in the ECS in 2019 larger than that observed in 2018 suggests that the age-1 cod in 2018 may not have survived to age-2. All previous reports of cod from the ECS have been of juvenile-sized fish (Barber et al., 1997; Mecklenburg et al., 2011, 2018; Logerwell et al., 2015). It seems that cod juveniles in the Chukchi Sea either suffer high mortality rates, or migrate to other areas prior to adulthood.

The juveniles in the Chukchi Sea may not be able to successfully grow and provision themselves well enough to survive to become adults. Condition (lipid densities and weight at length) was lower in the 2017 age-0 cod from the Chukchi Sea than those from the GOA. Lipid densities were also lower in the age-0 cod in this study than in co-occurring gadids in the Chukchi Sea in 2017 (Copeman et al., 2022). The age-0 cod in the Chukchi Sea in this study inhabited colder waters (2017, 2–6 °C) than age-0 cod during the summer in the EBS (~6–12 °C; Hurst et al., 2015; Hurst et al., 2018) and the Gulf of Alaska (~8–11 °C; Abookire et al., 2007; Laurel et al., 2016a). Further, summer temperatures in the Chukchi Sea are lower than those modeled for maximum growth (~11.0–11.5 °C) and maximum lipid accumulation (10 °C) in controlled laboratory growth experiments (Laurel et al., 2016b; Hurst et al., 2010, 2012b; Copeman et al., 2017). Thus, temperatures during the summer in the Chukchi Sea may be too low for juvenile cod to achieve sufficient size or energetic thresholds to survive long, low-productive Arctic winters. Future monitoring of age-0 cod in the Chukchi Sea should include both growth and condition metrics.

The abundance of age-0 cod in the ECS is potentially high enough to be ecologically meaningful if they could survive to adulthood. Only small numbers of juveniles were caught with our small-mesh benthic trawl, but catch rates in the nearshore areas of the ECS were similar to catch rates in EBS nursery areas using a similar trawl (Hurst et al., 2015, Table 3); however, they were one order of magnitude lower than catch rates in GOA nursery areas in high-abundance years (Table 3). An abundance estimate based on our limited number of stations in 2017 should be viewed with caution, but it provides a general sense of the potential number of cod juveniles in the ECS in 2017. Benthic trawl catch rates in the ECS were highest from 67 °N to 69 °N inshore of 40 m bottom depth, an area of approximately 14,500 km^2. Mean catch rates here were approximately 12,000 fish per km^2. Assuming the trawl caught all of the fish in the towpath, and our sampling was representative of the area, mean density multiplied by area would equal approximately 174 million fish present in 2017 within the area from 67°N to 69 °N inshore of 40 m bottom depth. Alternatively, estimating abundance from the mean catch rates and area of the entire survey area south of 70 °N provides an estimate of approximately 150 million fish. Even if these estimates are high, there were tens of millions of age-0 cod in the ECS in 2017. If these or future age-0 cod survive to adulthood, and either remain in the Chukchi Sea or successfully migrate to other

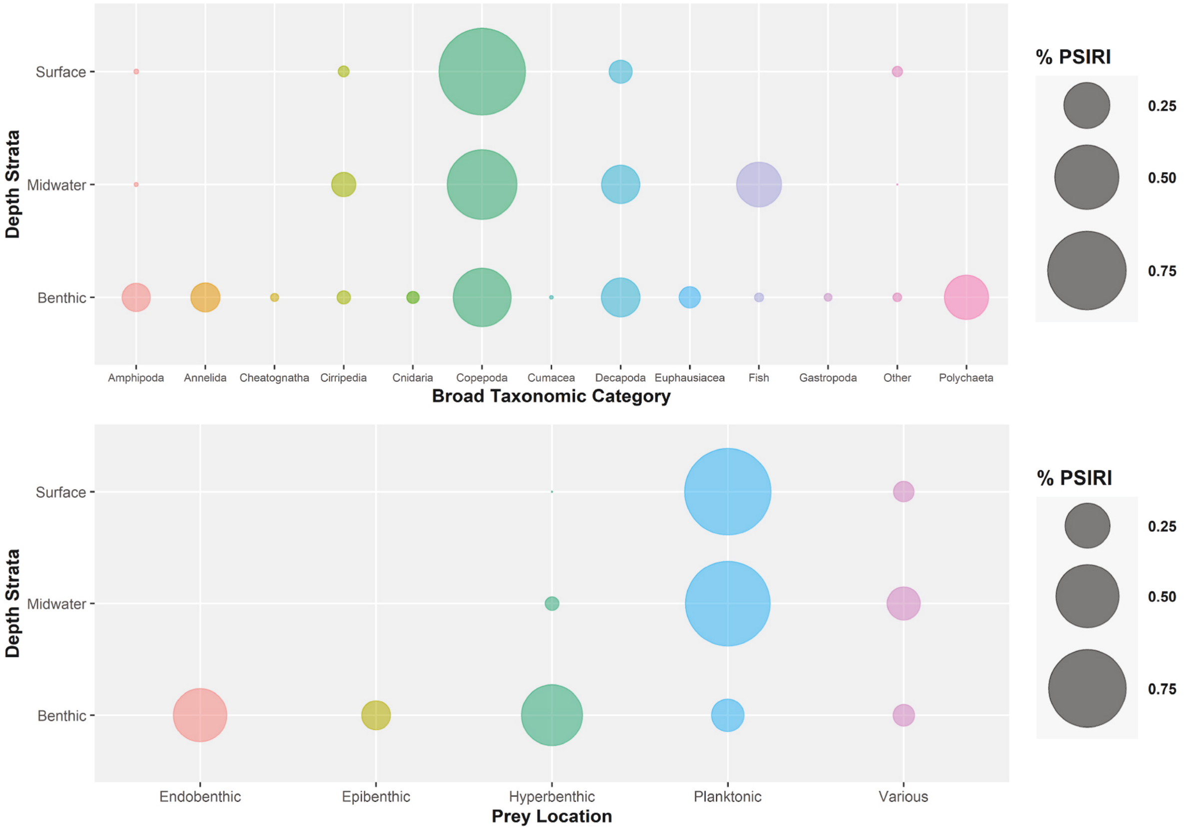

Fig. 10. Prey specific relative index of importance (PSIRI) of prey items in the diet of small juvenile Pacific cod caught in 2017. Top panel depicts PSIRI by prey taxonomic groups, and bottom panel depicts PSIRI by prey general habitat classification.

spawning areas, it would mean a northward expansion of cod nursery area habitat, which is one type of poleward distribution shift that has been documented in marine fish due to ocean warming (Rindorf and Lewy, 2006; Nye et al., 2009; Figueira and Booth, 2010).

Densities of adult and age-1 cod estimated in this study are very low compared to reports from the Bering Sea. CPUE by weight for combined age-1 and adult fish at stations where fish were present ranged from 0.0018 to 1.5 kg/ha in this study. Even in 2010, when cod were considered “almost completely absent” from the NBS, cod CPUE values at some stations were greater than 10 kg/ha, and CPUE values in the EBS may be greater than 50 kg/ha (Stevenson and Lauth, 2019). These catch rate comparisons are between the DT 27.1/24.4 bottom trawl used in the WCS in this study, and the 83–112 trawl used in the NBS and EBS, however, catchability differences seem unlikely to cause the much lower CPUE values observed in the WCS in this study. In the western Bering Sea (WBS), cod densities have been reported from surveys using the same large-mesh trawl as used in the WCS in this study (Shuntov et al., 2014). Cod densities in the WBS were summarized by statistical regions and depth range over the time period from 2006 through 2012. In regions and depth ranges where cod are present in the WBS, reported mean densities ranged from 235 to 7631 kg ha-1, however, these densities assumed that only 40% of fish encountering the trawl were retained by the trawl (Shuntov et al., 2014). To make these numbers comparable to the CPUE units used in this study (100% of fish retained), the values reported by Shuntov et al. (2014) were multiplied by 0.4. These converted mean CPUE values are 94 to 3052 kg ha-1 and are much higher than even the peak CPUE values observed in the Chukchi Sea in this study.

Although estimated densities were low, the adult cod observed in the WCS (and the one adult caught in the ECS) in this study are among the first known (to us) adult Pacific cod caught in the Chukchi Sea. The only other is an adult Pacific cod caught in a subsistence fishing net near Point Hope, AK, in August 2020, and reported as a novel occurrence to the Alaska Arctic Observatory and Knowledge Hub (AAOKH; Donna Hauser, International Arctic Research Center, University of Alaska Fairbanks, personal communication, January 29, 2021). The lack of observed intermediate size ranges of fish between age-1 and adults makes it likely that there is not a self-recruiting cod population in the Chukchi Sea, and that the adults likely moved northward from the Bering Sea, similar to how adults moved into the NBS from the EBS (Stevenson and Lauth, 2019). Only one adult was caught in the ECS during this study, but it was caught when the pelagic midwater trawl was incidentally fished on the bottom while targeting a deep acoustic layer. It is possible that adults and larger juveniles were also present at other sampling stations in the ECS in the recent warm years of this study, but avoided the pelagic and small-mesh benthic sampling gear. Adult cod are primarily benthic (Fadeev, 2005; Nichol et al., 2007) and would not be available to the pelagic trawls, and could also likely avoid the small-mesh benthic trawl due to the small mouth opening and slow fishing speeds (Itaya et al., 2007). Therefore, the presence of larger juvenile and adult cod in the ECS is unknown and will remain unknown until the area is surveyed across a range of habitats with gear suited to their capture (see Emelin et al., 2023).

Differences in abundance and distribution between the ECS and WCS for all life stages would be interesting to study, but trawl type differences in recent years make this difficult. The ECS has been surveyed with trawls likely to catch age-0 fish, and the WCS has been surveyed with gear likely to catch larger juveniles and adults.

The data presented here show that multiple life stages of Pacific cod were present in the Chukchi Sea in recent warm years, which suggests that the species is expanding into the Chukchi Sea by both recruitment of age-0 fish, and adult movement. However, the true extent of this range expansion, its potential to persist into the future, and the ultimate fate of individuals that move into the Chukchi Sea, are still unknown.

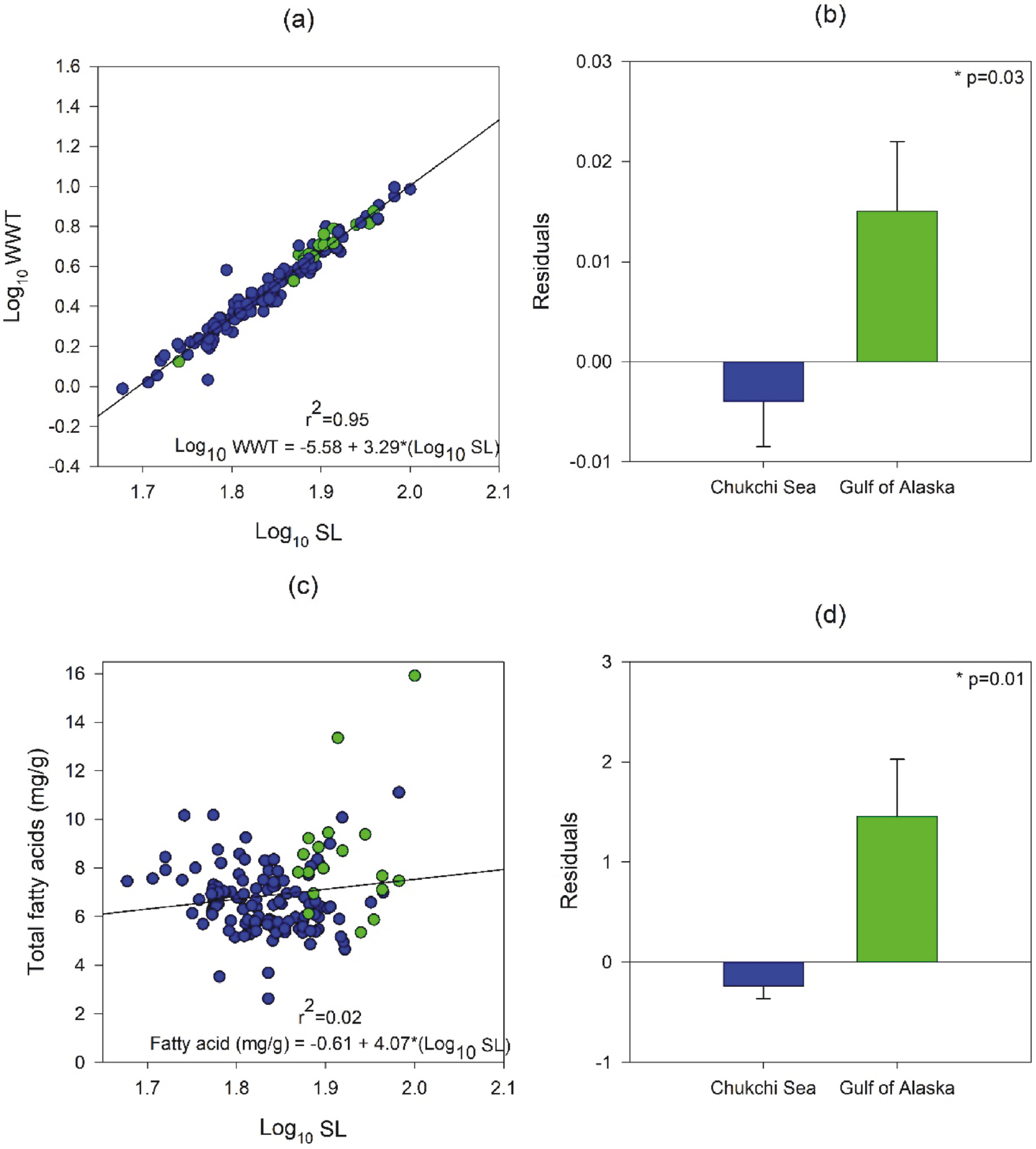

Fig. 11. The effect of sampling region on the relationship between age-0 Pacific cod length (Log_{10}, SL, mm) and (a) wet weight ((Log_{10}, WWT, g) as well as (c) lipid density. Residuals from these relationships showed a significant effect of region of capture on condition based on length-weight residuals (b) and a significant effect of region on condition based on fatty acids concentrations (d).

Monitoring surveys designed to estimate abundances and condition of multiple life stages are required to better understand this poleward distribution shift, and to assess its impacts to the ecosystem.

5. Conclusions

Age-0 sized Pacific cod were present in the eastern Chukchi Sea during a recent warm period and absent during a previous cold period. Pacific cod larvae were present south of the Bering Strait during June in a recent warm year. Increased springtime water temperatures near the Bering Strait and increased springtime northward transport through the Bering Strait during the recent warm period may allow larvae from the northern Bering Sea to be transported through the Bering Strait, and thus the northern Bering Sea is a likely source of the age-0 Pacific cod observed in the Chukchi Sea.

Age-1 sized Pacific cod were present in the western Chukchi Sea during the recent warm period suggesting that some of the age-0 fish in the Chukchi Sea may survive the first winter. However, condition of the age-0 fish was much lower in the Chukchi Sea than in the Gulf of Alaska. Poor age-0 condition and absence of any juveniles older than age-1 suggest that Pacific cod are not currently surviving to adulthood in the Chukchi Sea. Collection gear deployed in the western Chukchi Sea may not retain age-0 fish, and collection gear deployed in the eastern Chukchi Sea may not retain age-1 or older demersal fish limiting comparisons between the two areas.

Adult Pacific cod were present in both the western and eastern Chukchi Sea during the recent warm period. Absence of intermediate-sized juveniles suggest that these adults moved into the Chukchi Sea

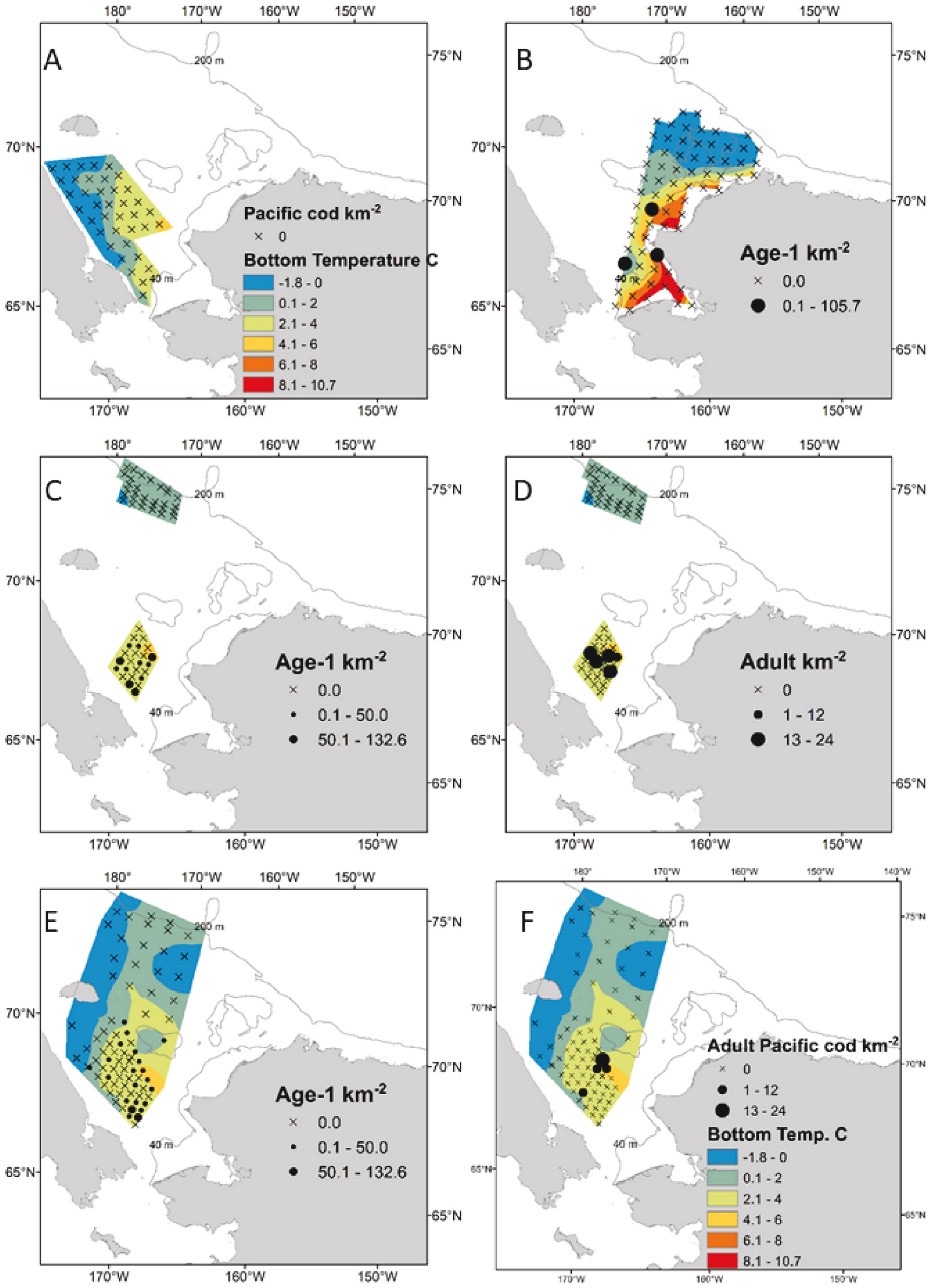

Fig. 12. Distribution and catch per unit effort of juvenile (age-1) and adult Pacific cod in large-mesh benthic trawl in the Chukchi Sea: (A) Age-1s and adults in 2010; (B) Age-1s in 2012; (C) Age-1s in 2018; (D) Adults in 2018; (E) Age-1s in 2019; (F) Adults in 2019.

Table 3
Comparison of Catch per Unit Effort (CPUE) in this and other studies from Alaskan waters using a similar 3-m beam trawl based on the design of Gunderson and Ellis (1986). Where noted, the trawls were based on the modified design of Abookire and Rose (2005).

Large Marine Ecosystem	Area	Year	Trawl Design	Mean Pacific cod km^{-2}	Reference
Chukchi Sea	20–29 m depth range	2017	Abookire and Rose (2005)	6200	This study
Chukchi Sea	30–39 m depth range	2017	Abookire and Rose (2005)	2800	This study
Chukchi Sea	20–29 m depth range	2019	Abookire and Rose (2005)	0	This study
Chukchi Sea	30–39 m depth range	2019	Abookire and Rose (2005)	1800	This study
Bering Sea	Alaska Peninsula <50 m depth	2012	Abookire and Rose (2005)	2200	Hurst et al. (2015)
Gulf of Alaska	Kachemak Bay	1994	Gunderson and Ellis (1986)	100	Abookire et al. (2001)
Gulf of Alaska	Kachemak Bay	1995	Gunderson and Ellis (1986)	48,700	Abookire et al. (2001)
Gulf of Alaska	Kachemak Bay	1996	Gunderson and Ellis (1986)	0	Abookire et al. (2001)
Gulf of Alaska	Kachemak Bay	1997	Gunderson and Ellis (1986)	50,300	Abookire et al. (2001)
Gulf of Alaska	Kachemak Bay	1998	Gunderson and Ellis (1986)	200	Abookire et al. (2001)
Gulf of Alaska	Kachemak Bay	1999	Gunderson and Ellis (1986)	600	Abookire et al. (2001)

from the Bering Sea.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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