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Contrasting coastal and shelf nursery habitats of Pacific cod in the southeastern Bering Sea

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Shallow, subtidal waters of coastal embayments are the primary nursery habitats of juvenile Pacific cod through much of their range. However, the importance of these habitats to the Bering Sea population is poorly understood as the Bering Sea offers relatively little of this habitat. In this study, we examined the use of demersal and pelagic habitats in the southeast Bering Sea by age-0 Pacific cod. In 4 years of demersal beam trawling on the shelf at depths of 20 – 146 m, fish were most abundant along the Alaska Peninsula (AKP) at depths to 50 m. In addition, 1 year of spatially intensive beam trawl sampling was conducted at depths of 5 – 30 m in a nearshore focal area along the central AKP. In this survey, age-0 cod were more abundant along the open coastline than they were in two coastal embayments, counter to patterns observed in the Gulf of Alaska. Demersal sampling in 2012 was conducted synoptically with surveys of surface and subsurface waters over the continental shelf. Age-0 cod were captured in pelagic waters over the middle and outer shelf, with maximum catches occurring over depths of 60 – 80 m. The similar size distributions of fish in coastal-demersal and shelf-surface habitats and the proximity of concentrations in the two habitat types suggests that habitat use in the Bering Sea occurs along a gradient from coastal to pelagic. While capture efficiencies may differ among trawl types, trawl-based estimates of age-0 cod density in demersal waters along the AKP was 10 times that observed in the highest density pelagic-shelf habitats, demonstrating the importance of coastal nursery habitats in this population. Despite representing a much smaller habitat area, the coastal waters along the AKP appear an important nursery area and support a significant fraction of the age-0 Pacific cod in the Bering Sea.

Keywords: Bering Sea, habitat, juvenile, nursery, pacific cod *Gadus macrocephalus*.

Introduction

The first summer of life is a critical period in the productivity of fish populations. Habitat conditions in juvenile nursery areas play a dominant role in determining growth, survival, and recruitment rates. However, very little is known about the distribution and habitat use of juvenile stages of a number of important North Pacific fishery species. Understanding juvenile habitat use is of particular importance for benthic and demersal species, as they must locate and settle to suitable benthic habitat, which may have specific physical and prey requirements. However, flexibility to exploit multiple habitats, either sequentially through ontogeny at the individual level or simultaneously at the population level, increases the range of operative nursery environments, even if these habitats are only transiently utilized *en route* to the principal nursery area. If species can exploit multiple habitats, it is important to determine which of these serve as principal nursery areas and which are subordinate habitats, an exercise best accomplished through critical evaluation of fish abundance distribution, growth trajectories, and mortality estimates.

Pacific cod (*Gadus macrocephalus*) are widely distributed, occurring on continental shelves throughout the eastern and western North Pacific Ocean and Bering Sea. They are an important component of regional fisheries and foodwebs. Along the West Coast of the United States, landings of Pacific cod trail only those of walleye pollock (*Gadus chalcogrammus*). As predators, they consume juvenile stages of other important resource species including walleye pollock and crabs (Urban, 2012). Except the early juvenile stages, the distribution and habitat use of Pacific cod in the southeastern Bering Sea (SEBS) has been well documented. Demersal subadults and adults are most abundant over the middle and outer shelf at depths of 50–200 m, generally moving deeper with age (Bakkala, 1984). Fish make spawning migrations to waters around Unimak Island and west of the Pribilof Islands (Shimada and Kimura, 1994; Figure 1). In addition, fish in spawning condition have been captured along the outer shelf between 100 and 200 m as far north as Zhemchug Canyon (Neidetcher *et al.*, in press). Pacific cod spawn demersal eggs; larvae rise to the surface immediately after hatch (Doyle *et al.*, 2009; Hurst *et al.*, 2009). Based on a divergence in flows between the Bering Slope and Bering Coastal Currents, larvae spawned near Unimak Island could be transported northward over the shelf or along the Alaska Peninsula (AKP; Lanksbury *et al.*, 2007; Stabeno *et al.*, 2009). To date, there has been little examination of the distribution and habitat use of juveniles in the Bering Sea population.

Nursery habitats of juvenile Pacific cod have been most closely examined in the central Gulf of Alaska. Sampling with trawls, seines, and baited cameras has demonstrated the importance of shallow water nursery areas (<10 m) for age-0 fish (Dean *et al.*, 2000; Abookire *et al.*, 2001, 2007; Laurel *et al.*, 2007). In several sites, age-0 cod were most abundant in waters <10 m depth (Abookire *et al.*, 2001; Laurel *et al.*, 2007) with fish moving to greater depths with age (Laurel *et al.*, 2009). In addition, in both field sampling and laboratory studies, juvenile Pacific cod have displayed a preference for kelp and eelgrass habitats (Dean *et al.*, 2000; Laurel *et al.*, 2007; Ottmar and Hurst, 2012). In the Gulf of Alaska, age-0 Pacific cod are rarely captured over the deeper continental shelf (Wilson, 2009). Shallow, and in some cases, vegetated habitats in coastal embayments also appear to be primary nursery habitats in other areas of the Pacific cod range with highly articulated shorelines, large areas of sheltered, shallow waters, and narrow continental margins, such as the Aleutian Islands (Thedinga *et al.*, 2008) and northern Japanese coast (Takatsu *et al.*, 2001).

In comparison to other parts of the Pacific cod range, the Bering Sea offers little of this sheltered coastal habitat. The southeastern Bering Sea (SEBS) is dominated by a broad, shallow continental shelf. Much of the coastline is straight with sand/gravel beaches and broad mud/sand/gravel flats (see Alaska Shore Zone Habitat Map, http://alaskafisheries.noaa.gov/shorezone/) and there are few sheltered bays and inlets. It is unclear if these types of shallow habitats are capable of supporting the large population of Pacific cod found over the Bering Sea shelf. In addition, it is clear that in the Bering Sea, age-0 Pacific cod are not restricted to shallow demersal habitats (Duffy-Anderson *et al.*, 2006). Two recent studies examined habitat use of fish captured in pelagic habitats over the continental shelf (Hurst *et al.*, 2012a; Parker-Stetter *et al.*, 2013).

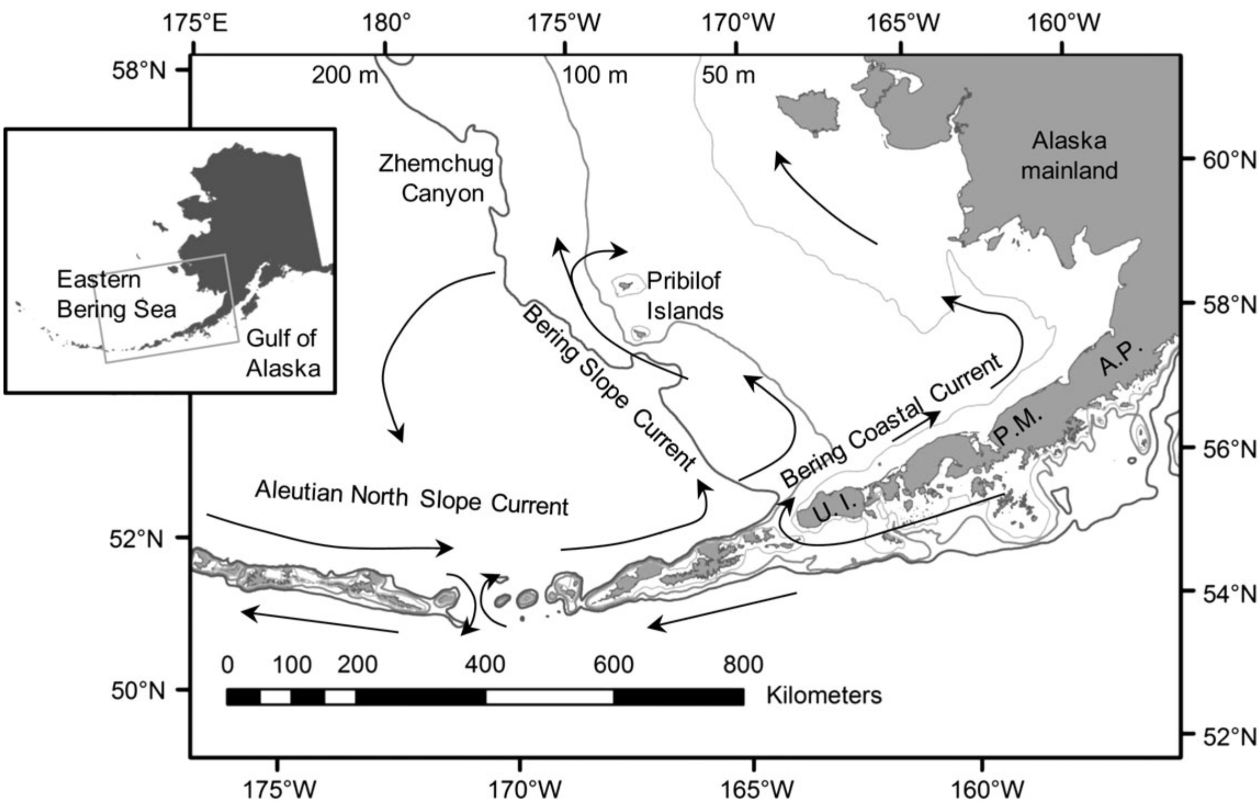

Figure 1. Eastern Bering Sea map with goegraphic landmarks and major surface circulation patterns (arrows). Circulation patterns are based on Stabeno *et al.* (1999). U.I., Unimak Island; P.M., Port Moller; A.P., Alaska Peninsula.

In multiple years of surface trawling and acoustic profiling, age-0 fish were most abundant on the middle shelf over bottom depths of 50–80 m. They tended to be more abundant near the surface (to ∼35 m depth) but were occasionally observed deeper in the water column over the outer shelf and slope (Parker-Stetter *et al.*, 2013). Fish were abundant offshore of the central AKP, near Port Moller, one of the largest coastal embayments of the eastern Bering Sea, suggesting that shallow waters along the western and central AKP could be important nursery habitats for juvenile cod (Hurst *et al.*, 2012a). Surface and demersal waters represent distinctly different habitat types with distinct patterns of thermal variation and structural features. They offer access to different prey types and expose fish to different suites of predators, potentially requiring distinct anti-predator behavioural strategies (Ottmar and Hurst, 2012). However, to date there has been little directed sampling to determine if age-0 fish use demersal in addition to surface habitats over the SEBS shelf. In addition, there has been no sampling of inlets and shallow coastal waters along the periphery of the Bering Sea to evaluate use of these coastal habitats as juvenile nursery areas for Pacific cod or other fishery resource species.

The goal of this project was to provide a more comprehensive perspective of habitat use by age-0 Pacific cod on the SEBS. Specifically, we wanted to evaluate the use of demersal habitats on the continental shelf and along the AKP coastline to complement existing knowledge of pelagic habitat use over the shelf. We describe the depth distribution of age-0 Pacific cod in demersal habitats based on 4 years (2006, 2008, 2010, and 2012) of demersal beam trawl sampling over the SEBS. We also present results from spatially intensive sampling of a nearshore focal area along the central AKP. The synoptic sampling of the nearshore focal area with surface, midwater, and demersal trawling across the shelf provides a more comprehensive description of habitat use of age-0 Pacific cod in the SEBS. Based on relative densities in these surveys and estimates of the areal extent of habitat types, we suggest that age-0 fish are common in the surface waters over the southern portion of the middle shelf, but this area may be secondary to demersal habitats along the AKP as the primary nursery area for the eastern Bering Sea population of Pacific cod.

Material and methods

Study area

The SEBS is a broad continental shelf bordered on the east and south by the Alaska mainland and the AKP, respectively (Figure 1). The steep shelf break marks the western boundary with the deep Aleutian Basin. Water comes onto the SEBS at the southern margin via the Aleutian North Slope Flow, from the Gulf of Alaska through Unimak Pass, and onshore at several slope canyons. Water flows weakly over the shelf to the northwest with the stronger Bering Coastal Current running northeast along the AKP before turning north along the mainland Alaska coast (Coachman, 1986). Sediments on the shelf are generally sandy with courser grains near the coastal margins and finer muds in deeper areas (Smith and McConnaughey, 1999). The shelf can be generally divided into three zones based on hydrographic characters. A well-mixed inner shelf is separated by the "inner front" at ∼50 m depth from the middle shelf where a seasonally warm surface layer sits atop a persistent "cold pool." A second, weaker front generally exists near 100 m depth, beyond which is the more weakly stratified outer shelf and slope (Kinder and Schumacher, 1981; Overland *et al.*, 1999).

The north side of the AKP is perforated by several inlets, the largest of which is the Port Moller-Herendeen Bay (PM-HB) system. PM-HB is a tidally dominated marine system with only minor freshwater inputs. The head of Herendeen Bay is fjord like with depths reaching to 100 m. Otherwise, PM-HB is characterized by extensive areas of intertidal and shallow subtidal (<10 m) sand/mud flats with deep, narrow tidal channels (to 20 m depth). These channels are naturally maintained and have coarser sediment with rocks and boulders. Outside the mouth of PM-HB, the AKP shoreline consists of gravel and sand beaches with depths increasing to 30 m within 10 km of the coast.

Demersal sampling over the Bering Sea shelf

Small-mesh beam trawling was conducted in late summer (August and September) over the SEBS shelf over 4 years at depths of 20–146 m (Table 1). This sampling targeted different regions of the SEBS in each year, but it included some sampling offshore of the AKP in each year (Figure 2). The number of beam trawl stations in each year ranged from 20 to 67 with the diel timing of collections varying across years due to scheduling constraints related to co-occurring sampling. Fish were collected with a 3-m beam trawl with 7-mm mesh and a 4-mm mesh codend based on the design of Gunderson and Ellis (1986) as modified by Abookire and Rose (2005). At each station, the net was towed along a consistent heading at ∼2 knots for 5–10 min, depending on the regional density of benthic fauna. A depth sounder mounted in the net 1 m behind the header rope providing real-time data to the ship was used to determine when the net contacted the seabed and confirmed that contact was maintained throughout the tow duration. Bottom temperatures (2 m off bottom) at each trawl location were measured with a thermister mounted in the trawl or a conductivity, temperature, and depth (CTD) profiler deployed in an independent vertical cast following trawl retrieval. See Cooper *et al.* (2014) for additional details of demersal shelf sampling. Upon retrieval, age-0 Pacific cod were sorted from the catch and measured (to 1.0 mm TL).

Global positioning system (GPS) coordinates were used to measure the length of each tow (mean = 459 m). Catch at each beam trawl station was converted to catch (number) per unit effort (cpue) in a standardized tow of 250 m. Based on preliminary analyses and habitat use patterns observed in juvenile northern rock sole (Cooper *et al.*, 2014), the SEBS was divided into two regions for analysis: the southern area offshore of the AKP and Unimak Island (Figure 2) and the eastern shelf, offshore from the Alaska mainland (eastern shelf, ES).

Demersal sampling in the nearshore focal area

Based on preliminary analysis of the available surface (Hurst *et al.*, 2012a) and beam trawling data (2006–2010, this study), fine-scale sampling was conducted in a nearshore focal area along the central AKP in summer 2012. The objective of this sampling was to evaluate habitat use in a large coastal embayment and shallow waters along the AKP that have not previously been sampled by larger research vessels working over the shelf.

Age-0 Pacific cod were sampled in the PM-HB coastal embayments and along the adjacent coastline in the Bering Sea from 19 to 27 August 2012 (Figure 3). A total of 75 tows, ranging in depth from 2 to 35 m, were made from the 13-m chartered fishing vessel FV *Bountiful*. Due to the presence of large rocks in the tidal channels which interfered with the trawl, only three successful collections

Table 1. Sampling effort for age-0 Pacific cod by year and gear type.

Year	Dates	Region	Gear	*n*	Sampling time	Depth range (water depth, m)	Vessel, length
2006	12 – 21 September	SEBS	3-m Beam trawl (demersal)	18	Daylight	25 – 138	NOAA *Miller Freeman*, 65 m
2008	11 – 20 September	SEBS	3-m Beam trawl (demersal)	49	24-h	22 – 113	NOAA *Miller Freeman*, 65 m
2010	11 – 18 September	SEBS	3-m Beam trawl (demersal)	58	24-h	20 – 110	NOAA *Miller Freeman*, 65 m
2012	20 August—1 September	SEBS	3-m Beam trawl (demersal)	64	Night-time	26 – 146	NOAA *Oscar Dyson*, 64 m
2012	19 Aug—14 October	SEBS	55-m Surface trawl	94	Daylight	28 – 1195	NOAA *Oscar Dyson*, 64 m
2012	19 August—7 October	SEBS	55-m Midwater trawl	24	Daylight	37 – 141	NOAA *Oscar Dyson*, 64 m
2012	17 – 27 August	PM-HB	3-m Beam trawl (demersal)	75	Daylight	2 – 35	FV *Bountiful*, 13 m

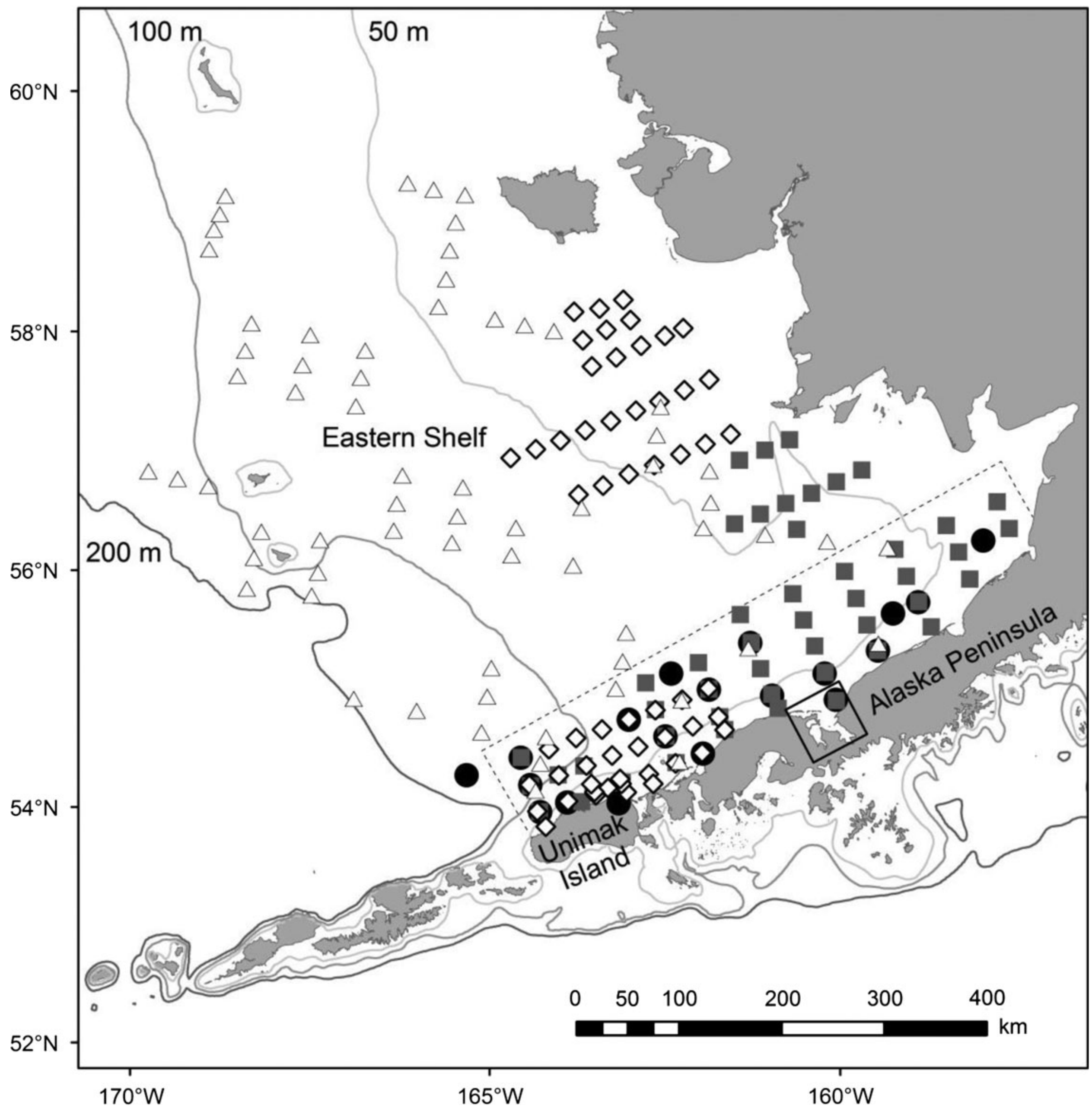

Figure 2. Beam trawl locations in the Southeast Bering Sea in 4 years of sampling. Circles: 2006; squares: 2008; diamonds: 2010; triangles: 2012. The large box (dashed line) represents the AKP sampling region. The small box (solid line) represents the location of the PM-HB nearshore focal region sampled in 2012; see Figure 3 for detailed map.

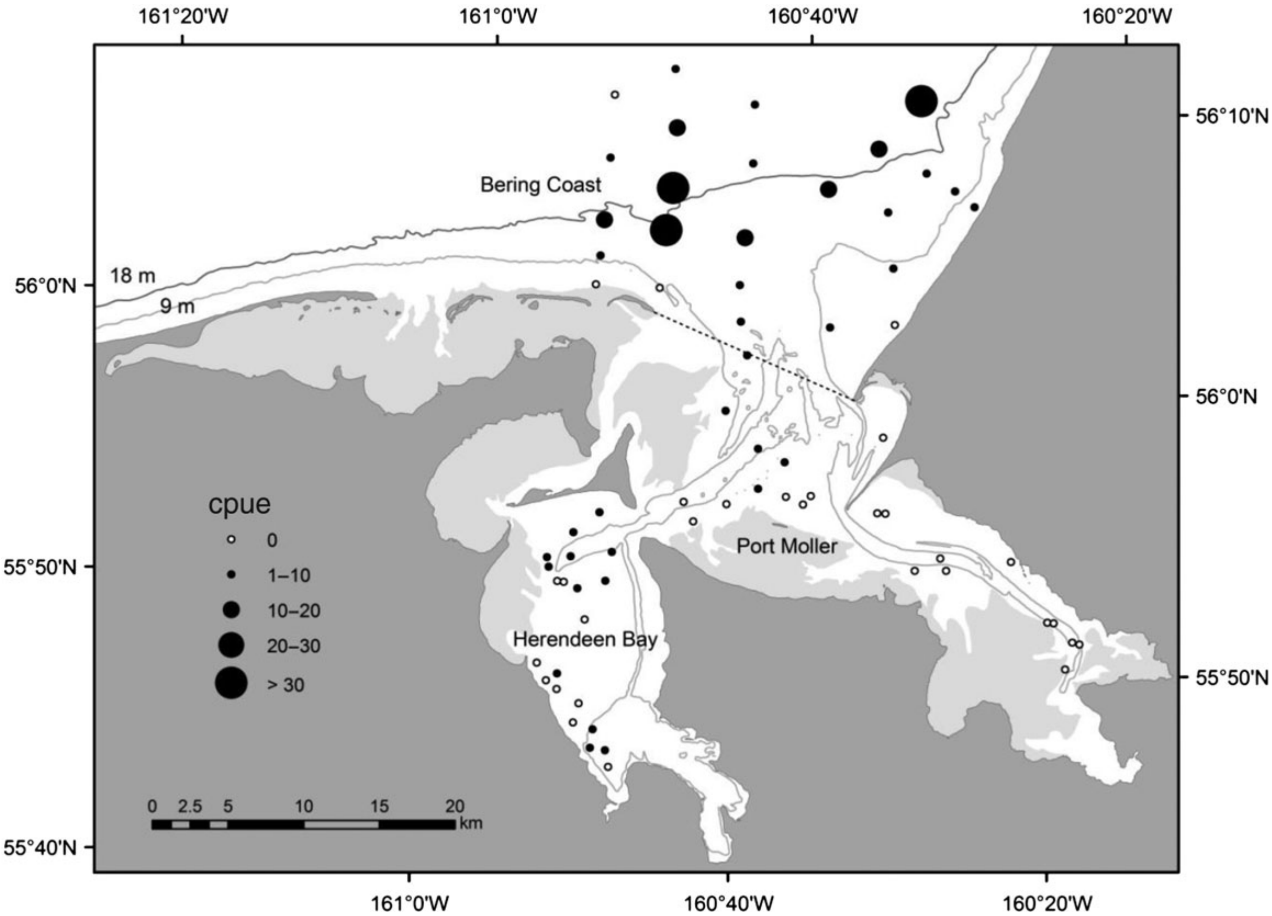

Figure 3. Beam trawl locations and catch rates in the PM-HB nearshore focal area sampled in August 2012. The dotted line marks the division of the BC sampling region from the coastal embayments of Port Moller (to the east) and Herendeen Bay (PM-HB). Shaded areas are intertidal sand/mud flats.

were made in these habitats, and we did not attempt to sample the head of Herendeen Bay due to its depth and fine sediments.

Sampling was conducted using a beam trawl of the same design as that used in the SEBS shelf sampling (described above). Trawling was conducted during daylight hours irrespective of tidal stage. At each station, the net was towed at 1.5 knots for 5 min against the prevailing tidal current. Tow line scopes (tow line length : water depth) were between 5 : 1 and 7 : 1, with larger scopes used in deeper water and during periods of high tidal flows. Additionally, during periods of high tidal flows, a 10 or 18 kg "sentinel" weight was attached to the tow line 15 m in front of the net bridle to keep the net in contact with the seabed. GPS coordinates were used to measure the length of each tow (mean = 247 ± 70 m s.d.). Upon retrieval of the net, all juvenile gadids (and flatfish) <125 mm total length (TL) were sorted from the catch and frozen for laboratory identification, measurement, and dissection. Larger fish were identified to species at sea and subsampled for length measurements (up to 50 of each species per tow). Following each tow, water temperature and salinity were measured at the surface and bottom (YSI model 85) at the midpoint of the tow transect. In the laboratory, age-0 Pacific cod were thawed and measured (to 0.1 mm TL). Catch at each station was converted to cpue in a standardized beam trawl tow of 250 m. Catch rates in the nearshore focal area were analysed within the subbasins of PM-HB and along the Bering Sea coast (BC) outside PM-HB.

Pelagic sampling over the Bering Sea shelf

As part of the Bering-Aleutian Salmon International Survey, surface and midwater trawling was conducted concurrently (and from the same research vessel, NOAA *Oscar Dyson*) with beam trawl sampling on the SEBS shelf in 2012 (Figure 4). The data from previous years of this survey (2004–2010) have been used to describe some aspects of the distribution of juvenile Pacific cod (Hurst *et al.*, 2012a; Parker-Stetter *et al.*, 2013). The 2012 data are included here to contribute to a comprehensive, synoptic evaluation of habitat use in the SEBS. A 198-m midwater rope trawl was used to sample fish at the surface and in acoustically identified midwater aggregations. The net has a mouth opening of 55 m width × 15 m height and is made up of hexagonal mesh wings with a 1.2-cm mesh codend liner. Ninety-four surface tows were conducted along an established grid over bottom depths of 28–1195 m during daylight hours. For the surface tows, the net was modified with additional flotation to keep the net at the water surface and was towed at speeds of 3.5–5.0 knots (6.5–9.3 km/h) for 30 min. GPS-derived start and end positions of each tow were used to determine the length of each tow. Additional details on surface trawling are provided in Farley *et al.* (2007). Water temperatures were measured at 1 m depth from a CTD cast made before each tow.

Surface trawl sampling on the SEBS conducted in 2012 was analysed according to the methods of Hurst *et al.* (2012a). Catch

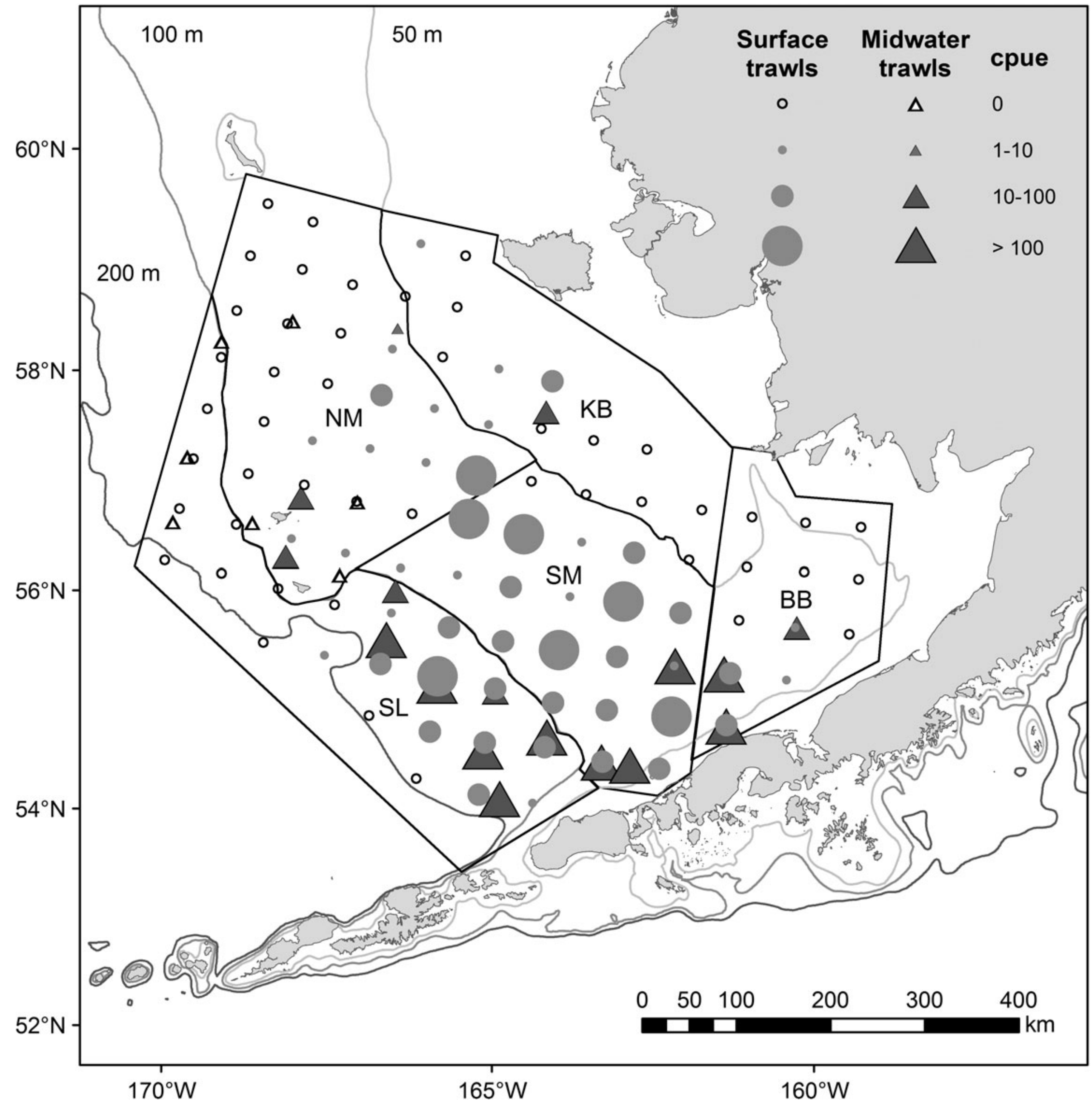

Figure 4. Sampling locations and catch rates in surface (circles) and midwater (triangles) trawls in the Southeast Bering Sea in 2012. The lines demark geographic sampling regions defined in Hurst *et al.* (2012a).

at each station was expressed as cpue of a standardized tow of 0.246 km^2. Catch rates in surface trawls were calculated in each of five regions defined by geographic landmarks and depth contours associated with recognized hydrographic boundaries (Kinder and Schumacher, 1981; Overland *et al.*, 1999; Hurst *et al.*, 2012a): Bristol Bay (BB), Kuskokwim (KB), south-middle (SM) shelf, north-middle (NM) shelf, and Slope (SL; the North region was not sampled for this study).

The primary goal of midwater sampling was to determine the species- and size composition of midwater acoustic targets occurring below the depth of surface net sampling (Parker-Stetter *et al.*, 2013). As a result, catch rates in midwater samples are used to infer general occurrence in midwater habitats and are not assumed to represent quantitative estimates of regional abundance. Twenty-four midwater trawls were conducted in 2012 over the middle and outer shelf, over bottom depths of 37–141 m. Additional information on midwater trawl sampling ("acoustic target identification trawls") is provided in Parker-Stetter *et al.* (2013). Upon retrieval of surface and midwater trawls, age-0 Pacific cod were sorted from the catch and individually measured (to 1.0 mm fork length) at sea. Measurements of fork length were converted to TL based on an empirical relationship. In instances of large catches, a subsample of the catch was sorted and used to estimate the total catch of age-0 Pacific cod.

Spatial distribution within habitat type

The primary patterns of habitat use of age-0 Pacific cod in the SEBS were described by spatial patterns of cpue for each of the sampling programmes as described above (Table 1). Across years, there was a trend toward higher catches in demersal beam trawls performed at night than during the day. However, this was partially an artefact of day and night-time tows not being evenly distributed across sampling regions or years. Focusing on the best subset of samples to evaluate this effect (<50 m depth along the AKP in 2008 and 2010), again there was a trend toward higher catches at night, but this effect was not significant ($p = 0.103$). Similarly, there was a significant difference in cpue among years, with 2012 having lower catch rates than the earlier years ($p < 0.01$), but this was primarily due to differences in spatial distribution of sampling effort. Therefore, data from the 4 years of beam trawling were pooled for identifying the primary spatial patterns in demersal habitat use across the Bering Sea. Catch at each beam trawl station was converted to cpue in a standardized tow of 250 m. Based on preliminary analyses and habitat use patterns observed in juvenile northern rock sole (Cooper *et al.*, 2014) the SEBS was divided into two regions for analysis: the southern area offshore of the AKP and Unimak Island (Figure 2) and the eastern shelf, offshore from the Alaska mainland (ES).

Within each survey, tows were grouped into 10 m depth bins (5 m bins in the nearshore focal area) and cpue was analysed as a function of depth and geographic sampling region. The role of temperature in habitat selection of Pacific cod was examined by comparing the mean temperatures measured during sampling (2012 only) in each region with the weighted mean temperature of capture (sampling depth temperatures weighted by $\log_{10}$ cpue).

Finally, size-frequency distributions of age-0 Pacific cod captured in 2012 were compared across sampling gears and regions of the SEBS. One-way ANOVA was used to compare fish sizes (pooled among sampling areas) among gear types. Because fish were not captured with all gear types in all habitat regions, separate one-way ANOVAs were used to compare mean lengths among sampled regions within each gear type. Mean length was also examined as a function of water temperature measured at the sampling depth in distinct sampling regions to explore the potential for thermal influences on growth or size-dependent habitat selection.

Nursery habitat evaluation

We used the synoptic sampling of the SEBS in August–September 2012 as the basis for an initial evaluation of basin-scale patterns in habitat use for age-0 Pacific cod. Nursery areas were defined as the combinations of habitat type (demersal or surface) and geographic regions supporting the greatest estimated cumulative abundances of age-0 Pacific cod from among the sampled habitat and region combinations. The cumulative abundances present in each habitat area were based on habitat-specific catch rates and the geographic area (km^2) of each region (Marshall and Frank, 1995). Because midwater tows targeted acoustically identified fish concentrations in the water column (primarily walleye pollock), these are not considered representative samples and were not included in these analyses. The cpue of demersal and surface trawls was converted from catch per standardized tow of each gear type to catch per kilometre squared based on the length of each tow, the effective net width of each trawl type, and the fraction of the vertical dimension of the habitat sampled by the gear. Acknowledging the potential for differences in catchability between the surface and demersal trawls, we believed that these analyses represent the best-available evaluation of fish densities across habitat types. For the beam trawls, an effective net width of 74% of beam length (Gunderson and Ellis, 1986) was applied. For the surface trawls, a previously measured net width of 55 m was adopted. In addition, the cpue in each surface trawl was multiplied by a factor representing the ratio of thickness of the surface layer (vertical distance from the surface to the bottom of the thermocline) to the vertical opening of the net (15 m). The surface layer thickness was calculated from CTD casts at each trawl station. At sites where the water column was well mixed (vertical temperature range of <1.5°C), the bottom depth was used as the surface layer thickness. Regional mean surface layer thickness ranged from 21.3 m in BB to 47.5 m in SL. Fish densities in each habitat (surface or demersal) and sampling region were expressed as the geometric mean cpue ($10^{[\sum \log(\text{cpue}+1)]/n} - 1$) and converted to cumulative abundance based on the spatial extent of that habitat region. The areal extent of five regions of surface-water habitats over the Bering Sea shelf and slope were based on the area designations defined in Hurst *et al.* (2012a). Based on observed patterns of depth distribution in demersal trawls (see below), we also divided the AKP and ES shelf sampling regions into areas shallower and deeper than 50 m.

Results

Demersal sampling over the Bering Sea shelf

In 4 years of beam trawl sampling over the SEBS shelf at depths of 19–146 m, age-0 Pacific cod were captured in 38% of tows and were most abundant in waters along the AKP to depths of 50 m. In the AKP sampling region, age-0 fish were captured in 48% of tows, with a mean cpue of 7.0 fish/tow. However, catch rate was significantly affected by sampling depth, decreasing rapidly at depths over 50 m (Figure 5). Along the AKP, mean cpue was 16.4 fish/tow at depths shallower than 50 m, but only 1.2 fish/tow deeper than 50 m. cpue declined from east to west along the AKP (correlation of cpue with longitude, $r = 0.233$, $p = 0.001$) due in part to the larger proportion of deeper tows offshore of the western peninsula and Unimak Island.

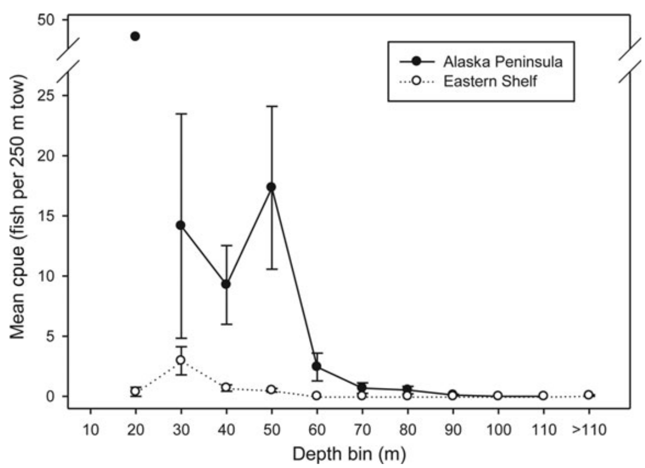

Figure 5. cpue of age-0 Pacific cod in SEBS beam trawls as a function of water depth. Points are mean ± standard error of catch corrected to a standardized tow length of 250 m over 4 years of sampling in 10-m depth bins along the AKP and on the ES. Note: only 1 tow was made in the 20-m depth bin in the AKP region.

Over the broad eastern shelf, the fraction of tows with age-0 Pacific cod was lower than that observed along the AKP (29%) and the mean cpue of 0.6 fish/tow was significantly lower. Highest cpue's was observed ~30 m depth.

During 2012, when sampling was conducted synoptically with sampling of pelagic waters and demersal sampling in the nearshore focal area, age-0 Pacific cod were captured in only 5 of 64 tows, as few tows were conducted in the region with the highest across-year densities (<50 m depth along the AKP). However, consistent with patterns in other years, the highest catch in 2012 (34 fish) occurred next to the AKP at 32 m depth.

Demersal sampling in the nearshore focal area

During sampling of the nearshore focal area in 2012, age-0 Pacific cod were more abundant in beam trawls along the BC than they were within the embayments of Port Moller and Herendeen Bay (Figure 3). Age-0 cod were caught in 21 of 25 tows along the Bering coast with a mean cpue of 9.8 fish/tow. Peak catch rates occurred at ~20 m depth in the Bering coast region (Figure 6) and fish were not captured in tows next to wave-exposed shorelines. Catch rates averaged 1.6 and 1.3 fish/tow in Outer Port Moller and Herendeen Bay, respectively, and no age-0 Pacific cod were captured in 11 tows in Inner Port Moller. Within PM-HB, there appeared no relationship between catch rate and sampling depth, despite sampling at depths where cod were most abundant in the coastal region. However, sampling in the deep, tidal channels was limited to a small number of successful samples due to problems with gear entanglement on large boulders.

Pelagic sampling over the Bering Sea shelf

Consistent with observations in previous years, catches of age-0 Pacific cod in surface trawls in 2012 were highest over the SM portion of the shelf (mean cpue = 224.6 fish/tow; Hurst *et al.*, 2012a; Parker-Stetter *et al.*, 2013). Moderate catches of 16.9 and 26.6 fish/tow were observed over the SM and NM, respectively (Figure 4). Average catches were <5 fish/tow in the BB and KB regions. Catches of age-0 Pacific cod in surface tows were highest over water depths of 60–90 m (Figure 7). A secondary peak in cpue over 130 m was driven by one large catch of 125 fish at 133 m (Figure 4).

Because midwater trawls targeted acoustically identified aggregations of small fish in the water column, catch rates are not representative of Pacific cod density in midwater habitats. However, catches of age-0 Pacific cod in these trawls suggest a general distribution consistent with that observed in the surface trawls. As in the surface trawls, highest catches of age-0 Pacific cod occurred over the SM and southern portion of the SL. They were absent from most tows over the NM and northern section of the SL (Figure 4).

Temperature and size variation

Bottom water temperatures during field sampling in 2012 ranged from 12.6°C in the shallow waters of Port Moller to <1°C within the demersal cold pool over the middle shelf at depths of 70–100 m (Figure 8). Temperatures decreased rapidly with depth moving away from the AKP, but due to the presence of the cold pool over the middle shelf, bottom temperatures were not strictly correlated with depth or latitude across the SEBS. Surface temperatures were less variable than bottom temperatures, generally decreasing with increasing latitude. Water temperatures at the sampling depth of midwater tows ranged from −0.5 to 9.9°C and were primarily related to sampling depth relative to the thermocline.

Water temperatures appeared to play a significant role in determining the use of demersal habitats but appeared to have less of an effect on the distribution of fish in surface waters or the size of fish across habitats and sampling regions. In the AKP and ES demersal sampling regions, mean temperature of capture was at least 3°C greater than the mean sampling temperature reflecting the use of warmer (and shallower) waters and avoidance of colder bottom areas. During surface trawl sampling, the mean temperature of capture was slightly higher than the mean sampling temperature (0.4–1.8°C difference) in all regions except for the SM region, where mean capture temperature was 0.8°C lower than the mean sampling temperature. And in the warm nearshore focal area, temperature did not appear to influence distribution as mean temperature of capture was similar to mean sampling temperature.

The size distributions of age-0 Pacific cod captured with different gears and across multiple habitats in the Bering Sea were not

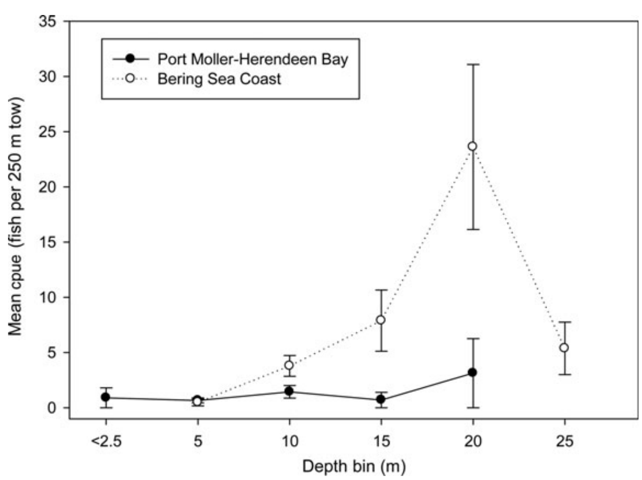

Figure 6. cpue of age-0 Pacific cod in the nearshore focal area as a function of water depth. Points are mean ± standard error of catch corrected to a standardized tow length of 250 m in 5-m depth bins in the PM-HB complex and adjacent coastal areas of the Bering Sea.

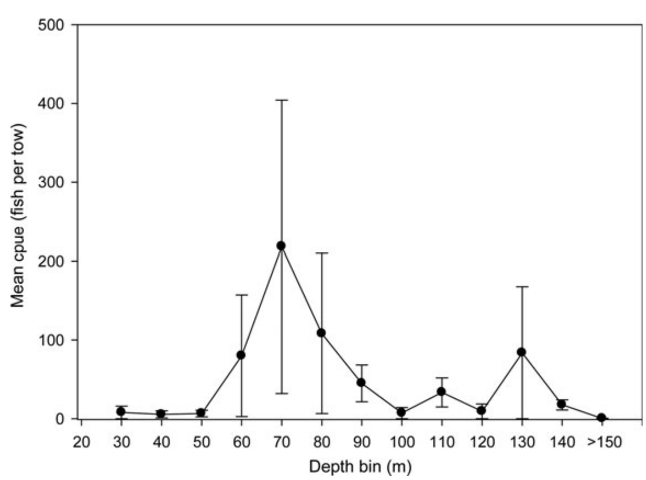

Figure 7. cpue of age-0 Pacific cod in surface trawls over the southeast Bering Sea shelf as a function of water depth. Points are mean ± standard error of standardized catch rates in 1 year of sampling (2012) in 10-m depth bins.

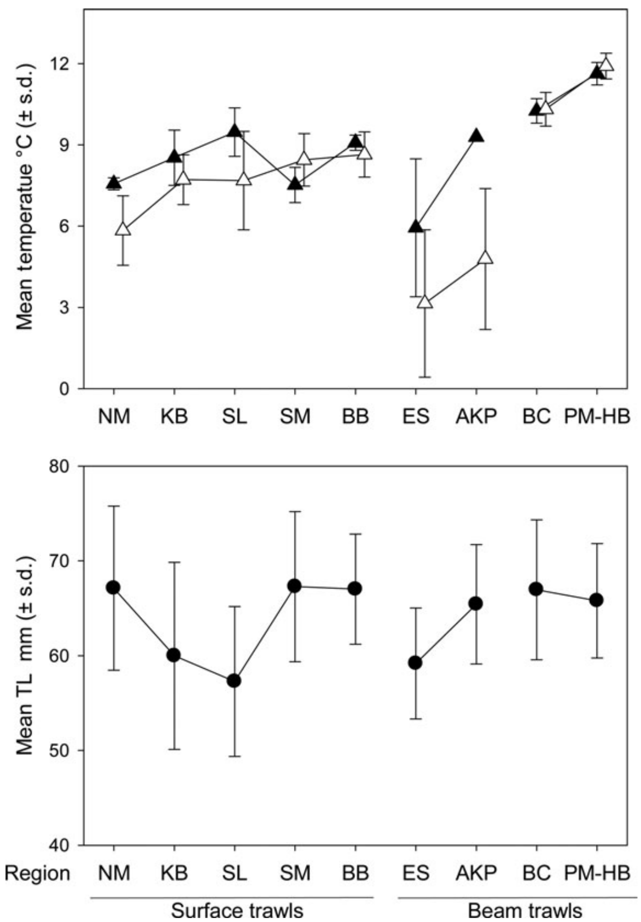

Figure 8. Mean sampling temperatures (± s.d.; open triangles), weighted mean temperature of capture (± s.d.; filled triangles), and mean lengths (± s.d.; circles) of age-0 Pacific cod collected in 2012 sampling as function of sampling region and gear type.

Table 2. Catch rates and habitat-region contributions of age-0 Pacific cod to the 2012 cohort in the SEBS.

Habitat region	***n*** (tows)	Density (fish/km^2)	Area (km^2)	Abundance (million)
Surface				
KB	15	3.39	65 389	0.22
NM	22	3.17	82 719	0.26
SL	23	11.27	43 888	0.49
BB	12	2.73	61 910	0.17
SM	20	187.50	69 329	11.61
Demersal				
PM-HB	44	22.81	200	$<$0.01
AKP $<$50 m[a]	27	2 203.05	23 018	50.71
AKP $>$50 m	7	0	39 628	0
ES $<$50 m	15	3.56	109 433	0.39
ES $>$50 m	43	0.19	207 806	0.04

Regional density is expressed as the geometric mean cpue ($10^{[\sum \log(\text{cpue}+1)]/n} - 1$). cpue is standardized across gear types to fish per kilometre squared.

[a]Note the AKP region $<$50 m depth includes samples taken during demersal sampling of the nearshore focal area outside the mouth of Port Moller ($n = 25$) and during demersal sampling of the shelf ($n = 2$).

markedly variable and did not appear strongly linked to water temperature at the capture location. Fish captured in beam trawls were slightly, but significantly larger (66.6 $\pm$ 7.1 mm TL; ANOVA, $F_{(2,2263)} = 13.86$, $p < 0.001$) than fish captured in surface (64.3 $\pm$ 9.2 mm) and midwater trawls (63.7 $\pm$ 8.1 mm). Within the SM region of the shelf where fish were captured with all three gears, the largest mean size was observed among fish caught by surface trawl, followed by beam trawl, and midwater trawl ($F_{(2,1111)} = 17.02$, $p < 0.001$).

Of the regions sampled with the demersal beam trawl, age-0 Pacific cod were slightly larger along the coast in the nearshore focal area (BC, 67.0 $\pm$ 7.3 mm TL; Figure 8) than they were within PM-HB or in the broader AKP sampling region (65.8 $\pm$ 6.0 and 65.4 $\pm$ 6.3 mm TL, respectively), but these differences were not significant ($F_{(2,345)} = 1.22$, $p = 0.296$). The few fish ($n = 10$) that were captured over the eastern shelf were much smaller (55.0 $\pm$ 2.83 mm TL) than those captured along the AKP or in PM-HB.

Size variation of fish caught in the surface trawl over the shelf was driven by small sizes observed in the KB and SL regions ($F_{(4,1371)} = 117.70$, $p < 0.001$; Figure 8). The largest mean size of fish in surface trawl samples was observed in the SM region which had a relatively high mean sampling temperature. Similarly sized fish were captured in the NM and BB regions which had the lowest and highest mean sampling temperatures, respectively. The fish captured by the midwater trawl in the KB region also tended to be smaller than those captured in other regions over the shelf ($F_{(2,345)} = 1.22$, $p = 0.296$).

Nursery area evaluation

A comparison of standardized catch rates with multiple gear types suggests that age-0 Pacific cod use two distinct habitat types in different regions of the SEBS as primary nursery areas: demersal waters $<$50 m depth along the AKP ("coastal-demersal") and surface waters over the southern portion of the middle shelf ("shelf-surface"). Estimated densities in waters $<$50 m depth along the AKP (Table 2) were 2–3 orders of magnitude greater than densities in demersal habitats of other sampling regions and $>$10 times those observed in the region with the highest catch rates in surface waters (SM). As a result, despite representing a relatively small geographic area ($\sim$6% of SEBS waters $<$200 m depth), this coastal-demersal nursery area appears to support a disproportionately large fraction of the age-0 fish in the SEBS ($\sim$79%).

The large area of surface waters over southern middle shelf had the second highest estimated density of fish, cumulatively supporting $\sim$18% of the cohort. While PM-HB was the only coastal embayment examined in this study, the low catch rates (compared with those observed along the adjacent coastline) and the small areal extent of these inshore waters along the periphery of the Bering Sea make it unlikely that these embayments constitute a substantial fraction of total habitat use of this population.

Discussion

Despite their importance as a commercial resource and critical predator on other resource species, little work has been done to identify essential habitats of juvenile Pacific cod in the Bering Sea. Interestingly, age-0 fish in this system appear to use two markedly different habitat types in different regions of their distribution. Recent work documented their distribution in surface and subsurface waters over the extensive continental shelf (Hurst *et al.*, 2012a; Parker-Stetter *et al.*, 2013). Consistent with those observations, we found concentrations of age-0 Pacific cod in surface trawls conducted over depths of 60–80 m on the southern middle shelf. Over most of the shelf, age-0 fish were more abundant in surface than demersal habitats. However, densities of age-0 fish in bottom waters along the central AKP at depths of 5–50 m were much higher than those observed in surface waters over any region of the shelf. These observations demonstrate that these previously unsampled coastal habitats of the southeast Bering Sea represent important nursery habitats for age-0 Pacific cod in this system. This use of (at least) two distinctly different habitat types (coastal-demersal and shelf-surface) has not been described in other parts of the species' range. The similarity in fish sizes between the habitat types suggests simultaneous, population-level habitat use, rather than a sequential (ontogenetic) shift from pelagic to demersal habitats. This use of a more diverse habitat portfolio may be unique to the Bering Sea population which has little access to sheltered coastal embayments, the primary habitat in other parts of the species' range. The use of diverse habitat types complicates efforts to quantitatively identify the essential habitats supporting this valuable resource species in the Bering Sea. While future work will be required to refine estimates of the extent of these high fish-density inshore habitats, preliminary comparisons of catch rates in synoptic coastal and shelf sampling suggest that nearshore coastal areas along the AKP are the primary nursery area and appear to support the most age-0 Pacific cod production in the SEBS.

As observed in other parts of their range, shallow coastal habitats appear to be critical nurseries for age-0 Pacific cod in the Bering Sea. However, on a finer scale within the broad categorization of "shallow coastal habitats", primary nursery habitat in the Bering Sea appears to differ from other parts of the range. In the Gulf of Alaska and along the coast of northern Japan age-0 Pacific cod appear most abundant in the shallow waters of sheltered marine embayments (Dean *et al.*, 2000; Takatsu *et al.*, 2001; Laurel *et al.*, 2007). Conversely, in this study, age-0 Pacific cod were less abundant within Port Moller and Herendeen Bay than they were along the adjacent open coastline. In addition, maximum densities of age-0 Pacific cod were found at significantly greater depths along the Bering Sea coastline than they are in the Gulf of Alaska. This difference between ocean basins is likely due to differences in coastal bathymetry and degree of shelter from high-energy waves and wind. The coastal bays around Kodiak Island and other parts of the Gulf of Alaska are "fjord like", having steep shorelines with rapidly increasing depths. Even the most exposed site examined by Laurel *et al.* (2007; Twin Creeks Beach) is only subject to strong surf conditions following prolonged episodes of wind from the northeast (***personal observation) and maximum densities of juvenile Pacific cod at this site were observed at 3 m depth. In contrast, the lower topographic relief of the AKP offers little protection to the extensive, shallow flats of the Port Moller System from wave-generating winds and the shoreline outside the bays is directly exposed to large swells from the Bering Sea, creating a high-energy surf zone. These forces appear to greatly restrict the development of seagrass and kelp beds along the north side of the AKP. Within the bays, age-0 Pacific cod tended to be caught near tidal channels and along the coast fish were not captured in shallow waters with strong wave surge near the entrance to Port Moller (Figure 3).

In contrast to other parts of the species' range, Pacific cod in the Bering Sea also use pelagic-shelf waters as juvenile nursery habitats. In these habitats, they co-occur with the closely related walleye pollock which have a more pelagic distribution throughout their lives (Brodeur and Wilson, 1996). Previous work has documented the general patterns of age-0 Pacific cod in these habitats and described some aspects of interannual variation (Hurst *et al.*, 2012a; Parker-Stetter *et al.*, 2013). The distributions of age-0 cod captured in surface and midwater trawls over the Bering Sea shelf in 2012 were similar to those observed in previous studies. However, at the time of those studies, it was not known if cod also used demersal habitats on the shelf, as most previous demersal shelf sampling used gear with much larger mesh sizes (e.g. Mueter and Litzow, 2008). By integrating demersal sampling using a small-mesh beam trawl with routine surface and subsurface sampling in 2012, we demonstrated that age-0 Pacific cod are largely absent from the demersal habitats over much of the eastern Bering Sea shelf, at least at depths over 50 m. When age-0 Pacific cod are found on the shelf, they are up in the water column or near the surface.

Broad-scale patterns of habitat use by age-0 Pacific cod and other juvenile fish in the Bering Sea appear related to temperature and the distribution of large-bodied demersal predators. Maximizing growth opportunities and minimizing the risk of predation are assumed to be critical in determining juvenile nursery habitat use (Beck *et al.*, 2001). In the Bering Sea, shallow coastal waters and, to a lesser extent pelagic surface waters, may represent habitats with high growth potential and lower predation risk compared with deeper demersal waters over the shelf. Temperature has a significant effect on the growth potential of juvenile Pacific cod with maximum growth rates occurring at $>10^{\circ}$C (Hurst *et al.*, 2010, 2012b) and age-0 fish have been shown to exhibit behavioural selection of near-optimal growth temperatures in laboratory experiments (Davis and Ottmar, 2009) and field collections (Hurst *et al.*, 2012a). In the Bering Sea, summertime bottom water temperatures decline rapidly with increasing depth from 10 to 12°C in nearshore areas along the AKP to $<2^{\circ}$C within a persistent cold pool over the middle shelf (Luchin *et al.*, 1999). However, the development of strong summertime stratification in shelf waters over 50 m in depth results in surface temperatures over the mid-shelf that are only slightly cooler than the bottom temperatures observed along the coast (Figure 8). The similarity in body lengths observed between fish in coastal and pelagic habitats provides additional support for the idea that thermal opportunities for growth are generally similar between the two primary habitat types. However, interannual variation in energetic status (lipid storage) of Pacific cod on the shelf appears more sensitive than body length to thermal and diet variation, and may be linked to overwinter survival (Farley *et al.*, in press). Therefore, future studies should include additional comparisons of nutritional status of fish in nearshore and offshore habitats and evaluate the relative contributions of each habitat to the adult population (Beck *et al.*, 2001). Recent work (Miller *et al.*, in press) has demonstrated spatial variation in otolith elemental composition in age-0 Pacific cod in the SEBS which can be used to evaluate the ultimate contribution of these distinct nursery areas.

The "shallow water (predation) refuge hypothesis" has frequently been invoked to explain the use of coastal and estuarine waters as juvenile nurseries for a wide diversity of fish species (Paterson and Whitfield, 2000; Linehan *et al.*, 2001). Although generally applied to shallow subtidal habitats (<5 m; but see Ryer *et al.*, 2010), the hypothesis is based on the observation that the mean body size of piscivores generally increases with water depth. In deeper waters of the Bering Sea shelf, juvenile fish would have limited thermal opportunities for growth while being exposed to a number of large-bodied demersal predators including arrowtooth flounder (*Atheresthes* *stomias*), Pacific halibut (*Hippoglossus stenolepis*), and cannibalistic older Pacific cod (Aydin and Mueter, 2007). Juvenile Pacific cod on the shelf could minimize exposure to these demersal predators by remaining in the upper portions of the water column or in shallow waters along the coast (although in surface waters over the shelf, they would potentially be exposed to other pelagic predators such as salmon (*Oncorhynchus* spp.; Karpenko *et al.*, 2007) and seabirds (Paredes *et al.*, 2012). Although they may be undersampled with the beam trawl, we noted a complete lack of predatory fish in the shallow (<30 m depth) demersal trawls, consistent with previously described distributions (Mito *et al.*, 1999). The only larger-bodied fish captured with age-0 Pacific cod in the coastal-demersal habitats were the non-piscivorous flatfish northern rock sole (*Lepidopsetta polyxystra*) and yellowfin sole (*Limanda aspera*). The nearshore waters along the AKP would appear to offer the advantage of highest thermal opportunities for growth and lowest predation risk. The observation of high abundances of juvenile northern rock sole and yellowfin sole in these coastal habitats (Cooper *et al.*, 2014; ***Hurst, unpublished data) suggests that the general benefits of these coastal-demersal habitats apply to an array of juvenile fish.

While not known to occur in other populations of Pacific cod, the use of both coastal-demersal and shelf-surface habitats is recognized in other populations of gadids. It is most clearly understood in Norwegian Atlantic cod (*Gadus morhua*) where two recognized population segments use distinctly different juvenile habitats (although the degree to which the groups represent genetically distinct populations remains unclear; Nordeide *et al.*, 2011). "Norwegian coastal cod" spawn in fjords along the western and southern coasts, larvae are retained within the fjords, and juveniles primarily inhabit shallow coastal waters (Salvanes *et al.*, 2004). In contrast, "Northeast Arctic cod" spawn outside the fjords and on nearshore banks along the west coast, larvae drift northward into the Barents Sea, and age-0 juveniles remain in the pelagic zone though the first summer of life (Bergstad *et al.*, 1987). In age-0 Pacific cod in the Bering Sea, the use of the two habitat types appears less discrete than observed in Norwegian Atlantic cod and more analogous to Atlantic cod around Newfoundland, Canada. In those populations, most age-0 fish appear to reside in shallow coastal nurseries (Dalley and Anderson, 1997; Laurel *et al.*, 2003) but fish are also found in surface waters over the shelf through the first summer of life (Anderson and Dalley, 1997). In the Bering Sea, the proximity of the surface concentrations of age-0 fish over the mid-shelf to the demersal concentrations observed along the AKP (Hurst *et al.*, 2012a) and the similarity of size distributions between these regions suggests that habitat use of age-0 Pacific cod in the Bering Sea occurs along a gradient from coastal to pelagic. It is also possible that fish along the AKP move between coastal-demersal and shelf-surface habitats.

The ability to utilize a mosaic of habitats as nursery areas may contribute to the persistence of the Pacific cod population in the Bering Sea. The Bering Sea represents the northern extent of the latitudinal range of cod and a flexible, heterogeneous habitat portfolio may be an example of adaptive diversification at the margin of the species' range. A dynamic and developing age-0 cod population that is distributed across habitat spectra is able to utilize the unique and possibly non-substitutable resources of each habitat locale. This adaptation fosters complementary use of landscape resources (Dunning *et al.*, 1992) and balances resource availability, use, and depletion in a geographic area where the population is potentially more vulnerable to strong limiting factors. Habitat alternatives also afford protection from localized predation and competition. For example, Hunsicker *et al.* (2013) demonstrated that the interaction of arrowtooth flounder abundance and temperature influenced the degree of overlap between flounder (predator) and juvenile walleye pollock (prey). In this case, a flexible temperature tolerance would permit movement to areas with decreased predator abundances.

Sampling of multiple habitat types in the SEBS demonstrated that age-0 Pacific cod occupy pelagic waters over the shelf and inshore coastal waters, two distinctly different habitat types. Recognizing that direct comparisons of cpue across habitats and gear types is limited by a number of simplifying assumptions, we believe that our initial evaluation of relative abundances based on coordinated, synoptic sampling provides a reliable description of the basin-scale distribution of age-0 Pacific cod in the SEBS, significantly improving the understanding of nursery habitat use in this species. The high catch rates observed in demersal habitats along the AKP suggest that a disproportionately large fraction of age-0 fish resides in this region. Catch rates in this area were more than 10 times those observed in the region of surface habitat with the highest catch rates (SM) and >100 times the shelf-wide average in surface waters. As a result, estimated cumulative abundances along the AKP were four times those in surface waters over the entire SEBS shelf and slope (Table 2). Catch rates in demersal waters over the shelf were lower than those observed in surface waters, such that the estimated cohort contribution of demersal habitats deeper than 50 m is <1%. Similarly, while the PM-HB system was the only coastal embayment examined in this study, the low catch rates (compared with those observed along the adjacent coastline) and the limited areal extent of these inshore waters along the periphery of the Bering Sea make it unlikely that they could contribute substantially to the total productivity of this population.

Finally, we caution that the estimated contribution of habitat regions to basin-scale patterns of habitat use is based on direct comparison of catch rates from 1 year of sampling and that environmental or density-dependent processes may influence some aspects of habitat use patterns. For example, spring warming was delayed in 2012 and heavy ice cover persisted along the AKP and in the Port Moller system into mid-May. Perhaps the late warming may have resulted in reduced recruitment into and use of these coastal embayments. However, we believe that the general patterns of habitat use described here are robust to such effects. Through 4 years of beam trawling, we observed a consistent pattern of maximum abundances along the AKP at depths <50 m, and Hurst *et al.* (2012a) found that the distribution of fish in surface waters was not strongly influenced by cohort strength or thermal conditions. The use of pelagic waters over the shelf appears a regular component of juvenile habitat use in the Bering Sea and indices of abundance in surface waters may be useful as an early indicator of population recruitment (Anderson and Dalley, 1997; Stige *et al.*, 2013). However, such predictions should be used with caution as shelf-surface waters appear secondary to demersal-coastal areas as the primary habitat of age-0 Pacific cod in the Bering Sea. Additional research should be directed at understanding the biotic and abiotic factors driving growth and survival in these coastal nurseries due to the significant role these areas would appear to play in population productivity.

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