



Distributional patterns of 0-group Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea under variable recruitment and thermal conditions

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Despite the importance of Pacific cod in Bering Sea fisheries and foodwebs, little is known about the habitat use and the distribution of early life stages. We analysed 6 years of catch data for 0-group Pacific cod in fishery-independent surveys of the Bering Sea shelf. Juvenile cod were most commonly captured on the middle shelf over depths of 50–80 m and were rarely captured north of 58°N. Consistently high catches were observed east of the Pribilof Islands and north of Port Moller along the Alaska Peninsula. There was evidence of density-dependent habitat selection at the local scale as the frequency of occurrence increased with regional catch per unit effort. At the basin scale, the southerly distribution of the weak 2009 cohort suggested the possibility of a range contraction for small cohorts. There was no consistent shift in the distribution of juvenile Pacific cod in response to interannual climate variability. These results for Pacific cod contrast with those observed for walleye pollock, which appears to exhibit greater variance in distribution, but are similar to patterns observed for juvenile Atlantic cod. Future work should focus on distribution in nearshore habitats and examine the patterns of dispersal and the connectivity of the Bering Sea and Gulf of Alaska populations.

Keywords: Bering Sea, density-dependence, distribution, habitat, Pacific cod, temperature.

Introduction

The question of which factors determine species distributions has persisted in theoretical and applied ecology for a century. It is widely accepted that no single factor is likely responsible for defining range limits; the limiting factor may vary throughout the range or may change with environmental variation. In fisheries ecology, research on this topic has focused on describing variation in the distribution of major coastal fishery and forage species (Murawski, 1993). Many marine fish species undertake extensive seasonal migrations, have dispersive larval stages, and are not constrained by specific geographic barriers to the movement of either larvae or spawners. As a result, their distributions have the potential to shift in response to environmental or demographic factors on short time-scales.

MacCall's (1990) application of the ideal free distribution model (Fretwell, 1972) to marine fish stocks (in the “basin

model”) synthesized the study of density-dependent habitat selection in this group. Marine fish stocks have frequently been observed to expand their distribution during periods of high abundance and contract the distribution during periods of low abundance (Atkinson *et al.*, 1997; Barange *et al.*, 2009). In addition to the potential for cannibalism among predatory species, changes in potential competition for prey and refuge sites are assumed to be the general mechanisms governing the density-dependent behaviour of individuals and populations. Marine fish distributions also respond to changes in the environment. A poleward expansion of species' ranges is predicted for many marine species in response to the warming of coastal waters (Walther *et al.*, 2002; Roessig *et al.*, 2004), and several such shifts have already been documented in high-latitude marine systems (Perry *et al.*, 2005; Spencer, 2008; van Hal *et al.*, 2010).

Time-series of catch data from spatially extensive, fishery-independent trawl surveys in the North Atlantic and North Pacific have regularly been applied to questions of population biogeography (Perry and Smith, 1994). For example, distribution shifts in aggregate populations of groundfish in the Northwest Atlantic have been linked to both interannual variation and long-term trends in temperature (Murawski, 1993; Nye et al., 2009) and stock size (Swain, 1997; Simpson and Walsh, 2004; Nye et al., 2009). However, these studies have also demonstrated variation in the responsiveness among species within a community with some species exhibiting stable distributions (Perry et al., 2005; Dulvy et al., 2008; Nye et al., 2009).

Fewer studies have specifically examined the juvenile prerecruit stages of these species (but see Schneider et al., 1997; Abella et al., 2008; Moss et al., 2009). Patterns in juveniles may differ from those observed in adults as juveniles may have limited capacity for long-distance movements and may have more specific habitat requirements than older fish. And the impact of environmental variation may differ among early life-history stages. For example, increases in temperature may accelerate development, potentially reducing realized dispersal distances of larvae (O'Connor et al., 2007). Identifying the patterns of variation among multiple life stages will improve our understanding of the mechanisms responsible for distribution shifts over time (Rindorf and Lewy, 2006). Further, understanding of the distributional variability of juvenile fish has implications for how surveys to evaluate recruitment strength are designed (Blanchard et al., 2007; Woillez et al., 2009).

The wide continental shelf of the eastern Bering Sea supports important fisheries for walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and several flatfish and crab species. Water from the Alaska Stream and Aleutian North Slope Current is advected onto the southeast Bering Sea shelf. Flows on the shelf are generally northwards and water exits through the Bering Strait (Stabeno et al., 1999). The oceanography of the eastern Bering Sea is significantly influenced by sea-ice formation and melting. The maximum extent of the ice and the rate of melting are tightly linked to surface stratification, spring heating, and lower trophic level productivity (Hunt and Stabeno, 2002). There has been a rapid loss in the extent and thickness of sea ice in the Bering Sea associated with climate warming and increases in surface and bottom temperatures are predicted for the next century (Overland and Wang, 2007). The influence of climate variation on the distribution of walleye pollock (Wyllie Echeverria and Wooster, 1998; Moss et al., 2009) and red king crab in the Bering Sea (*Paralithodes camtschaticus*; Loher and Armstrong, 2005) has been described. In addition, McConnaughey (1995) and Spencer (2008) explored the effects of climate and population size on the distribution of Bering Sea flatfish.

Pacific cod is a widespread marine species, occurring on continental shelves throughout the eastern and western North Pacific and Bering Sea. An improved understanding of the stock structure, dispersal, and movement patterns of Pacific cod has been identified as a critical knowledge gap. Pacific cod spawn demersal eggs with larvae rising to the surface waters immediately after hatch (Doyle et al., 2009; Hurst et al., 2009). Larvae are transported from discrete spawning grounds by prevailing water currents, but the degree of mixing among regions remains unknown. In the Bering Sea, 0-group Pacific cod do not appear to be restricted to shallow nearshore habitats as they are commonly captured across the shelf in both demersal and pelagic trawl surveys. Laboratory studies have demonstrated the effects of

temperature on the behaviour (Davis and Ottmar, 2009; Hurst et al., 2009) and swimming activity (T.P. Hurst, unpublished data) of Pacific cod, but larger-scale patterns in distribution and habitat use have yet to be explored.

Here, we describe the distribution of juvenile (0-group) Pacific cod in the eastern Bering Sea based on 6 years of fishery-independent survey data. The period examined (2004–2009) was characterized by significant variation in the cohort strength of Pacific cod and thermal regime in the Bering Sea, allowing us to consider the potential for density-dependent effects and climate-induced changes in distribution at the northern limit of the species' range. Finally, we evaluate the local scale habitat selection in relation to fish density and water temperature. This paper is part of a larger project examining the patterns of dispersal and population connectivity in Bering Sea Pacific cod through the application of otolith chemistry (DiMaria et al., 2010).

Methods

Fish sampling

The late summer distribution of 0-group Pacific cod (hereafter “juvenile cod”) in the eastern Bering Sea was described for six cohorts (2004–2009), based on catches in the Bering–Aleutian Salmon International Survey (BASIS). Surveys were conducted from chartered fishing vessels (38-m FV “Sea Storm” and 49-m FV “Northwest Explorer”) or the 64-m NOAA Ship RV “Oscar Dyson”. In each year, field sampling efforts began in eastern Bristol Bay and moved northwest through the eastern Bering Sea (Figure 1). Surveys were conducted at similar times each year (late-August to late-September), with slight changes in survey locations, sampling dates, and the number of stations sampled due to weather conditions and other factors. A summary of annual sampling is provided in Table 1. Fish were collected with a 198-m midwater rope trawl modified to fish at the water surface (Farley et al., 2005). The net has a mouth opening of 55 m wide × 15 m deep and was made up of hexagonal mesh wings with a 1.2-cm mesh codend liner. The net was towed at speeds from 3.5 to 5.0 knots (~6.5–9.3 km h⁻¹) for 30 min during daylight hours. Water temperature was recorded at the start of each haul from a hull-mounted thermister positioned 3 m below the waterline or obtained from a CTD cast made before each haul (the measurement at 3-m depth was taken from the CTD cast).

The contents of the trawl were emptied into a sorting table on deck, and 0-group Pacific cod were sorted from other life stages and species. Fish were individually measured (to 1 mm L_F) and counted. For large catches, a subsample of juvenile cod was processed and used to estimate the total number of juvenile cod. Most Pacific cod captured during the survey were ≤ 100 mm L_F , and all fish ≤ 140 mm L_F were included in these analyses. Changes in the precision of length measurements and variation in cohort strengths precluded accurate identification of 0-group size limits yearly. As a result, the applied size limit of 140 mm L_F would likely have included a small number of age-1 fish in these analyses.

The trawl used in this research was designed to herd fish towards the codend of the net. Juvenile cod were larger than the codend liner (1.2-cm mesh) but smaller than the mesh in other parts of the net. Therefore, catches reported here should be considered relative rather than true estimates of juvenile cod abundance

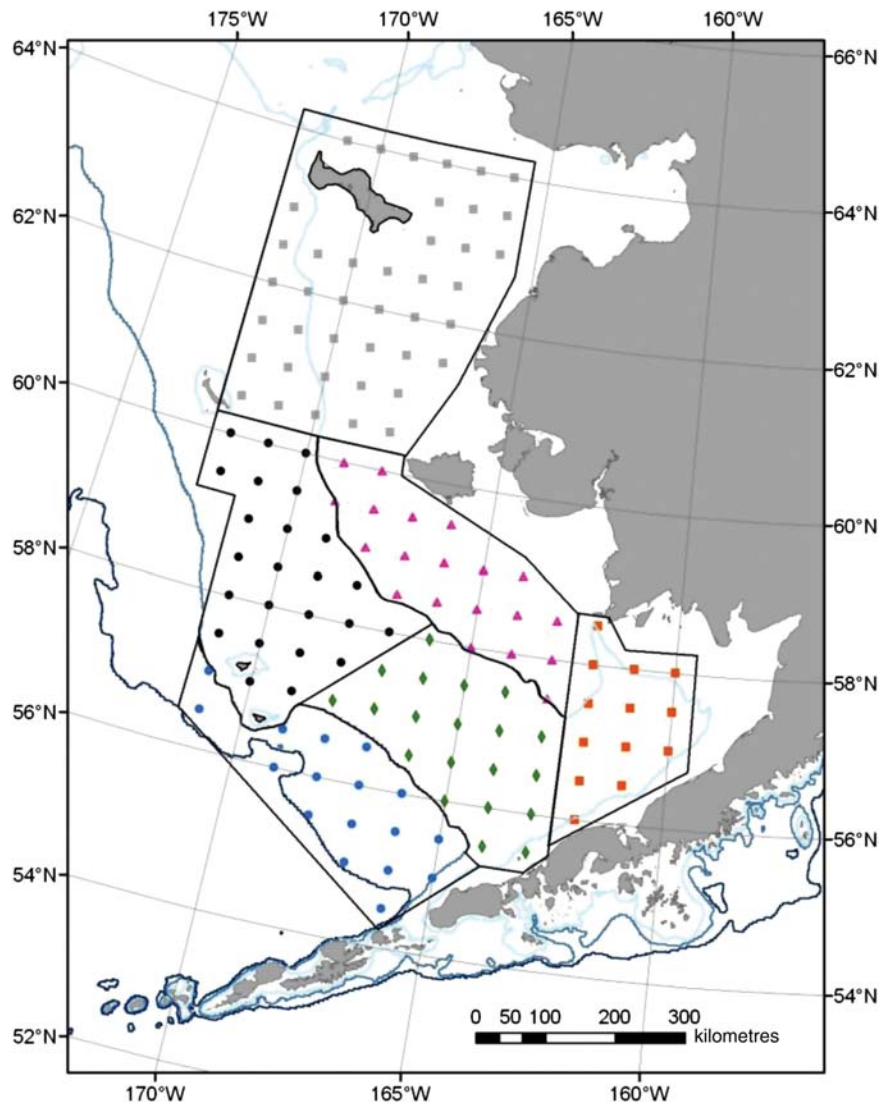


Figure 1. Statistical sampling regions of the Bering Sea used for analysis of the distribution of juvenile Pacific cod. Stations were included in the set of “core” stations (shown on map), if they were sampled at least four times in the 2004–2009 BASIS. Region boundaries were based on geographic landmarks and recognized hydrographic domains associated with depth-dependent stratification. Regions are: North (grey), North-Middle (black), South-Middle (green), Slope (blue), Kuskokwim (pink), and Bristol Bay (orange).

in the survey region. The start and end positions of each tow were used to determine the length of each tow and were used with the measures of net spread to determine the area swept by each tow (in km^2). Catch of juvenile cod at each station was expressed as catch per unit effort (cpue) of a standardized tow of 0.246 km^2 .

Although this survey was not designed to sample 0-group Pacific cod, they are a regular component of the catch and catch rates in this survey are correlated with those of age-1 fish in the AFSC’s eastern Bering Sea shelf bottom-trawl survey ($r = 0.901$, $p = 0.014$ from 2004 to 2009). Little sampling has been conducted inshore along the Bering Sea coastline, and cod may also use shallow inshore habitats as they do in the Gulf of Alaska and along the Aleutian Islands (Laurel *et al.*, 2007). In addition, 0-group Pacific cod are occasionally captured in Bering Sea bottom-trawl surveys, but generally at much lesser abundances than in the surface trawls; the process by which and time interval when Pacific cod adopt a fully benthic lifestyle are unknown.

Recognizing that this survey does not provide a comprehensive description of habitat use for juvenile cod, we assume that catches in the BASIS survey adequately represent basin-scale patterns in the distribution of juvenile Pacific cod.

To minimize the influence of interannual variation in the spatial coverage of sampling effort on apparent distribution (especially at the edges of the surveyed region), a subset of all sampling stations was included in this analysis: stations included in the analysis were sampled at least four times between 2004 and 2009. This resulted in the inclusion of 120 sampling sites in the “core” sampling area. For some analyses, these sites were then divided into six regions (Figure 1): Bristol Bay (13 stations), Kuskokwim (19 stations), South-Middle (20 stations), North-Middle (24 stations), Slope (12 stations), and North (41 stations). Region boundaries were based on geographic landmarks and depth contours associated with recognized hydrographic domains (Kinder and Schumacher, 1981; Overland *et al.*, 1999). The vertically

Table 1. Sampling effort by year and region.

Region	Area (km ²)	2004	2005	2006	2007	2008	2009
Sampling dates		14 August – 30 September	14 August – 6 October	16 August – 20 September	15 August – 8 October	11 September – 27 September	30 August – 27 September
Bristol Bay	61 910	11 (16)	11 (15)	11 (12)	11 (13)	4 (4)	4 (4)
Kuskokwim	65 389	19 (20)	19 (20)	18 (19)	19 (20)	9 (9)	9 (9)
South-Middle	69 329	20 (20)	20 (20)	22 (22)	20 (20)	10 (10)	11 (11)
North-Middle	82 719	20 (22)	16 (20)	21 (29)	21 (26)	5 (6)	9 (14)
Slope	43 888	10 (10)	12 (14)	14 (32)	12 (27)	2 (2)	7 (16)
North	144 739	37 (55)	32 (38)	37 (44)	37 (76)	0 (0)	37 (45)
Total	467 972	117 (143)	110 (127)	123 (158)	120 (182)	30 (31)	77 (99)

Stations used in core area analyses (all stations sampled).

isothermal inner domain generally extends to ~50-m depth where it is separated from the stratified middle domain by the “inner front”. A second, weaker front generally exists near 100 m depth, beyond which the reduced effectiveness of tidal mixing and intrusion of slope waters results in a less strongly stratified three-layer system (Overland *et al.*, 1999).

Over the 6 years of sampling, a total of 740 samples was collected, including 577 samples included in the core area. Sampling effort was most restricted in 2008 when 31 core stations were sampled, including only two stations in the Slope region and no stations in the North region. In all other years, the total number of core stations sampled was >75 and each region was represented by at least four samples in each year. Because it was not sampled in 2008, the North region was eliminated from some analyses.

Cohort strength

Estimates of the basin-wide recruitment of 0-group Pacific cod were obtained from the Bering Sea–Aleutian Islands Pacific cod stock assessment (Thompson and Lauth, 2011). The estimate of recruitment is developed using stock synthesis (Methot, 2011) incorporating data on catches in both the commercial fishery and research surveys and cohort-specific length-at-age data. The initial assessment of 0-group recruitment for each cohort is made in the year following recruitment based on the abundance of age-1 fish captured in the AFSC groundfish survey. Information on catch rates of 0-group Pacific cod from the BASIS survey is not incorporated into the assessment. Cohort strength varied nearly tenfold over the 6 years of this study (Table 2). For analyses, the cohort size (R_0) was binned into three levels (small, medium, and large) based on the most recent stock assessment (Thompson and Lauth, 2011). Large cohorts occurred in 2006 and 2008, which were both well above the 30-year average. Conversely, estimated cohort strength in 2009 was the lowest observed in the past 20 years. Medium size cohorts were produced in 2004, 2005, and 2007.

Thermal regime

Interannual variation in thermal regime in the eastern Bering Sea was described by regional climate indicators before the survey period and temperatures observed during sampling (Table 2). The ice retreat index and anomalies from the May sea surface temperature (SST) index were used to describe interannual variation in basin-scale warming patterns and conditions during the larval and early juvenile stages. The Bering Sea ice retreat index is calculated as the number of days with ice cover after 15 March in the region 56–58°N and 163–165°W. The May SST is measured

Table 2. Summary of climate conditions and abundance of juvenile Pacific cod in the eastern Bering Sea.

Cohort	Ice retreat index	May SST deviation	Sampling temperature	Mean cpue	Age-0 recruitment (millions)
2004	23	+1.10	10.61	27.07	279
2005	0	+0.85	11.72	68.24	316
2006	13	–1.63	10.00	309.93	1 153
2007	25	–1.73	10.16	22.55	385
2008	35	–2.59	8.66	65.81	1 360
2009	39	–1.60	8.69	2.30	168

across 54.3–60°N and 161.2–172.5°W. Temperatures measured during field sampling (at 3 m depth) were negatively correlated with the ice retreat index ($r = -0.908$, $p = 0.012$) and positively correlated with the May SST ($r = 0.814$, $p = 0.049$) during the 6 years of this study. Based on these indices, thermal conditions in the Bering Sea (T_{BS}) were classified as warm in 2004 and 2005, cool in 2006 and 2007, and cold in 2008 and 2009 (Table 2).

Analysis of distribution

In addition to the qualitative examination of cpue plots, quantitative assessments of the distribution and habitat characteristics of 0-group Pacific cod were conducted. These analyses examined both the basin- and regional-scale patterns in distribution and habitat selection with the goal of evaluating density-dependent and climate-related shifts. Spatial patterns in cpue of juvenile cod were analysed using the delta-generalized linear model approach (Stefansson, 1996). This approach combines separate generalized linear models for the description of presence/absence (with a binomial model) and cpue at sites where juvenile cod were present to produce an index of abundance. The log-normal distribution consistently outperformed the gamma distribution (lower model AIC scores) and was applied throughout the analyses of catch rates in positive tows. Analyses were conducted in the R programming environment. This approach was used to estimate annual cpue and frequency of positive catches in each of the geographic areas. For each cohort, the fraction of the cohort present in each region (“regional contribution”) was calculated based on the annual abundance index and the geographic area of the region (Marshall and Frank, 1995).

To examine the general patterns of juvenile cod distribution over the 6 years of sampling, presence/absence and cpue in positive tows were modelled as functions of depth (in three bins with breaks at 50 and 100 m; D_{bin}), latitude (Lat), and water temperature (relative to annual mean temperatures measured during sampling; T_{dev}), and their two-way interactions. Identification of significant effects was based on a stepwise removal of terms (based on decreasing AIC scores) from the full model; the removal of main effect terms was tested for models containing no significant interactions including that term.

A second set of expanded models examined variation in catch distribution among years in relation to variation in cohort size and thermal regime. Rather than including year as a nominal term, these models included terms for binned cohort size (R_0) and thermal regime (T_{BS}) to reflect the functional factors potentially influencing fish distribution. The spatial terms Lat, D_{bin} , and T_{dev} were included as well as the interaction between D_{bin} and T_{dev} which was identified as significant in the previous analyses. The presence of basin-scale density-dependence or thermal-dependence, respectively, would be indicated by a significant interaction between R_0 or T_{BS} with the spatial terms Lat, D_{bin} , or T_{dev} in either component of the model. A separate analysis tested for interactions between R_0 or T_{BS} with the geographic region.

Results

General distribution

The distribution of juvenile cod in the eastern Bering Sea was relatively stable across years and did not appear to shift in response to interannual variation in thermal regime. However, there were indications of distribution changes associated with

variation in cohort size. Across years, fish were most abundant at intermediate depths (peak catches at 50–80 m) and were only rarely captured in the colder waters of the North region (north of 60°N; Figure 2). Two clusters of sampling stations had mean catch rates across years of over 100 fish per tow: these were in the southern middle shelf over depths of 55–85 m; and north of the Alaska Peninsula, offshore of Port Moller to depths of 70 m (Figure 3). These areas of concentration are consistent with previous observations of juvenile cod in the eastern Bering Sea (Duffy-Anderson *et al.*, 2006; J.T. Duffy-Anderson, unpublished data).

Statistical analysis of catch data indicated significant effects of latitude, depth, temperature, and an interaction between depth and temperature on both the presence/absence of juvenile cod and the cpue in positive tows (Table 3). Juvenile cod were generally captured in the warmer waters sampled during the survey, consistent with their distribution centres the Bristol Bay and South-Middle regions, which had the warmest average surface temperatures. In addition, there was a significant interaction between depth and latitude on catch rates in positive tows reflecting the low catches at all depths in the northern samples.

Catch models expanded to include variation in the recruitment level (R_0) and thermal regime (T_{BS}) found significant interactions of these terms with water temperature (T_{dev}) on the presence/absence of juvenile cod (Table 4). Interestingly, the effect of water temperature on the presence/absence of juvenile cod appeared weakest (smallest difference in water temperature at occupied vs. unoccupied sites) in the cold years, due to the spatial homogeneity of surface temperatures. There were also significant interactive effects of R_0 and T_{BS} with latitude on the abundance of cod in positive tows. As would be predicted based on density-dependent expansion, the interaction between R_0 and latitude reflected a pattern of higher catches at higher latitudes in years of high recruitment (mean latitude of captured fish was highest for the large 2008 cohort). But this effect was primarily driven by the single small cohort in the study period (2009) having been captured exclusively in the southern portions of the SM and Slope regions. The mean latitude of capture differed by only 0.3° between years with medium and large cohorts. There was a counter-intuitive interaction between T_{BS} and latitude with mid-latitude catch rates being higher in cold conditions than in cool and warm conditions. But being based only on positive catches, this effect was driven by the large 2008 cohort that had the highest latitude of occurrence, rather than the small 2009 cohort which had the lowest latitude of occurrence, both of which occurred in cold years.

When distribution was examined in the six geographic regions, the highest catch rates were generally observed in the South-Middle region (four of six years) of the eastern Bering Sea (Table 5). Despite representing only 15% of the survey area, the South-Middle region contributed an average of 49% of juvenile cod in the study region (annual range 28–67%). Average regional contributions of the Bristol Bay and North-Middle regions were 22 and 15%, respectively. There were no significant interactions between R_0 or T_{BS} and region on the presence/absence of juvenile cod suggesting that regional distribution was maintained across years (Table 6). However, there was a significant interaction between R_0 and region on the cpue in positive tows as the catch rates of fish in positive Bristol Bay tows did not increase as would have been expected during the high recruitment years of 2006 and 2008.

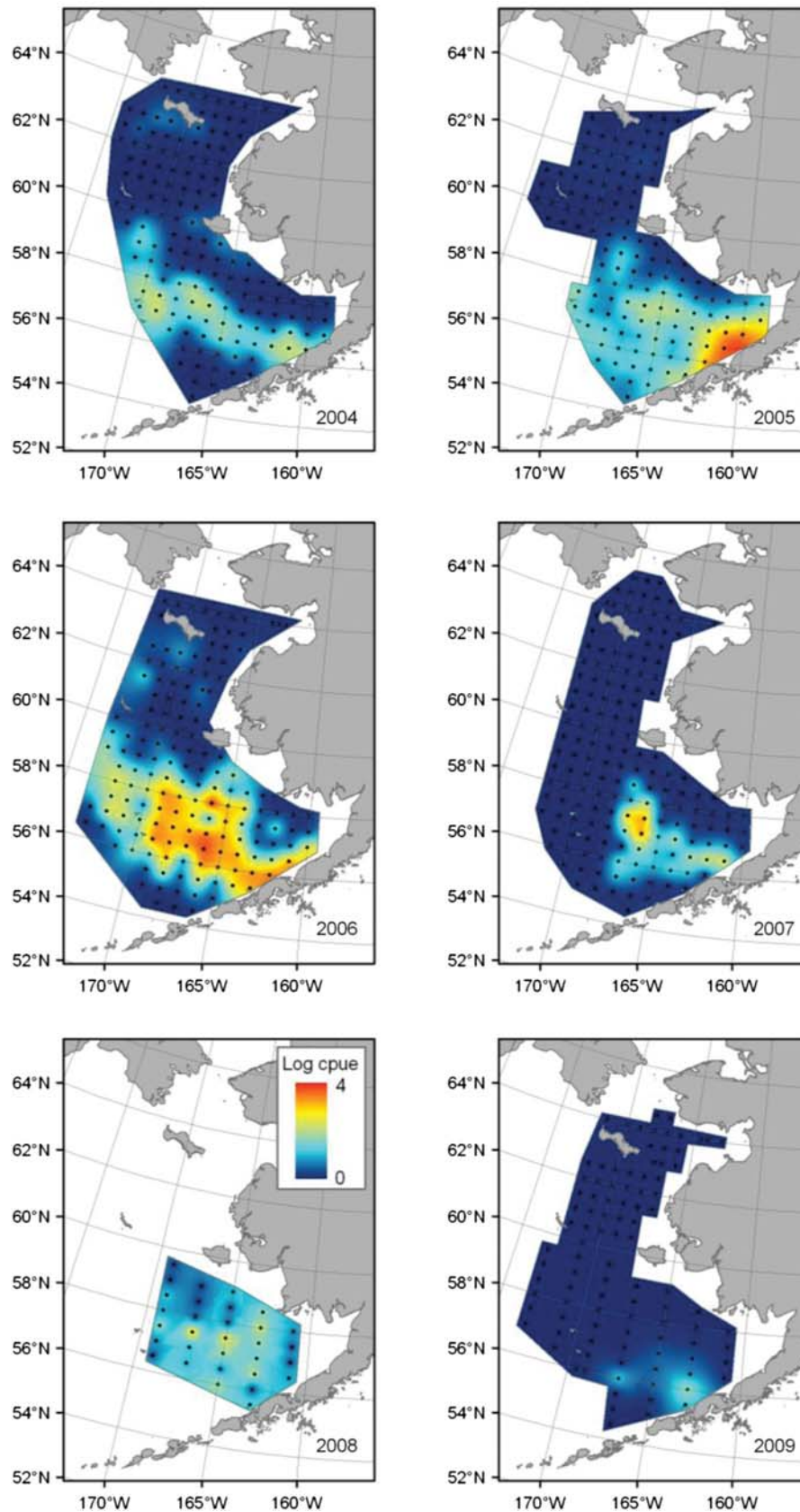


Figure 2. Cpue of age-0 Pacific cod in the BASIS for 6 years (2004–2009). Values are $\log(\text{cpue} + 1)$; cpue is the number of fish captured in each tow corrected to a standardized samples tow area of 0.246 km^2 .

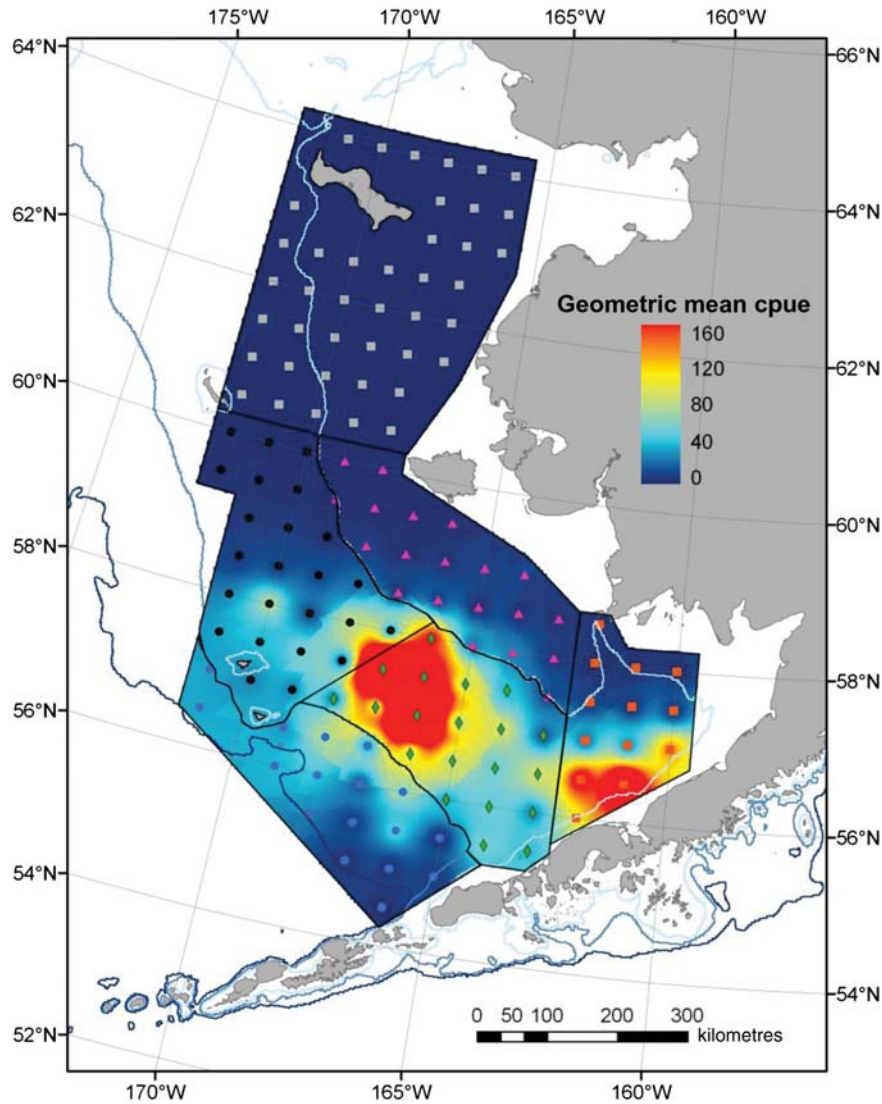


Figure 3. Geometric mean cpue ($10^{(\sum \log(\text{cpue}+1))/n} - 1$) of Pacific cod (< 140 mm L_F) across years (2004–2009) at each core sampling station in the BASIS.

Table 3. Model selection results for delta-generalized linear model of 0-group Pacific cod in the eastern Bering Sea.

Model	d.f.	AIC
Presence/absence model (Bernoulli)		
Final model: Lat + D_{bin} + T_{dev} + $D_{\text{bin}}:T_{\text{dev}}$	7	536.4
Term removal		
$D_{\text{bin}}:T_{\text{dev}}$	2	544.6
Lat	1	564.6
Positive catch model (lognormal)		
Final model: Lat + D_{bin} + T_{dev} + $D_{\text{bin}}:\text{Lat}$ + $D_{\text{bin}}:T_{\text{dev}}$	9	815.6
Term removal		
$D_{\text{bin}}:T_{\text{dev}}$	2	820.3
$D_{\text{bin}}:\text{Lat}$	2	821.7

Presence/absence and cpue in positive tows were modelled as functions of latitude (Lat), depth (D_{bin}), and temperature (T_{dev}) and their interactions. Terms were removed from the full model by backwards selection based on decreasing AIC scores. These results show the final accepted model and increases in AIC scores with additional terms removed.

Local habitat selection

Habitat selection by juvenile cod at the local scale mimicked patterns observed at the basin scale. When analysed within year–region combinations, there was a significant positive effect of T_{dev} on both presence/absence and catch rates, indicating active temperature selection rather than a consequence of larger temperature gradients through the Bering Sea range. In addition, we observed indications of density-dependent habitat selection at the local scale. The fraction of survey stations at which juvenile Pacific cod were captured in a region increased with regional mean cpue for that year in an asymptotic pattern (approximately linear on the logarithmic scale; Figure 4). Because sampling was conducted with regular grid spacing, similar results were obtained when the presence/absence data were analysed as the “positive area” (Woillez *et al.*, 2009).

Discussion

This is the first study to examine the distribution of juvenile Pacific cod in the Bering Sea. Juvenile cod were most abundant in surface

Table 4. Model selection results examining the temperature- and density-dependence of catch distribution of 0-group Pacific cod in the eastern Bering Sea.

Model	d.f.	AIC
Presence/absence model (Bernoulli)		
Final model: $R_0 + T_{BS} + \text{Lat} + D_{bin} + T_{dev} + R_0:T_{dev} + T_{BS}:T_{dev}$	13	520.7
Term removal		
$T_{BS}:T_{dev}$	2	525.6
$R_0:T_{dev}$	1	525.8
D_{bin}	2	529.9
Lat	1	540.3
Positive catch model (lognormal)		
Final model: $R_0 + T_{BS} + \text{Lat} + D_{bin} + T_{dev} + D_{bin}:T_{dev} + R_0:\text{Lat} + T_{BS}:\text{Lat}$	13	757.2
Term removal		
$D_{bin}:T_{dev}$	2	763.5
$T_{BS}:\text{Lat}$	2	765.4
$R_0:\text{Lat}$	2	765.8

Recruitment level (R_0) and thermal regime (T_{BS}) are included as factors and examined for interactive effects on catch as a function of latitude (Lat), depth (D_{bin}), and temperature (T_{dev}). Terms were removed from the full model by backwards selection based on decreasing AIC scores. These results show the final accepted model and increases in AIC scores with additional terms removed.

Table 5. Catch rates and regional contribution of juvenile Pacific cod in the eastern Bering Sea.

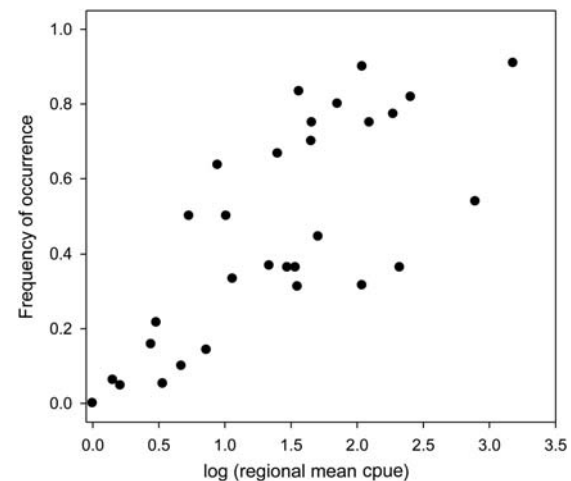
Region	2004	2005	2006	2007	2008	2009
cpue						
Bristol Bay	33.28	253.81	209.65	28.76	4.37	0.00
Kuskokwim	1.77	20.74	108.39	2.40	79.99	0.00
South-Middle	44.57	123.21	1 516.59	70.17	108.587	7.83
North-Middle	44.18	34.49	187.36	0.63	24.11	0.00
Slope	3.70	35.43	785.01	10.47	9.27	6.26
North	0.00	0.43	2.041	0.00	n.d.	0.00
Regional contribution						
Bristol Bay	0.23	0.52	0.07	0.24	0.02	0.00
Kuskokwim	0.01	0.05	0.04	0.02	0.24	0.00
South-Middle	0.34	0.28	0.60	0.67	0.56	0.66
North-Middle	0.40	0.10	0.08	0.01	0.15	0.00
Slope	0.02	0.05	0.20	0.06	0.03	0.34
North	0.00	<0.01	<0.01	0.00	n.d.	0.00

Regional cpue is based on the analysis of presence/absence and catch rates in positive tows using the delta-generalized linear model for each year/region.

Table 6. Model selection results examining the temperature- and density-dependence of the catch distribution of 0-group Pacific cod in six regions of the eastern Bering Sea.

Model	d.f.	AIC
Presence/absence model (Bernoulli)		
Final model: $R_0 + T_{BS} + \text{region}$	10	566.1
Term removal		
T_{BS}	2	566.3
R_0	2	603.5
Region	5	720.1
Positive catch model (lognormal)		
Final model: $R_0 + T_{BS} + \text{region} + R_0:\text{region}$	16	804.6
Term removal		
$R_0:\text{region}$	6	806.9
T_{BS}	2	830.2

Recruitment level (R_0) and thermal regime (T_{BS}) are included as factors and examined for interactive effects on catch by region. Terms were removed from the full model by backwards selection based on decreasing AIC scores. These results show the final accepted model and increases in AIC scores with additional terms removed.

**Figure 4.** Positive relationship between region-specific cpue of juvenile Pacific cod and frequency of occurrence in samples in that region indicating local density-dependent habitat selection.

trawls over the southern middle portion of the Bering Sea shelf, with highest concentrations found east of the Pribilof Islands and north of Port Moller. Data from 6 years of standardized surveys indicated that the oceanic distribution of juvenile cod was relatively stable and did not shift markedly in response to interannual variation in thermal regime. However, the southerly distribution of the 2009 cohort and habitat selection at the local scale suggests a possible range contraction when poor recruitment coincides with cold conditions. The locations of observed high concentrations and temporal stability may be a consequence of distributional limits which are established at earlier life-history stages, or a reflection of the species' general use of coastal margin habitats in the Bering Sea.

Little effort has been directed towards understanding the distribution and habitat characteristics of juvenile cod in the Bering Sea. Studies of juvenile cod in the Gulf of Alaska (and to a lesser extent the Aleutian Islands) have found cod to be abundant near the shoreline in coastal embayments (Abookire et al., 2007; Laurel et al., 2009) in association with submerged macrophytes (Laurel et al., 2007), but rare over the deeper continental shelf

(Wilson, 2009). However, in comparison, the Bering Sea offers little of that type of habitat and juvenile cod appear to be more commonly captured over the broad continental shelf, suggesting differences in habitat use at large scales. It is likely that juvenile cod use those inshore habitats where they occur in the eastern Bering Sea (along the Alaska Peninsula and Pribilof Islands) and that their distribution as observed in shelf surveys parallels distribution patterns along the adjacent coastlines. Additional sampling of inshore waters is clearly needed to obtain a more comprehensive understanding of habitat use in juvenile Pacific cod in the Bering Sea.

The distribution of juvenile cod in the eastern Bering Sea described here is consistent with observations made from samples taken in different years from more spatially restricted surveys with a variety of gear types. Juvenile cod were commonly captured in midwater trawls during 5 years (1996–2000) of sampling on the middle and outer shelf east of the Pribilof Islands (Duffy-Anderson *et al.*, 2006). More recently, demersal sampling in 2006 and 2008 found high abundances of juvenile cod along the Alaska Peninsula, especially in the area north of Port Moller (J. T. Duffy-Anderson, NOAA-AFSC, unpublished data). That sampling found fewer juvenile cod off Cape Newenham (in the northern half of our Bristol Bay region). Demersal sampling in our Kuskokwim region in 2003 captured very few juvenile cod (Norcross and Holladay, 2005), consistent with our observations. Sampling in our North region and farther north into the Chukchi and Barents Seas did not encounter juvenile cod (Norcross *et al.*, 2010; Rand and Logerwell, 2011). The range of juvenile cod in the Bering Sea appears to be more restricted than that for adults. Whereas juvenile cod were rare north of 58°N, adult cod were commonly captured in summer surveys at least as far north as 64°N (Hamazaki *et al.*, 2005).

Habitat selection and distribution

The distribution of organisms at any particular life stage can reflect the response of that life stage to environmental heterogeneity, with organisms selecting habitats with preferable biotic (e.g. prey availability) or abiotic (e.g. temperature) conditions. Alternatively, the distribution may reflect the persistence of patterns established by habitat selection or dispersal patterns at earlier life stages (Rindorf and Lewy, 2006). For example, species distribution in estuaries is often more reflective of salinity regimes during the settlement period than salinity conditions observed during sampling (e.g. Hurst *et al.*, 2004).

The distribution of cod appeared linked to both basin- and regional-scale thermal patterns. Temperature (expressed as T_{dev}) had a significant effect on catch rates. At the basin scale, juvenile cod were found primarily in the warmer South-Middle, Bristol Bay, and North-Middle regions of the Bering Sea. Although there was a significant interaction of thermal regime with latitude on catch rates of juvenile cod, there was no consistent pattern of shifting distributions in response to climate conditions as might be expected near the northern limit of a species range (Roessig *et al.*, 2004). The large 2008 cohort and small 2009 cohort both occurred in cold years and had the highest and lowest mean latitude of capture, respectively. However, when analysed within each region, juvenile cod were more commonly captured and had higher catch rates in positive tows at stations with higher water temperatures at the time of sampling. This finer-scale discrimination reflects an active pattern of selection for habitats offering the greatest thermal opportunities for growth (Hurst *et al.*, 2010).

Patterns of density-dependent habitat selection in juvenile cod were most apparent at the local scale. The southerly distribution of the weak 2009 cohort suggests the possibility of range contractions associated with poor recruitment, but the distribution of additional weak cohorts would need to be examined to confirm this effect. Otherwise, there was little indication of density-dependent expansion in response to high recruitment events, as there was no clear pattern of abundant cohorts occupying areas that were not occupied by fish in years of average recruitment. Conversely, the significant correlation between regional abundance and the fraction of sites occupied reflects a pattern of density-dependent habitat selection at the regional scale (Tyler and Hargrove, 1997; Shepherd and Litvak, 2004). As with other fish where increases in the area of occupancy have been associated with increased abundances, the exact mechanism responsible for the change in behaviour is unclear (Robichaud and Rose, 2006; Barange *et al.*, 2009). However, it is generally assumed to represent a response to patterns in foraging and growth opportunities due to varying local abundances of conspecifics (MacCall, 1990).

The temporal stability of the distribution of juvenile cod in the Bering Sea may be functionally linked to patterns of spawning activity and prevailing flow regimes (Hare and Cowen, 1996; Abella *et al.*, 2008; Duffy-Anderson *et al.*, 2010). While the distribution of spawning effort in Bering Sea Pacific cod is not fully known, the regions around Unimak Island (“cod alley”) and west of the Pribilof Islands appear to be major spawning areas (Shimada and Kimura, 1994). In addition, spawning and pre-spawning females have been frequently captured along the shelf break between 100- and 200-m depth as far north as 61°N (S. Neidetcher, National Marine Fisheries Service, unpublished data). Despite the 5–9 months between hatching and the survey, it is reasonable to infer linkages between observed aggregations of spawners and juveniles. Based on the divergence of flows in the Bering Slope and Bering Coastal Currents (Stabeno *et al.*, 1999), it is plausible that spawning activity in the Unimak Island region could be the natal source of fish in both observed aggregations of juvenile cod (Lanksbury *et al.*, 2007). Alternatively, juveniles captured near the Pribilof Islands could have been retained from local spawning by anticyclonic eddies or have been transported from spawning along the Aleutian Islands via the Aleutian North Slope Current and Bering Slope Current (Stabeno *et al.*, 1999). Interestingly, despite the widespread occurrence of fish in spawning condition along the shelf break, juvenile cod were very rarely captured north of 58°N. The presence of a persistent “inner front” near the 50-m isobaths may represent a transport barrier for larval cod into the Kuskokwim region as has been suggested for other species (Norcross and Holladay, 2005).

Comparison with observations for walleye pollock and Atlantic cod

These observations of a relatively stable distribution for juvenile Bering Sea Pacific cod contrast to those for juvenile walleye pollock based on catches in the same surveys (Moss *et al.*, 2009). During 2 years of high abundance, the distribution of 0-group walleye pollock was significantly more widespread, with much higher catches along the outer shelf and in the northern regions, than in years of low recruitment. The difference in response between the two species may reflect differences in behavioural ecology and species range. Walleye pollock are known to have a highly plastic behavioural strategy as juveniles, exhibiting

responses to variation in light, feeding conditions, and temperature (Olla *et al.*, 1995; Hurst, 2007). Laboratory experiments have demonstrated differing behavioural responses of juvenile walleye pollock and Pacific cod to temperature variation (Hurst, 2007; T.P. Hurst, unpublished data). In addition, walleye pollock are more widely distributed than Pacific cod, extending farther north into the Chukchi and Barents Seas (Norcross *et al.*, 2010; Rand and Logerwell, 2011). The wider range and behavioural flexibility of juvenile walleye pollock may result in a more dynamic distribution that more readily responds to demographic and climatic drivers.

Studies of the distribution of 0-group Atlantic cod in relation to abundance revealed similar patterns to those observed for Pacific cod, with results depending on the scale of the analyses. Examining habitat use within a coastal embayment with a local spawning aggregation, Robichaud and Rose (2006) found that 0-group Atlantic cod distribution expanded with catch rates and Laurel *et al.* (2004) demonstrated habitat-specific behaviours believed to be associated with density-dependent habitat selection. However, Schneider *et al.* (1997) found no evidence that the distribution of juvenile Atlantic cod along 1500 km of the Canadian coastline, expanded in years of high recruitment. Similarly, in the North Sea, the distribution of juvenile Atlantic cod was not related to density (Rindorf and Lewy, 2006). The later study also examined the potential influence of temperature variation on the distribution of juvenile Atlantic cod. As observed for juvenile Pacific cod in this study, temperatures at the time of sampling did not appear to impact the broad distribution of juvenile Atlantic cod. However, they did find evidence that temperatures and wind direction during the winter spawning period influenced the distribution of the resulting cohort (Rindorf and Lewy, 2006).

Conclusions

Change in habitat use and distribution of fish species is one expected consequence of climate variation at short and long time-scales (Roessig *et al.*, 2004). These responses may be the result of directed movements of fish into areas with preferred habitats, or greater survival and recruitment of offspring in areas that were previously unproductive, or a combination of the two (Shepherd and Litvak, 2004; Rijnsdorp *et al.*, 2009). Many studies have demonstrated relationships between short-term changes in the distribution of multiple age classes and environmental variability, suggesting that directed movements of adults and subadults are responsible for a significant part of the response (Spencer, 2008; Ruppert *et al.*, 2009). In comparison, juvenile fish may have less capacity for large-scale movements, and initial distributions of larval and juvenile fish may be more strongly defined by flow regimes and spatial patterns of survival in the early life stages (Abella *et al.*, 2008; Wilson, 2009). In this study, we found that the distribution of juvenile Pacific cod in the Bering Sea was relatively stable across thermal regimes but may contract during years of low recruitment. The lack of short-term variation does not imply that the distribution of Pacific cod will be resistant to long-term climate variation. Rather, the distribution of juveniles may be linked to spawning distribution via transport and retention patterns or consistent spatial gradients in temperature. As such, significant shifts in the distribution of juvenile cod in the Bering Sea may be dependent on changes in flowfield or spawner distribution (Frank *et al.*, 1996; Rindorf and Lewy, 2006). Understanding the processes responsible for biogeographic shifts in response to

climate variation would be enhanced by additional study directed at early life stages at a range of spatial scales.

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