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Juvenile northern rock sole (*Lepidopsetta polyxystra*) spatial distribution and abundance patterns in the eastern Bering Sea: spatially dependent production linked to temperature

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Annual spatial distribution and relative abundance of age-2 and age-3 northern rock sole (*Lepidopsetta polyxystra*) and summer bottom temperatures were analysed using data from eastern Bering Sea summer trawl surveys from 1982 through 2012. Previously observed differences in age-0 northern rock sole distribution persisted until age-2 and age-3. Latitudinal distributions of age-2 and age-3 fish were correlated most strongly with summer bottom temperatures 2 and 3 years prior to the survey year, during the time that the fish would have been age-0. Thus, temperature during the age-0 year may affect spatial distribution for the first few years of life. Distribution of age-2 and age-3 fish shifted northwards 2 years after the beginning of a warming trend from 1999 to 2003, and shifted southwards 2 years after a cooling trend from 2004 through 2010. Northerly distributions were correlated with high abundances. Density dependence was ruled out as a reason for northward shifts in distribution given a lack of correlation between latitudinal distributions and the annual abundances within the southern part of the distribution. We propose that the large northern nursery area produces large cohorts of northern rock sole, and that bottom temperatures in the age-0 year affect use of the northern nursery area.

Keywords: juvenile, *Lepidopsetta polyxystra*, Northern rock sole, nursery area, nursery area hypothesis, temperature.

Introduction

Shifts in population spatial distribution are often studied in ecology and fisheries science, in part because they are frequently associated with changes in abundance. Mechanisms for spatial shifts due to climate variability include adult movement (Mueter and Litzow, 2008; Nye *et al.*, 2009; Kotwicki and Lauth, 2013), changes in spawning location (van Hal *et al.*, 2010), variable egg and larval transport (Rindorf and Lewy, 2006), and expansion into marginal habitat during periods of high abundance (MacCall, 1990).

Climate variability may exert more control over early life history stages than adults for multiple reasons. Wind and current patterns can affect pelagic larval drift (Werner *et al.*, 1997; Rijnsdorp *et al.*, 2009), and early life stages are more sensitive to temperature-mediated growth (Teal *et al.*, 2008; Matta *et al.*, 2010). They can also have more narrow temperature range requirements than adults (Pörtner and Farrell, 2008; Rijnsdorp *et al.*, 2009).

Like all fish, flatfish population size depends on the survival of juvenile stages. For flatfish, juvenile survival depends on the quantity and quality of benthic nursery habitat (Gibson, 1994). For some flatfish species, the amount of juvenile nursery habitat is a bottleneck that can limit population size (Rijnsdorp *et al.*, 1992; Gibson, 1994; van der Veer, 2000).

In the eastern Bering Sea (EBS), northern rock sole (*Lepidopsetta polyxystra*), spawn over the outer continental shelf (Cooper *et al.*, 2013; Figure 1), and pelagic larvae are transported by prevailing currents. Larvae spawned north of Unimak Island and the Alaska Peninsula are advected eastward along the Alaska Peninsula towards Bristol Bay, and larvae spawned off the continental shelf south of the Pribilof Islands move northwards towards the Pribilof Islands (Lanksbury *et al.*, 2007; Cooper *et al.*, 2013). After settlement, age-0 juveniles inhabit areas with sandy sediment at depths <50 m (Cooper *et al.*, 2014). Potential age-0 habitat (<50 m depth) occurs

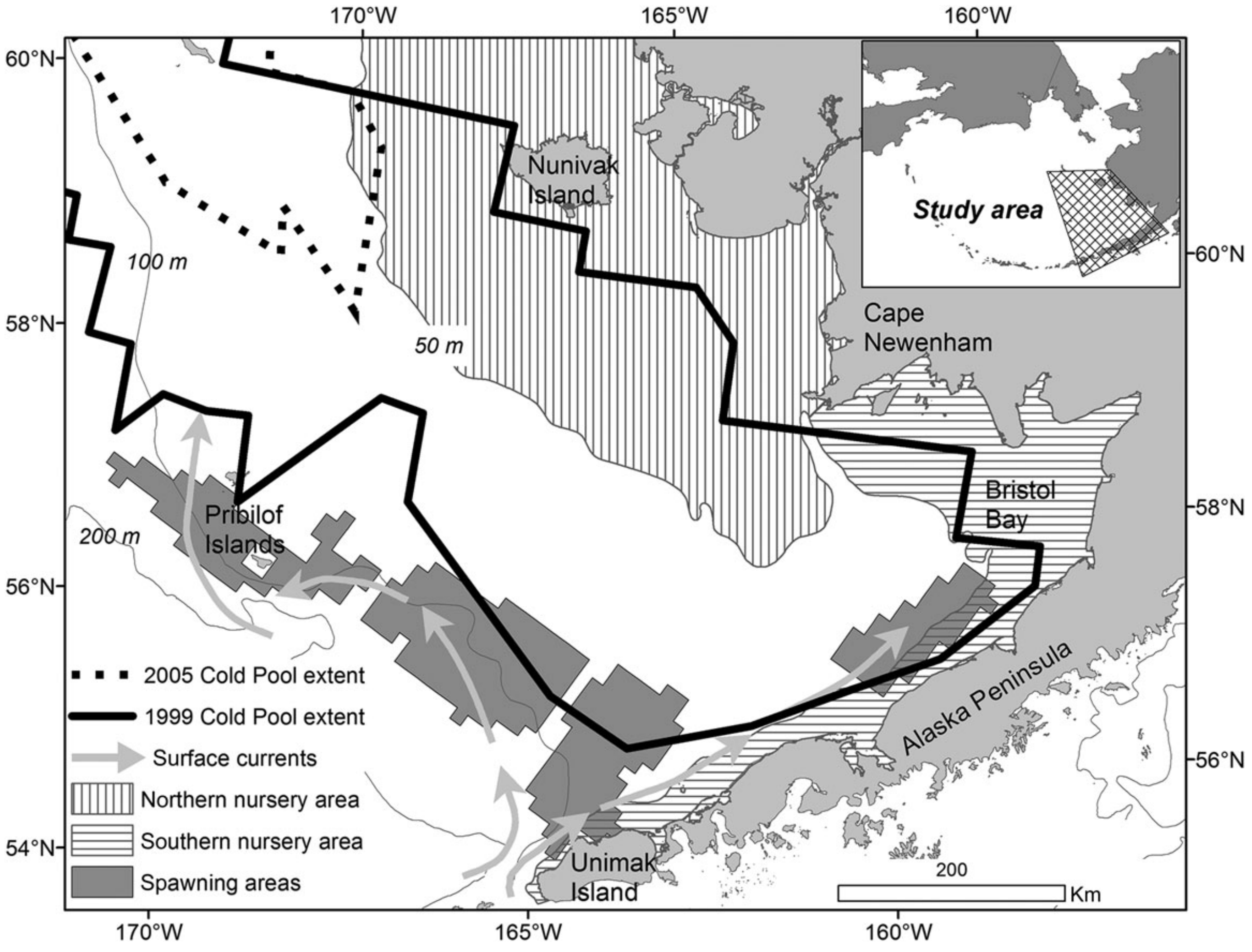

Figure 1. Map of the eastern Bering Sea. Northern rock sole spawning areas (from Cooper *et al.*, 2013) depicted by grey polygons. Depths <50 m depicted by vertical striped lines north of Cape Newenham (northern nursery area) and by horizontal striped lines south of Cape Newenham (southern nursery area). The EBS summer trawl survey area with bottom temperatures <2°C is outlined in 2005 by a dotted black line and in 1999 by a solid black line. Surface currents are depicted by light grey arrows (from Stabeno *et al.*, 1999).

in a relatively narrowband along the Alaska Peninsula, but in a much larger area along the Alaska coastline north of Cape Newenham, thus offering more potential juvenile northern rock sole habitat in the north (Figure 1). Hereafter, the region encompassing <50 m bottom depth between Cape Newenham and ~60°N will be referred to as the northern nursery area, and the region encompassing <50 m bottom depth south of Cape Newenham will be referred to as the southern nursery area.

The EBS shelf is also characterized by annual changes in oceanographic conditions, which may affect the suitability of juvenile northern rock sole habitat. Perhaps the most prominent feature of the EBS shelf is the annual formation of a pool of cold bottom water (Cold Pool, bottom temperatures <2°C) in the middle shelf (50–100 m depth) that can persist into spring and early summer (Stabeno *et al.*, 2001). The Cold Pool results from winter sea ice conditions, and its size and southern extent vary annually (Stabeno *et al.*, 2001). Prior to 1999, annual EBS temperatures varied without discernible multiyear trends; however, from 1999 through 2013, the EBS exhibited a multiyear warming trend and warm period followed by a multiyear cool period (Overland *et al.*, 2012; Stabeno *et al.*, 2012). In 1999, EBS summer bottom temperatures were the coldest in the time series, and the summer cold pool extended to near the Alaska Peninsula (Figure 1). Starting in 2000, the EBS began to warm, and stayed warm through 2005, when the southern extent of the summer cold pool was between the Pribilof Islands and Nunivak Island (Figure 1). Following 2005, there was a cool period in summer bottom temperatures from 2006 through 2013.

The spatial extent of the Cold Pool may influence the amount of available nursery habitat in the EBS for juvenile northern rock sole. Age-0 and age-1 fish were abundant in the northern nursery area during a warm year (2003), but not in two cold years (2008 and 2010), leading to the hypothesis that juveniles use this area as nursery habitat only in warm years, when the spatial extent of the cold pool is at a minimum (Cooper *et al.*, 2014). The large size of the northern nursery area and high densities of age-0 and age-1 juveniles observed there also led to the hypothesis that variable juvenile production in the northern nursery area impacts year-class strength (Cooper *et al.*, 2014).

The Alaska Fisheries Science Center (AFSC) of the National Oceanic and Atmospheric Administration (NOAA) has conducted an annual summer bottom trawl survey (BT survey) on the EBS continental shelf from 1982 to present (Lauth and Nichol, 2013). Catch data of 6–11 cm fork length (FL) northern rock sole collected in this survey allow the study of abundance and spatial distribution patterns of an important life stage. Fish in the 6–11 cm size range are age-2 and age-3 juveniles, and will hereafter be referred to as small juveniles. Although the BT survey does not sample age-0 and age-1 juveniles (<6 cm FL) due to size selectivity of the trawl, environmental factors during age-0 years can be related to spatial distributions of age-2 and age-3 juveniles to assess possible impacts when juveniles were age-0.

Our first objective was to compare age-0 distributions from the available 2 years of small-mesh trawl surveys (Cooper *et al.*, 2014) with later small juvenile distributions in the annual BT survey to determine whether the observed variability in age-0 spatial distribution persists until the cohorts recruit to the BT survey. Our second objective was to use the BT survey data to test the hypothesis that summer bottom temperature in the age-0 year affects spatial distribution of small juveniles collected 2 and 3 years later in BT survey. Our final objective was to test the hypothesis that the use of the northern nursery area corresponds to a higher abundance of small juveniles.

Methods

Comparison of age-0 fish distributions with later small juvenile distributions

Density estimates and distribution of age-0 northern rock sole were obtained from small-mesh BT surveys conducted in 2003 (1–26 August) and 2010 (11–18 September). Fish were collected using a 3.05-m plumb staff beam trawl with 7 mm mesh and 4 mm codend liner (see Cooper *et al.*, 2014). Density was estimated as catch per unit effort (cpue) of age-0 northern rock sole for each tow, and was calculated as number of fish caught divided by the area swept by the trawl, i.e. distance towed multiplied by the effective net width (2.26 m; Gunderson and Ellis, 1986). Age-0 fish were identified as the smallest length mode in both years (18–51 mm TL in 2003, and 22–50 mm TL in 2010), and in 2010 this length mode was verified to be age-0 by the absence of an annulus on the sagittal otolith (Cooper *et al.*, 2014).

For small juveniles (6–11 cm FL), distribution and relative abundance data were obtained from the 1982 through 2012 BT surveys (Lauth and Nichol, 2013). These surveys annually sampled a standard set of 330 fixed stations located 37.04 km (20 nautical miles) apart from each other, starting in inner Bristol Bay, extending west to a bottom depth of 200 m, south along the Alaska Peninsula, and north to latitude 61°N. Standardized BT survey gear and methodologies were used throughout the time series (Stauffer, 2004).

Small juvenile density was estimated as the cpue at each station, which was calculated as the number of individuals 6–11 cm FL captured per area trawled (hectares). Prior to 1996, rock sole (genus *Lepidopsetta*) were not identified to the currently recognized species level (northern rock sole, *L. polyxystra*; southern rock sole, *L. bilineata*), and therefore genus level data were used during these years. This was considered inconsequential because southern rock sole biomass has averaged <0.04% of the total rock sole biomass in the EBS (Wilderbuer and Nichol, 2013).

Otoliths from up to 17 fish per centimetre length increment of small juveniles were collected each year from the BT survey. Ages were assigned by the AFSC Age and Growth Program and used to estimate the age composition of the small juvenile size range. Most fish in this study were aged by surface reading under reflected light, although some fish with questionable annuli were aged using break and burn methods (Matta and Kimura, 2012). Small juveniles collected during the BT surveys were age-1 (3%), age-2 (47%), and age-3 (50%) fish.

To determine if differences in age-0 distributions in the northern nursery area observed in the small-mesh trawl studies persisted until age-2, we plotted cpue values of age-0 fish observed in 2003 and 2010 during the small-mesh surveys and compared them with cpue values of small juveniles 2 years later during the BT survey.

Relating small juvenile spatial distributions to bottom temperatures in the age-0 year

To examine whether temperature during the age-0 year significantly affected the spatial distribution of small juveniles 2 or 3 years later, we tested for correlation between latitudes of the annual geographic centre points of the small juvenile distributions and mean summer bottom temperatures during the survey year as well as 1–4 years prior. If temperatures during the age-0 year were the most critical, then higher correlations between temperatures and latitudinal distributions would occur with latitudinal distributions time-lagged by 2 or 3 years. Mean annual summer bottom temperatures were calculated using station bottom temperatures measured during BT surveys (Lauth and Nichol, 2013). Bottom temperatures are measured during the survey from late May until late July, and temperatures are warming during this period. Annual temperatures are made as comparable as possible by starting the survey in the southeast corner of the grid and working towards the northeast corner of the grid each year. Coordinates of the annual geographic centre points of the small juvenile distributions, weighted by cpue ($\bar{X}$, $\bar{Y}$) were then calculated for each year by:

$$\bar{X}_w = \frac{\sum_{i=1}^{n} w_i x_i}{\sum_{i=1}^{n} w_i}, \quad \bar{Y}_w = \frac{\sum_{i=1}^{n} w_i y_i}{\sum_{i=1}^{n} w_i},$$

where w_i is the weight (cpue) at station i, x_i and y_i are the coordinates for station i, and n is the total number of stations (Burt *et al.*, 2009). Calculations were performed using the Mean Center tool, weighted by cpue, in ArcMap. Correlations were tested using a cross-correlation function, which is defined as the set of correlations between latitudinal distribution and temperature in the current year as well as 1–4 years prior (Chatfield, 1989; SYSTAT v. 13). Finally, to visualize the effect of age-0 temperatures on small juvenile distributions, the annual geographic centres of small juvenile distribution were mapped using symbols corresponding to the annual mean EBS summer temperatures 2 and 3 years prior when the small juveniles were age-0. For this, annual mean EBS summer bottom temperatures were binned into three categories: warm years (warmest 25% of the temperature range), moderate years (25%–75% of the temperature range), and cold years (coldest 25% of the temperature range).

Comparison of small juvenile spatial distributions and abundances

We tested for correlation between the latitudes of annual geographic centre point of the small juvenile distribution and the annual indices of abundance over the entire survey time series. The annual index of abundance was calculated as the mean cpue of the station grid. A positive correlation between northerly spatial distributions and abundances would be expected if the use of the northern nursery area produced higher abundances of small juveniles.

To determine if density-dependent movement may have caused the observed positive correlation between abundances and northerly geographic distributions (see Results), we tested the hypothesis that small juveniles spread northward from the southern nursery area into the northern nursery area during years of high abundance. From the set of geographic centre points, we selected 3 years having the most southerly distributions. We defined the area encompassing the centre of small juvenile distributions in these 3 years as the main southern nursery area. To do this, we used the Standard Deviational Ellipse tool in ArcMap, weighted by cpue, to delineate the area encompassing 1 SD (∼68%) of the cpue for each of the 3 years with the most southerly distributions. The standard deviational ellipse is a method to objectively generalize the centre of distribution of point data (Raine, 1978). Finally, we tested for correlation between annual mean cpues within the main southern nursery area bounds and the latitudes of the annual geographic centre points of the distributions for small juveniles for all years of the BT survey. A positive correlation would indicate that small juveniles spread northward during years of high abundance in the southern area.

Results

Comparison of age-0 fish distributions with later small juvenile distributions

The comparison between distributions of age-0 fish and small juveniles (age-2 and age-3) sampled 2 years later revealed similar patterns in both abundance and distribution. In 2003, age-0 fish were abundant in the northern nursery area (Figure 2a), as were small juveniles sampled 2 years later in 2005 (Figure 2b). In 2010, age-0 fish were absent from the northern nursery area (Figure 2c), and small juvenile cpue values were subsequently low 2 years later in 2012 (Figure 2d).

Relating small juvenile spatial distributions to bottom temperatures in the age-0 year

Latitudes of the annual geographic centre points of small juvenile distributions were most strongly correlated with summer EBS bottom temperatures 2 and 3 years prior to the survey year (Figure 3), with a peak correlation 2 years prior to the survey year

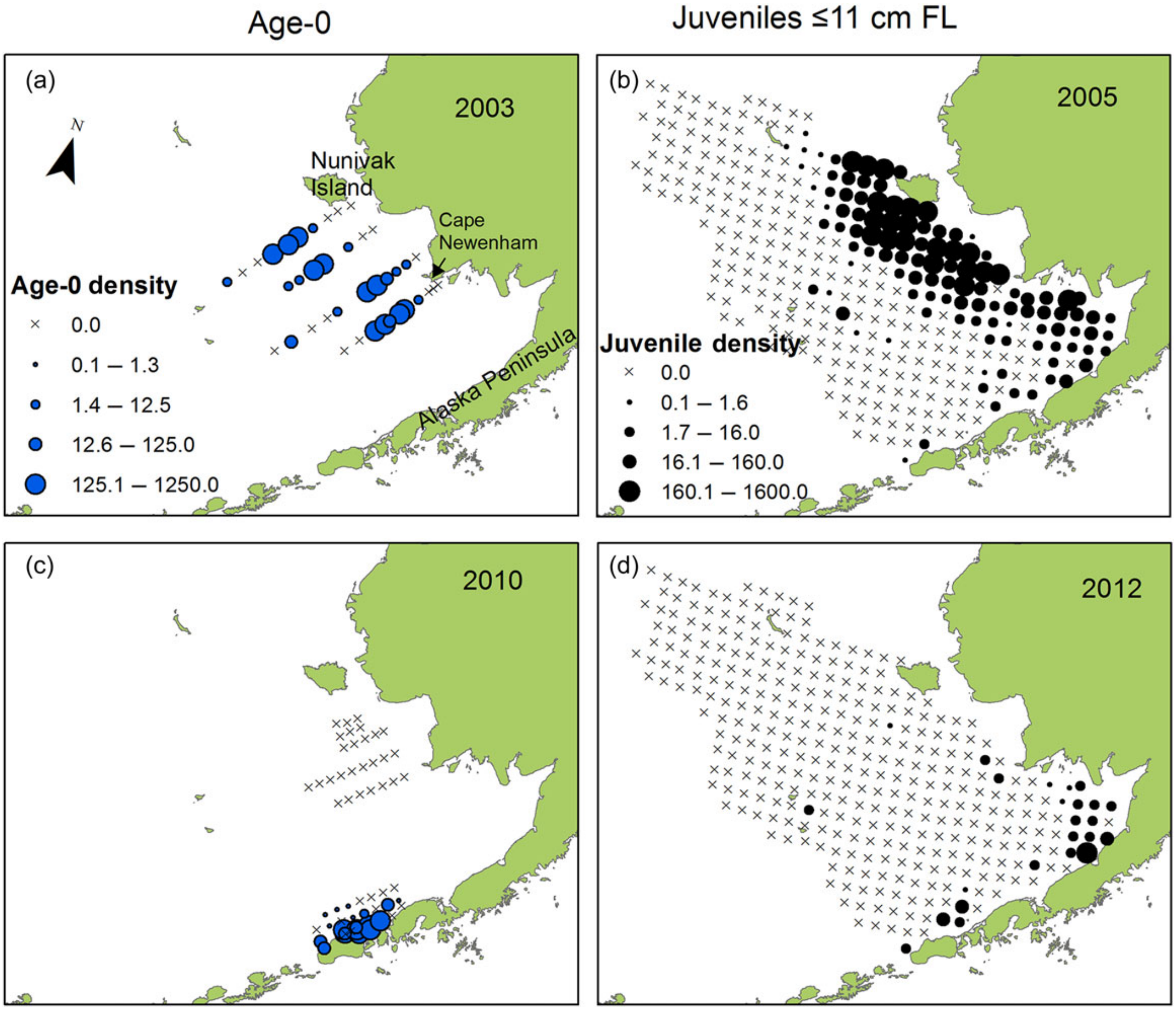

Figure 2. Northern rock sole age-0 catch per unit effort (cpue) and resulting catch per unit effort of small juveniles (≤11 cm) 2 years later. (a) Age-0 cpue (number of fish /1000 m^2) in August 2003 and (b) resulting small juvenile cpue (number of fish/hectare) in summer 2005. (c) Age-0 cpue (number of fish/1000 m^2) in 2010, and (d) resulting small juvenile cpue (number of fish/hectare) in 2012. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

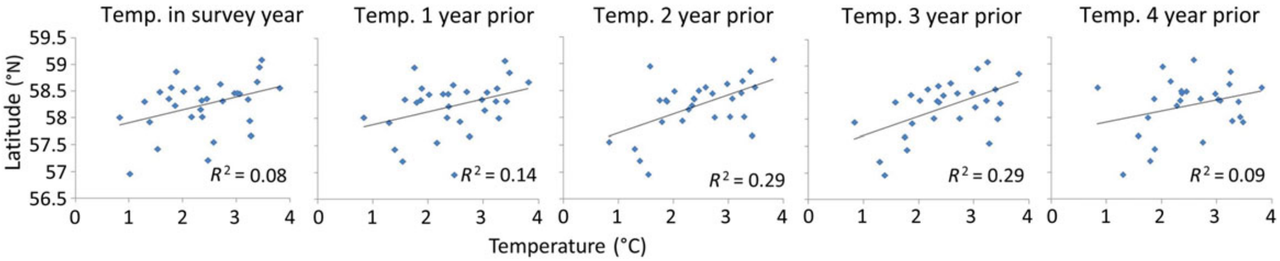

Figure 3. Latitude temperature time-lagged correlations. Scatterplots of annual latitudinal centre points of small juvenile distributions compared with current and 1–4 years previous mean eastern Bering Sea summer bottom temperatures for 1982–2012. The first column compares the latitudinal distribution centre points with temperatures from the same (current) year and column 2–5 compare the latitudinal centre point with temperature from 1 to 4 years prior. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

(Table 1), consistent with the hypothesis that distributions are most strongly related with temperature conditions 2 and 3 years prior to the survey when the small juveniles were age-0s. Although not as strong, there was also a significant correlation during the survey year, indicating that current temperatures may also have influenced small juvenile distributions. The time-lagged correlations were most evident during the period of multiyear warming and cooling from 1999 through 2010 (Figure 4). From 1999 through 2003, when EBS bottom temperatures increased, the small juvenile distributions shifted north with a two year lag; and from 2003 to 2010 when bottom temperatures decreased, the distributions shifted south, again with a 2-year lag (Figure 4). The 3 years (2010, 2011, and 2012) with the most southerly centres of small juvenile distribution had cold bottom temperatures both 2 and 3 years prior (both years when small juveniles were age-0), and these 3 survey years (2010, 2011, and 2012) were the only years with cold temperatures both 2 and 3 years prior (Figure 5). The most northerly distributions of small juveniles occurred in survey years following successive warm age-0 years (such as survey years 2005 and 2006); however, northerly small juvenile distributions also occurred in years following two moderate age-0 temperature years (such as 1991 and 1992), or even following moderate and cold age-0 years (such as 1996; Figure 5).

Comparison of small juvenile spatial distributions and abundances

Small juveniles were more northerly distributed during years when their abundance was higher (Figure 6d–f) when compared with lower (Figure 6a–c). Annual centres of small juvenile distributions ranged from near the Alaska Peninsula inside Bristol Bay to the northeast towards Nunivak Island (Figure 5). Juvenile abundances were significantly correlated ($R^2 = 0.53$, Pearson correlation $P \ll 0.001$) with latitude (Figure 7).

Annual mean cpue values within the main southern nursery area were not correlated with the latitudinal centres of the small juvenile distributions (Figure 8), as would be expected if high densities in the main southern nursery area caused fish to move northwards. Consequently, no evidence was found indicating density-dependent movement during years of high abundance and more northerly distributions.

Discussion

Comparison of age-0 fish distributions with later small juvenile distributions

Year classes either used the northern nursery as age-0s and remained there until age-2, or did not use the northern nursery area at all from age-0 through age-2. Age-0 fish settle offshore and move shoreward by age-1, then move offshore again according to Heinke's law by age-2 and age-3 (Cooper *et al.*, 2014); however, the available data indicate a general latitudinal pattern is set by the time the age-0 fish settle. It must be emphasized to note that only summer distribution data are available, and it is unknown whether these juvenile fish move throughout the seasons.

Table 1. Cross-correlation function (CCF) coefficients of centre of latitude of small juvenile distribution and summer bottom temperatures in the survey year (0 years prior to the survey) and 1–4 years prior to the survey year for the 1982–2012 time series.

Temperature precedes latitude of small juveniles by	CCF correlation	95% CI	$P < 0.05$
0 Years	0.39	0.35	Yes
1 Year	0.34	0.36	No
2 Years	0.50	0.37	Yes
3 Years	0.48	0.38	Yes
4 Years	0.25	0.38	No

Relating small juvenile spatial distributions to bottom temperatures in the age-0 year

The relationship between small juvenile distribution and temperature in the age-0 year suggests that latitudinal distribution patterns in small juveniles are partially determined by environmental conditions in the age-0 year. Bottom temperature could impact juvenile distribution in the age-0 year by multiple mechanisms. One possible mechanism is temperature-mediated nursery area suitability. The northern nursery area is within or partially within the Cold Pool in cold summers when rock sole are settling (Cooper *et al.*, 2014). Northern rock sole growth is reduced in the laboratory at colder temperatures (Hurst and Abookire, 2006), but lower temperature limits for growth in the Bering Sea are unknown. Northerly distributions of small juveniles occurred following age-0 years with moderate or even moderate and cold years, and thus it may be that the northern area is only uninhabitable by age-0 fish in the coldest years, such as in 2008–2010, which resulted in the survey years with the most southerly small juvenile distributions (2010–2012).

Another potential mechanism is a shift of adult spawning distribution with temperature. Northern rock sole spawn in winter and early spring (Wilderbuer and Nichol, 2013). In warm years, spawning fish may move north. Van Hal *et al.* (2010) report that populations of two species of flatfish in the North Sea shifted northwards during warming trends because adults first migrated north, then

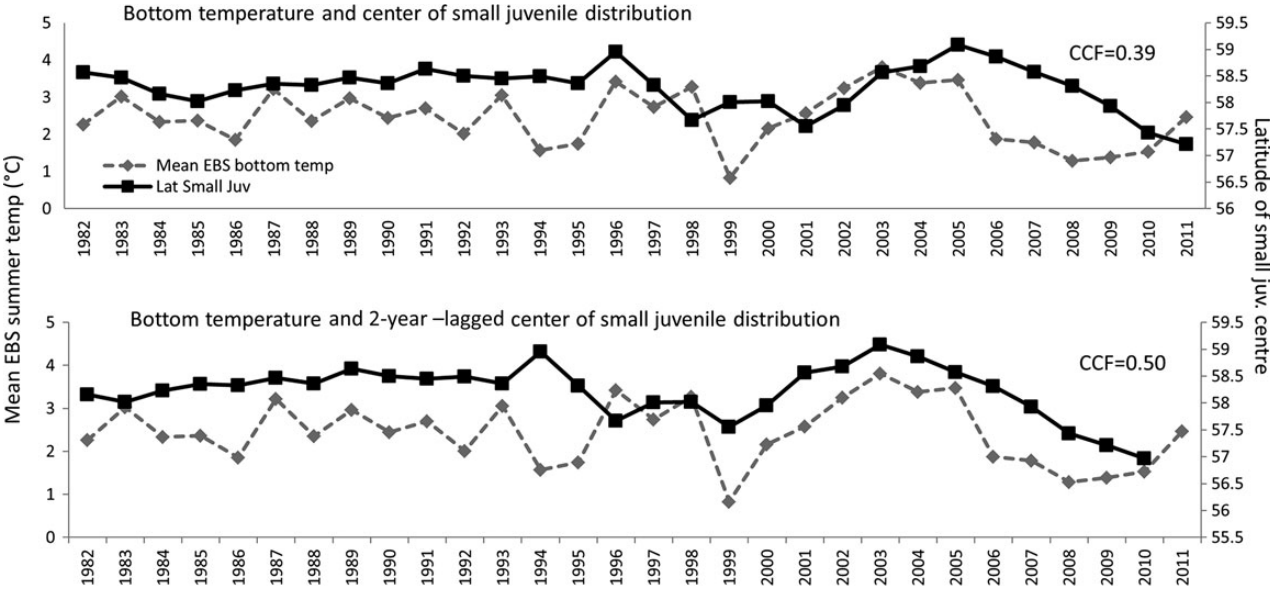

Figure 4. Trends in annual mean EBS summer bottom temperature from the Alaska Fisheries Science Center eastern Bering Sea summer trawl survey and latitude of the mean centre of northern rock sole small juvenile distributions. The top panel is bottom temperature and latitude of the centres of distribution in the same year. In the bottom panel, mean centre of small juvenile distributions is lagged by 2 years.

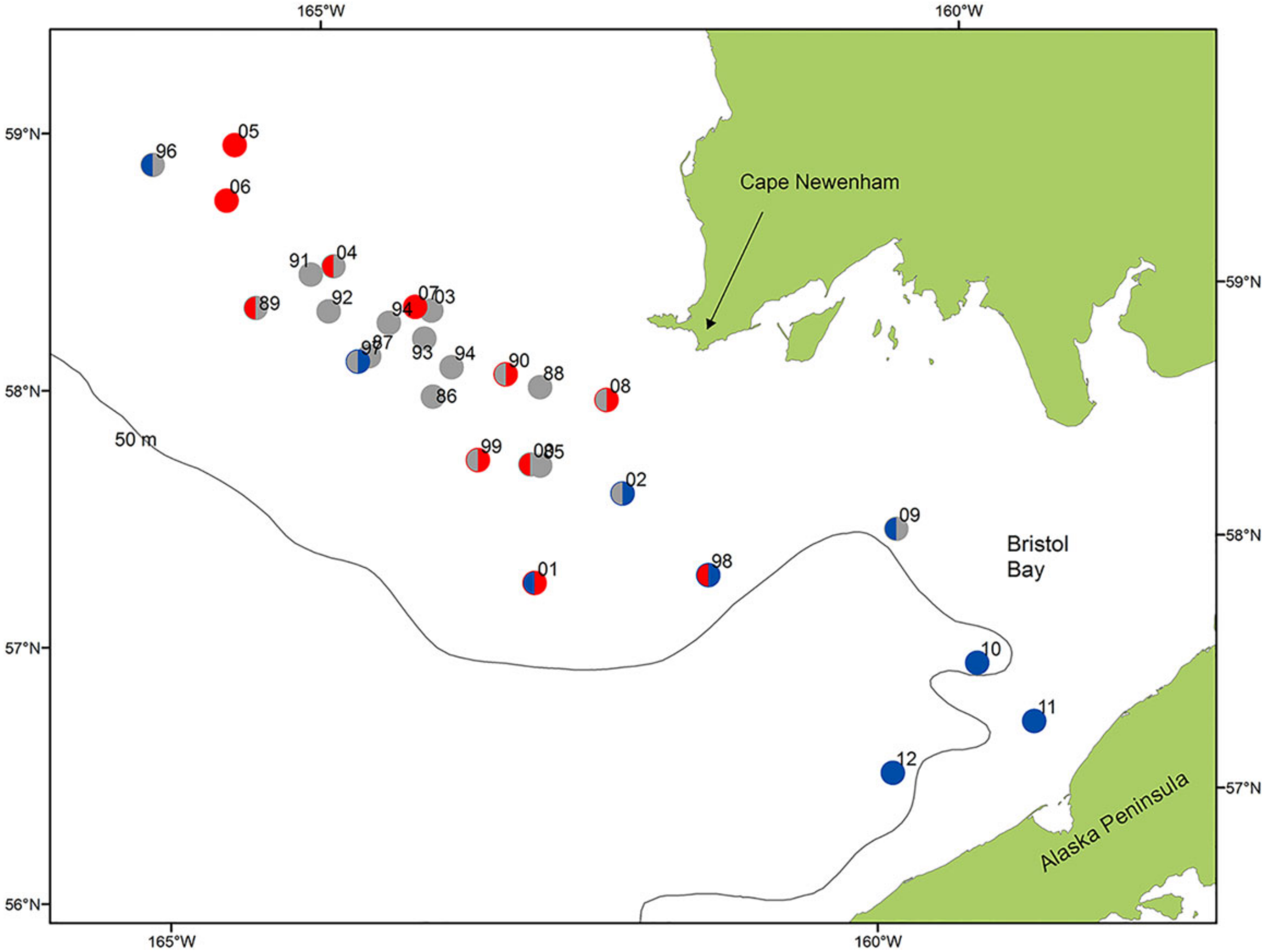

Figure 5. Geographic mean centres of annual northern rock sole small juvenile distributions for 1982–2012. Each circle with numeric year label represents the centre of geographic distribution weighted by catch per unit effort from the Alaska Fisheries Science Center eastern Bering Sea trawl survey for one year. The circles are composed of two semi-circles with the colour representing mean EBS summer bottom temperatures (<1.55°C represented by blue, 1.55–2.3°C represented by grey, and >2.3°C represented by red) 2 (left semi-circle) and 3 (right semi-circle) years prior to the survey. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

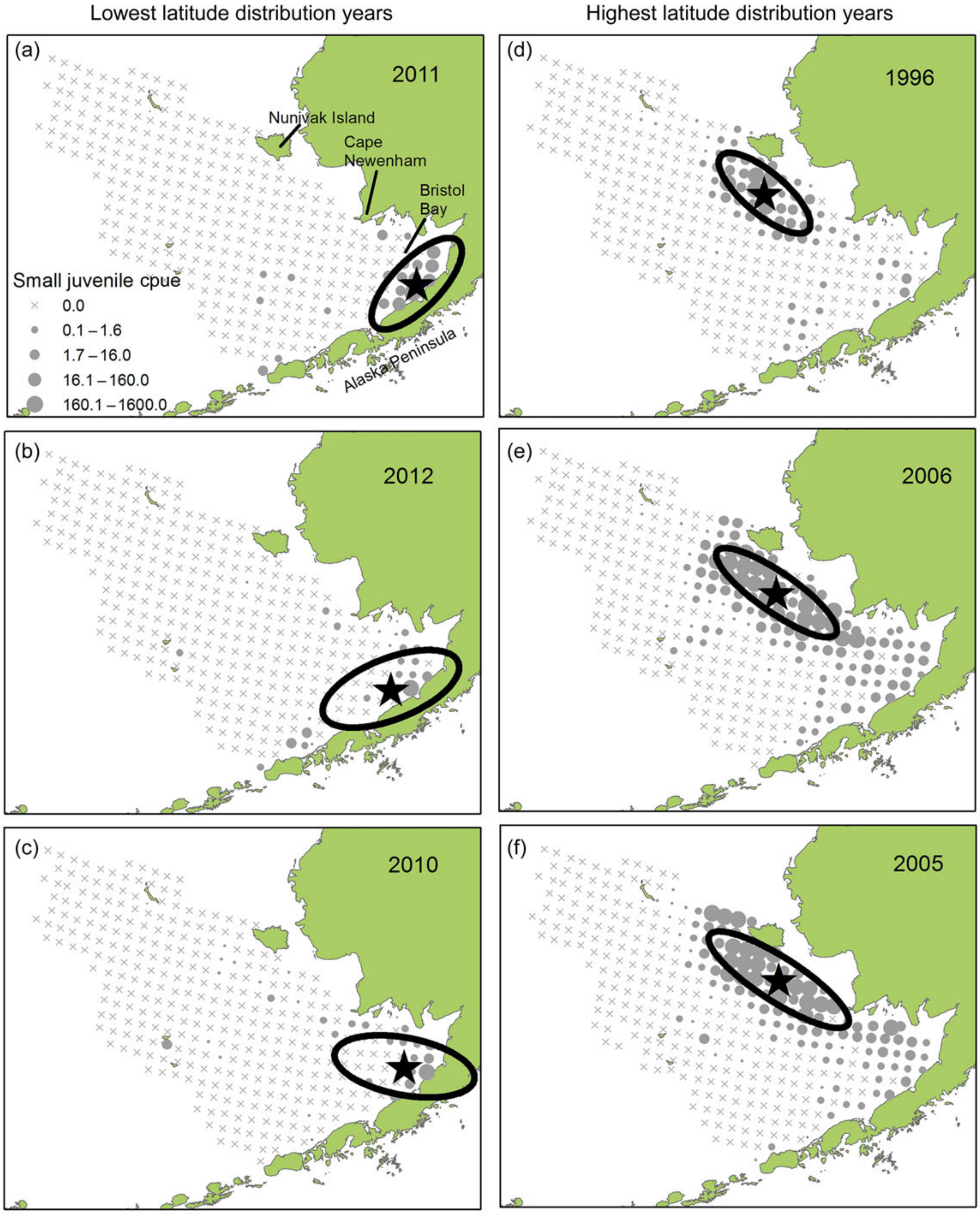

Figure 6. Variability in latitudinal distribution of northern rock sole small juveniles (≤11 cm) for 6 years with the three lowest (a–c) and three highest (d–f) latitudinal centres of distribution from the summer AFSC EBS trawl survey from 1982 to 2012. cpue at each survey station (number of fish per hectare) are shown with variably sized grey circles. Mean geographic centre of distribution weighted by cpue for each year is shown with a black star. Black ellipses encompass the area of ~68% of the catch in each survey year. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

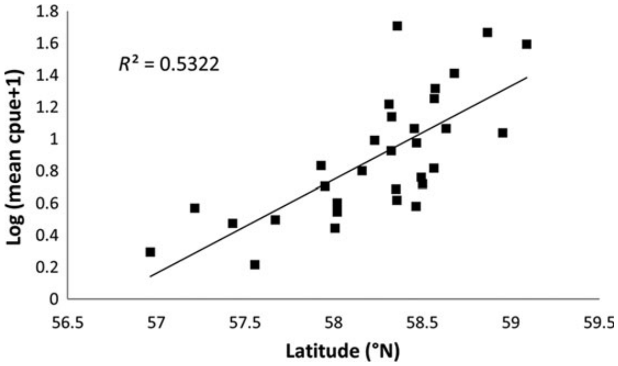

Figure 7. Mean annual index of abundance ((log(mean cpue + 1)) of small juvenile northern rock sole in relation to the annual latitudinal centre point of the small juvenile distribution, 1982–2012.

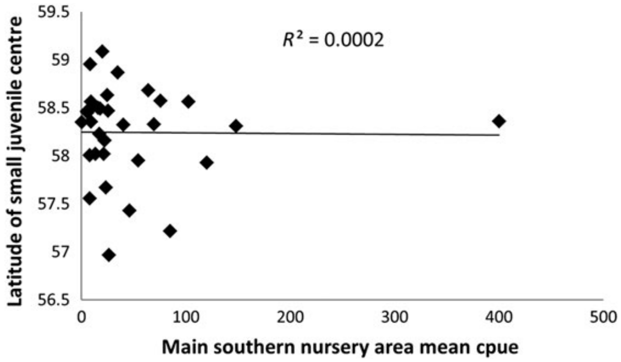

Figure 8. Mean cpue of small juvenile northern rock sole in the main southern nursery area in relation to latitudinal centre of distribution for each year from 1982 through 2012.

successfully reproduced, and this may also occur with northern rock sole in the EBS. Modelling suggests that walleye pollock spawning distributions in the EBS contract away from sea-ice cover and cold temperatures (Petrik *et al.*, 2014).

Another plausible mechanism for bottom temperature to impact age-0 distribution is climate-mediated change in ocean currents and larval transport. Near-surface currents in the EBS differ between warm and cold years (Stabeno *et al.*, 2012). During spring, when northern rock sole are transported as planktonic larvae (Lanksbury *et al.*, 2007), mean near-surface currents tend to flow westward during cold years, which may transport larvae offshore and away from the northern nursery area. During warm years, mean near-surface currents in the EBS move shoreward, potentially transporting larvae inshore to the northern nursery area (Cooper *et al.*, 2014). Wilderbuer *et al.* (2002, 2013) report increased recruitment in years with easterly winds during the larval transport period, which may transport larvae from spawning areas (Cooper *et al.*, 2013) to the northern nursery area.

The years with the most southerly distributions of small juveniles (2010–2102) all followed years with some of the coldest bottom temperatures (2008–2010) both 2 and 3 years prior. It may be that the northern nursery area is unused as nursery habitat only in the coldest years observed in this time series, and the necessary grouping of age-2 and age-3 fish in this study only allowed for the detection of the cold pool effects during the period of multiple cold years from 2008 to 2010.

Comparison of small juvenile spatial distributions and abundances

Northerly distributions of small juvenile northern rock sole occurred during years of high abundances. A possible reason is that the large northern nursery area produces large abundances. Rijnsdorp *et al.* (1992) noted a correlation between maximum recruitment and surface area of age-0 nursery habitat among five stocks of sole (*Solea solea*) and hypothesized that nursery area size may determine stock size. Van der Veer *et al.* (2000) reviewed evidence of this "nursery area hypothesis", and found additional supporting evidence of plaice stocks in the north sea and near Iceland, and also cites data from Gibson (1994) which shows interspecific evidence of the nursery area hypothesis in the Northeast Atlantic. Evidence of the nursery area hypothesis has also been found in round fish (Sundblad *et al.*, 2014).

An alternate explanation for the correlation between abundance and northerly distribution is density-dependent movement. According to the basin theory, at low abundances, fish would inhabit the preferred nursery area (MacCall, 1990), and in this case low abundances are associated with southerly spatial distributions. High abundances would overcrowd this preferred nursery habitat, and cause some juveniles to move northwards to marginal habitat. However, if this is true and the northern nursery area is marginal habitat, then the population should move north when densities in the southern nursery area (the preferred habitat if the basin theory is correct) are high. This was not observed.

It may be fruitful for future studies of population distribution shifts and abundance dynamics of northern rock sole to include the effects of climate during early life stages. The distribution of adult and subadult northern rock sole has been studied in relation to climate (Mueter and Litzow, 2008; Spencer, 2008; Kotwicki and Lauth, 2013) and population density (Spencer, 2008; Kotwicki and Lauth, 2013). These studies examined shifts in spatial distribution of the entire surveyed population, and report shifts in centroids of distribution of up to ~50 km among years (from Spencer, 2008). Our study demonstrated that small juveniles enter the surveyed population each year with greater spatial variability in annual centres (up to 400 km), from as far north as Nunivak Island to as far south as near the Alaska Peninsula. It is unknown how long these cohort specific spatial patterns persist, but some of the observed shifts in adult populations could arise from the large annual spatial variability of juveniles entering the surveyed population. Spencer (2008) and Kotwicki and Lauth (2013) also studied the possible effects of population density on spatial distribution assuming density-dependent movement. It may be that the causal relationship between density and spatial distribution is actually reversed, i.e. that the northerly distributions in the juvenile stage cause increased abundances through increased production of the northern nursery area.

The northern nursery area produces large abundances of juvenile northern rock sole, and the use of the northern nursery area may be related to temperature in the age-0 year. Variable juvenile production in the northern nursery area could be important to both year-class strength and population distribution.

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