Original Article

Nursery areas of juvenile northern rock sole (*Lepidopsetta polyxystra*) in the eastern Bering Sea in relation to hydrography and thermal regimes

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Age-0 and age-1 northern rock sole were collected over large-scale areas of the eastern Bering Sea in the summers of 2003, 2008 and 2010. Age-0 presence was poorly predicted by a published resource selection model developed for the Gulf of Alaska, and the failure of that model may have been caused by oceanographic features in the eastern Bering Sea. Where a front (inner front) separated the well-mixed coastal domain from the stratified middle domain, age-0 fish were less abundant and occurred at fewer stations in the nearshore, thermally mixed coastal domain than expected by the Gulf of Alaska model. In contrast, where the inner front was not established, age-0 fish were present in the highest densities in nearshore and thermally mixed waters. North of Unimak Island, the same hydrographic pattern that inhibits the formation of the inner front also likely transports larvae near shore. Age-1 densities were highest in the coastal domain, and age-0 length decreased with distance from shore, suggesting northern rock sole move shoreward after settlement. Juvenile northern rock sole were abundant in a nursery area between Nunivak Island and Cape Newenham in a warm period (2003), but were almost completely absent in cold periods (2008 and 2010), leading to the hypothesis that climate variability limits the utility of this nursery area during cold periods.

Keywords: Climate, habitat, inner front, juvenile, *Lepidopsetta polyxystra*, northern rock sole.

Introduction

Hydrodynamic patterns affect dispersal and retention of larval fish. Spawning locations of some species are adapted to supply larvae to persistent hydrodynamic features such as fronts and currents, which transport (Bailey, 1981; Hare and Cowen, 1996) or retain (Iles and Sinclair, 1982; Munk *et al.*, 2009) larvae near suitable juvenile habitat. Climate variation can alter persistent hydrodynamic features and be a cause of year-class variation (Methot, 1983; Hinrichsen *et al.*, 2001; Bailey and Picquelle, 2002).

Young-of-the-year flatfishes are good harbingers of ecosystem perturbation due to climate variability, because they are exposed to variations in winds and currents during pelagic larval drift (Werner *et al.*, 1997, Rijnsdorp *et al.*, 2009), feed on dynamic low trophic levels (van der Veer *et al.*, 2000), and have temperature-mediated growth (Teal *et al.*, 2008, Matta *et al.*, 2010). In addition, they can be subjected to temperature- (Bailey, 1994) or density-related (van der Veer *et al.*, 2000) predation, and early life stages can have more narrow temperature requirements than adults (Pörtner and Farrell, 2008; Rijnsdorp *et al.*, 2009).

Northern rock sole (*Lepidopsetta polyxystra*) in the eastern Bering Sea support a commercial fishery, and the distribution and habitat use of mature stages is well studied (McConnaughey and Smith, 2000; Mueter and Litzow, 2008; Spencer, 2008; Wilderbuer and Nichol, 2010). However, juvenile nursery areas in the eastern Bering Sea have not been previously characterized, and the factors influencing habitat use are poorly understood. Habitat for age-0 post-settlement rock sole (*Lepidopsetta* spp.) during the first summer has been described for a few areas in the Gulf of Alaska,

where summer habitat is characterized as sand and mixed-sand substrates at depths <50 m (Norcross *et al.*, 1995, 1997; Stoner *et al.*, 2007). A model developed for that region (Norcross *et al.*, 1999) predicts presence/absence of age-0 rock sole in the summer based on depth and sediment type, and provides a useful tool for examining rock sole habitat use in other marine ecosystems.

Northern rock sole larvae have been collected in the eastern Bering Sea north of Unimak Island and the Alaska Peninsula in May (Lanksbury *et al.*, 2007), and transport of these larvae is likely influenced by two currents: the Bering Coastal Current (BCC), a seasonal current which flows to the northeast parallel to the Alaska Peninsula, and a baroclinic current that flows northwards from Unimak Pass (Lanksbury *et al.*, 2007; Cooper *et al.*, 2012), (Figure 1). In Bristol Bay, the BCC turns and roughly parallels bathymetry as it travels northwest along the west coast of the Alaskan mainland. As the continental shelf broadens in Bristol Bay, the current moves farther from shore. The BCC is located in the vicinity of the inner front, a tidal or structural front that separates the well-mixed coastal domain from the stratified middle domain (Coachman, 1986; Kachel *et al.*, 2002). Cross-shelf flow at the inner front is so small that the inner front is "an effective barrier" to cross-shelf flux (Coachman, 1986), which potentially limits

ingress of northern rock sole larvae into the coastal domain. Simulated northern rock sole larvae transported by the baroclinic flow north from Unimak Island exhibit limited cross-shelf ingress into the coastal domain, as demonstrated by an individual-based biophysical coupled model (Cooper *et al.*, 2012).

The climate pattern in the eastern Bering Sea has shifted from inconsistent interannual temperature variability to 4–6 year alternating periods of warmer and cooler temperatures (Stabeno *et al.*, 2012). Late 1999 through autumn 2005 was a warm period that was followed by a cool period extending from autumn 2005 to the present (Stabeno *et al.*, 2012). Expanded winter ice coverage during cool periods causes a cold pool of <2°C bottom temperature water to extend south nearly to the Alaska Peninsula during the spring and summer months (Stabeno *et al.*, 2012), which would alter the thermal experience of pelagic and post-settlement age-0 northern rock sole in the eastern Bering Sea between warm and cold periods.

The purpose of this study was to examine the habitat of age-0 and age-1 juvenile northern rock sole in relation to the hydrography in the eastern Bering Sea. The first objective was to test the efficacy of a resource selection model developed in the Gulf of Alaska (Norcross *et al.*, 1999) on age-0 rock sole in the eastern Bering Sea. The second objective was to test the hypothesis that ingress of age-0 fish
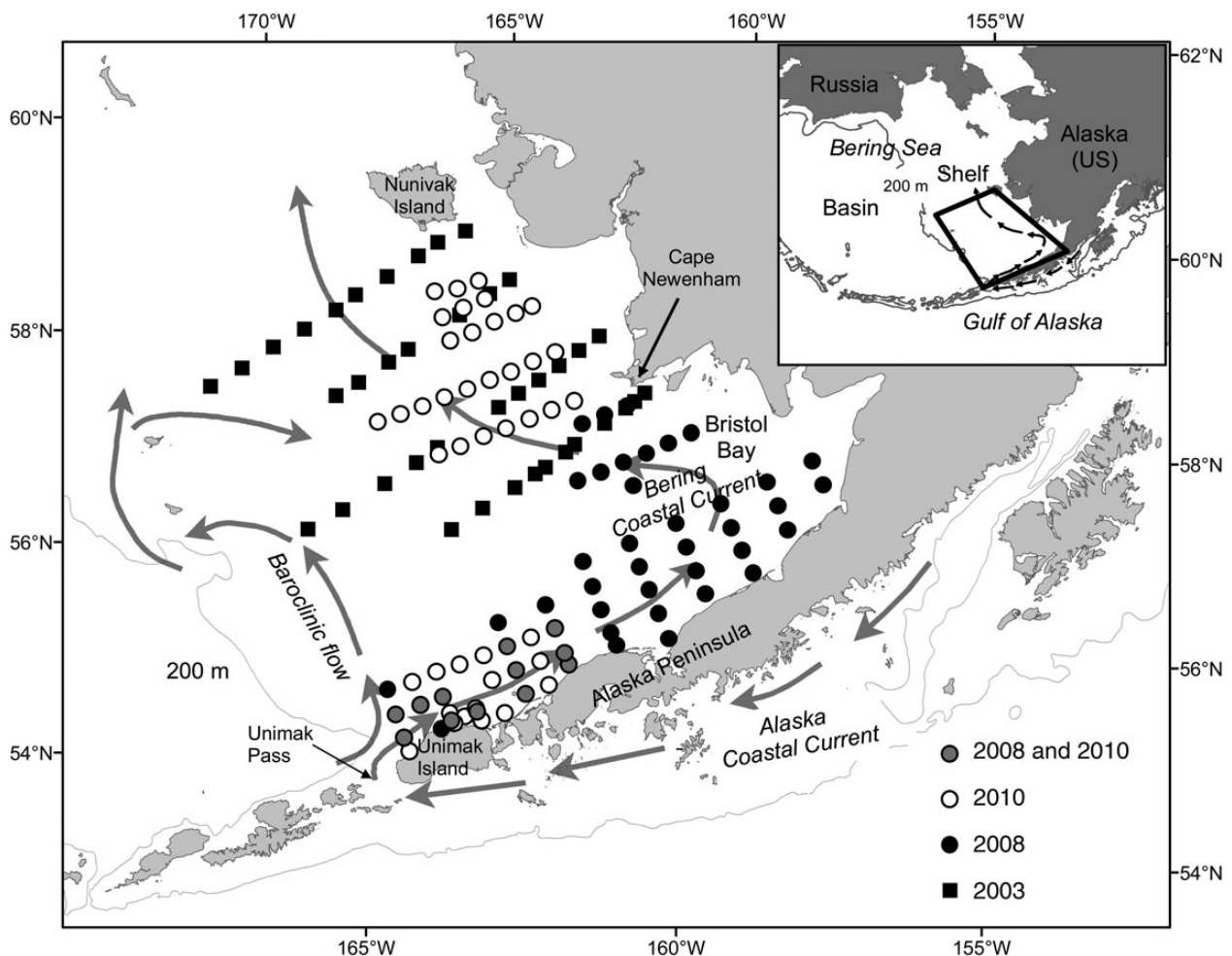

Figure 1. Map of the survey area and stations sampled each year. Stations depicted by grey circles were sampled in both 2008 and 2010. Inset shows relation of survey to the surrounding area and the eastern Bering Sea shelf inshore of the 200-m isobath. Grey arrows represent surface currents (Stabeno *et al.* 1999).

into the coastal domain is limited by the presence of the inner front. Specifically, we hypothesized that age-0 northern rock sole would be present at fewer stations in the coastal domain than predicted by the resource selection model. A corollary to this hypothesis is that age-0 densities would be lower in the coastal domain than in the inner front. We assumed that lack of larval ingress into the coastal domain during the spring by pelagic larvae would be reflected in the broad-scale summer distribution of settled age-0 fish. The third objective was to analyse age-0 and age-1 distributions and age-0 length patterns to determine if young-of-the-year northern rock sole exhibit large-scale movements after settlement. The final objective was to examine interannual spatial variation between warm and cold years to determine whether climate variability modulates those patterns relative to the hydrography described above.

Methods
Field collections
Data were collected on three cruises spanning eight years. In 2003, a research cruise was conducted aboard the FV "Big Valley" from 11–26 August. Four SW–NE survey transects were conducted across the inner front between Nunivak Island and Cape Newenham, approximately 5–120 nautical miles (nmi) from shore (Figure 1). From 11–20 September 2008, a research cruise was conducted aboard the NOAA ship "Miller Freeman", primarily along the north side of Unimak Island and the Alaska Peninsula, with some northern stations offshore of Cape Newenham (Figure 1). From 11–18 September 2010, a research cruise aboard the "Miller Freeman" surveyed an area between Nunivak Island and Cape Newenham similar to the area surveyed in 2003, and an area north of Unimak Island and the Alaska Peninsula (Figure 1). A combined total of 146 stations were sampled during the three cruises.

Fish were collected using a 3.05-m plumb staff beam trawl with 7-mm mesh and 4-mm codend liner (after Gunderson and Ellis, 1986). In 2003, the trawl had additional 15 cm lengths of hanging chain attached every 15 cm on the lead-lined footrope. In 2008 and 2010, the trawl was equipped with an extended top panel to increase catchability of gadiform fish, as described by Abookire and Rose (2005). In 2003, tows were made in daylight (08:00–20:00 h). In 2008 and 2010, tows were conducted at all hours of the day and night. Towing speed was ∼ 0.5 m s^{-1} (1.0 knot) in 2003, and 1 m s^{-1} in 2008 and 2010. The vessels maintained a single heading during tows; beginning and ending positions of each tow were recorded using standard global positioning systems (GPSs) and used to calculate distance towed. Depth was recorded from the depth sounder on the vessels. Tows were of variable distance (122–1000 m in 2003, 240–1400 m in 2008, and 138–797 m in 2010). Target tow durations were 10 min in 2003, and 20 min in 2008 and 2010, but in areas with high catches, subsequent tows were shortened to reduce risk of catch spilling out of the net mouth. Catch-per-unit-effort (cpue) of age-0 and age-1 northern rock sole for each tow 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 (3.05 m beam length × 74%; Gunderson and Ellis, 1986). One tow in 2008 was not considered quantitative, and therefore was excluded from density calculations, but included in the presence/absence analysis.

A vertical profile of hydrographic data was recorded at each station using a conductivity, temperature and depth (CTD) profiler (Sea-bird Electronics, SBE 19 in 2003, SBE 19 *plus* in 2008, and SBE 39 in 2010). In 2003, the CTD profiler was deployed at the bottom of the ship's wire, and data were collected on each downcast. In 2008, the CTD profiler was attached above a bongo net, and data were collected on each upcast. In 2010, the temperature profile and bottom temperature were recorded using an SBE 39 temperature profiler attached to the beam of the beam trawl. Bottom temperatures were interpolated for mapping using the inverse distance weighted (IDW) tool in ARCMAP 9.3 (ESRI).

Sediment was collected at each trawl location using a van Veen sediment grab. The grab was opened from the top, and sediment for grain-size analysis was scooped from the top 5 cm of the substrate.

In 2003 and 2010, total length (TL) of northern rock sole was recorded to the nearest mm. In 2008, northern rock sole were measured to standard length (SL) if <80 mm SL and to TL if >80 mm SL. Standard lengths were converted to total lengths using conversion factors developed by measuring both standard and total length of frozen northern rock sole. For fish <40 mm SL, the conversion factor was TL = 1.2044(SL) + 0.0415, $r^2 = 0.95$, $n = 120$; and for fish >40 mm SL, the conversion factor was TL = 1.231(SL) − 1.325, $r^2 = 0.99$, $n = 106$. In all years, subsamples of at least 25 fish were measured if a size class of fish contained too many individuals to measure in the available time.

Oceanographic domain categorization
Stations were categorized as within the middle domain, inner front, or coastal domain based on the methods developed for transects crossing the inner front in the southeast Bering Sea by Kachel *et al.* (2002). In 2003, stations were occupied in transects that crossed the inner front. In 2008 and 2010, stations were occupied in a grid pattern (Figure 1), and stations along the Alaska Peninsula were occupied from north to south or south to north. In 2008, stations on the eastern side of the grid were not occupied in order across the inner front, however these stations were occupied within a 3 d period. The offshore edge of the inner front is where the temperature gradient of the stratified middle domain weakens, and was defined by Kachel *et al.* (2002) as:

$$|dT/dZ|_{maxS} < 1/2|dT/dZ|_{maxT},$$

where dT = change in temperature (°C), dZ = change in depth (m), $maxS$ = maximum value for the station, and $maxT$ = maximum value for the transect, with the additional constraint that:

$$\left|dT/dZ\right|_{\max S} < 1°Cm^{-1}.$$

The inshore edge of the inner front is where the water becomes nearly thermally unstratified, and was defined as:

$$\left|dT/dZ\right|_{\max S} < 0.05°Cm^{-1}.$$

One deviation from the methods described in Kachel *et al.* (2002) was that in 2008 and 2010 there were four stations with $|dT/dZ|_{\max S} > 0.05$°C m^{-1} that were included in the coastal domain because the temperature stratification was only slightly above 0.05°C m^{-1}, the warming was only in the uppermost 10 m, and these stations were sampled after weeks of calm weather. These four stations had $|dT/dZ|_{\max S} = 0.058$°C m^{-1} at a depth of 10 m, 0.052°C m^{-1} at a depth of 10 m, 0.122°C m^{-1} at a depth of 6 m, and 0.061°C m^{-1} at a depth of 8 m. Warming in the upper water column at these stations was considered ephemeral and not the dynamic partial temperature stratification associated with the inner front.

Temperature contours were plotted along offshore–inshore transects using Ocean Data View software (Schlitzer, 2010).

Sediment analysis

Percentage sand in sediment samples was determined from a procedure modified from Folk (1980). Sediment samples were rinsed with fresh water through a 63-µm sieve to separate the bulk of the mud from the rest of the sample. Both fractions were dried in a drying oven at ~80°C. The fraction that passed through the 63-µm sieve (mud) was weighed. The fraction remaining on the 63-µm sieve (gravel, sand, plus some remaining mud) was placed on the top of a series of sieves of sizes: 9.42 mm, 4.59 mm, 2.00 mm, 1.00 mm, 0.50 mm and 63 µm. The sieves were stacked over a collecting tray and shaken with a rotating and tapping sieve shaker for 10 min. The fraction on each sieve and the collecting tray were weighed. Sediment remaining on the 1.00-mm, 0.50-mm and 63-µm sieves was classified as sand, and percentage sand of total weight of the sample was calculated. Sediment samples were unavailable from 21 of the 146 stations, and sediment data for these stations were obtained from the nearest sediment data location in the EBSSED database (Smith and McConnaughey, 1999).

Age class determination

For 2003 data, ages of age-0 and age-1 northern rock sole were assigned based on length frequency analysis, as has been done for rock sole in the Gulf of Alaska (Norcross et al., 1997; Abookire and Norcross, 1998). For 2008 and 2010 data, there were not distinct length modes for age-1 fish, and the length category for age-1 fish was determined by creating age–length keys using otoliths sampled from 20 fish per haul in the length range from 0–49 mm TL, and from 10 fish per haul in the length range from 50–100 mm TL. Age was determined by counting annual increments of whole otoliths in water under reflected light.

Resource selection model

A resource selection model developed for age-0 rock sole in the Gulf of Alaska (Norcross et al., 1999) was used to determine expected presence or absence of age-0 northern rock sole in the eastern Bering Sea based on depth and sediment type:

$$w(x) = \frac{e^{(1.25-0.06D+0.04S)}}{1 + e^{(1.25-0.06D+0.04S)}},$$

Where $w(x)$ = the probability of age-0 northern rock sole presence, D = depth (m) and S = percentage sand in the sediment.

Statistical analyses

To test the efficacy of the Norcross et al. (1999) resource selection model, we separately applied two goodness-of-fit tests appropriate for logistic regression to the resource selection model-predicted probabilities of age-0 presence/absence and the observed presence/absence data: the "Hosmer–Lemeshow test" as well as the global "le Cessie–van Houwelingen–Copas–Hosmer test" (Hosmer et al., 1997). These tests were applied using R software with the function "HLgof.test" in the "MKmisc" package, available from www.stamats.de/software.htm (last accessed October 2013).

Statistical tests of cpue and length were performed using statistical software (SYSTAT 13, SYSTAT Inc.). To test the hypothesis that the inner front limits larval ingress into the coastal domain, the survey area in each year was divided into an area (North) offshore of mainland Alaska from Cape Newenham to Nunivak Island, and

the remainder of the survey area along the north side of Unimak Island and the Alaska Peninsula, because larvae sources and transport currents in these two areas are likely different (Cooper et al., 2012). The Kruskal–Wallis test was used to compare cpue among oceanographic domains when three domains were present. When differences were present, the Conover–Inman test was used for pairwise comparisons. Where an inner front was not present, the Mann–Whitney test was used to test for differences in cpue between the offshore and thermally mixed nearshore water masses. Differences in mean length of age-0 northern rock sole at

Table 1. Number of northern rock sole (*Lepidopsetta polyxystra*) per length increment collected in 2003, 2008 and 2010.

Total length (mm)	2003	2008	2010
0–20	7	0	0
20.1–25	52	4	11
25.1–30	181	129	316
30.1–35	313	272	986
35.1–40	306	166	1258
40.1–45	95	13	1688
45.1–50	16	1	331
50.1–55	13	2	4
55.1–60	48	2	21
60.1–65	111	5	6
65.1–70	168	17	14
70.1–75	226	17	19
75.1–80	146	13	16
80.1–85	114	12	20
85.1–90	62	17	14
90.1–95	21	59	11
95.1–100	12	65	10
100.1–105	13	124	2
105.1–110	11	80	3
110.1–115	20	93	3
115.1–120	25	102	5
>120.1	149	1515	573
Total	2109	2708	5311

Table 2. Northern rock sole (*Lepidopsetta polyxystra*) age-length key from collections in 2008 and 2010.

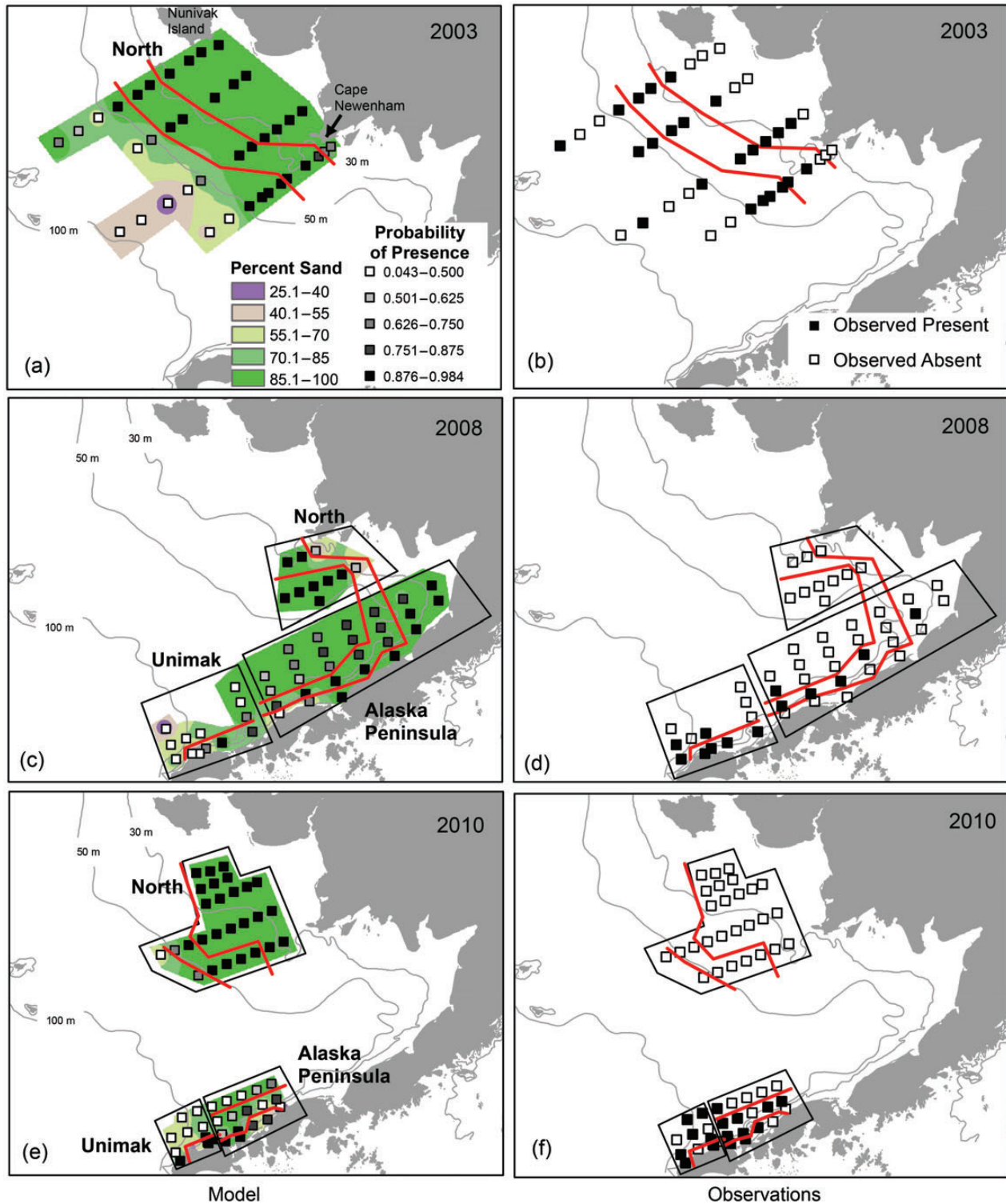| Total length (mm)	2008			2010		
	Age-0	Age-1	Age-2	Age-0	Age-1	Age-2
0–20	–	–	–	–	–	–
20.1–25	2	–	–	3	–	–
25.1–30	10	–	–	23	–	–
30.1–35	30	–	–	92	–	–
35.1–40	33	–	–	77	–	–
40.1–45	7	–	–	33	–	–
45.1–50	–	–	–	10	–	–
50.1–55	–	2	–	–	1	–
55.1–60	–	3	–	–	1	–
60.1–65	–	6	–	–	6	–
65.1–70	–	10	–	–	3	–
70.1–75	–	5	–	–	8	–
75.1–80	–	6	–	–	7	–
80.1–85	–	7	–	–	11	1
85.1–90	–	2	3	–	11	–
90.1–95	–	–	7	–	2	–
95.1–100	–	–	9	–	1	2
100.1–105	–	1	1	–	–	1
105.1–110	–	–	1	–	1	–

Figure 2. Maps of model predicted and observed age-0 northern rock sole (*Lepidopsetta polyxystra*) presence and absence in August (2003) and September (2008 and 2010). For model-predicted maps (a, c, e), >50% model-predicted probability of presence (predicted presence) is indicated by grey or black squares, and <50% model-predicted probability of presence (predicted absence) is indicated by a white square. For observed presence maps (b, d, f), observed presence is indicated by a black square, and observed absence is indicated by a white square. (**a**) Model predicted in 2003, (**b**) observed in 2003, (**c**) model predicted in 2008, (**d**) observed in 2008, (**e**) model predicted in 2010, (**f**) observed in 2010. Interpolations of percentage sand in the sediment at each station are included in the maps of model predictions. The approximate boundaries of the Inner Front in the North and Alaska Peninsula areas, and between the thermally mixed "coastal" and non-thermally mixed "offshore" regions in the Unimak Area, are shown in red.

each station by distance from shore and temperature were tested with ANOVA.

Results

Year classes

Northern rock sole age-0 and age-1 length categories were apparent as distinct length frequency modes in 2003 (Table 1). There was a length mode of fish from 18–51 mm TL that was classified as age-0, and a length mode of fish from 51–105 mm TL that was classified as age-1. In 2008 there was a length mode of fish from 21–46 mm TL (Table 1), and length–age data indicated these were age-0 fish (Table 2). The age-1 and older year classes were not separated into length modes (Table 1). All aged fish from 50–88 mm TL were age-1 (Table 2), and this length range was presented as age-1 for 2008. In 2010 there was a length mode of fish from 22–50 mm TL (Table 1), and length–age data indicated these were age-0 fish (Table 2). Age-1 fish were defined as 51–100 mm TL in 2010 (Table 2).

Gulf of Alaska model efficacy in the Bering Sea

The model predicted age-0 presence (probability of presence > 0.5) at most (114 of 146) stations in the surveyed area (Figure 2). Stations with model-predicted presences generally had depths < 50 m and sediments with > 85% sand. Stations with model-predicted absences generally were deeper than 50 m, had sediments with <85% sand, and included areas offshore from Nunivak to Cape Newenham, offshore of Unimak Island and the Alaska Peninsula, and a few inshore stations near Unimak Island and the Alaska Peninsula.

Age-0 northern rock sole presence/absence significantly differed in all of the three sample years from the resource selection model developed in the GOA using sand and depth ($p < 0.001$ in all three years for both Hosmer–Lemmeshow and le Cessie–van Houwelingen–Copas–Hosmer tests). The model correctly predicted presence or absence at 59 of 146 stations (Figure 3). Model error was more often due to model-predicted presence and actual absence (73 stations) and less often due to model-predicted absence and actual presence (14 stations).

Juvenile distribution by oceanographic domains and year

The oceanographic domains were not distinct in all areas and at all times. The inner front was present in the sampling area in 2003 (Figure 4, Transect 1), and separated the coastal domain from the middle domain. In 2008 and 2010, the inner front, coastal domain, and middle domain were established on the eastern part of the survey area (Figure 4, Transects 2 and 3), but not in an area near Unimak Island (Figure 4, Transect 4). An inner front did not exist in the vicinity of Unimak Island because although temperatures decreased with depth (Figure 4, Transect 4), the thermal stratification in the offshore area was multilayered over 10s of metres of depth rather than the abrupt two-layered stratification in the middle domain in areas with the inner front. The sampling stations closest to shore in this area met the same thermally well-mixed definition as the coastal domain (defined as $|dT/dZ|_{\max S} < 0.05°$ C m^{-1}), and are referred to as thermally mixed or "coastal" for comparison with stations in the coastal domain in areas where the inner front was established. In 2010, the inner front again was absent north of Unimak Island, however it was established farther west than in 2008 (Figure 2c and e).
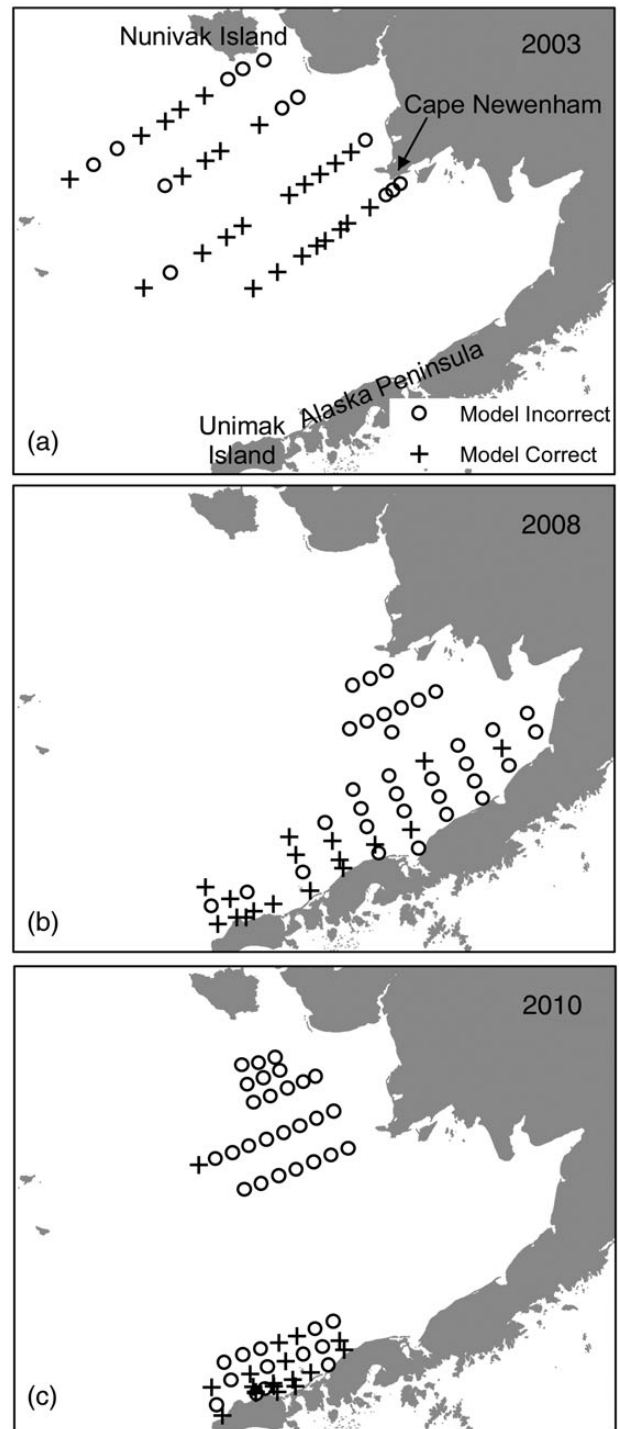

Figure 3. Maps of resource selection model success or failure in (**a**) August 2003, (**b**) September 2008, and (**c**) September 2010. Crossed lines indicate model success, and open circles indicate model failure.

To analyse fish density and distribution data relative to the inner front, the survey stations were subdivided *a priori* into three areas. An area (North) between Nunivak Island and Cape Newenham was defined as a separate area because it has a hypothesized different larval source current. The remainder of the survey area was divided into two areas by the presence or absence of the inner front. The north side of the Alaska Peninsula (Alaska Peninsula) had an
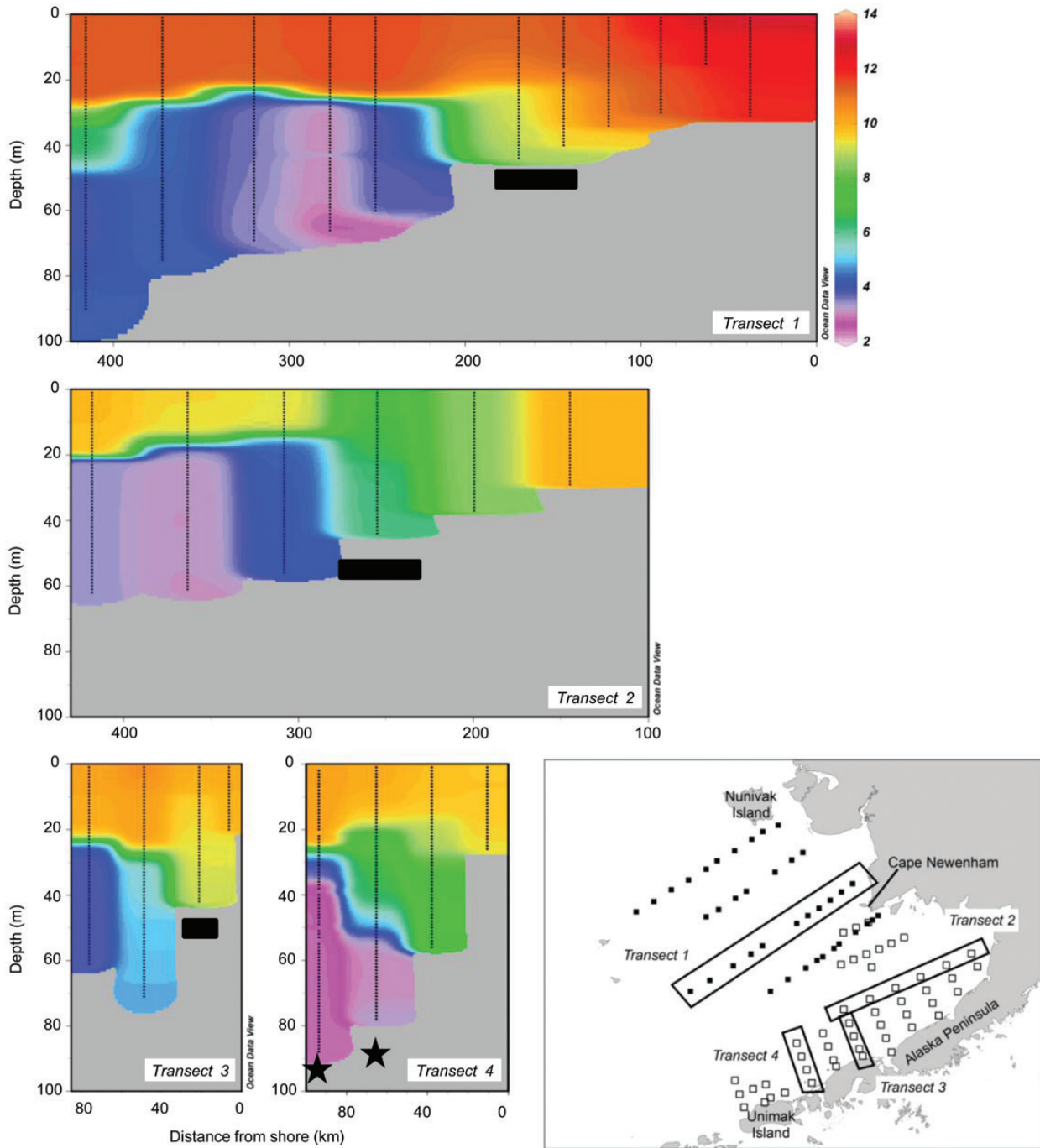
Figure 4. Oceanographic domain transects. Temperatures (°C) recorded 18–23 August 2003 (Transect 1) and 13–15 September 2008 (Transects 2, 3, and 4). Map indicates position of transects. CTD casts at each station are represented by broken lines, and the areas between stations are temperature interpolations. Stations in Transects 1–3 located within the Inner Front are denoted by a black bar at the bottom of each transect. Coastal stations are inshore of the Inner Front stations, and the water column is thermally mixed. Stations offshore of the Inner Front are thermally stratified, with an abrupt thermocline. Note that in Transect 4, the temperatures at profiles marked with stars decrease more gradually with depth (over 10s of metres), indicating that the two-layer abrupt thermal stratification of the middle domain is not present.

established inner front in all years examined. The area north of Unimak Island (Unimak) was marked by the absence of the inner front in all study years. The inner front was established farther west in 2010 than in 2008, and thus the boundary between the Unimak and Alaska Peninsula areas is not the same for 2008 and 2010 (Figure 2c and e).

North

In 2003, age-0 northern rock sole were observed at fewer stations in the coastal domain than expected (Figure 2a and b), and mean density in the coastal domain was significantly lower than in the inner front (Kruskal–Wallis, $p = 0.001$; Figures 5a and 6a). The
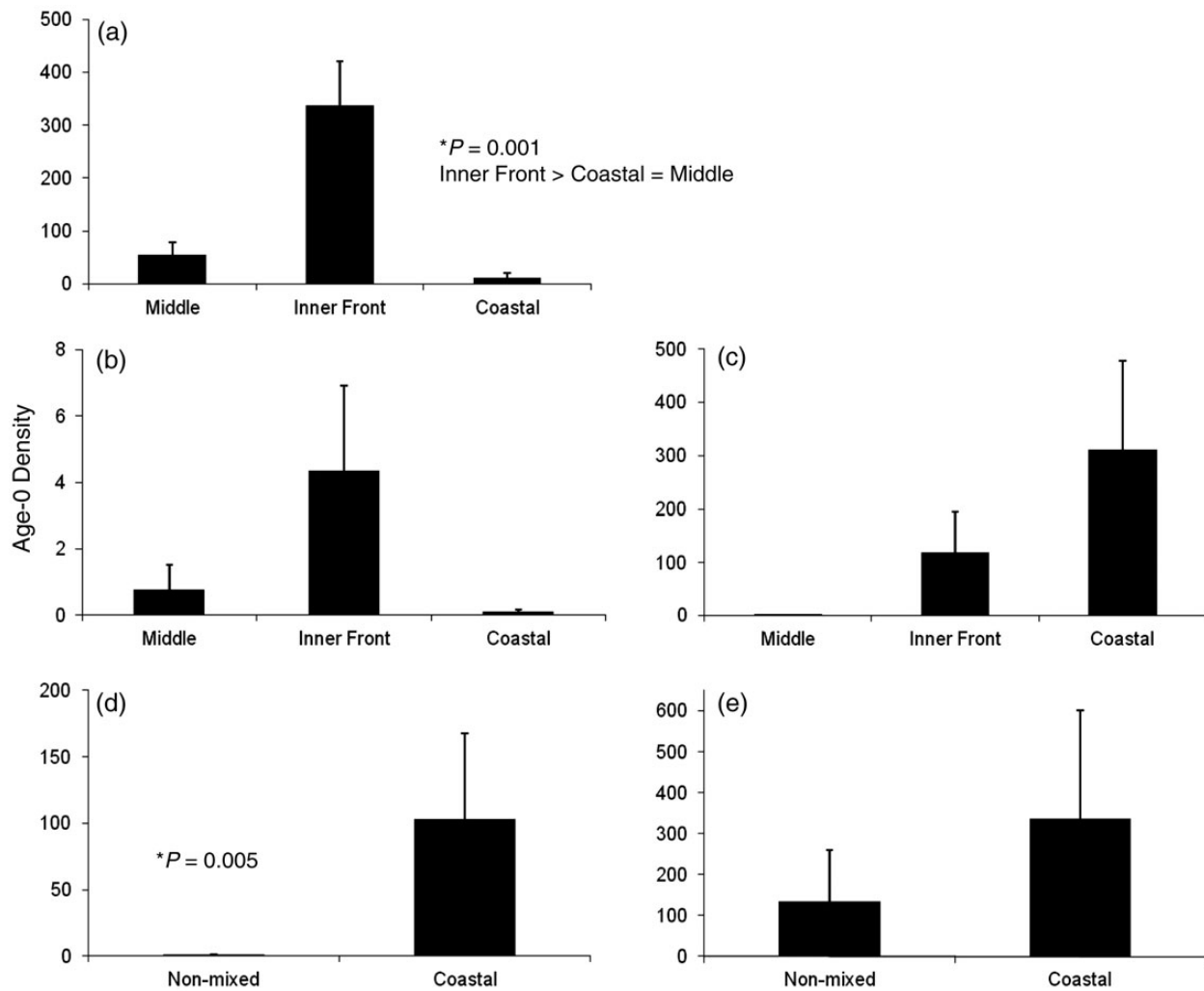
Figure 5. Mean densities (number of fish 1000 m^{-2} ± SE) of age-0 northern rock sole (*Lepidopsetta polyxystra*) by oceanographic domain. (**a**) North area in 2003; densities in the inner front were significantly greater ($p = 0.001$) than densities in the coastal or middle domains. (**b**) Alaska Peninsula in 2008. (**c**) Alaska Peninsula in 2010. (**d**) Unimak in 2008; densities in the thermally mixed "coastal" domain were significantly greater ($p = 0.005$) than densities in the non-mixed offshore area. (**e**) Unimak in 2010.

resource selection model was more accurate in the inner front and middle domains (Figure 3a).

Only the North area was surveyed in both warm (2003) and cool (2008 and 2010) years. Both age-0 and age-1 juveniles were abundant in the North area in 2003 (Figure 6a, and b). Age-0 fish were present at eight of nine stations in the inner front at a mean density of 337 fish 1000 m^{-2} (Figure 6a). The approximate area surveyed in the inner front was 21 500 km^2. Age-1 fish were present in all stations in the coastal domain or inner front at a mean density of 67 fish 1000 m^{-2} (Figure 6b), and the area surveyed in the inner front and coastal domain was ∼ 47 300 km^2. Age-0 fish were absent in the North area in both 2008 and 2010 (Figure 6c and e). Age-1 fish were present in the coastal domain or inner front at one of four stations in 2008 (Figure 6d) at a density of 0.5 fish 1000 m^{-2}, and at one of 25 stations in 2010 (Figure 6f) at a density of 2 fish 1000 m^{-2}. Age-1 densities were highest in the coastal domain in 2003 (Table 3, Figure 6b).

Alaska Peninsula

In 2008, age-0 northern rock sole were present in fewer stations than predicted by the model in all oceanographic domains

(Figure 2c and d). Similar to the North area in 2003, densities of age-0 fish were higher in the inner front than in the coastal domain (Figures 5b and 6c), but the difference was not significant at the $\alpha = 0.05$ level (Kruskal–Wallis, $p = 0.078$). In 2010, observed age-0 northern rock sole presence more closely agreed with resource model predictions (Figure 2e and f) and densities were highest in the coastal domain (Figure 5c), although densities in the inner front and coastal domain were not statistically different (Conover–Inman, $p = 0.44$). Age-1 densities were highest in the coastal domain in both 2008 and 2010 (Table 3, Figure 6d and f).

Unimak

In 2008, observed age-0 presence exceeded the model prediction in both the thermally mixed "coastal" domain and non-thermally mixed deeper areas (Figure 2c and d), and in 2010, observed presence exceeded predicted presence in the non-thermally mixed stations, but not in the thermally mixed "coastal" domain stations (Figure 2e and f). Mean densities were higher in thermally mixed "coastal" domain areas than in the thermally non-mixed deeper stations in both years (Figure 5d and e). The difference was significant
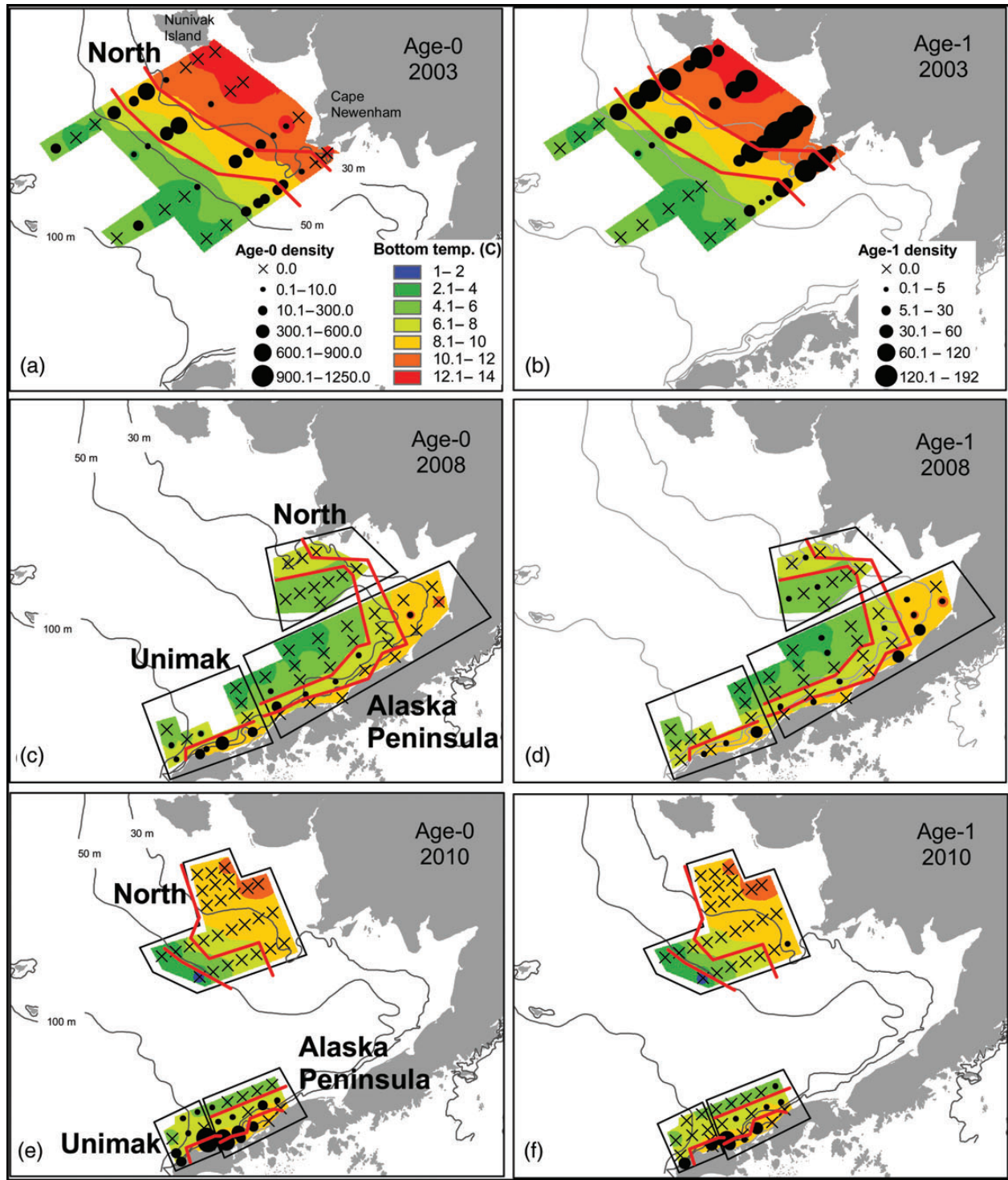
Figure 6. Observed densities (number of fish 1000 m^{-2}) of northern rock sole (*Lepidopsetta polyxystra*) juveniles in August (2003) and September (2008 and 2010). (**a**) age-0 in 2003, (**b**) age-1 in 2003, (**c**) age-0 in 2008, (**d**) age-1 in 2008, (**e**) age-0 in 2010, and (**f**) age-1 in 2010. The approximate boundaries of the Inner Front in the North and Alaska Peninsula areas, and the thermally mixed region in the Unimak Area, are shown in red. Bottom temperature interpolations from the time of sampling are included with each map.

in 2008 (Mann–Whitney $p = 0.005$) but not in 2010 (Mann–Whitney $p = 0.86$). Age-1 densities were highest in the "coastal" domain in both 2008 and 2010 (Table 3, Figure 6d and f).

Age-0 length patterns

Mean length of age-0 fish at each station significantly decreased with distance from shore in all years (2003, $p = 0.001$; 2008, $p = 0.002$;

Table 3. Mean age-1 northern rock sole (*Lepidopsetta polyxystra*) catch-per-unit-effort (cpue; number of fish 1000 m^{-2}) and Standard Error (SE) for each year, study area, and oceanographic domain.

	2003		2008		2010	
Area	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
North						
Middle Domain	6.4	3.67	0.2	0.10	0.0	0.00
Inner Front	58.6	9.56	0.0	0.00	0.0	0.00
Coastal	72.3	15.07	0.1	0.11	0.1	0.10
Alaska Peninsula						
Middle Domain	–	–	0.3	0.23	0.2	0.22
Inner Front	–	–	0.3	0.14	5.3	4.47
Coastal	–	–	3.6	1.73	12.3	7.05
Unimak Island						
Non-mixed	–	–	0.0	0.00	1.8	1.77
Coastal (mixed)	–	–	3.1	1.37	3.2	1.52

and 2010, $p = 0.001$) and increased with temperature in all years (2003, $p = 0.002$; 2008, $p = 0.01$; and 2010, $p = 0.003$). Temperature and distance from shore were not independent, as temperature decreased with distance from shore in all areas (Figure 6).

Discussion

This is the first published report of northern rock sole juvenile nursery areas in the eastern Bering Sea. The resource selection model developed for age-0 fish in the Gulf of Alaska (Norcross *et al.*, 1999) poorly predicted the presence/absence of age-0 rock sole in the Bering Sea. Age-0 distributions and abundance patterns were consistent with the hypothesis of reduced ingress into the coastal domain, although juvenile spatial distribution may have been altered by annually varying thermal regimes.

During the summer, age-0 and age-1 northern rock sole can potentially inhabit a broad expanse in the eastern Bering Sea, including the area north of Unimak Island and along the north side of the Alaska Peninsula, as well as the area offshore of mainland Alaska from Nunivak Island to Cape Newenham. Cross-shelf patterns of juvenile abundance in each of these areas vary relative to the presence of the inner front.

In the North area in 2003 and along the Alaska Peninsula in 2008, age-0 northern rock sole distributions and densities were consistent with our hypothesis that the inner front limits larval ingress into the coastal domain. The resource selection model indicated that depth and sediment type in the coastal domain were suitable for age-0 rock sole, therefore the reduced occurrence and low densities are attributable to another factor or factors. Ingress into the coastal domain is likely limited by the presence of the inner front, which entrains early life stages in its predominantly along-isobath flow, effectively limiting cross-shelf delivery of larvae.

The densities of age-0 fish on the north side of Unimak Island were highest in the thermally mixed nearshore "coastal" water where the inner front was not established. Water coming through Unimak Pass from the Gulf of Alaska into the Bering Sea prevents a two-layer midshelf structure from establishing on the north side of Unimak Island (Kachel *et al.*, 2002); the advection of water from the Gulf of Alaska may also be a source of northern rock sole larvae.

In the Alaska Peninsula area, age-0 ingress into the coastal domain appeared reduced in 2008, but age-0 densities were highest in the coastal domain in 2010. We suggest this may be due

to difference in the spatial extent surveyed in 2008 and 2010, and our method of determining the boundary between the Unimak and Alaska Peninsula areas using the presence of the inner front at the time of sampling in September. In 2008, the survey extended farther east along the Alaska Peninsula, where the inner front may have limited larval ingress into the coastal domain. In 2010, the highest densities of age-0 fish in the Alaska Peninsula area were north of Unimak Island and adjacent to stations with the highest densities of age-0 fish in the Unimak Area. In 2010, age-0 fish may have moved into the coastal domain in the Alaska Peninsula area by the same larval delivery mechanisms as the adjacent age-0 fish in the Unimak Island area, perhaps because the inner front was not established in this location in the spring when the pelagic larvae were in the water column, or because larvae moved into the coastal domain on the adjacent Unimak Area side of the boundary.
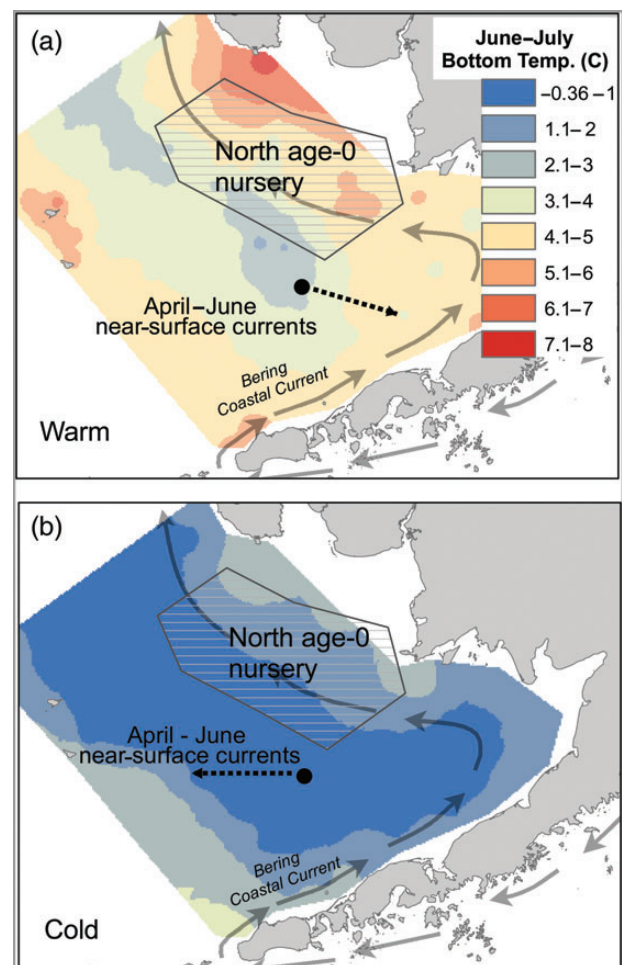

Figure 7. Schematic of summer bottom temperature differences and possible differences in larval transport between warm (top panel) and cold (bottom panel) years. The area where northern rock sole (*Lepidopsetta polyxystra*) were present in 2003 is labelled the North age-0 nursery. Summer (June–July) bottom temperature interpolations are from the eastern Bering Sea National Marine Fisheries Service groundfish survey in 2003 (top panel) and 2008 (bottom panel). Differences in direction of near-surface currents in warm and cold years are from Stabeno *et al.* (2012) at the M2 mooring (black circle) and are depicted by broken arrows.

Table 4. Reported densities of age-0 and age-1 rock sole (*Lepidopsetta spp.*) from areas in the Gulf of Alaska.

Area	Number of age-0 rock sole 1000 m^{-2}	Number of age-1 rock sole 1000 m^{-2}	Source
Kodiak Island bays	Ranged from 0 to 1300	Not reported	Stoner *et al.* (2007)
Kachemak Bay	Mean of ∼70 on sand	Mean of ∼12 on sand	Abookire and Norcross (1998)
South side of Alaska Peninsula	Mean of ∼80	Mean of ∼12	Norcross *et al.* (1999)

Both the inner front along the Alaska Peninsula and mainland Alaska, as well as the advection of water onshore at Unimak Island, are annually recurring and seasonally persistent hydrodynamic features that deliver northern rock sole larvae to age-0 benthic habitat. Persistent oceanographic features such as fronts and annually recurring currents have the potential to influence community composition (Sabates and Olivar, 1996; Darnell-Jimenez *et al.*, 2009) and population structure (Iles and Sinclair, 1982), and larval uses of persistent oceanographic features have been documented in several areas across the globe (Methot, 1983; Hinrichsen *et al.*, 2001; Bailey and Picquelle, 2002). However, though persistent oceanographic features can be capable of exerting significant structuring influence on larval distributions, their influence may be modified by other factors. We noted that the North area appeared to function as a juvenile nursery in warm years, but not in cold years. Climate variation may alter larval transport or the thermal properties of the North nursery area. Near-surface currents in the eastern Bering Sea can be different in warm and cold years (Stabeno *et al.*, 2012). During the months of April, May and June, when northern rock sole are being transported as planktonic larvae (Lanksbury *et al.*, 2007), mean near-surface currents are to the east in cold years, which may transport larvae offshore and away from the North nursery area (Figure 7). In warm years, mean near-surface currents in the eastern Bering Sea move shoreward, which may keep northern rock sole larvae entrained in the BCC and transport them to the North nursery area (Figure 7). This study did not examine either distribution of northern rock sole larvae or transport differences during the larval period, however this could be a future avenue of study that may explain differences in subsequent juvenile distribution in warm and cold years. Other possibilities are that larvae were delivered to the North area in 2008 and 2010, but temperatures were too cold for suitable nursery habitat, or that thermally reduced growth rates caused the larvae to be too small to settle in this habitat. June–July bottom temperatures in the North area can vary between from below zero to 3°C in cold years and 2–7°C in warm years (Figure 7). These differences could be enough to significantly affect growth and growth-mediated mortality of age-0 fish. Indeed, age-0 northern rock sole growth rate decreased at colder temperatures in a range of 2–13°C in laboratory growth experiments (Hurst and Abookire, 2006); growth rate at temperatures below 2°C and the lower thermal limit for suitable nursery habitat are unknown.

The resource selection model (Norcross *et al.*, 1999) created in a separate marine ecosystem for this species was not applicable to the eastern Bering Sea. The model seemed to fail because the model is incomplete in the eastern Bering Sea, not because the fish use nursery habitat with different characteristics in the eastern Bering Sea than in the Gulf of Alaska. Most model error occurred when fish were not present at locations predicted by the resource selection model, i.e. with suitable sediment and depths. As we discuss above, we suggest this is due to oceanographic features and possibly climate variability, which may limit larval transport to some areas. Stoner *et al.* (2007) hypothesized that differences in age-0 northern rock sole densities among Gulf of Alaska bays result from differences in larval supply, and that larval supply increases in importance as a factor in age-0 distribution at larger geographic scales, and our conclusion that the inner front affects pelagic larval distribution and subsequent age-0 distribution is consistent with their hypothesis. Large-scale differences in age-0 plaice (*Pleuronectes platessa*) densities near the Skagerrak off the coast of Sweden have also been related to differences in larval supply (Wennhage and Pihl, 2001).

Flatfish stock sizes are often related to the size of juvenile nursery habitat (van der Veer *et al.*, 2000). The large size of the North area surveyed in 2003 and the spatially homogenous sandy sediment create the potential for this area to provide habitat for a large number of juvenile northern rock sole. The inner front covers a large surface area in the North because although termed a "front", it can be over 100 km wide here (Kachel *et al.*, 2002). In 2003, mean densities of over 300 age-0 fish 1000 m^{-2} in the inner front and 67 age-1 fish 1000 m^{-2} in the inner front and coastal domain are of roughly the same magnitude as northern rock sole densities near Unimak Island and the Alaska Peninsula from this study and juvenile rock sole densities at reported nursery areas in the Gulf of Alaska in the summer (Table 4). Extrapolating observed densities in the North area surveyed in 2003 yields around 7 billion age-0 and 3 billion age-1 fish. Although these numbers are very rough estimates due to the small number of stations sampled over the large North area, they provide a sense of the potential contribution of the North area to the overall northern rock sole population in the eastern Bering Sea, where the mean annual recruitment of age-4 northern rock sole is estimated to be about 1 billion fish (Wilderbuer and Nichol, 2010). Climate variability could influence the ability of this area to function as a nursery area and have a large impact on adult population size, highlighting the potential importance of the interaction between larval delivery to age-0 habitat by the inner front and climate variability.

The higher densities of age-0 fish in the inner front and age-1 fish in the coastal domain, and the increased size of age-0 fish closer to shore, indicate possible post-settlement movement shoreward. This is similar to what has been reported for Dover sole (*Microstomus pacificus*), which settle offshore and then move shoreward in the western Pacific (Toole *et al.*, 1997), and winter flounder (*Pseudopleuronectes americanus*), which can settle in coves and then move to other nursery areas in the Northwest Atlantic (Curran and Able, 2002). Multiple cruises during a summer, or reading daily otolith growth rings, would be required to determine the rate of age-0 movement from the inner front to the coastal domain.

The use of habitat by juvenile northern rock sole in the eastern Bering Sea appears to be influenced by persistent hydrographic features that likely deliver pelagic larvae to juvenile nursery habitat. However, differences in juvenile habitat use between warm and cold periods suggest that climate variation may modify juvenile northern rock sole nursery areas.

Acknowledgements

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