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Modeled connectivity between northern rock sole (*Lepidopsetta polyxystra*) spawning and nursery areas in the eastern Bering Sea

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ABSTRACT

Connectivity between spawning and potential nursery areas of northern rock sole, *Lepidopsetta polyxystra*, in the eastern Bering Sea was examined using an individual-based biophysical-coupled model. Presumed spawning areas were identified using historical field-collected ichthyoplankton data, and nursery habitats were characterized based on previously described settlement areas. Simulated larvae were released from spawning areas near the Pribilof Islands, south of the Pribilof Islands along the outer continental shelf, on the north side of the Alaska Peninsula, and in the Gulf of Alaska south of Unimak Island. Simulated larvae were transported along two general pathways: 1) northwards along the outer continental shelf from Unimak Island towards the Pribilof Islands and further north offshore of mainland Alaska, and 2) eastward along the Alaska Peninsula. At the end of the 2-month simulation, drift pathways placed pre-settlement stage larvae offshore of known nursery areas of older juveniles near mainland Alaska, consistent with a hypothesis that initial settlement may be followed by substantial post-settlement redistribution.

1. Introduction

Connectivity in marine populations has been the focus of intense interest, both among invertebrate and vertebrate marine populations, due to its ecological (biogeographic structuring, population dynamics, climate change) and management (stock structure, essential fish habitat, marine protected areas) implications. Considerable work on the topic has been done in tropical systems where locating, orienting toward, and settling to coral reef habitat is of critical importance to recruitment success (Cowen and Sponaugle, 2009; Sale, 2004). Complementary work in high-latitude systems has centered on flatfishes, as these forms face similar constraints as reef-associated species, in particular the requirement of delivery to suitable nursery habitats prior to assuming a settled existence. For these and other substrate-reliant fishes, locations of spawning areas may be highly evolved such that they are located in areas where prevailing hydrodynamic patterns transport eggs and larvae to juvenile nursery habitat (Bailey et al., 2005; Hinckley et al., 2001). Such a strategy may be critical for flatfishes as it maximizes the likelihood that settlement-ready stages are in close proximity to appropriate benthic habitat, which may be decisive if a species cannot delay metamorphosis until suitable habitat can be found. Accordingly, studies that examine the transport and timing of dispersal of pelagic flatfish stages are of importance to the study of flatfish advection, survival, and recruitment.

Northern rock sole is commercially fished in the Bering Sea (BS) and Gulf of Alaska (GOA). The species has a large biomass (estimated at over 1.8 million tons in the eastern BS; Wilderbuer and Nichol, 2011) and is an important component of the BS ecosystem (Zador, 2011). Annual differences in wind direction and resulting larval transport variations are hypothesized to explain northern rock sole recruitment variability in the eastern BS (Wilderbuer et al., 2002), and disruptions in connectivity between spawning and nursery areas are one postulated mechanism for variable recruitment. However, links between spawning and nursery habitat have not been directly investigated, and transport trajectories and source-sink relationships remain unknown.

Northern rock sole spawn in December through March (Wilderbuer and Nichol, 2011). Eggs are demersal and “semi-adhesive,” and incubation ranges from about 15 days at 9 °C to about 36 days at 2 °C (Laurel and Blood, 2011). Larvae hatch between 3.0 and 5.4 millimeters (mm) standard length (SL) (Laurel and Blood, 2011). Larvae are most abundant in Alaskan waters in April (Matarese et al., 2003) and have been reported in the eastern BS and the GOA near Unimak Island, along the north side of the Alaska Peninsula in May (Lanksbury et al., 2007), and near the Pribilof Islands in July and August (Duffy-Anderson et al., 2006). Lanksbury et al. (2007) have hypothesized several unique larval dispersal pathways for northern rock sole larvae in the southeast BS (Fig. 1), but to date there have been no directed studies evaluating trajectory variations in time and space.

Compared to what is known about larvae, less is known about the distribution of juvenile northern rock sole in the BS. Recent work

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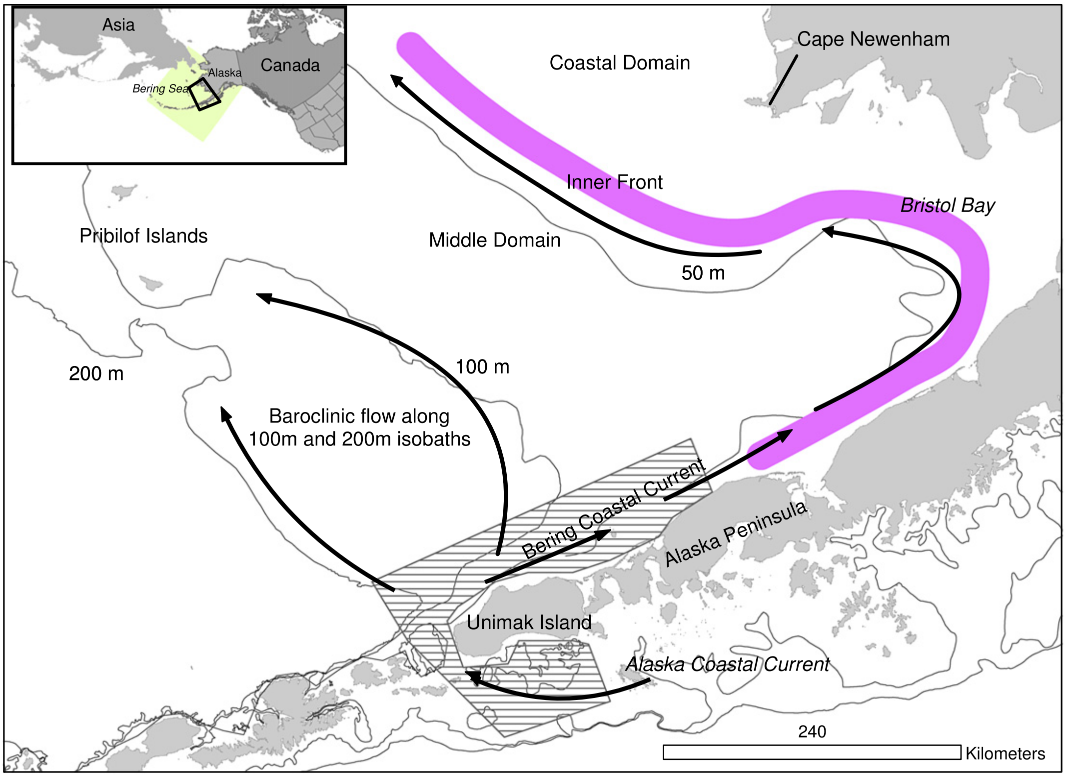

Fig. 1. Area (gray cross hatch) with reported concentrations of northern rock sole larvae in May. Arrows show hypothesized larval transport following the Bering Coastal Current to the northeast along the Alaska Peninsula, and baroclinic flow to the north towards the Pribilof Islands. The approximate location of the Inner Front is depicted in purple. The inset map shows the study area (black polygon) and the area of the regional ocean modeling system (ROMS; green shading) used in this study.
From Lanksbury et al., 2007.

over a relatively small geographic area has found age-0 northern rock sole off of mainland Alaska from Nunivak Island to Cape Newenham, and along the north side of Unimak Island and the Alaska Peninsula (Fig. 2). Age-0 northern rock sole have highest densities offshore of the coast (Fig. 2), in the vicinity of a seasonal front (Inner Front, IF) near the 50-m isobath and the Bering Coastal Current (BCC), which separates the thermally-mixed coastal domain from the thermally-stratified middle domain (Kachel et al., 2002; Fig. 1). Interestingly, in the absence of the IF along the north side of Unimak Island and the Alaska Peninsula, age-0s are readily collected inshore (Fig. 2). No other distributional information is available for the eastern BS. More data on settlement locations and juvenile habitat are available for the GOA, and from that, additional settlement areas in the BS can be inferred. In the GOA, age-0 post-settlement juveniles spend the first summer on sand and mixed sand sediment, primarily at <50 meters (m) depth (Norcross et al., 1999; Stoner et al., 2007); however, age-0 northern rock sole have been observed at lower densities on sand and mixed sand sediment to 80 m depth (Norcross et al., 1999). Based on the depth and sediment in the eastern BS shelf (McConnaughey and Smith, 2000), presence of settled juveniles in the BS might be expected in other geographic areas such as around the Pribilof Islands, in Bristol Bay, or in the vicinity of Cape Newenham (Fig. 1).

Our objectives are to examine connectivity of northern rock sole from spawning to nursery areas in the eastern BS using field data and biophysical modeling to determine the relative contributions of various source areas to corresponding settlement areas, and to examine temporal and spatial variations in larval dispersal. This research will refine our understanding of the scales over which larvae may be transported and the potential degree of connectivity between spawning and suitable nursery grounds.

2. Methods

2.1. Spawning areas

Spawning areas, and thus larval source areas for the individual-based biophysical-coupled model, were determined from locations where small larvae (≤4 mm SL) were collected in the eastern BS and south of Unimak Island from historical data obtained from surveys conducted by the Alaska Fisheries Science Center (AFSC) Recruitment Processes Program. Data for cruises were found in the AFSC ichthyoplankton cruise database.[1] Ichthyoplankton data are accessible in the AFSC larval fish database (ICHBASE). For the eastern BS, data from 1592 oblique plankton tows (60 cm bongo nets and 1 m Tucker trawls) from 17 years of sampling from 1988 to 2008 were used. In the GOA, data from 105 plankton tows from 14 years of sampling from 1982 to 2007 in the vicinity of Unimak Island were used. Matarese et al. (2003) contains detailed sampling protocols. Northern rock sole eggs are demersal (Laurel and Blood, 2011; Orr and Matarese, 2000), so eggs were not present in historical plankton records. Small (≤4 mm SL) planktonic larvae are considered to be suitable proxy data for spawning grounds since transport of demersal and semi-adhesive eggs is likely to be minimal and emergent larvae would be observed in proximity to egg deposition areas. Mean densities of newly-hatched (≤4 mm SL) northern rock sole larvae collected in plankton tows in April and May were averaged by 20×20 kilometer (km) grid squares and mapped. Areas with high densities were delineated, and subsets of these areas based on reported spawning depth

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[1] Ichthyoplankton Cruise Database, NOAA-NMFS, Alaska Fisheries Science Center. Available from: http://access.afsc.noaa.gov/icc/index.cfm, accessed Feb. 2010.

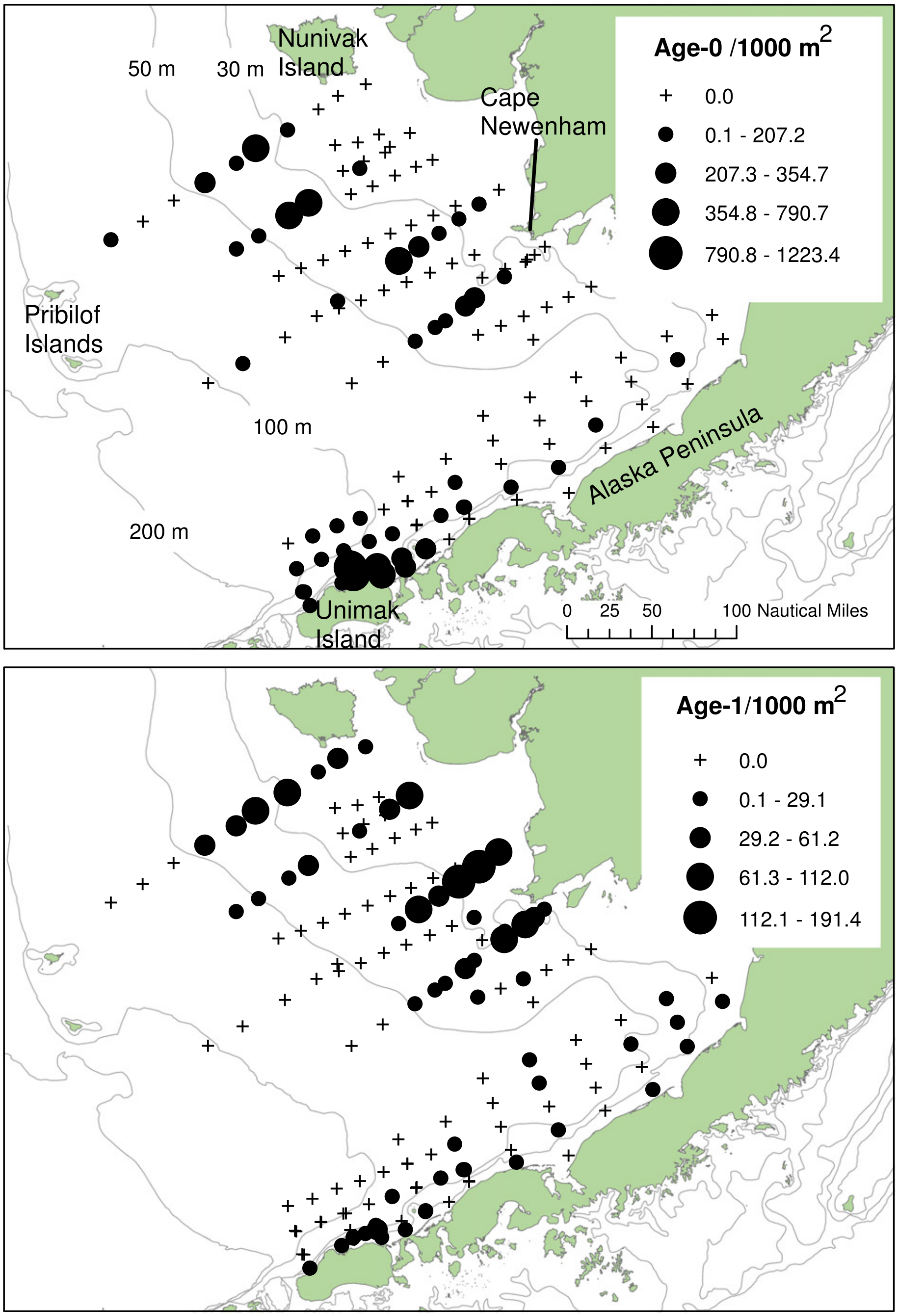

Fig. 2. Densities (fish per 1000 m^2) of northern rock sole age-0 (top panel) and age-1 (bottom panel) from 3 years (2003, 2008, 2010) of August and September trawl sampling. Adapted from Cooper et al. (in preparation).

between 40 m (Stark and Somerton, 2002) and the shelf break (200 m) were used as source areas for the model.

2.2. Settlement areas

Potential settlement areas were delineated into broad geographic areas based on depth and latitude (Fig. 3). Potential settlement areas for the model extended from approximately 54°N to 66°N were numbered from north to south from 1 through 16, and a settlement area around the Pribilof Islands was numbered 17 (Fig. 3). Settlement areas were defined as from 0 to 50 m or 50 to 80 m depth. An exception was an area around the Pribilof Islands (area 17), where a geographical area within 50 km of the shoreline was identified as the settlement area, and not constrained by depth (Fig. 3). Shallow water areas (<80 m) off the Pribilof Islands are limited and bounded by a steep seaward bathymetry, and this approach assumed that larvae in close proximity to the Pribilof Islands, but over deep water, would have some ability to move closer to shore to settle in suitable depths. While it is not known whether northern rock sole settle over this entire range, selected data from field observations (Fig. 2) and from inferences made from observations in the GOA (Norcross et al., 1999) suggest that these are appropriate potential settlement areas.

2.3. DisMELS model

We used the DisMELS, (Dispersal Model for Early Life Stages) model to simulate the dispersion of northern rock sole larvae in the

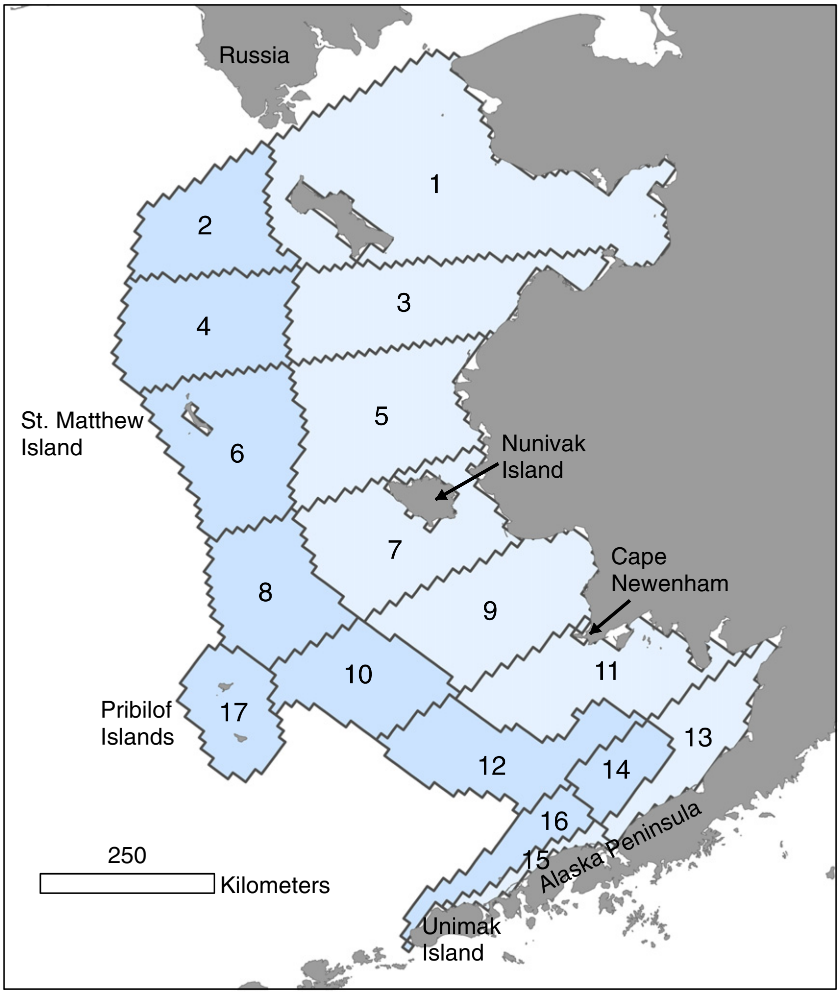

Fig. 3. Potential settlement areas (1–17) from shore to the 50-m isobath (light blue), between the 50 and 100 m isobath and within 50 km of the Pribilof Islands (dark blue) used in the DisMELS model in the eastern Bering Sea.

eastern BS from presumed spawning areas to shallow nursery grounds, to elucidate likely transport pathways, and to assess the inter-annual temporal variability in those pathways. DisMELS is a coupled biophysical model that combines an individual-based model (IBM) framework with simulated environmental conditions from an ocean circulation model to predict the growth, mortality, and dispersion of pelagic eggs and larvae of flatfish and other benthic marine species. DisMELS uses stored output of 4-dimensional (4D: 3 spatial dimensions + time) oceanographic currents, temperature, and salinity fields from the oceanographic circulation model to perform Lagrangian particle tracking. It also simulates advective transport of pelagic eggs and larvae with simple behaviors, including active vertical migration. Growth, mortality, and life stage of individuals are tracked through time. Ontogenetic shifts in vertical behavior, growth, and/or mortality rates are incorporated by defining a series of stages through which individuals grow. Values for minimum size and age are used to define when individuals change stages and when they are competent to settle to the benthos. Settlement, however, can only occur within predefined nursery areas and competent individuals that fail to reach suitable settlement habitat within an allotted time frame perish.

For this study, we used daily-averaged fields of 2-dimensional sea surface height and 3-dimensional salinity, temperature, horizontal velocity (u,v components), and scaled vertical flux (Ω) (from an oceanographic model) for the northeast Pacific Ocean to simulate the physical environment experienced by individual flatfish. The oceanographic model was implemented using the Regional Ocean Modeling System (ROMS; http://www.myroms.org). ROMS is a free-surface, hydrostatic, primitive equation ocean model that employs orthogonal curvilinear coordinates in the horizontal, and stretched terrain-following ("sigma") coordinates in the vertical (Haidvogel et al., 2000; Shchepetkin and McWilliams, 2005; Wilkin et al., 2005). The stretched coordinates allow increased resolution in areas of interest, such as the thermocline and bottom boundary layers.

The ROMS model simulation was run on a regional, intermediate resolution grid (North East Pacific grid version 4, NEP4) of a suite of nested computational domains extending from the basin scale to coastal regions (Curchitser et al., 2005; Hermann et al., 2009). The version of ROMS utilized for this work has been expanded to include a sea ice module therefore the model effectively accounts for sea ice flux and thermodynamics. The NEP4 computational grid consisted of 212 × 572 curvilinear/orthogonal cells, with an approximate cell size of 10 × 10 km in the horizontal and 42 stretched-coordinate layers in the vertical. No matter the water depth, the model possessed 42 vertical layers, and the highest vertical resolution was concentrated near the sea surface. Although this class of model exhibits strong sensitivity to topography, resulting in pressure gradient errors (Haidvogel and Beckmann, 1999), the numerical algorithm in ROMS is designed to reduce such errors (Shchepetkin and McWilliams, 2003). Duffy-Anderson et al. (2013) compared the ROMS NEP4 simulated velocity field with observational data collected from 1995 to 2004. In general, they concluded there was good agreement between the ROMS model and observational values, though they noted that simulated currents were slightly weaker than field observations, and they described a somewhat stronger tendency for topographic steering in the model than in the field. ROMS, with and without an individual based model component (IBM), has been used to examine the drift and transport of a variety of North Pacific marine species including Greenland halibut (Duffy-Anderson et al., 2013), Pacific halibut (Sohn, personal communication), snow crab (Parada et al., 2010) and walleye pollock (Duffy-Anderson, personal communication).

A multi-decadal (1958–2004) simulation of currents and temperatures was conducted using this 10 × 10 km grid. Air–water surface boundary conditions were derived from a hindcast simulation using the Community Climate System Model (CCSM; Collins et al., 2006) version of the Parallel Ocean Program (POP; Smith and Gent, 2002). Daily surface forcing functions (at 2° × 2° resolution) were obtained from the Common Ocean-Ice Reference Experiments (CORE) developed by Large and Yeager (2004). Tidal forcing was not included in the model. To reduce storage requirements, the output was spatially "clipped" to a horizontal region 180 × 180 cells square centered on the eastern BS while retaining all 42 vertical layers.

For the IBM components of the model, we defined two larval stages, an "early" stage (<8.5 mm SL) and a "late" stage (≥8.5 mm SL), to reflect ontogenetic changes in the vertical position of larvae in the water column (Table 1). Between 378 and 612 simulated larvae were released, evenly spaced over each of the 6 larval source areas, for a total of 2966 simulated larvae released per year. Simulated larvae were released in the model on 15 April each year at an initial size of 3.8 mm SL (Table 1). Early stage and late-stage larvae grew at a linear rate of 0.25 mm day^{-1} every year based on published growth rates of newly-settled juveniles (Hurst and Abookire, 2006). A "preferred" depth range for early stage larvae was 10–20 m depth, regardless of time of day. In contrast, late-stage individuals underwent diel vertical migration, with minimum and maximum depth parameters set such that the "preferred" depth ranges were 0–10 m at night and 20–30 m during the day. Active larval behavior included directed vertical swimming and vertical random walks. Directed vertical swimming occurred when larvae were outside their "preferred" depth range, possibly as a consequence of vertical advection or random movement. Vertical position also included a random walk component implemented as a normally-distributed random velocity updated at each model time step with fixed variance. Individuals that were outside these "preferred" depth ranges would actively "swim" up or down until entering the preferred depth range Transition between daytime and nighttime behaviors for late-stage larvae was dependent on times of sunrise and sunset, as determined by year-day and individual location. The IBM model was iterated over 20-minute time steps. Individual locations were updated on the native NEP4 curvilinear grid using a 4th-order Milne predictor/4th-order Hamming corrector algorithm (Lapidus and Seinfeld, 1971) for Lagrangian particle tracking similar to that used in ROMS. Horizontal and vertical current velocities were spatially interpolated bilinearly from the daily ROMS model output to each individual's position at the current IBM time step for the predictor step, and to its predicted position at the subsequent time step for the corrector step. Attributes (life stage, age, size, location) for each simulated individual were saved to an output file at a daily time step. Locations were converted from NEP4 grid coordinates to physical coordinates (latitude, longitude, depth) prior to output.

Table 1
Parameter values and data sources for northern rock sole hatch date, initial size, growth rate, and vertical position used in the dispersal model for early life stages (DisMELS) model.

Model parameter	Value	Source
Model years	1979–2004	
Hatch date	15 April	Matarese et al. (2003)
Initial larval size	3.8 mm SL	IIS[a]
Growth rate	0.25 mm/day	Hurst and Abookire (2006)
Settlement size	20 mm SL	This study
Vertical position (meters, m)		
simulated larvae <8.5 mm SL	10–20 m	Lanksbury et al. (2007)
simulated larvae ≥8.5 mm SL	Day: 20–30 m; night: 0–10 m	Lanksbury et al. (2007)

[a] Ichthyoplankton Information System (IIS), NOAA-NMFS, Alaska Fisheries Science Center. Available from http://access.afsc.noaa.gov/ichthyo/index.cfm (access date 04 May 2011).

To estimate the settlement size of northern rock sole larvae, and therefore the appropriate end date for the model runs, comparisons were made of maximum sizes of larvae collected in plankton tows with minimum sizes of demersal juveniles. Length frequency data of northern rock sole caught in historical plankton tows in the eastern BS (April through September 1979–2008) were obtained from ICHBASE, and compared with length frequencies of demersal age-0 fish caught using demersal beam trawls conducted by the AFSC Recruitment Processes Program in the eastern BS in September 2008. Few northern rock sole > 20 mm SL were caught in the plankton nets, and there were few <20 mm SL caught using the demersal beam trawls (Fig. 4), thus the model run concluded when larvae reached 20 mm SL (20 June every year for all simulated larvae).

Connectivity between spawning and nursery areas was calculated for each source area in each model year as the fraction of simulated larvae originating in the source area which were transported to each settlement area. Overall mean connectivity was calculated for each source area by averaging connectivity over all 26 years of the model. Variability in modeled transport from each source was visualized by plotting the center of the distribution of the end points of simulated larvae for each model year.

3. Results

3.1. Field observations

Observations from field-collected data indicated that densities of small northern rock sole larvae (<4 mm SL) were concentrated around the Pribilof Islands (designated model larval source areas 1 and 2), southeast from the Pribilof Islands toward the Alaska Peninsula (larval source area 3), along the Alaska Peninsula (larval source area 4), and north (larval source area 5) and south (larval source area 6) of Unimak Island (Fig. 5). A few isolated records north of the Pribilof Islands indicated nearby spawning (Fig. 5), but observations were based on only a very few historical ichthyoplankton records so these areas were not used as spawning locations in the model.

3.2. Model-derived observations

Simulated larvae released from source areas near the Pribilof Islands (sources 1–3) moved northwards, as shown by tracks from

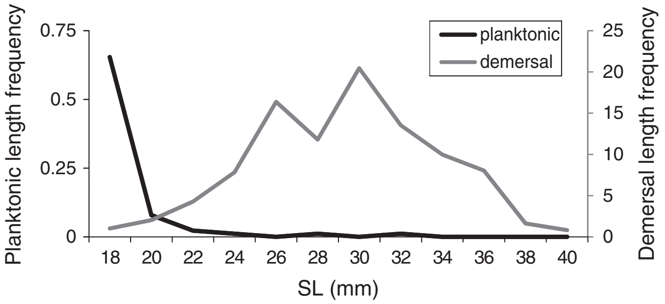

Fig. 4. Length frequencies of northern rock sole caught by plankton nets (black line) throughout the year from 1988 through 2008 and demersal nets (gray line) in the eastern Bering Sea in September 2008.

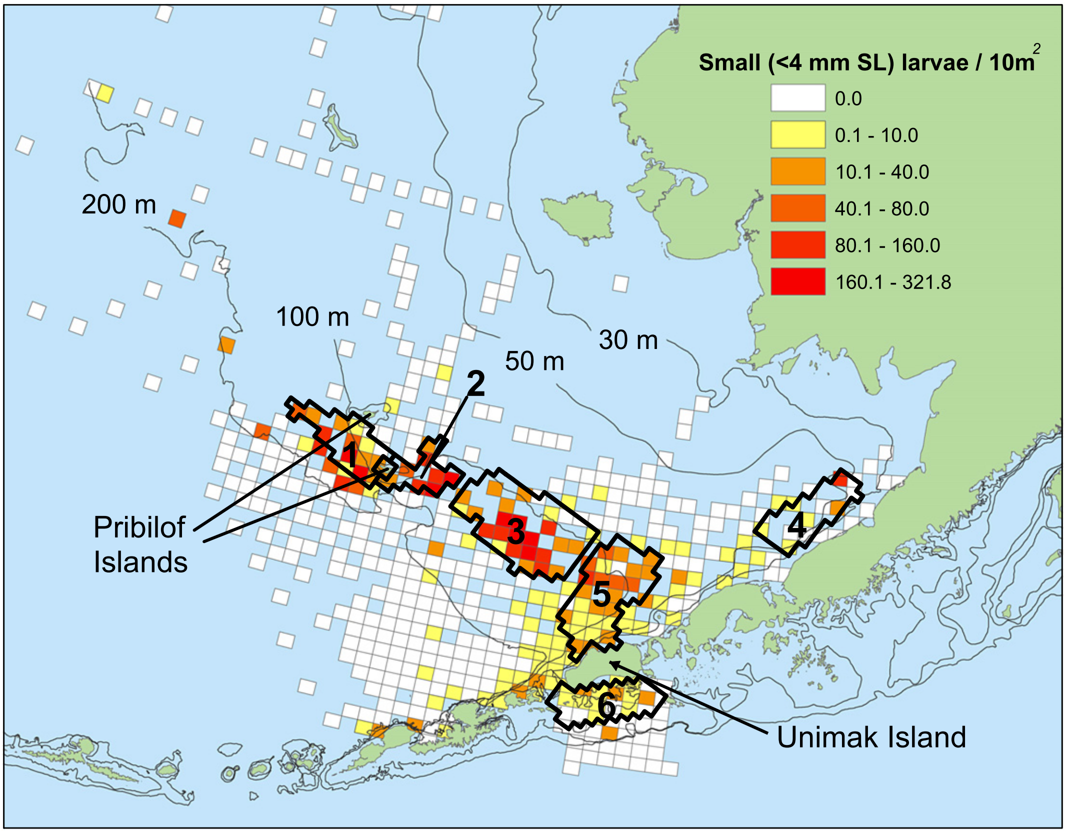

Fig. 5. Northern rock sole spawning areas (black polygons 1–6) used as larval start areas for the DisMELS model. Mean density (number of fish/10 m^2) of small ($\leq$4 mm SL) northern rock sole larvae in 20×20 km grid squares from 60-cm bongo net data collected in the eastern Bering Sea 1988–2008, and south of Unimak Island 1982–2007, are represented by white or colored 20×20 km squares.

one model year (Fig. 6). Mean simulated larval transport over all years from sources 1–3 was primarily to settlement areas to the north (Fig. 7a–c). There was variability in the northward distance traveled, however transport was northward in every model year (Fig. 8a–c). No simulated particles from these three sources were predicted by the model to settle inshore of the 50 m isobath off mainland Alaska in any year. Simulated larvae settled in areas more than 180 to 300 km from shore (Fig. 7a–c) at water depths > 50 m.

Most simulated larvae released from source 4, along the Alaska Peninsula, were transported to the east along the Alaska Peninsula with some turning to the northwest inside Bristol Bay (Fig. 6). The mean transport pathways over all model years reflect this pathway, with simulated larvae moving to settlement areas to the east along the Alaska Peninsula or to nearby settlement areas to the north (Fig. 7d). Unlike the simulated larvae settling offshore of the 50-m isobath from sources 1–3, the model predicted settlement here in areas < 50 m (Fig. 7d). Transport from source 4 was to the north or northeast in every year and variability was lower than in the other areas (Fig. 8d).

Simulated larvae from north and south of Unimak Island (sources 5 and 6) were transported along one of two general pathways, as shown by tracks of the simulated larvae in one model year (Fig. 6). Some were transported along a pathway to the north, in a manner resembling that of simulated larvae from sources 1–3, reaching settlement areas < 50 m along the coast of mainland Alaska or near the Pribilof Islands (Fig. 6). Others were transported to the east along the Alaska Peninsula, much the same as simulated larvae from source 4, and reached settlement areas both inshore and offshore of the 50-m isobath (Fig. 6). Mean transport of simulated larvae from sources 5 and 6 over all model years reflects these multiple pathways, with connectivity to settlement areas to the north and also to the east along the Alaska Peninsula (Fig. 7e, f). Inter-annual variability in transport in the east–west direction was high for sources 5 and 6 (Fig. 8e, f) because simulated larvae from these sources were transported both along the Alaska Peninsula to the east, and to the north towards the Pribilof Islands, moreover the proportion of larvae transported along these different pathways was variable among years (Fig. 9).

Zero simulated larvae were predicted to settle in areas north of St. Matthew Island in any year. Simulated larvae from sources 1, 2, 3, 5, and 6 did settle near the Pribilof Islands (Fig. 7), and some larvae were transported in a circular pattern around the Pribilof Islands (Fig. 6).

4. Discussion

Our model results suggest that, off mainland Alaska, initial settlement areas of northern rock sole could be located quite far from juvenile nursery habitat areas located near shore. Model results failed to deliver larvae any closer than hundreds of kilometers offshore of mainland Alaska, and field data (Fig. 2) are consistent with age-0 settlement offshore and subsequent shoreward movement. By age-1, northern rock sole are using nursery areas closer to shore in the coastal domain near mainland Alaska (Fig. 2). We hypothesize that settlement in northern rock sole is a multi-step process, involving exchange of larvae from spawning areas to an initial settlement zone, and transfer from the initial settlement sites to more favorable, prolonged-use nursery areas inshore. This hypothesized scenario may even be somewhat idealized; the actual settlement process may involve numerous iterative steps between initial settlement site and final nursery habitat.

An interesting follow-up question to the above is, why don't adult northern rock sole spawn in areas that allow larvae to settle closer to shore? Such a strategy would minimize the post-settlement searching

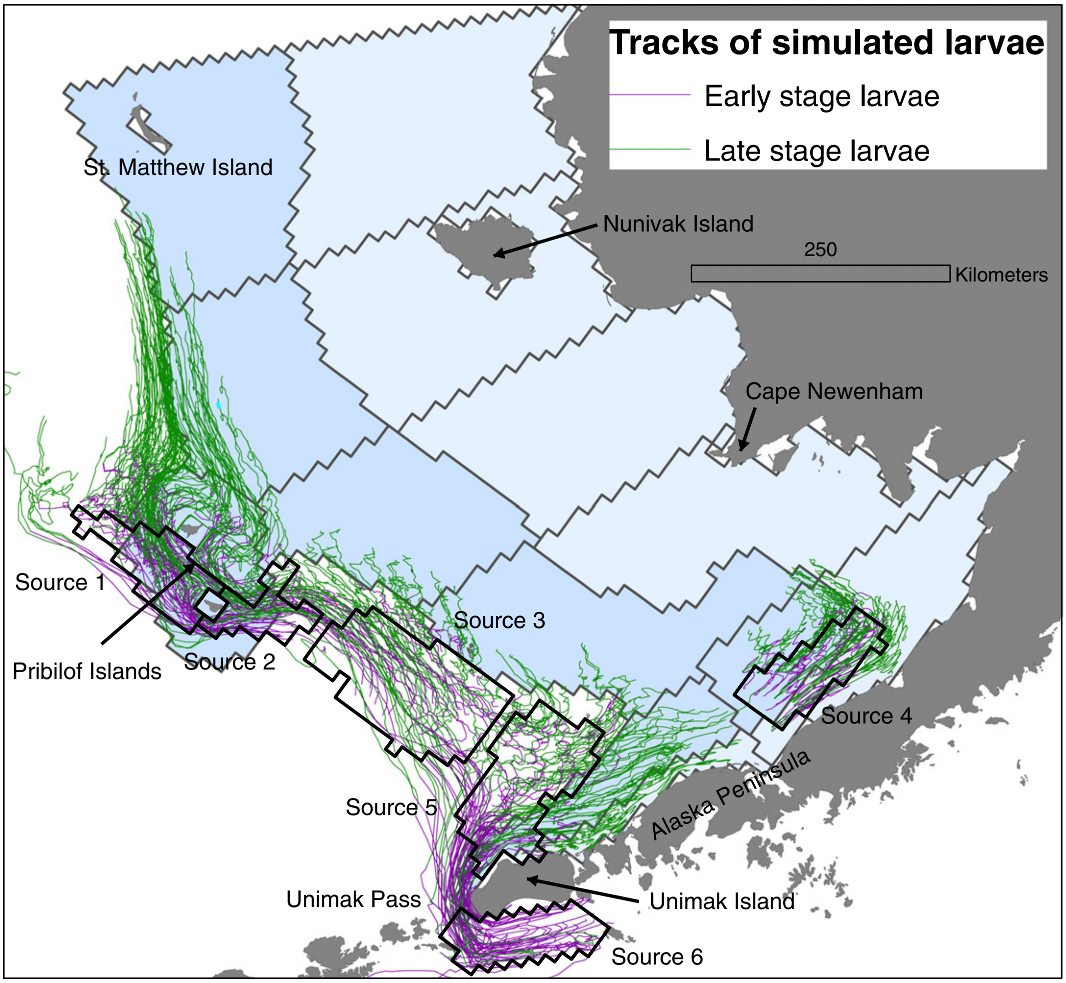

Fig. 6. Simulated larval trajectories for one example year (2004). Small (<8.5 mm SL) simulated larval tracks shown in purple. Larger (≥8.5 mm SL) simulated larval tracks shown in green. A random 10% of simulated larvae are displayed to better view pathways.

phase that appears to be necessary to connect newly-settled fish to nursery habitat. Common sole (*Solea solea*) and plaice (*Pleuronectes platessa*) can spawn either nearshore or offshore in different geographic areas depending on how local hydrodynamic patterns retain or transport eggs and larvae to nearshore nursery areas (as cited in Bailey et al., 2005). It would seem northern rock sole could do similarly by spawning in the vicinity of nursery areas near mainland Alaska. In fact, northern rock sole is not an obligate deep-water spawner, as they are known to spawn near beaches in Puget Sound, Washington (Orr and Matarese, 2000).

One possibility for settlement far from shore is that the area near shore of mainland Alaska is not suitable habitat for northern rock sole eggs and larvae during the spawning season (December through March). This area is often ice-covered during the spawning season (Stabeno et al., 2001), and sub-zero temperatures (°C) under sea ice (Stabeno et al., 1998) may be inhospitable for demersal northern rock sole egg and larval development. By spawning deeper along the shelf edge, eggs could develop in warmer water and be transported to the IF later in the spring. In the summer when the ice is gone and the water in the coastal domain warms, age-0 fish could move shoreward to nursery areas.

Another possibility is that the offshore settlement area offers desirable habitat for newly-settled fish. Length data indicate age-0 fish settle and then move shoreward, (Fig. 10), but also indicate that age-0 fish continue to grow with shoreward movement (Fig. 10). The settlement area is in the vicinity of the IF, which is highly productive (Hunt et al., 2011), and may offer increased prey resources, or perhaps biogenic structure which may be favorable for age-0 northern rock sole survival (Stoner et al., 2007). The bottom sediment in the vicinity of the inner front is predominately sand (McConnaughey and Smith, 2000), which is suitable sediment for age-0 rock sole larvae in the summer in the Gulf of Alaska (Norcross et al., 1999; Stoner et al., 2007). Of course, offshore zones are also important habitat for a variety of larger, piscivorous species including Pacific halibut, arrowtooth flounder, and Pacific cod. As such, the value of these areas may be mitigated by their inherent risk of predation.

An abundance of prey resources in the vicinity of the IF could be of significant value to newly-settling rock sole larvae given their long exposure to the strongly stratified middle domain (Ladd and Stabeno, 2012), during the transport between spawning and settlement areas. A strongly stratified middle domain, particularly in cold years with significant seasonal ice coverage, may vertically separate feeding larvae from prey resources. Unless larvae are well maintained in the thermally mixed layer (0–30 m), feeding opportunities during the transport process may be transient. Accordingly, placement of settling larvae near the well-mixed IF and costal domain could result in much-needed feeding opportunities for settlement-ready fish.

Long distance movement of post-settlement and metamorphosed flatfish is not commonly reported in the literature. In winter flounder (*Pseudopleuronectes americanus*), larvae are transported to settlement areas, and post-settlement fish move to nearby nursery areas; however, the reported movement is on a scale of less than 10 km and little growth happens during the transition (Curran and Able, 2002). Other flatfish

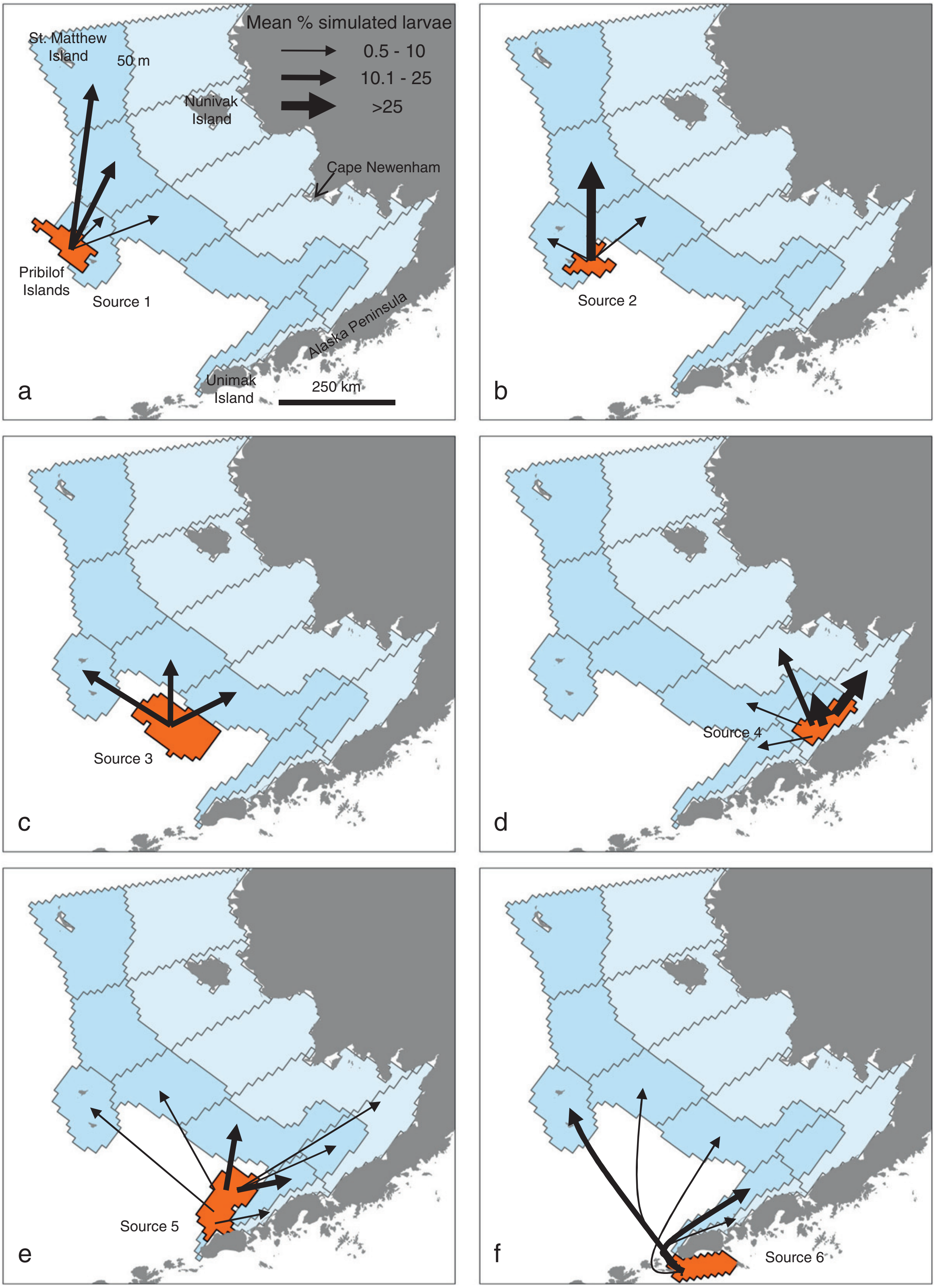

Fig. 7. Connectivity between modeled spawning and settlement areas. Arrows represent mean percent of simulated larvae for 26 years of model results originating in a spawning area and settling in a settlement area. a) source area 1; b) source area 2; c) source area 3; d) source area 4, e) source area 5; and f) source area 6.

species settle offshore, and move shoreward during an extended transformation stage (Boehlert and Mundy, 1987; Toole et al., 1997). Evidence for northern rock sole in the BS suggests that age-0 northern rock sole are conducting shoreward movement while fully metamorphosed into the juvenile stage, at a development stage and size where, in other geographic areas, they are already located in prolonged-use nursery habitats (Norcross et al., 1999; Stoner et al., 2007).

Two general transport pathways for simulated larvae are evident in this study: one occurs northwards from Unimak Pass to the Pribilof Islands and then continues north, and the other is to the east along

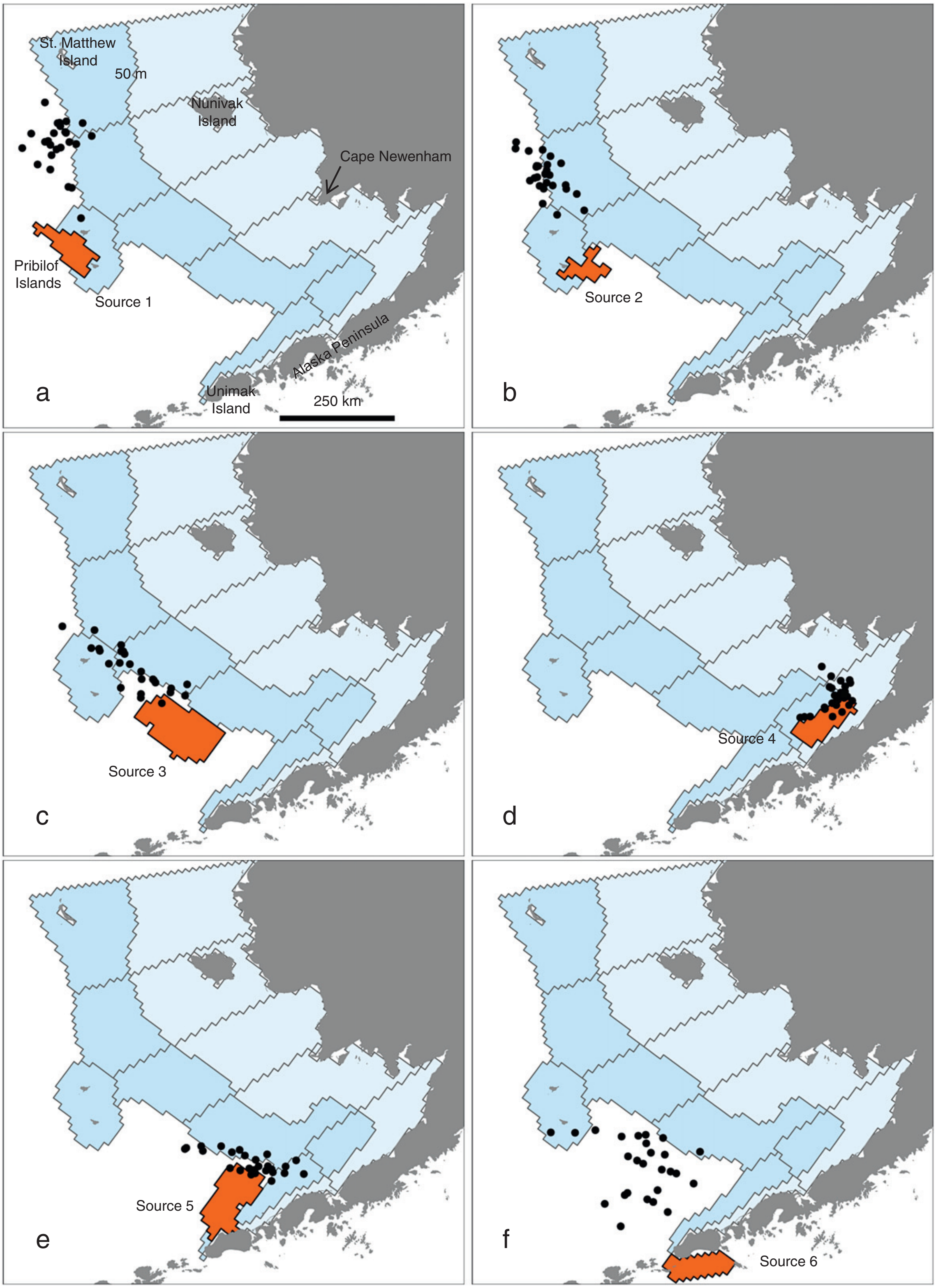

Fig. 8. Variability of transport of simulated larvae. Each black dot represents the mean center of distribution for one model year of simulated larvae released from a) source area 1; b) source area 2; c) source area 3; d) source area 4, e) source area 5; and f) source area 6.

the Alaska Peninsula. Each of these pathways was predicted by Lanksbury et al. (2007) because the pathways follow the predominant currents in the area during the northern rock sole larval period: the baroclinic flow from Unimak Pass northwards to the Pribilof Islands and continuing farther north, and the BCC from Unimak Island to the east along the Alaska Peninsula.

Differences in the properties of the currents along these two pathways may explain settlement offshore of mainland Alaska, but closer to shore along the Alaska Peninsula. The northwards baroclinic current along the outer shelf does not have a strong cross-shelf component (Coachman, 1986), and this lack of cross-shelf transport is reflected in the ROMS model and ultimately the DisMELS model

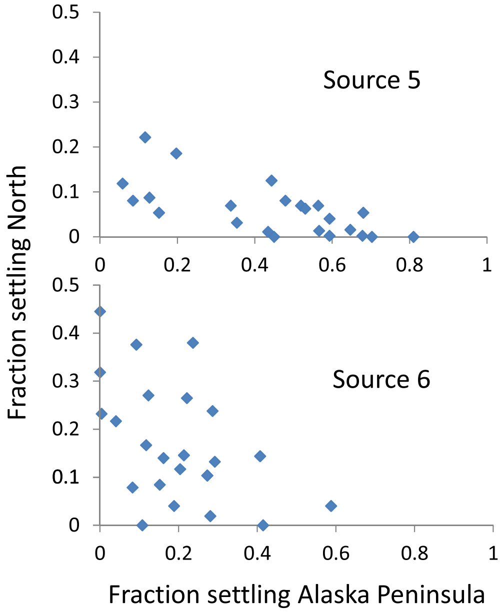

Fig. 9. a) Fraction of simulated larvae released from larval source areas 5 and 6 settling along the Alaska Peninsula (settlement areas 11, 13, 14, 15, 16) versus areas to the north (settlement areas 6, 8, 10, 17). Each point represents 1 year.

which does not transport simulated larvae inshore of the 50-m isobath in this area. Field data from this area confirm age-0 northern rock sole ingress into the coastal domain is limited during the summer (Fig. 2). Along Unimak Island and the Alaska Peninsula, the BCC is closer to the shore, which is consistent with the model-predicted settlers and field data observations of age-0 fish in the 0–50 m depth range near shore (Fig. 2).

Settlement near the Pribilof Islands may be enhanced by a tidally-induced clockwise flow pattern (Kowalik and Stabeno, 1999), which may entrain larvae and increase larval residence. The Pribilof Islands are isolated and remote, located more than 300 km away from the next nearest suitable rock sole nursery habitat.

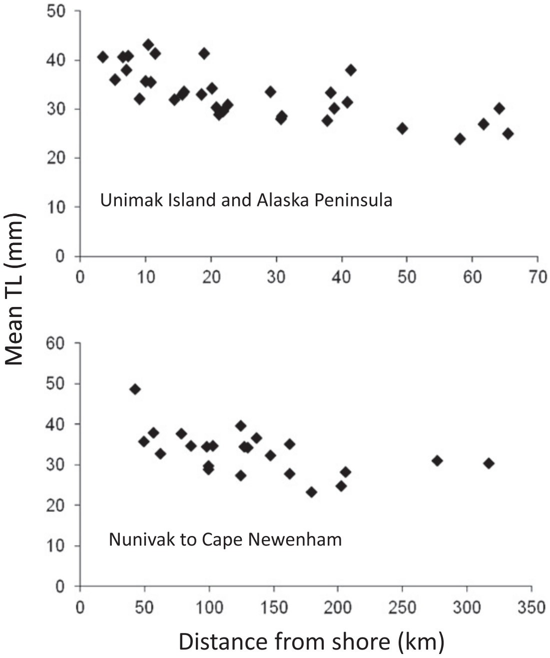

Fig. 10. Mean total length (mm) of age-0 northern rock sole by distance from shore (km) for beam trawl stations along Unimak Island and the Alaska Peninsula (top panel) and between Nunivak Island and Cape Newenham (bottom panel). Each point represents one trawl station.
Adapted from Cooper et al. (in preparation).

The model parameters for larval release date, larval release locations, growth rate, vertical distribution, and pelagic larval duration were constant for all years, and thus model results do not reflect the effects of real inter- or intra-annual changes in these parameters. Of particular note, the model does not incorporate tides, or possible changes in larval vertical distribution related to tides and resulting selective tidal stream transport (STST). In the ocean, northern rock sole larvae may use variability in any of these parameters to facilitate transport that is not predicted by our model. Substantial inter-annual differences in transport, or directed divergence in transport from predominate currents are possible, especially in later ontogenetic stages when swimming abilities increase and there are fewer data on vertical distribution. Additional field work is required to determine inter-annual variability in these parameters, investigate possible STST, and further refine our understanding of larval transport.

Model-predicted settlement did not occur north of St. Matthew Island in this study, though adult northern rock sole are reported north of St. Matthew Island (Lauth, 2011). Northern rock sole larvae are possibly delivered to the northern BS from spawning areas not included as starting points in our model, such as the isolated areas north of the Pribilof Islands, where small northern rock sole were documented in sporadic historical ichthyoplankton records. Additional field sampling to identify both spawning and nursery areas north of the Pribilof Islands is needed to completely understand connectivity from spawning to nursery areas in the entire BS for this species.

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