Received: 21 February 2020 | Revised: 9 July 2020 | Accepted: 15 July 2020

DOI: 10.1111/fog.12492

ORIGINAL ARTICLE

FISHERIES OCEANOGRAPHY WILEY

Red king crab larval advection in Bristol Bay: Implications for recruitment variability

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Funding information
North Pacific Research Board, Grant/Award Number: Project # 1402

Abstract

Recruitment variability is poorly understood for Bering Sea crab stocks. The nearshore area in southwest Bristol Bay (Alaska, USA) is hypothesized as having historically (i.e., prior to ~ 1980) been the most important spawning ground for Bristol Bay red king crab (*Paralithodes camtschaticus*) because post-larvae are thought to have been most likely to reach optimal settlement habitat along the Alaska Peninsula when hatched from this area as part of an endless-belt reproductive strategy. We coupled a biophysical and oceanographic circulation model to test this hypothesis, investigate larval connectivity of more recent female spatial distributions, and evaluate the importance of climate variability on larval advection trajectories. Predicted settlement success varied through changes in larval pelagic duration and oceanographic circulation patterns: Shorter advective distance was associated with warmer conditions, causing higher rates of local retention relative to cold conditions. Contrary to earlier models, most larvae hatched in southwest Bristol Bay were advected offshore away from good habitat, whereas larvae hatched in central and nearshore Bristol Bay were retained in or advected to good habitat along the Alaska Peninsula. Our results suggest contemporary spatial distributions can supply settlement-competent larvae to nurseries along the Alaska Peninsula and that under certain conditions, larvae may reach the Pribilof Islands when hatched from southwest Bristol Bay. Our study informs the role of environmental variability on larval transport and provides context within which to structure future investigations of recruitment mechanisms.

KEYWORDS

Bristol Bay, connectivity, larval advection, *Paralithodes camtschaticus*, recruitment, red king crab, retention

1 | INTRODUCTION

Red king crabs (*Paralithodes camtschaticus*) have significant commercial and ecological importance throughout the North Pacific, and Bristol Bay red king crab supports the longest existing crab fishery in Alaska, USA. Population abundances have fluctuated over the past several decades and are currently at low levels relative to the late 1970s and early 1980s (Zheng & Siddeek, 2018), but our

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understanding of mechanisms driving recruitment variability is limited (Zheng & Kruse, 2006) and recruitment is only weakly related to spawning stock abundance (Zheng & Kruse, 2003). Very little information exists on processes or factors affecting red king crab survival at the early life stages, and the linkage between oceanographic processes and population dynamics has been largely speculative.

Larval advection is an important process for recruitment in benthic invertebrates as the supply of settlement-competent larvae to a given area typically depends upon larval hatch that occurs elsewhere. For species with long larval pelagic duration, substantial transport distances may occur before reaching the settling stage (Shanks, 2009). As such, variable rates of connectivity and retention can result in large-scale population trends. For example, long periods of localized retention support the existence of sub-stocks of eastern Bering Sea (EBS) Tanner crab (*Chionoecetes bairdi*) (Richar, Kruse, Curchitser, & Hermann, 2015). Similarly, connectivity analysis highlights the importance of geographic/oceanographic subsystems for Bering Sea snow crab (*Chionoecetes opilio*) (Parada, Armstrong, Ernst, Hinckley, & Orensanz, 2010). For Bristol Bay red king crab, the location of ovigerous females at larval release may control the location of post-larvae relative to optimal settling habitat. Nearshore grounds north of Unimak Island and the Black Hills (Figure 1) have long been hypothesized as the population's most important hatching ground for supplying recruits to the population because the predicted location of settling post-larvae after dispersal corresponds with favorable nearshore benthic habitat (Armstrong, Incze, Wencker, & Armstrong, 1986; Armstrong, Wainwright, Jensen, Dinnel, & Andersen, 1993; Evans, Fey, Foy, & Olson, 2012; Haynes, 1974; Hebard, 1959; Hsu, 1987; Loher, 2001). This theory has been suggested as an evolutionary strategy referred to as an endless-belt

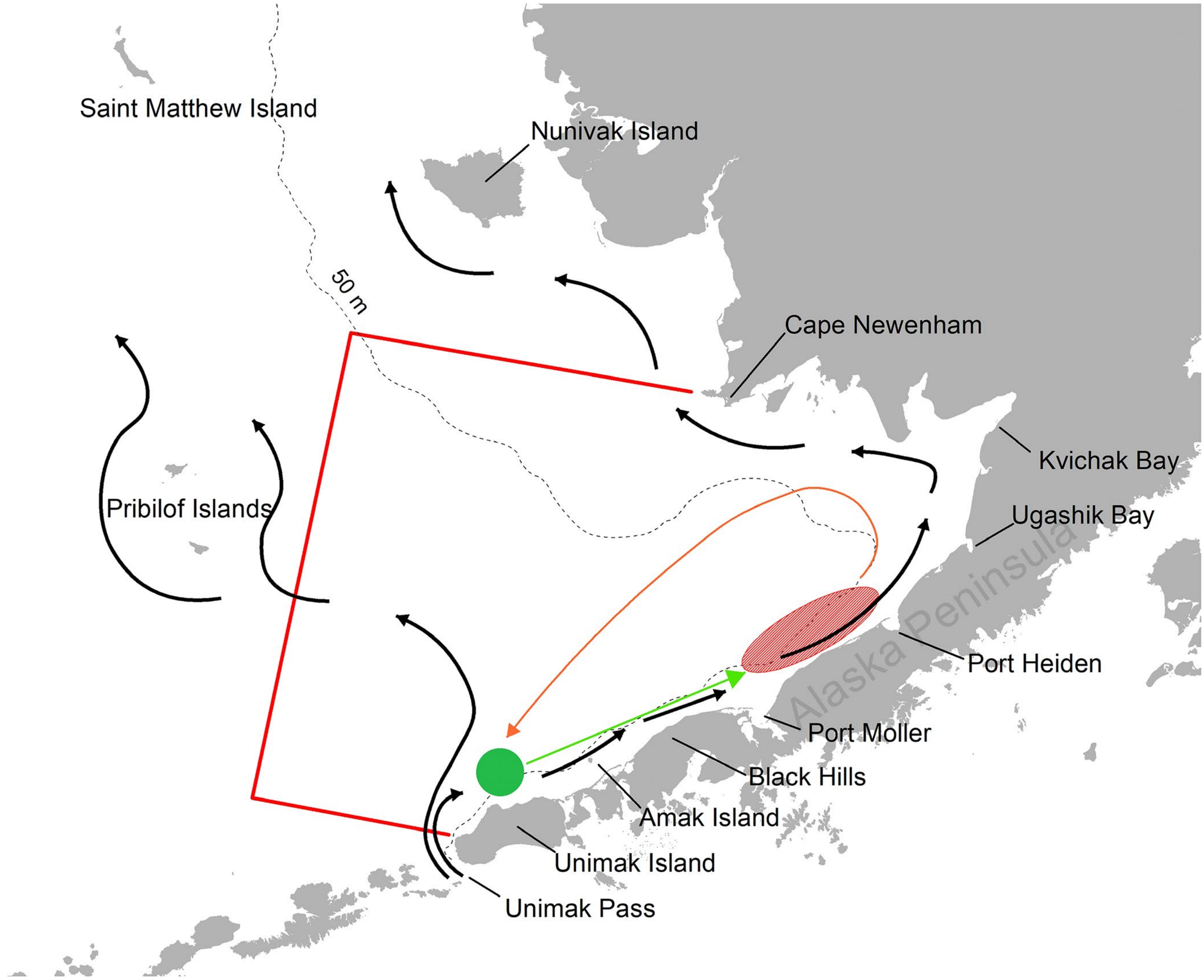


FIGURE 1 Diagram of the endless-belt reproductive strategy for red king crab (*Paralithodes camtschaticus*), depicting how the location of larval release and the prevailing currents might affect settlement location. The black arrows depict general current structure on the eastern Bering Sea shelf (adapted from this study and Stabeno et al., (2001)), the orange arrow indicates a theoretical adult female migration route, the green circle indicates a theoretical larval release (hatch) area, the green arrow indicates a theoretical larval advection trajectory, the pink oval indicates a theoretical post-larval settlement area, and the red line indicates the management boundary for Bristol Bay red king crab [Colour figure can be viewed at wileyonlinelibrary.com]

reproductive strategy, in which ovigerous females migrate from northeast Bristol Bay to southwest Bristol Bay to concentrate the larval source up-current of nursery grounds (Figure 1).

The component of the Bristol Bay red king crab broodstock that was located along the north shore of Unimak Island disappeared in the early 1980s, concurrent with the sharp decline in overall abundance (Armstrong et al., 1993; Loher & Armstrong, 2005). Since then, most of the broodstock has occurred to the northeast near the center of Bristol Bay. It is unclear whether the mature female redistribution was caused by large-scale migrations to the northeast or from spatially explicit mortality. Loher and Armstrong (2005) hypothesized that changes in bottom temperature caused the spatial shift, while Dew and McConnaughey (2005) hypothesized that high rates of trawl bycatch mortality caused the disappearance. Regardless of the cause, if Bristol Bay red king crab use an endless-belt reproductive strategy, the loss of Unimak broodstock would thereby decouple nursery habitat from the larval source impeding the population's ability to produce recruits (Loher, 2001).

Red king crabs have a complex life cycle including four pelagic larval (zoeal) stages, a post-larval (glaucothoe) stage, and benthic juvenile and adult stages (Marukawa, 1933). Ovigerous female red king crabs mate in spring/summer and brood their embryos for approximately 11 months. Pelagic larvae (zoeae) spend several months in the water column feeding on phytoplankton and zooplankton. Field collections suggest larvae remain in the mixed layer (~upper 40 m) and migrate between 10 m and 40 m (Haynes, 1983; McMurray, Vogel, Fishman, Armstrong, & Jewett, 1986; Shirley & Shirley, 1987; Wainwright et al., 1991). After molting through the larval stages, red king crab zoeae metamorphose into the semi-benthic, non-feeding, post-larval (glaucothoe) stage and then settle and molt into the first juvenile benthic instar.

Virtually, all decapod crustacean species have specific habitat requirements during settlement, and early benthic phase king crabs have received much-focused research over the past several decades (see Stevens (2014a) for a review). Settling red king crab post-larvae and recently settled juveniles are thigmotactic, and their preference for structural complexity has been well documented in various laboratory, aquaculture, and field studies (Blau & Byersdorfer, 1994; Daly, Swingle, & Eckert, 2009; Dew, 1991; Loher & Armstrong, 2000; Pirtle & Stoner, 2010; Stevens, 2003). In the wild, early benthic phase red king crabs have been observed in association with complex habitats such as macroalgae, hydroids, polychaete tubes, bryozoans, shell hash, gravel, and cobble (see Stevens (2014a) for a review). Predation is probably the single most important factor influencing survival immediately following post-larval settlement; thus, complex structures with specific crevice spaces are needed to provide adequate refuge (Daly, Eckert, & White, 2013; Loher & Armstrong, 2000; Pirtle, Eckert, & Stoner, 2012; Stoner, 2009). A limited availability of complex habitat may create a survival bottleneck for settling post-larvae.

Larval advection has been explored using hydrodynamic and biophysical models for a range of species, which has yielded valuable insight into population dynamics (e.g., Stockhausen et al., 2019). In this study, our goal was to re-evaluate the endless-belt hypothesis in the context of climate variability. The importance of red king crab female spatial distribution, particularly in southwest Bristol Bay, for successful juvenile recruitment to the population is generally supported by studies using simpler modeling techniques than our current study (Loher (2014) and references therein). Although basic models can be informative, advancements in computer technology and modeling development allow for an improved investigation. Our hydrodynamic model builds on past model versions and allows for fine-scale (2-km) spatial resolution that can capture small-scale oceanographic features such as tides, eddy structures, fronts, and storm events. Many of these fine-scale features cannot be captured by long-term average flow, and larval advection trajectories may therefore be vastly different than what long-term average currents may suggest. We hypothesized that (a) because changes in temperature will affect growth of larvae along their advection trajectories, temperature will affect when and where settlement occurs, (b) changes in circulation patterns between warm and cold years will lead to differences in larval trajectories and, thus, in post-larval settlement areas, and (c) under present average conditions, larvae released from southwest Bristol Bay will be transported to southeast Bristol Bay along the Alaska Peninsula, while larvae released from central Bristol Bay will be transported to the northeast and northwest.

2 | MATERIAL AND METHODS

Our overall goal was to understand the spatial connection between red king crab larval release and post-larval settlement areas in Bristol Bay by modeling larval trajectories by (a) improving an existing hydrodynamic model (based on the Regional Ocean Modeling System, ROMS) and developing a finer-scale (2-km) horizontal resolution grid; (b) modifying an existing snow crab individual-based model (IBM) (Parada et al., 2010) for red king crab; and (c) running model simulations to develop larval trajectories and predict post-larval settlement locations (Daly et al., 2018).

2.1 | Grids

Several environmental grids were used in various components of this project (Daly et al., 2018) and will be described subsequently. Briefly, the study's hydrodynamic model was a spatially refined subset of a previously used ROMS grid (Hermann et al., 2013) and had an approximately 2-km horizontal resolution with 32 vertical layers. This spatially refined model was used to generate oceanographic current vectors (speed and direction), temperature, and salinity. The IBM was driven by the ROMS output, hence used the same grid spatial resolution. Estimates of ovigerous female red king crab distributions were obtained from the US National Oceanic and Atmospheric Administration's (NOAA), National Marine Fisheries Service (NMFS) eastern Bering Sea (EBS) bottom trawl survey that uses a grid with 37-km × 37-km squares (Lang et al., 2018); thus, the IBM initial conditions conformed to this spatial resolution. The study's habitat grid was based a regularized version of the ROMS grid with approximately 37-km resolution. The connectivity grid (map) was composed of polygons of irregular shape and size, which was used to test project hypotheses by calculating proportional connectivity or retention among grid areas. Spatial resolution of initial conditions and the habitat grid was based on NOAA EBS survey grid and the spatial density of the habitat data.

2.2 | Hydrodynamic model

We developed a 2-km horizontal resolution hydrodynamic model of the southeastern Bering Sea shelf, derived from an existing 10-km resolution hydrodynamic ROMS model of the entire Bering Sea (Hermann et al., 2013, 2016, 2019) (Figure S1). The 2-km model grid was centered on Bristol Bay, Alaska, USA, where the finer horizontal resolution relative to 10-km gridding substantially improved our resolution of coastal currents (and their interannual variability), as well as better-describing shelf currents and the seasonal retreat of the cold pool. As in the 10-km model, this new version included both ice and tidal dynamics. Additionally, we included estimates of coastal freshwater runoff (Kearney, 2019). Boundary conditions were derived from presently archived and newly generated 10-km model output. In hindcast mode, the 10-km model used global output from the NOAA Climate Forecast System Reanalysis (Saha et al., 2010) for its initial and boundary conditions. This effectively created a three-level (~50 → 10→2 km) nested downscaling of global conditions. Vertical resolution in the 2-km model was 32 layers. Further details on model structure are available in Daly et al. (2018). Because multiple, multidecadal runs of the 2-km model are computationally prohibitive, we focused on representative cold and warm years from the recent past, and a predicted warm, future year within the time span of 2030–2040 based on United Nations Intergovernmental Panel on Climate Change (IPCC) projected conditions (CMIP3, CMIP5; IPCC, 2014).

We chose years for analyses based, in part, on the physical oceanographic conditions measured during the EBS bottom trawl survey, which has been conducted by NOAA scientists since 1975. Sampling stations are regularly spaced over an approximately 37-km × 37-km grid and sampled every year, primarily in June–July each year. The survey provides a robust data set spanning over four decades with extensive abundance and distribution data for immature and mature red king crabs. We chose ROMS simulations from 1999 and 2005 as representative cold and warm years from the recent past, respectively, to contrast environmental conditions in the biophysical model. We chose year 2037 from the CMIP5 projection of the MIROC global model (Watanabe et al., 2011) as the driver for the ROMS forecast simulations, as it was predicted to be a relatively warm year under emission scenario rcp8.5. 2005 was warmer than 1999, and 2037 is projected to be considerably warmer than either 1999 or 2005 (Daly et al., 2018, Figure S2).

2.3 | Habitat map

Because of the acknowledged importance of habitat quality for successful settlement of red king crab post-larvae (Stevens, 2014b), we assembled a spatial database of suitable habitat locations in the EBS, with a focus on Bristol Bay. This was mapped in order to post-process IBM results: We designated which particles (post-larvae) survived based on the habitat into which they settled (see glaucothoe settlement behavior below).

Data for the habitat map were divided into abiotic (sediments, rocks, and shells) and biological (epibenthos) categories using various data sources including published and unpublished digital data, paper data sheets, and cruise logbooks (Figures S3, S4, S5, S6, S7, S8, and S9). We created a grid for the habitat information that represented a regularized version of the ROMS grid with cell size of 37 km × 37 km because the habitat data could not be resolved at the circulation model's finely divided (2 km × 2 km) scale. Each sample location in the habitat database was classified as either good habitat (if gravel >50%, shells, rocks, or appropriate biogenic materials were found; n = 10,320) or bad habitat (if no appropriate habitat was found; n = 40,331). Each location in the habitat database was assigned to a cell of the habitat grid, and each cell was then classified as good habitat or bad habitat (Figure 2). Cells containing both good and bad habitat were classified as good habitat, while cells in the grid containing no samples were classified as unknown habitat (Figure 2).

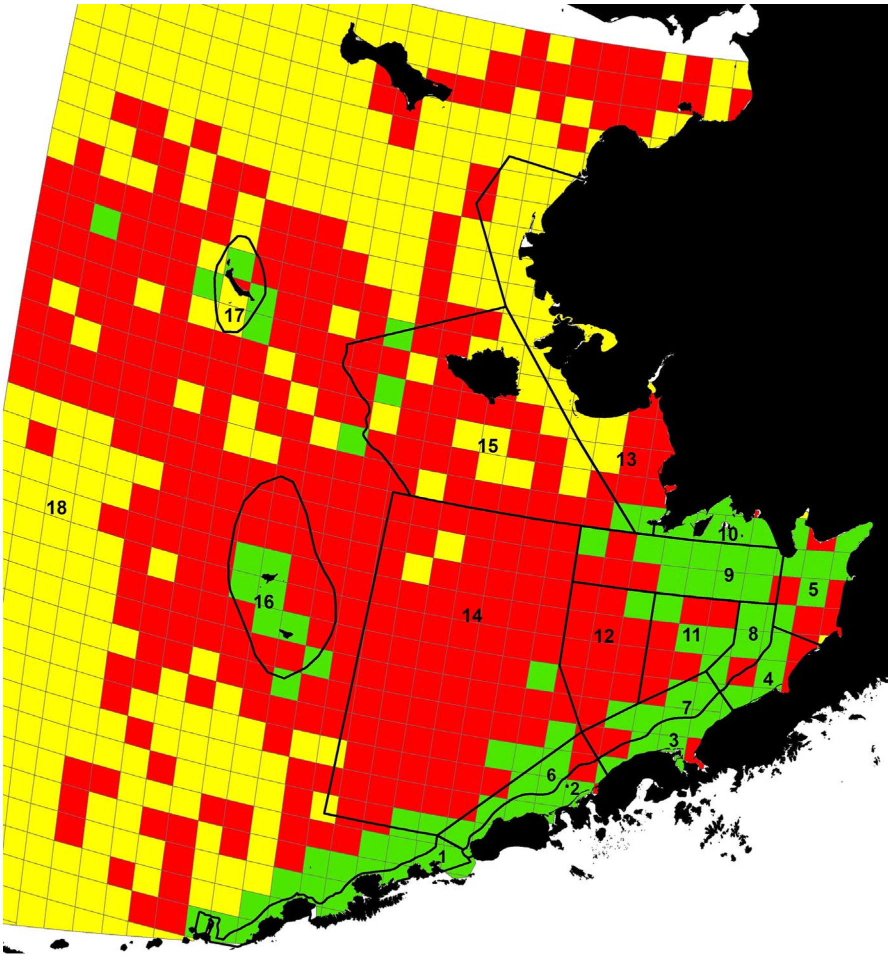
2.4 | Biological model

We modified an existing snow crab (*Chionoecetes opilio*) IBM (Parada et al., 2010) to represent the appropriate biology for red king crab. The biophysical model (ROMS model coupled to an IBM) used was a modified version of the Ichthyop modeling tool (Lett et al., 2008) and was adapted to the Bering Sea system. The Ichthyop tool is designed to study the effects of physical and biological factors on ichthyoplankton dynamics. Salinity, temperature, sea level, and current fields obtained from ROMS were used to force the red king crab IBM over the same time frame and spatial resolution as the physical model. The biology of the early life history stages of red king crab from larval release to settlement was represented through the following mechanisms or processes: larval abundance at release, spatial distribution of larvae at release, hatching time, vertical movement, growth, horizontal movement, post-larval settlement rules, and settlement habitat availability (i.e., initial benthic mortality).

2.5 | Larval abundance and spatial distribution at release

The spatial location of larval release was configured for two conditions: realistic and hypothetical initial conditions. Realistic initial

FIGURE 2 Connectivity and habitat maps, combined, that were used in the current red king crab (*Paralithodes camtschaticus*) larval advection study. Green cells indicate good habitat for settling red king crab post-larvae, red cells indicate bad habitat (i.e., where samples were taken but no good habitat was found), and yellow cells indicate unknown habitat (i.e., where no samples were taken). Connectivity zone names are as follows: 1 = Aleutians; 2 = nearshore Unimak; 3 = nearshore Port Moller; 4 = nearshore Port Heiden; 5 = Nushagak; 6 = offshore Unimak; 7 = offshore Port Moller; 8 = offshore Port Heiden; 9 = northern Bristol Bay; 10 = Togiak; 11 = east-central Bristol Bay; 12 = west-central Bristol Bay; 13 = Newenham; 14 = western Bristol Bay; 15 = Nunivak; 16 = Pribilof Islands; 17 = Saint Matthew Island; and 18 = eastern Bering Sea shelf [Colour figure can be viewed at wileyonlinelibrary.com]



conditions were based on abundance estimates of mature females as estimated from the NOAA-NMFS EBS bottom trawl survey (Lang et al., 2018). Fecundity increases with crab size (Swiney, Long, Eckert, & Kruse, 2012); thus, the number of larvae released was estimated using:

$$F = m\mathrm{CL} + b,$$

where F is the fecundity in number of embryos, CL is the carapace length of the spawning female in millimeters, m is the slope, and b is the intercept. Split-point model parameters (Swiney et al., 2012) were applied to estimated pre-molt size (Stevens & Swiney, 2007a) of all benthic females in the population by trawl survey station. Because the total estimated number of larvae released in Bristol Bay was on the order of trillions, a smaller number (20,000) of super-individuals (Scheffer, Baveco, DeAngelis, Rose, & van Nes, 1995) were released in the advection model and thereafter tracked. A total of 20,000 particles (super-individuals) per simulation (i.e., modeled year/month) were divided among grid cells based on the proportion of total female fecundity within a given grid cell (Figure 3). Given that mature female spatial distribution cannot be known for 2037 but that this is predicted to be a warm year, we used the 2005 initial spatial distribution as a proxy for 2037 (Figure 3) and categorized 2037 as "realistic" because it used the real 2005 distributions. Hypothetical initial conditions were generated to explore the importance of spawning areas of historical interest (zones 2—nearshore Unimak; 5—Nushagak; 6—offshore Unimak; and 10—Togiak; see Figures 2 and 3) that were not present in the realistic-initial-conditions simulation years.

2.6 | Hatch timing

Generally, embryonic development and hatch timing of red king crab larvae are dependent on temperature, wherein later hatch timing is likely a result of cold temperatures delaying embryonic development (Shirley et al., 1989; Stevens, Swiney, & Buck, 2008; Chilton et al., 2010). Precise estimates of annual hatch timing in Bristol Bay are not possible with existing data; however, proportions of females with eyed embryos (i.e., extruded the previous year) versus newly extruded embryos at the time of survey can be obtained (Chilton et al., 2010). Considering that primiparous female red king crabs extrude eggs up to 26 days earlier and hatch larvae 12–16 days earlier than multiparous females (Stevens & Swiney, 2007b), we modeled hatching as occurring on April 15, May 15, and June 15 of each simulation year, as coarse-level temporal approximations to explore population-level variability in hatch timing.

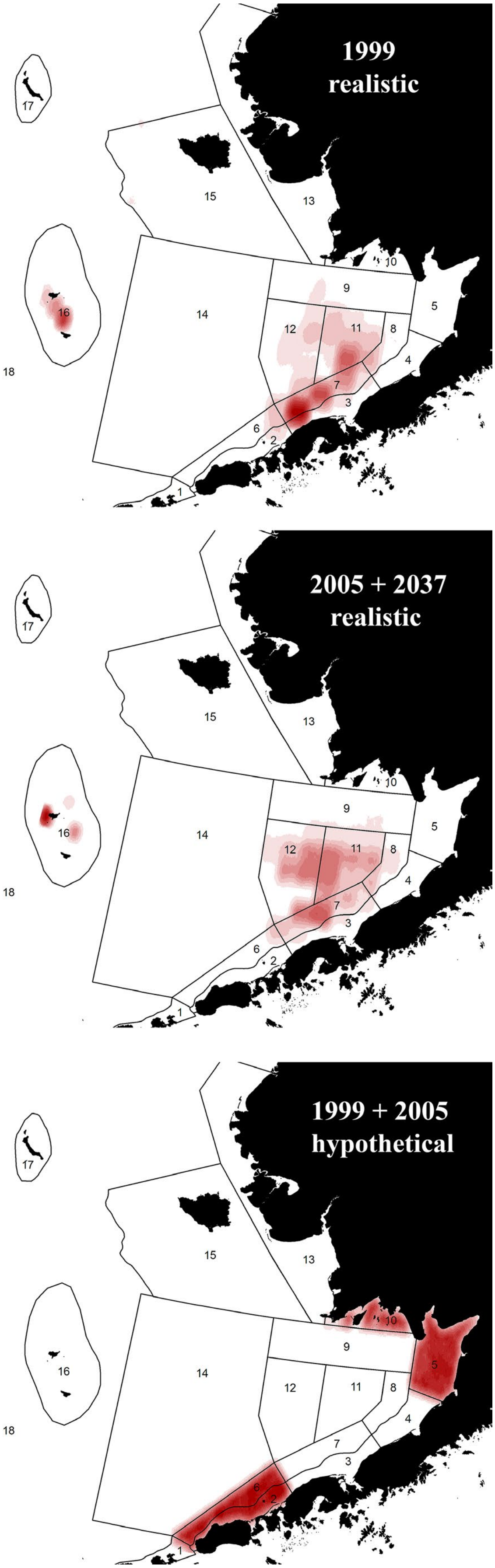


FIGURE 3 Initial conditions (i.e., hatch locations) of 20,000 super-individuals used for red king crab (*Paralithodes camtschaticus*) larval advection simulations. Realistic initial conditions were based on fecundity estimates of ovigerous females captured in US National Marine Fisheries Service eastern Bering Sea (EBS) bottom trawl surveys, while hypothetical initial conditions represent areas of interest given historical adult female distributions. Initial conditions were the same for each April, May, and June release within each year and real/hypothetical scenario. The shade of red indicates relative particle density (darker shades correspond to higher densities) [Colour figure can be viewed at wileyonlinelibrary.com]

2.7 | Vertical movement

Little information exists regarding the position of king crab larvae in the water column; however, some information shows that densities vary with depth over a 24-hr cycle (Takeuchi, 1962; Haynes, 1983; Wolotira et al., 1984; Armstrong et al., 1986; McMurray et al., 1986; Shirley & Shirley, 1987; Wainwright et al., 1991). It is unknown whether red king crab larvae actively vertically migrate in a manner that influences their horizontal migration, or which environmental cues may initiate their behavioral response to alter their depth (e.g., light cycle, tidal phase). Positive phototaxis has been demonstrated for red king crab zoeae in the laboratory using point source light (Epelbaum, Borisov, & Kovatcheva, 2007; Shirley & Shirley, 1987, 1988). However, more recent studies determined that negative phototaxis occurs for some species of brachyuran crab at low light intensities following light acclimation, and it is believed that positive phototaxis from some historical studies using narrow chambers has been a laboratory artifact (Epifanio & Cohen, 2016). Field collections of red king crab larvae suggest a diurnal influence, yet the timing is contradictory: In Bristol Bay, larvae are most abundant in shallower waters during the night and deeper waters during the day (McMurray et al., 1986; Takeuchi, 1962; Wainwright et al., 1991), whereas the opposite has been demonstrated in Kodiak waters (Wolotira et al., 1984) and in southeast Alaska (Shirley & Shirley, 1987). Because of uncertainty around vertical behaviors, we conducted a preliminary sensitivity analysis and compared four behavioral scenarios in the IBM: (a) diel vertical migration (DVM; shallower at night than during daylight), (b) reverse diel vertical migration (RDVM; shallower during daylight), (c) random walk, and (d) passive drifters (Lagrangian) (Figure S10). The extent and direction of the advection of particles in the sensitivity analysis varied with behavior; however, differences were not large and the broad-scale horizontal distribution patterns were similar for all simulated behaviors (Figure S11). This result suggests that predicted advection trajectories are fairly robust to differences in behavior, and is supported by other studies (Loher, 2001). Because sparse evidence suggests DVM is more common in wild red king crab larvae (McMurray et al., 1986; Takeuchi, 1962; Wainwright et al., 1991), and due to the fact sensitivity analyses comparing DVM to RDVM yielded relatively similar trajectories, we used DVM in the final IBM, reported subsequently.

We made the following DVM assumptions in the IBM: (a) Larvae remain in the mixed layer (upper 40 m) and migrate between 10 m and 40 m, (b) larvae maintain their vertical position until the onset of sunrise and sunset, (c) swimming and sinking rates are equal for all zoeal stages, and (d) larval behavior is coupled with local vertical velocities where net upward or downward movement was defined as the vertical current field plus the swimming (or sinking) speed 0.75 cm/s. Active swimming ascent rates of 1.50 cm/s (for zoeal stages 1–3) and passive sinking rates of 0.75 cm/s (for zoeal stages 1–2) have been shown in laboratory studies (Shirley & Shirley, 1988). Field data, although limited, suggest much slower rates, but likely underestimate speed because of low temporal resolution of samples (Wolotira et al., 1984; McMurray et al., 1986; Shirley & Shirley, 1987; Wainwright et al., 1991). We defined two migration periods each day as occurring over a period of 1 hr after sunrise and 1 hr after sunset. During those migration periods, larvae ascended constantly at one half of the maximum speed (i.e., at 0.75 cm/s), representing their assumed average speed if larval swimming speed accelerated constantly from 0 to the maximum of 1.50 cm/s over that one-hour period. Larvae descended at a constant sinking rate of 0.75 cm/sec. Thus, all migration speeds regardless of direction (up or down) were 0.75 cm/s. Net upward or downward movement was defined as the vertical current field plus the swimming (or sinking) speed 0.75 cm/s.

2.8 | Larval growth

Larvae went through four pelagic zoeal stages, which ended at the settling post-larval (glaucothoe) stage (Marukawa, 1933). We assumed that larvae were released at the sea floor and rose toward the ocean surface and that larvae settled upon reaching the glaucothoe stage based on settlement rules implemented below. We modeled temperature-dependent growth as a function of sea surface temperature where the duration of each zoeal stage was modeled after Nakanishi (1987):

$$\ln(D) = m - b\ln(T),$$

where D is intermolt duration (days), T is temperature (°C), m is the slope, and b is the intercept.

2.9 | Horizontal movement

Horizontal larval trajectories were followed using the Euler tracking algorithm via Ichthyop version 3.1 as a platform (Lett et al., 2008). Velocities of particles in every time step were calculated as:

$$\frac{\mathrm{dxp}}{\mathrm{dt}} = u_{\mathrm{water}}$$

$$\frac{\mathrm{dyp}}{\mathrm{dt}} = v_{\mathrm{water}}$$

where u_{water} and v_{water} are the east–west and north–south velocity components, respectively, of the ROMS model. The position of particles at a given time was approximated with an Eulerian forward solution where x and y are the two-dimensional positions of the particles at time t and x_{t+1} and y_{t+1} are positions of particles at time t + 1.

$$x_{t+1} = x_t + u_{\mathrm{water}}\,\mathrm{dt}$$

$$y_{t+1} = y_t + v_{\mathrm{water}}\,\mathrm{dt}$$

2.10 | Post-larval settlement

The post-larval (glaucothoe) stage lasts several weeks (Marukawa, 1933), but the timing of settlement during that period is unclear. Laboratory studies suggest most settlement to the substrate occurs within the first several days after metamorphosis, but can be delayed when exposed to suboptimal habitat (Stevens, 2003; Stevens & Kittaka, 1998) and allows potential for additional dispersal. We made the following assumptions regarding the glaucothoe stage and settlement consistent with laboratory observations (Stevens, 2003; Stevens & Kittaka, 1998): (a) Swimming speeds will be as described for zoeae, (b) successful settlement will occur if glaucothoe reach favorable habitat at the time of metamorphosis, (c) glaucothoe that are not above favorable habitat at the time of metamorphosis will ascend to the next vertical layer during daylight hours, and settle on the bottom during hours of darkness, (d) glaucothoe will extend their pelagic duration for up to 14 days if favorable habitat is not encountered at the time of metamorphosis, and (e) glaucothoe that have not reached favorable settlement habitat within 14 days will die. Surviving post-larvae are individuals that reach good habitat within the model domain. No other mortality sources were implemented.

2.11 | Connectivity map

IBM output consisted of larval ("particle") spatial trajectories from starting locations to settlement locations predicted by the model. We used a connectivity map to quantify rates of connectivity and retention between and among regions (Figure 2) and to test underlying hypotheses. We defined nearshore zones in Bristol Bay along the northern shore of the Alaska Peninsula and subdivided central Bristol Bay to evaluate regional-scale processes. Connectivity indices consisted of the proportion of modeled particles from a given release area that were transported to (or retained within) a given settlement zone based on the simulated larval advection trajectories.

3 | RESULTS

3.1 | Oceanographic variability

In simulations for both 1999 and 2005, flow toward Bristol Bay was weak to non-existent in April and May, and especially weak in 2005. Only later in the year did substantial northeastward flows develop along the coast between Unimak Pass and Bristol Bay. The lack of continuous flow from Unimak to Bristol Bay during spring was surprising, as it contradicted our initial expectations of climatological flows in the region. While the model's salt bias on the outer shelf and Unimak Pass may be a contributing factor (Hermann et al., 2016), this result may be largely driven by wind forcing. In 2005, spring winds were southwestward, hence diminishing any existing northeastward flow toward Bristol Bay. It is unlikely that substantial northeastward surface flows would be present along the northern side of the Aleutian chain under these conditions. Interestingly, projected along-shore transport toward Bristol Bay in 2037 was enhanced in April, May, and June.

3.2 | General settlement patterns

Environmental conditions affected predicted red king crab larval advection trajectories through complex interactions with the oceanographic current structure and pelagic duration. Our IBM results show complex advection trajectories with large-scale intra- and interannual variability with some common trends (Figure 4). Generally, modeled larvae experienced warmer temperatures in 2005 and 2037 compared to 1999 and experienced increasingly warmer temperatures at later hatch dates within each year (Figure 5). Intermolt duration declined with later hatch due to warmer seasonal temperature. The intra- and interannual differences in growth patterns affected horizontal transport (i.e., straight-line distance between release and

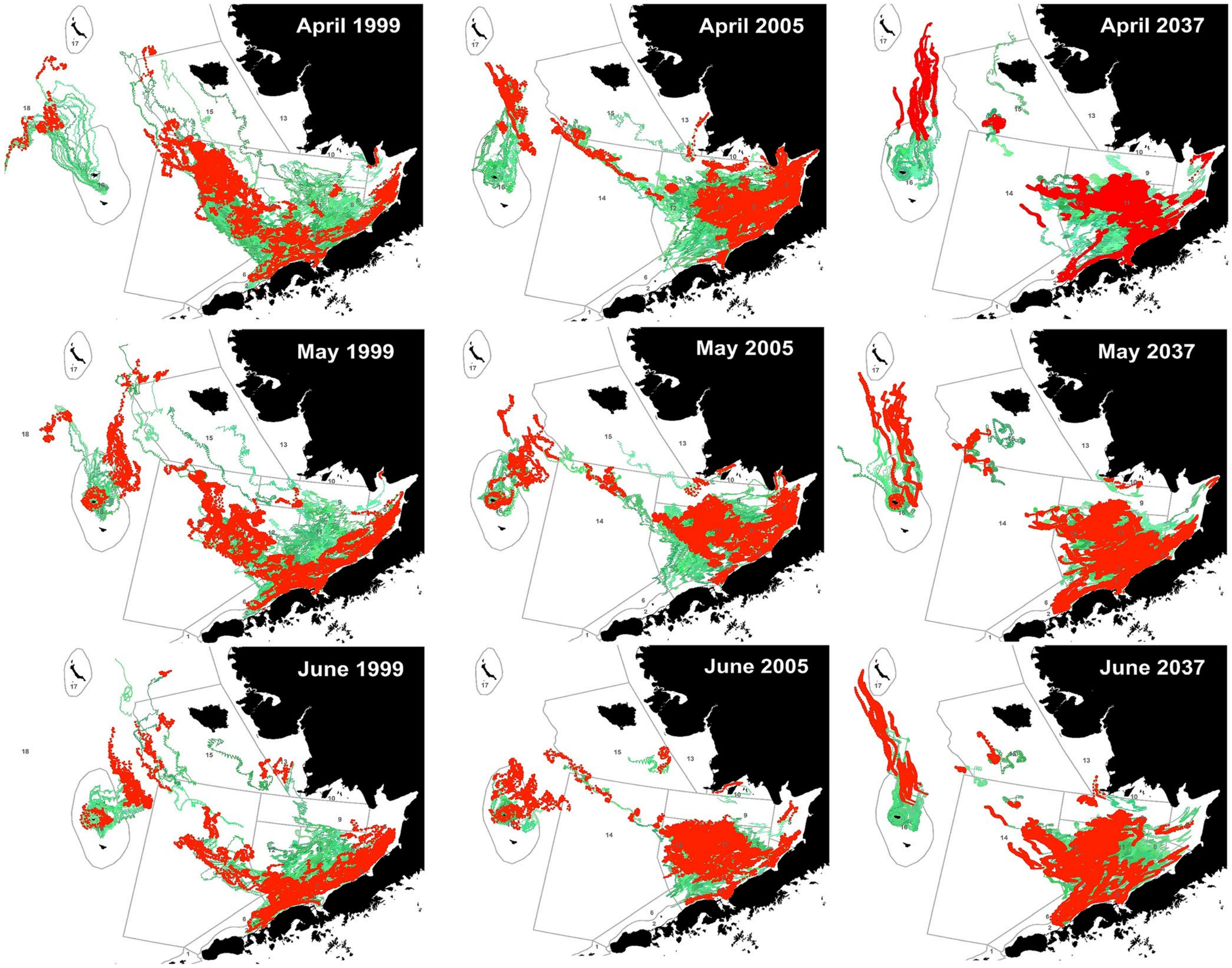


FIGURE 4 Advection trajectories for modeled red king crab (*Paralithodes camtschaticus*) larvae based on ***realistic*** initial release distributions when released into simulated currents during April, May, and June of 1999, 2005, and 2037. Green lines represent individual larval trajectories where red indicates the post-larval settlement stage. For visual purposes, we show every 100th particle of the total 20,000 super-individuals for each month/year simulation [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 5 Box plot of mean temperature experienced by simulated red king crab (*Paralithodes camtschaticus*) larvae along advection trajectories in Bristol Bay, Alaska, USA. The bottom and top (i.e., separated by the bold horizontal line) of each box are their lower and upper quartiles, respectively, the band near the middle of the box is the 50th percentile (the median), and the extreme lines ("whiskers") indicate the highest and lowest values excluding outliers (i.e., 1.5*the interquartile range)

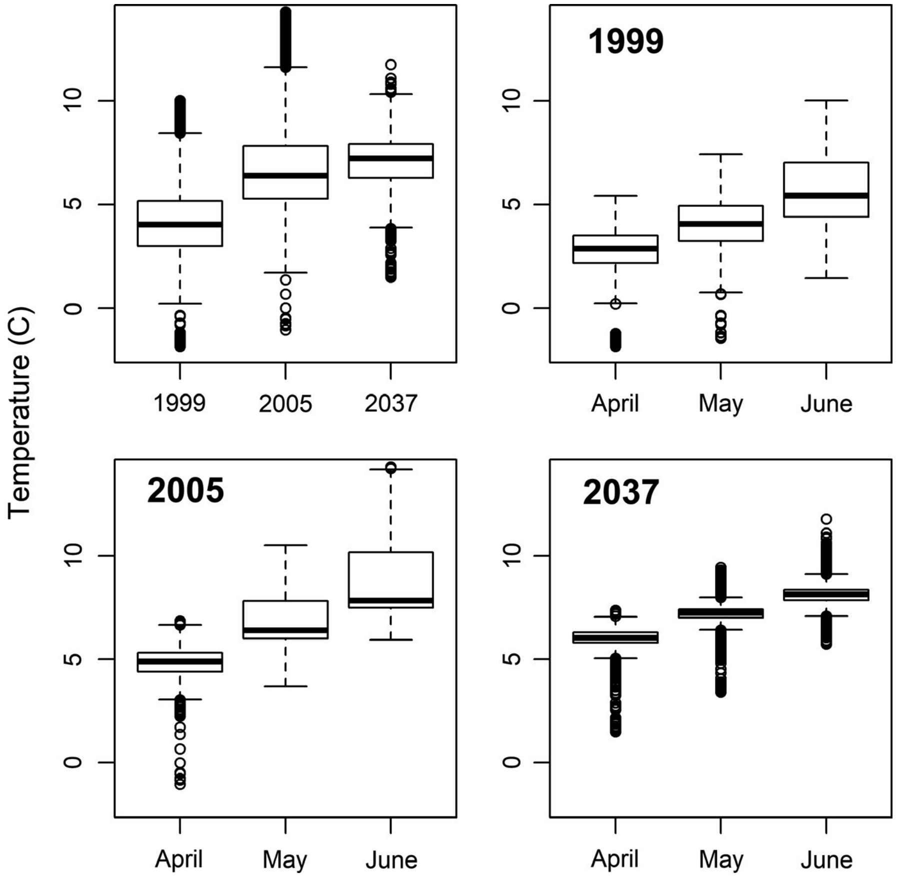
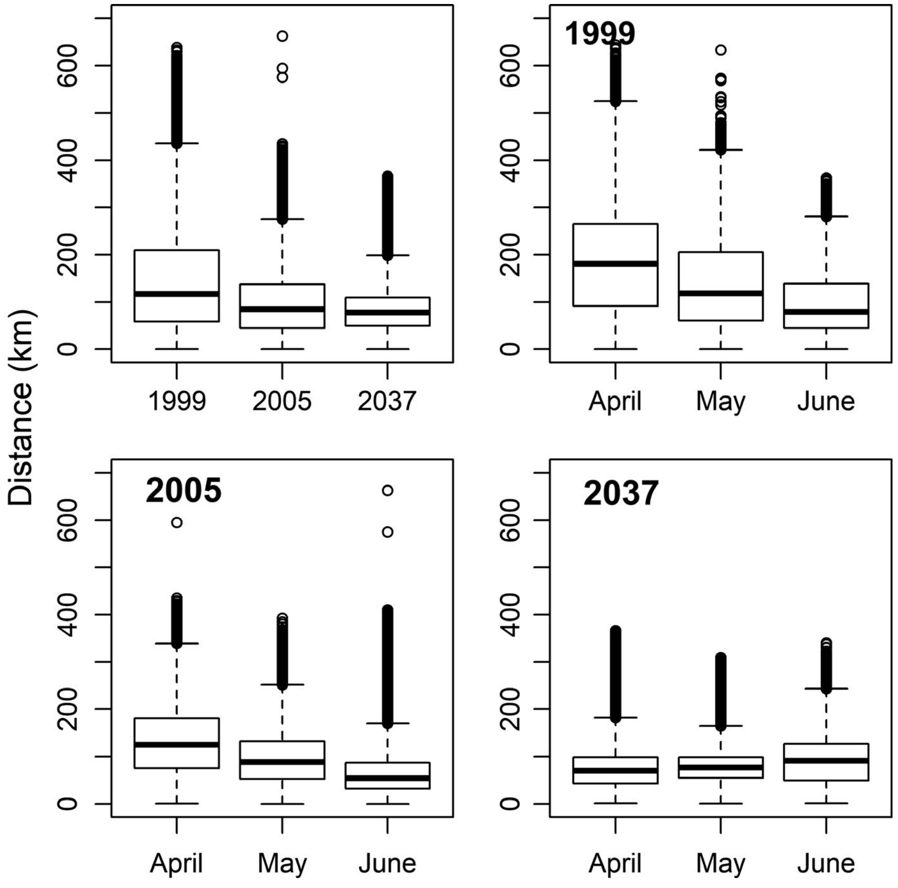


FIGURE 6 Box plot of mean horizontal displacement (km) traveled by modeled red king crab (*Paralithodes camtschaticus*) larvae released into simulated currents in Bristol Bay, Alaska, USA. Distance was calculated as the horizontal (straight-line) distance between the location of release, and the location where an individual reached the glaucothoe (settling) stage, regardless of whether those individuals reached suitable habitat. The bottom and top (i.e., separated by the bold horizontal line) of each box are their lower and upper quartiles, respectively, the band near the middle of the box is the 50th percentile (the median), and the extreme lines ("whiskers") indicate the highest and lowest values excluding outliers (i.e., 1.5*the interquartile range)



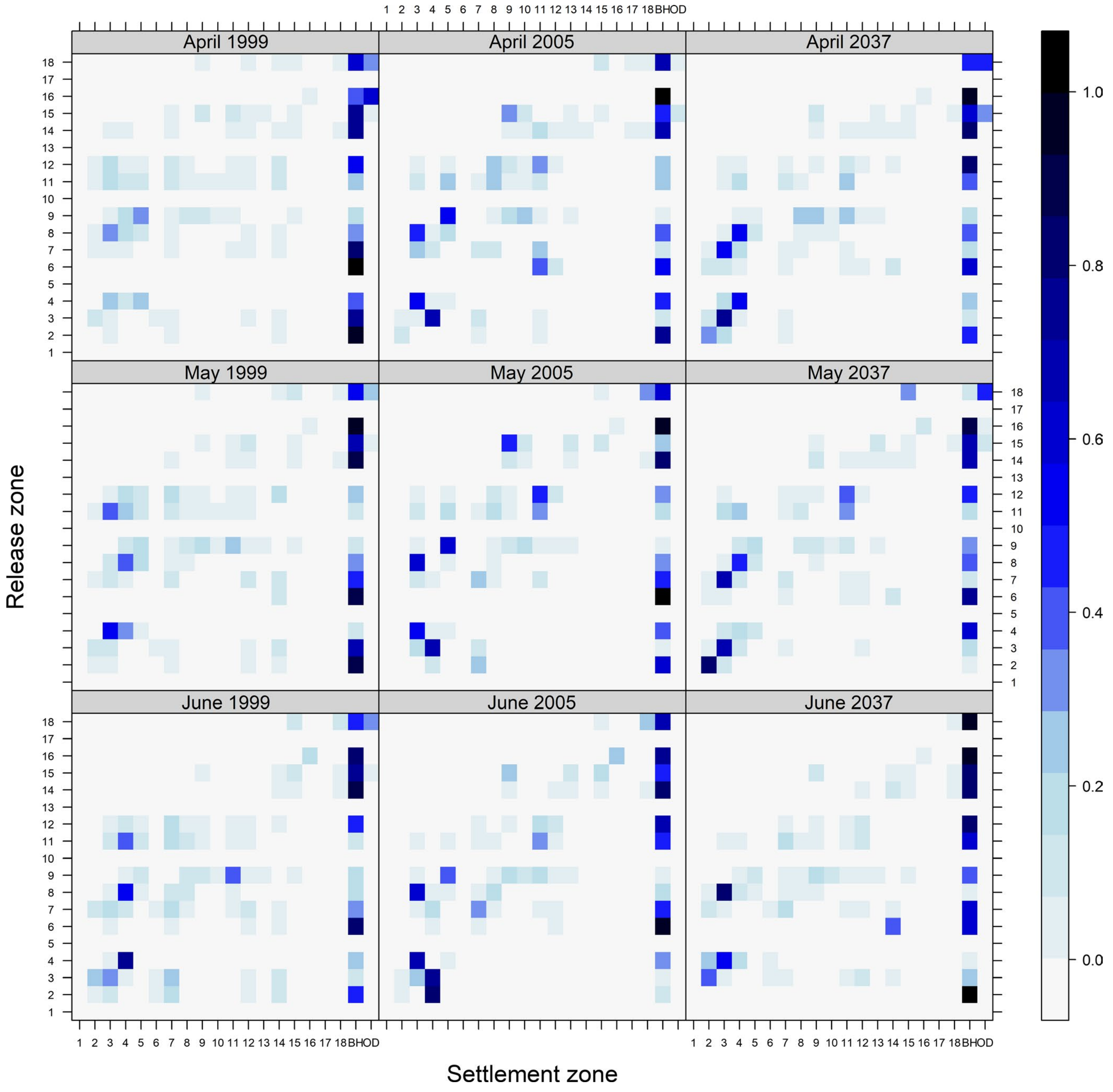


FIGURE 7 Connectivity matrix for modeled red king crab (*Paralithodes camtschaticus*) larvae released into simulated currents in Bristol Bay, Alaska, USA, during April, May, and June of 1999, 2005, and 2037 using ***realistic*** initial release distributions based on the distribution of ovigerous females from US National Marine Fisheries Service eastern Bering Sea (EBS) bottom trawl surveys. Colors indicate the proportion of modeled red king crab larvae reaching settlement zones by release zone, where light blue corresponds to low proportions and dark blue represents high proportions. Connectivity zone names (see also Figure 2) are as follows: 1 = Aleutians; 2 = nearshore Unimak; 3 = nearshore Port Moller; 4 = nearshore Port Heiden; 5 = Nushagak; 6 = offshore Unimak; 7 = offshore Port Moller; 8 = offshore Port Heiden; 9 = northern Bristol Bay; 10 = Togiak; 11 = east-central Bristol Bay; 12 = west-central Bristol Bay; 13 = Newenham; 14 = western Bristol Bay; 15 = Nunivak; 16 = Pribilof Islands; 17 = Saint Matthew Island; and 18 = eastern Bering Sea shelf. The “BH” (bad habitat) column indicates larvae that died due to a failure to find good habitat, while the “OD” (out of domain) column indicates larvae that were advected out of the study domain [Colour figure can be viewed at wileyonlinelibrary.com]

settlement, as opposed to distance traveled along the trajectory) of larvae because the onset of the settling post-larval stage occurred sooner (by 7–18 days). This temperature-driven reduction of the pelagic stage duration generally corresponded to reduced horizontal displacement, with the exception of 2037, the latter perhaps due to enhanced along-shore transport in April, May, and June of 2037. Overall, larvae had greater horizontal transport in 1999 than in 2005 and 2037, as well as reduced transport with later hatch timing (Figure 6). Horizontal transport varied by release area with larvae traveling the farthest when released from western Bristol Bay and

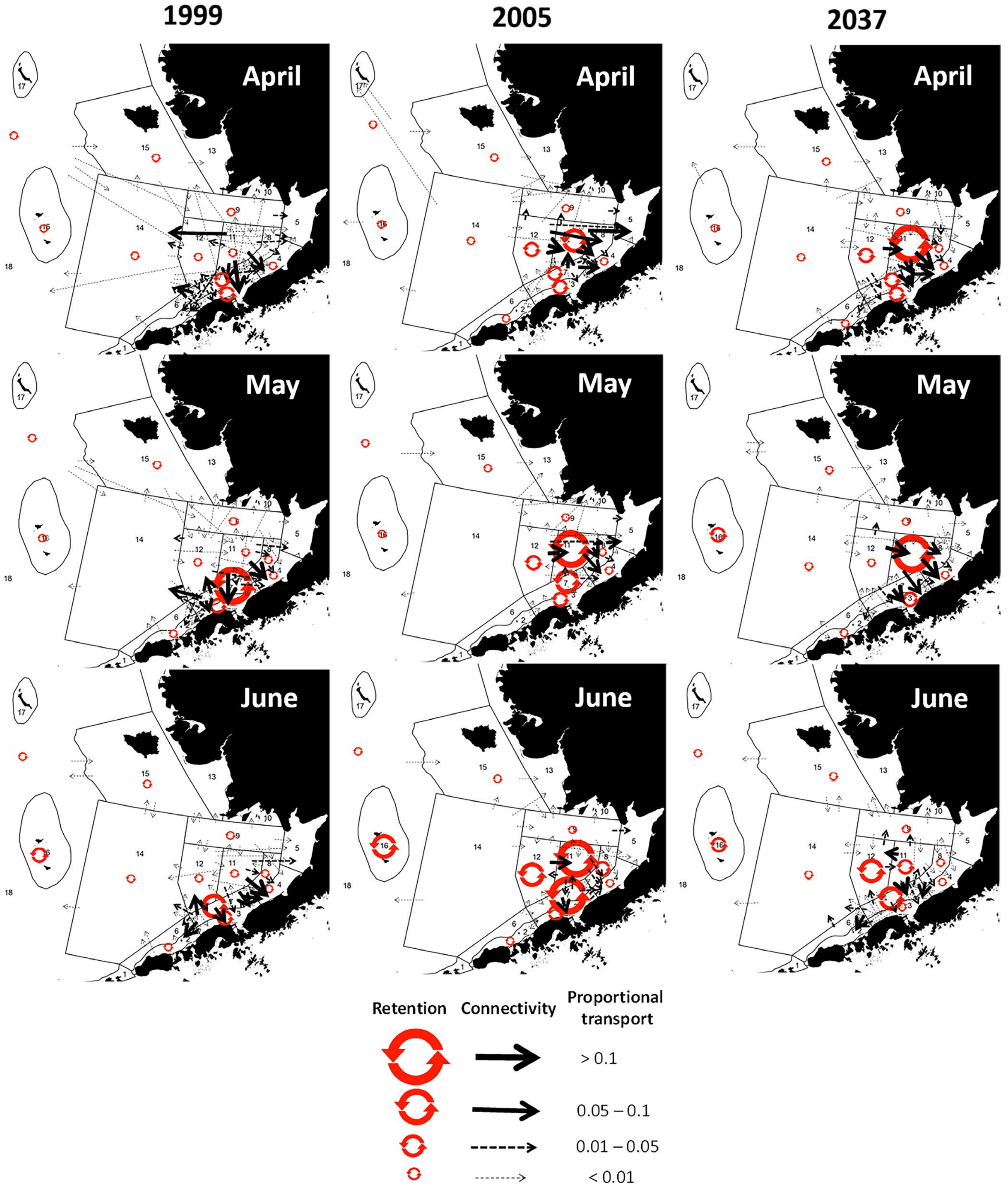


FIGURE 8 Connectivity maps for modeled red king crab (*Paralithodes camtschaticus*) larvae released into simulated currents in Bristol Bay, Alaska, USA, during April, May, and June of 1999, 2005, and 2037. The size of the arrows and circles corresponds to the proportion of total larvae that successfully reached settlement habitat in each year and month. Simulations shown here used ***realistic*** initial release distributions based on US National Marine Fisheries Service eastern Bering Sea (EBS) bottom trawl survey data for ovigerous females [Colour figure can be viewed at wileyonlinelibrary.com]

around the Pribilof Islands (zones 2—nearshore Unimak; 6—offshore Unimak; 14—western Bristol Bay; 15—Nunivak; 16—Pribilof Islands; 18—eastern Bering Sea shelf), while particles released in inner and central Bristol Bay generally did not travel as far. The highest proportion of dead particles (i.e., failing to reach good habitat) were released from the western zones including the area around Unimak Island.

3.3 | Connectivity and retention

Intra- and interannual variability in connectivity and retention occurred (Figures 7-9). Because temperature largely drives pelagic duration, and thus, horizontal distance traveled, retention generally increased with increasing temperature such that 1999 had the lowest

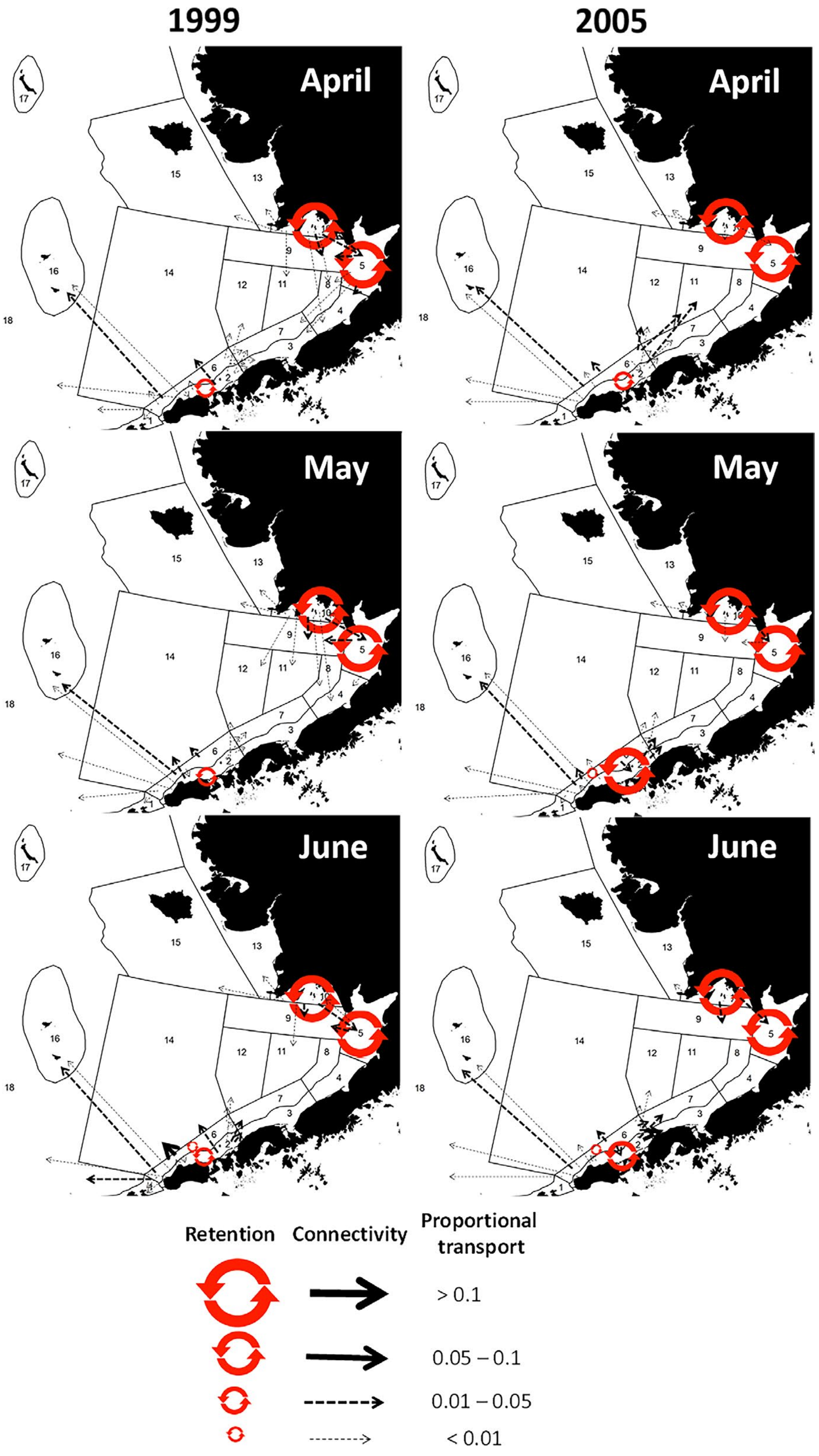


FIGURE 9 Connectivity maps for modeled red king crab (*Paralithodes camtschaticus*) larvae released into simulated currents in Bristol Bay, Alaska, USA, during April, May, and June of 1999 and 2005. The size of the arrows and circles corresponds to the proportion of total larvae that successfully reached settlement habitat in each year and month. Simulations shown here used ***hypothetical*** initial release distributions representing areas of interest given historical adult female distributions [Colour figure can be viewed at wileyonlinelibrary.com]

predicted rates of retention, and 2037 had highest rates of retention. In 1999, the proportion of particles reaching good habitat increased with later hatch date, whereas highest settlement in 2005 occurred for larvae that hatched during April. In 2005 and 2037, high retention occurred in east-central Bristol Bay (zone 11) and nearshore, with strong transport from the central Bristol Bay zones to the nearshore zones, and these patterns were strongest in warmer conditions. Particles released from western Bristol Bay (zones 2—nearshore Unimak; 6—offshore Unimak; and 14—western Bristol Bay), around Nunivak (zone 15), and around the Pribilof Islands (zone 16) had the lowest chance of reaching good settlement habitat (Figure S12). In all three years examined, particles released from contemporary spatial distributions including central Bristol Bay and the nearshore area surrounding Port Moller were capable of reaching good settlement habitat, including the Unimak area (zones 2—nearshore Unimak; and 6—offshore Unimak). Particles released from the Unimak area (hypothetical initial conditions: zones 2—nearshore Unimak; and 6—offshore Unimak) in 1999 were mostly advected offshore (Figure 10) with low successful settlement, whereas moderate-to-high nearshore retention occurred in 2005 for larvae that were released

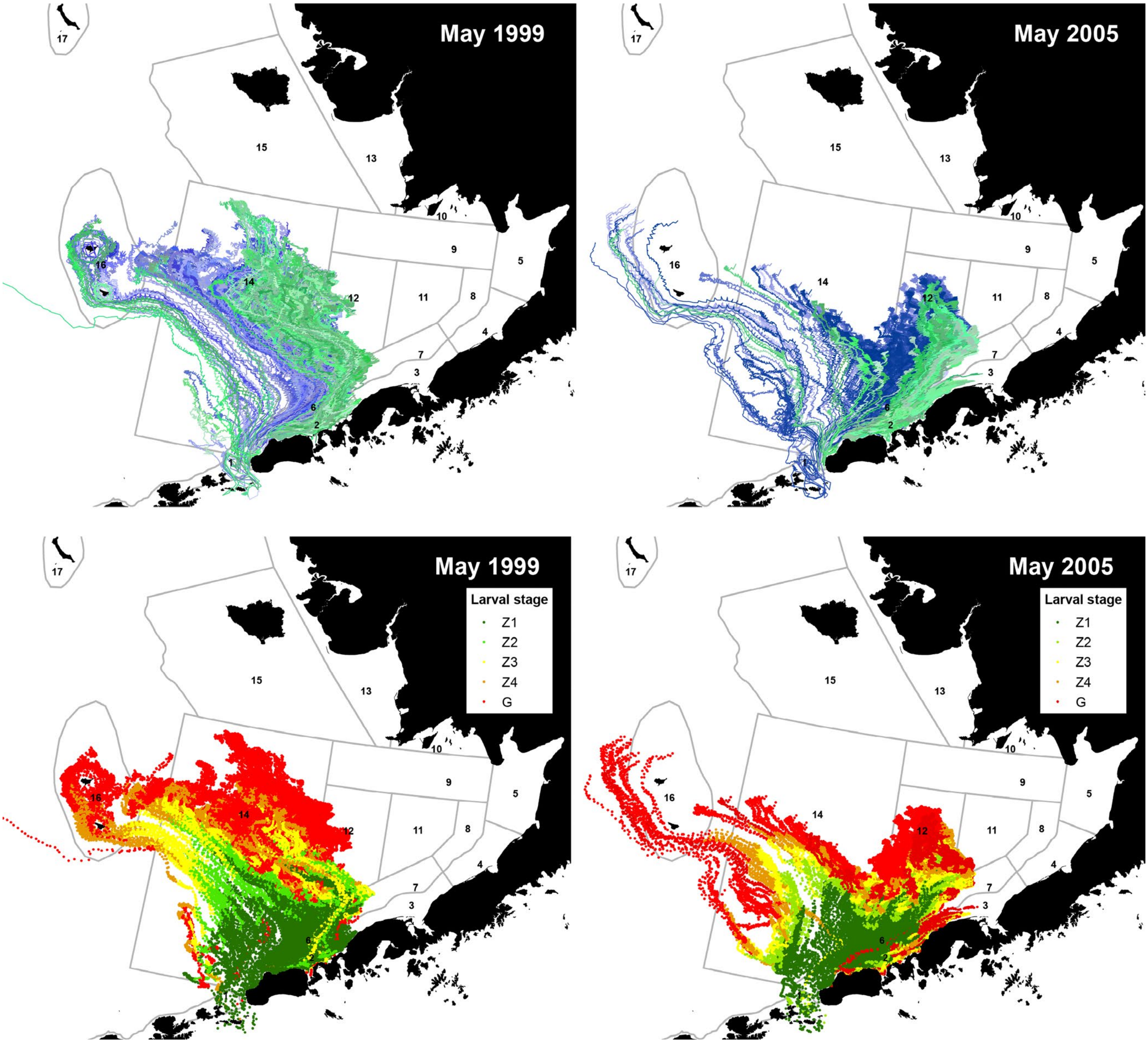


FIGURE 10 Transport of modeled red king crab (*Paralithodes camtschaticus*) larvae released into simulated currents from nearshore Unimak using ***hypothetical*** initial release distributions during 1999 and 2005. Here, we show May releases as examples of varying trajectory patterns between years and depict every twentieth modeled larvae to assist visualization of individual trajectories. The top panels indicate trajectories in zone 2 (green lines) and zone 6 (blue lines). The bottom panels indicate larval stage along trajectories using an 8-hr time step where dark green corresponds to Z1 larvae and red corresponds to settling post-larvae. Modeled larvae depicted here are not filtered by habitat-mediated mortality [Colour figure can be viewed at wileyonlinelibrary.com]

during May and June. Within the nearshore Unimak area (zone 2), most successful nearshore settlement occurred when particles were released between mid-Unimak and the Black Hills, whereas particles released from the western end of Unimak Island were mostly advected offshore along the 100-m isobath (Figure 11). Particles released from Bristol Bay could reach the Pribilof Islands (zone 16), but only if released from the Unimak area (zones 2—nearshore Unimak; and 6—offshore Unimak in hypothetical initial conditions; Figure 10).

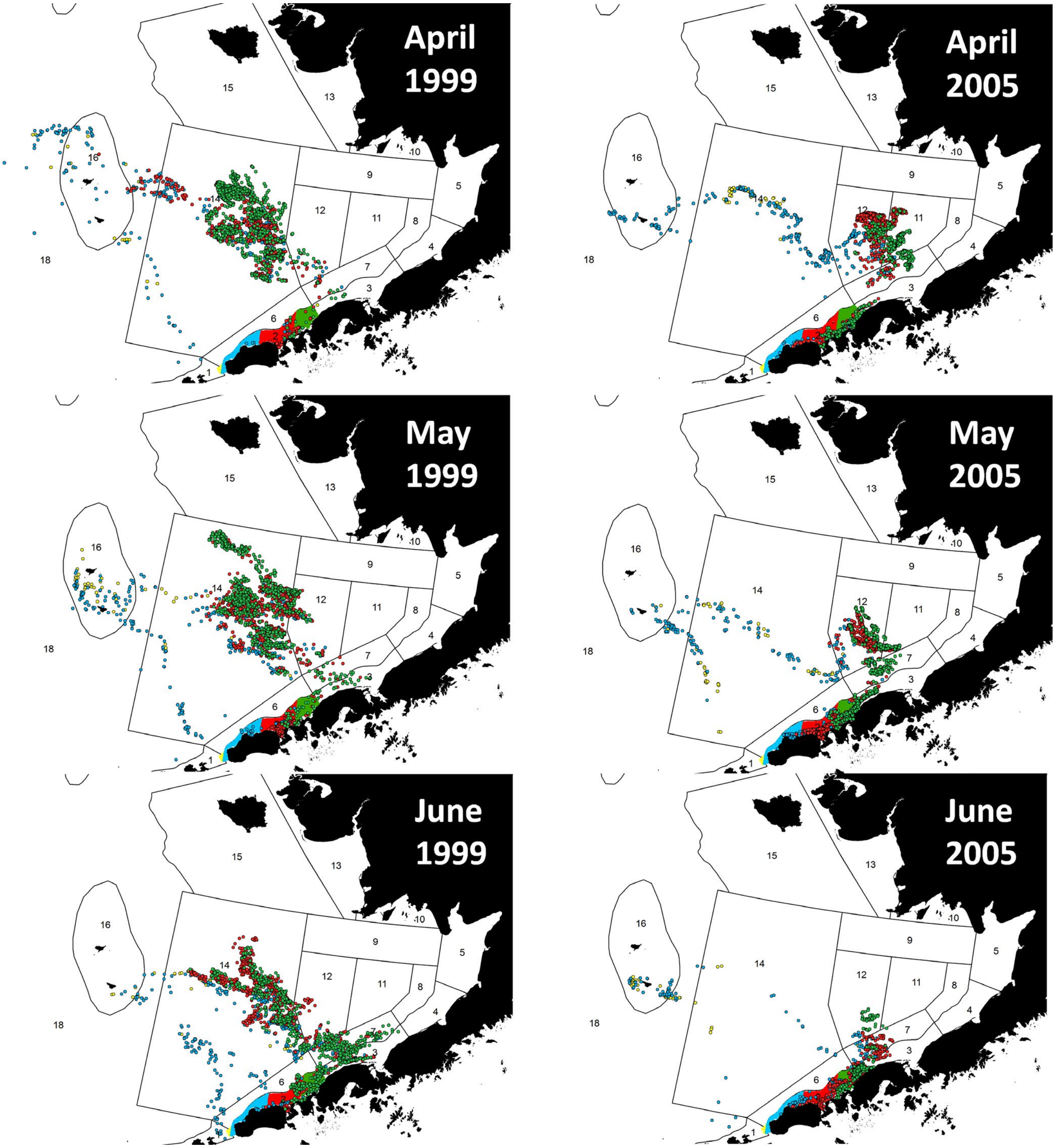


FIGURE 11 Transport of modeled red king crab (*Paralithodes camtschaticus*) larvae released into simulated currents from nearshore Unimak (zone 2) using ***hypothetical*** initial release distributions during April, May, and June of 1999 and 2005. Zone 2 was subdivided by degree of longitude to explore advection patterns on a finer spatial scale. Sub-zones are indicated by color, where the color of the dots indicates settlement locations and corresponds to release areas of the same color polygon. Particles shown here were not filtered by settlement success via habitat quality [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Settlement success

Successful settlement varied by release zone. Generally, particles released in east-central Bristol Bay had higher settlement rates than those in western Bristol Bay, particularly from nearshore Unimak (zones 2—nearshore Unimak; and 6—offshore Unimak; Figure S13). Successful settlement rates increased with distance between Unimak Pass and the release location, and this trend was more pronounced in 1999 compared to 2005 (Figures 11 and 12). Virtual settlement sinks were located predominantly in east-central Bristol Bay and in nearshore zones around Port Moller and Port Heiden. Western Bristol Bay (zone 14) was a virtual sink in 1999, but only in the very small portion of the zone where good habitat was located (Figures S14 and S15), and the ability of larvae to reach this area was likely a result of the extended larval duration. Because successful settlement was affected solely by habitat availability in our study, it is not surprising that virtual sinks correspond with areas of good habitat. While particles released in 1999 were generally advected farther, nearshore settlement was observed in part due to the initial release locations: Ovigerous females were more aggregated, particularly in zones 7—offshore Port Moller, and 11—east-central Bristol Bay. In contrast, ovigerous female distribution was more diffuse in 2005 and modeled similarly for 2037. Thus, coupled with shorter larval duration, female distribution patterns likely explain settlement in east-central Bristol Bay zones in 2005 and 2037. However, particles released in April and May 2037 also displayed nearshore settlement in zones 3—nearshore Port Moller; and 4—nearshore Port Heiden, due to a more pronounced shoreward current structure and reduced pelagic larval duration. Highest simulated settlement rates occurred in April and May, which are more likely to have represented peak hatch timing in 1999 and 2005 than would the June simulations. In 1999, approximately 50% of ovigerous females captured in the NOAA EBS bottom trawl survey contained unhatched embryos by June 12, and in 2005, nearly all ovigerous females had hatched their larvae by June 20, suggesting that most of the hatching had occurred prior to mid-June.

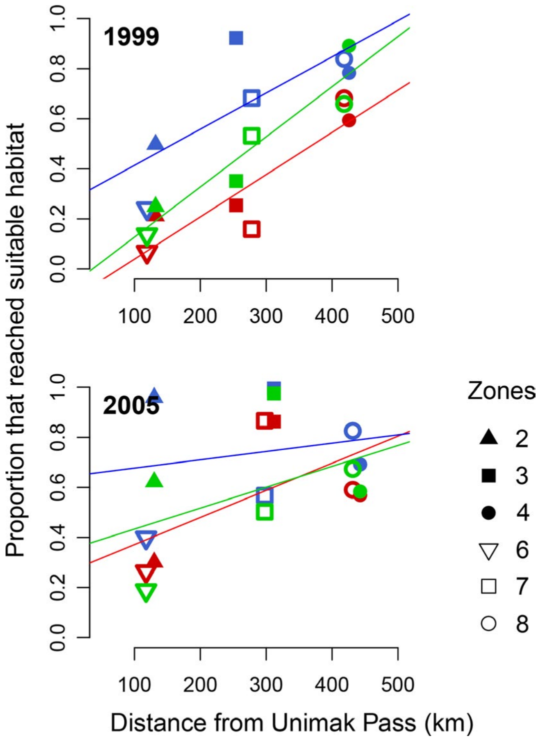


FIGURE 12 Proportion of modeled red king crab (*Paralithodes camtschaticus*) larvae released into simulated currents that successfully reached suitable settlement habitat by distance (km) between hatch location and Unimak Pass using ***hypothetical*** initial release distributions. Data points (shapes) represent release zones (see also Figure 2) as follows: 2—nearshore Unimak; 3—nearshore Port Moller; 4—nearshore Port Heiden; 6—offshore Unimak; 7—offshore Port Moller; and 8—offshore Port Heiden by year and month. Colors correspond to release months, where red indicates April, green indicates May, and blue indicates June. Lines indicate linear regression [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our results contradict the theory that broodstock in southwest Bristol Bay are needed to supply recruits to coastal nurseries as part of an endless-belt reproductive strategy. We suggest that contemporary spatial distributions of ovigerous females are capable of supplying settlement-competent larvae to the north shore of the Alaska Peninsula in both cold and warm environmental conditions. Previous studies (Armstrong et al., 1993; Evans et al., 2012; Haynes, 1974; Hsu, 1987; Loher, 2001; McMurray et al., 1986) hypothesized that central Bristol Bay may be relatively poor spawning habitat compared to historical adult distributions on the basis of being advectively decoupled from suitable settlement habitat and that the present geographic broodstock distribution is therefore "evolutionarily counterintuitive" (Loher, 2001). Our modeling results suggest that, for all years that were simulated, high retention nearshore along the Alaska Peninsula and in parts of central Bristol Bay, and advection to those regions from other source locations, occurred. Settlement success for larvae released from the nearshore Unimak area (zone 2) was predicted to be lower than expected, as many particles were advected to the northwest away from good settlement habitat in Bristol Bay. Nearshore retention around Unimak Island occurred in warm conditions, yet we expected to see more pronounced advection to the northeast via nearshore currents. Surprisingly, our simulations show advection to the south from central Bristol Bay occurs across a range of temperature conditions.

Why do past advection studies support the importance of southwest Bristol Bay as the populations most important spawning ground? Previous larval transport modeling work has lacked the ability to replicate smaller-scale oceanographic processes and focused on broad-scale current patterns that suggest relatively linear west-to-east advection along the northern Alaska Peninsula and relatively little mean directional advection seaward of the 50-m isobath (reviewed by Loher, 2014). The ability of contemporary high-resolution models to capture small-scale oceanographic features affects the nature of simulated particle trajectories. Our 2-km ROMS model operates at one of the finest spatial resolutions to date for the eastern Bering Sea and captures intra- and interannual variability in features such as coastal currents, shelf currents, seasonal retreat of the cold pool, sea ice, tides, storm events, and freshwater runoff in ways that prior models could not. These fine-scale features likely affect local current vectors such that overall advection trajectories differ from those that are forced by long-term average currents. Contrary to our expectations, simulations showed lack of spring nearshore flow from Unimak Pass into Bristol Bay, which may be due to southwestward winds diminishing any existing northeastward flow. Discrepancies between long-term average current patterns and simulated horizontal transport are not unprecedented. Systems with complex flow regimes and spatially heterogeneous habitat often have lower than expected dispersal distances and high rates of local retention. Pedersen, Nilssen, Jorgensen, and Slagstad (2006) demonstrated this on the northern coast of Norway, where some simulated red king crab larval advection trajectories differed from regional long-term circulation patterns, possibly due to wind-driven forcing. Similarly, simulations of lobster (*Homarus americanus*) larval advection in the Gulf of Maine, USA, displayed transport against the prevailing direction of the coastal current system and smaller overall horizontal displacement than the currents might suggest (Incze et al., 2010).

Local retention and shorter regional connections may be more important for Bristol Bay red king crab population dynamics than once thought. In our simulations, successfully settled post-larvae generally originated either within a given connectivity zone (i.e., were retained) or within one to two immediately adjacent zones. As stated above, this was partly due to water temperature: Warmer conditions caused a shorter pelagic duration, reduced horizontal transport, and increased retention rates. It should be noted that actual hatching would have likely occurred later in 1999 (June) and earlier in 2005 (April) (Stevens et al., 2008). Simulated larvae, when hatched in these months, experienced similar temperatures (~5°C, Figure 5) with comparable mean horizontal displacement (~100 km, Figure 6), which could dampen any differences caused by overall temperature change. Yet, dispersal may not be affected by pelagic duration in areas with strong recirculation patterns. In contrast, where currents are largely advective, nuances of hatch location and timing may be more influential. Current structure bifurcates to the north of Unimak Pass, where some flow continues to the northwest toward the Pribilof Islands along the 100-m isobath and some flow turns to the northeast along the Alaska Peninsula. Simulated particles that were released using the "hypothetical" initial release locations around western Unimak Island were largely influenced by the northwestward, not the eastward flow. In fact, settlement success improved as distance between larval source location and Unimak Pass increased, which may be a function of a reduced impact of the northwestward flow fields. Some field studies support this observation. Recently hatched red king crab larvae have been observed in high densities near Unimak Pass and Port Moller, with the distribution near the Port Moller area shifting to the east and farther toward the head of Bristol Bay as the season progressed, while seasonal progression of observed larvae near Unimak Island inferred a northwest drift trajectory (Haynes, 1974). This aligns with our observation of diverging current structures and offshore transport from the Unimak area, with optimal hatching grounds farther northeast, toward the Black Hills–Port Moller area and into central Bristol Bay. Within the Unimak nearshore area (zone 2), a greater number of particles were delivered to nearshore habitat if released from the eastern portion of the zone (164°W to 162°W: approximately mid-Unimak Island to the Black Hills). While our simulations suggest lower larval delivery rates from this region to coastal Alaska Peninsula than we had hypothesized, one cannot ignore the possibility that the current structure in the 1970s may have better facilitated coastal advection than the years that we investigated.

In addition to interannual variability that may not have been captured due to the limited number of years that we were able to simulate, larval behavior could also have a substantial and unknown impact on horizontal displacement (Kunze, Morgan, & Lwiza, 2013; Miller & Morgan, 2013; Queiroga & Blanton, 2005). Red king crab larvae exhibit swimming behavior via positive phototaxis and rheotaxis in laboratory conditions (Shirley & Shirley, 1987, 1988), but how these behaviors operate in the field to affect transport is unclear. Our sensitivity analysis (Appendix S1) showed relatively small differences in advection trajectories between diel vertical migration, reverse diel vertical migration, and random walk behaviors; however, this result was based on weekly averaged ROMS output from a previous study. Because of this, the sensitivity analysis was not as robust to impacts of diel behaviors than if hourly averages were used, making it difficult to compare differences in horizontal displacement among larval behaviors operating on a 24-hr cycle. In most studies, vertically stratified collections were conducted over a single 24-hr period (McMurray et al., 1986; Wainwright et al., 1991) making it unclear what environmental cues caused the observed depth distributions. Simulated larval trajectories could also differ greatly if larvae used tides for directed transport, as documented for other species (i.e., *Callinectes sapidus*, Forward, Tankersley, & Welch, 2003). Tidal-stream transport would likely have a more pronounced effect on larval delivery than diel vertical migration because larvae alter depth in response to current strength and direction to focus transport (or retention) in a targeted direction. There is no published evidence that red king crab larvae alter their depth distribution to make use of tides via selective tidal-stream transport, but this remains relatively unstudied in the species. Still, red king crab larvae likely remain in the mixed layer where tidal cues may be less pronounced than near the benthos. In the absence of correspondence between tidal periodicity and diel migration, the end result of tidal advection may be minimal in the Bristol Bay region due to the elliptical nature of tidal currents in the region (Pearson, Mojfeld, & Tripp, 1981) that would be expected to result in little net directional transport over the long periods associated with full larval development. Rather, diel vertical migration may have more influence on advection by varying the amount of time that larvae are subjected to wind-driven surface currents, especially as day length varies over the course of the larval rearing season. Cues for larval red king crab vertical depth distribution and the potential role of tidal transport warrant future study.

Population structure is a subject of ongoing debate for EBS crabs, and recent research has focused on examining whether populations are isolated versus a component of a larger metapopulation, with either persistent or transient connectivity between core and satellite populations. For example, simulated larval trajectories suggest that the EBS Tanner crab stock consists of a metapopulation composed of multiple subunits that are connected via variable dispersal rates, and the Bristol Bay component is quasi-isolated relying heavily on local retention for the supply of recruits (Richar et al., 2015). Similar analyses suggest the existence of asymmetrically connected subsystems for EBS snow crab with larval transport predominantly occurring from the southeast to the northwest section of the eastern Bering Sea middle domain (Parada et al., 2010). The Pribilof Islands blue king crab population shows a lack of connectivity to the Saint Matthew Island population via simulated larval trajectories (C. Parada, unpublished data), and this result has some support by genetic analyses (Stoutamore, 2014). Our simulations suggest that ovigerous red king crabs can supply recruits to areas outside of the Bristol Bay management area. Particles released from the western Unimak area were delivered to the Pribilof Islands in 1999 and 2005 simulations, which suggests that ovigerous female red king crabs observed in the Unimak area in the late 1970s could have seeded the Pribilof Islands. Assuming a lag of 6–10 years between hatching and maturity, the increase in mature Pribilof Islands red king crab abundance in the late 1980s may be attributed, in part, to the presence of ovigerous females in southwest Bristol Bay. Larvae released from regions other than the western Unimak area did not reach the Pribilof Islands in the current study, suggesting disconnection of the Pribilof Islands from the present-day Bristol Bay red king crab population.

The potential for future environmental change to affect red king crab populations is uncertain (Armstrong et al., 2010). A range of factors associated with predicted global climate change such as temperature increases, ocean acidification, range expansions of competing or predatory species, and broodstock spatial shifts may play a role in future population dynamics of Bristol Bay red king crab. Warm oceanographic conditions may allow for favorable red king crab advection trajectories within Bristol Bay, but future broodstock spatial distribution is unknown. It is unclear why the Bristol Bay red king crab population underwent a spatial shift in the late 1970s (Armstrong et al., 1993; Loher & Armstrong, 2005). One theory suggests spatially explicit mortality from increased trawling north of Unimak either decimated that portion of the broodstock and/or has prevented it from returning in subsequent cold years (Dew & McConnaughey, 2005), while others attribute redistribution to environmental change. A well-documented regime shift occurred in the North Pacific Ocean in 1976/77 that was characterized, in part, by an increase in water temperature. The extent of the Bering Sea cold pool fluctuates with environmental conditions and alters spatial distribution of many species (Mueter & Litzow, 2008). Loher and Armstrong (2005) hypothesized that changes in bottom temperature caused the spatial shift in mature female red king crabs via preferred temperature ranges, and Orensanz, Ernst, Armstrong, Stabeno, and Livingston (2005) proposed a similar hypothesis for shifts in snow crab spatial distribution. Yet, the role of cold pool extent on red king crab spatial distribution is uncertain because it is difficult to test whether changes in spatial distribution are a direct response to temperature. If ovigerous females avoid water that is cold enough to delay embryogenesis during brooding (Stone, O'Clair, & Shirley, 1992), then one might expect to see mature females in southwestern Bristol Bay in cold years when the cold pool extends to the Alaska Peninsula. Why, then, has broodstock been absent from the Unimak area since the 1970s? The answer may be related to the temporal scale of temperature changes. Single or a few consecutive cold years may not be adequate to initiate the large-scale spatial migrations required to reach the Unimak area. If spatial distribution is linked to an optimal thermal range, it is unsurprising that individuals spread rapidly to the northeast in concert with the retraction of the cold pool extent in the late 1970s. In 1999, mature female distribution was encompassed by the cold pool and was slightly more aggregated toward the Alaska Peninsula compared to 2005; however, it is unclear whether this is directly related to temperature. To avoid the cold pool in 1999, ovigerous females would have been forced laterally along the shore of the Alaska Peninsula to western Bristol Bay. Perhaps the temporal scale at which temperature fluctuations operate must extend to the order of decades (i.e., a regime shift), where sustained periods of cold temperatures (i.e., a reduction in the spatial extent of suitable habitat) are needed to for reestablishment in southwest Bristol Bay. That is, if water temperature is a key environmental feature structuring distribution, the population may be more resistant to redistribution to the southwest than to the northeast, especially if spatially explicit bycatch mortality is at play in southwest Bristol Bay (Dew & McConnaughey, 2005) and larval transport from central to southwest Bristol Bay is limited. Predicted warm conditions in 2037 simulations allowed for high retention and nearshore advection in favorable habitat, but we used 2005 initial spatial conditions. The spatial distribution of ovigerous females in future years may shift dramatically. Predicted global warming could cause cold-adapted species such as red king crab to undergo large-scale spatial migrations. A significant shift northward may hinder southerly larval transport to areas in central Bristol Bay or nearshore along the Alaska Peninsula, a phenomenon similar to the "environmental ratchet hypothesis" described for Bering Sea snow crab (Orensanz et al., 2005). Other factors associated with future oceanographic conditions will interact to affect larval advection trajectories and affect future recruitment success for Bristol Bay red king crab. For example, increases in atmospheric and oceanographic CO_2 since the Industrial Revolution are well documented (Feely et al., 2004), and associated reductions of pH levels may lead to decreases in red king crab survival during the larval stages (Long, Swiney, & Foy, 2013).

As with all modeling studies, caution should be used when interpreting our results. In the wild, larval mortality is likely high, variable, and from multiple sources. For example, red king crab larvae must begin feeding within 3 days of hatching or survival decreases dramatically (Paul & Paul, 1980); thus, physical conditions in the Bering Sea could cause a temporal or spatial mismatch with prey fields (Hunt et al., 2002; Stabeno, Bond, Kachel, Salo, & Schumacher, 2001) resulting in low survival rates. We were primarily interested in investigating spatial patterns of relative larval delivery that would be expected to remain robust over a range total mortality, if that mortality lacks a strong spatial component. However, spatial mortality patterns could fundamentally alter the final distribution of larval settlement relative to the results reported herein. Additional limitations of our analysis include our limited understanding of larval behavior, likely overestimation estimation of good red king crab habitat, and ignoring effects of starvation and predation. Dispersal distances are generally overestimated for passively dispersed organisms with long pelagic duration (Shanks, 2009) implying that larval behavior can modulate horizontal displacement. While the best available information supports diel vertical migration of red king crab larvae, its use in our model may be oversimplified or wrong. The difference in spatial resolution between that of available benthic samples and the model's habitat grid may have caused an overestimation of good red king crab settlement habitat. In the North American lobster (*Homarus americanus*), it has been suggested that total recruitment may be a function of the amount of crevice space that is available to cryptic juvenile stages (Wahle & Steneck, 1991). If a similar process governs the survival of early benthic phase red king crab (Loher & Armstrong, 2000), it may be necessary to more precisely define the amount of suitable habitat that exists within each settlement zone to determine their relative numerical potential to generate recruits.

Difficulty in defining underlying physical and biological processes that influence larval supply and survival to the juvenile stages is ubiquitous for crabs and lobsters and, as a result, significant stock–recruit relationships are rare (Wahle, 2003). The Bristol Bay red king crab stock–recruit relationship has some density-dependent effects, but recruitment trends are consistent with decadal climate shifts (Zheng & Kruse, 2003), suggesting the importance of environmental factors (Zheng & Kruse, 2006; Zheng & Siddeek, 2018). While our results fall short of having the ability to predict future recruitment, our study helps inform the role of environmental variability on larval transport and provides a context within which to structure future investigations of larval and juvenile distribution. Ultimately, modeling exercises represent refined hypotheses that should be followed by in situ validation studies designed to test their predictions. In the case of Bristol Bay red king crab, an ideal scenario would be to conduct regularly gridded larval sampling throughout the region predicted by modeling to encompass the current population's larval pool, at intervals throughout the pelagic development period, and compare observed larval densities with model-predicted values. This would be followed by benthic sampling to establish relationships between overlying larval supply and realized settlement densities, to quantify threshold larval abundances that are required to seed—or oversupply—nursery habitat, thus allowing for model-predicted particle densities arriving at settlement sites to be placed into an ecological context. Finally, predictions about future recruitment must consider how other factors such as physiological tolerances to fluctuating abiotic conditions and large-scale ecosystem reorganization will interact to affect larval advection trajectories and affect future recruitment success. As our understanding of underlying recruitment mechanisms evolves, we will improve the assessment and overall conservation of Bristol Bay red king crab and other Bering Sea crab stocks.

ACKNOWLEDGEMENTS

This research was made possible by funding from the North Pacific Research Board, Project # 1402. We thank Robert McConnaughey for providing data that were used in developing the habitat map and Robert Foy for providing NOAA crab survey data and insight during the early stages of the project. We also thank Arny Blanchard, Carla Moore, and Bradley Stevens for assistance in accessing historical Bristol Bay data used to develop the habitat map.

CONFLICT OF INTERESTS

The authors state that there are no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

The listed authors have made substantial contributions to project conception and design, model simulations, and interpretation of simulation results. Benjamin Daly compiled and drafted the manuscript, while all other authors contributed sections of text and reviewed it critically.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at: https://search.dataone.org/view/10.24431/rw1k44p
https://search.dataone.org/view/10.24431/rw1k44q
https://search.dataone.org/view/10.24431/rw1k44r

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Daly B, Parada C, Loher T, Hinckley S, Hermann AJ, Armstrong D. Red king crab larval advection in Bristol Bay: Implications for recruitment variability. *Fish Oceanogr*. 2020;29:505–525. https://doi.org/10.1111/fog.12492