frontiers in Marine Science

ORIGINAL RESEARCH
published: 15 May 2018
doi: 10.3389/fmars.2018.00161

Nearshore Larval Retention and Cross-Shelf Migration of Benthic Crustaceans at an Upwelling Center

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Planktonic larvae are thought to be very susceptible to offshore advection in upwelling regimes, increasing dispersal and decreasing recruitment. However, larvae of 42 species of nearshore benthic crustaceans primarily developed on the inner shelf at locations both in (98.5%) and away (99.8%) from a perennial upwelling center in the upwelling season of a recruitment-limited region characterized by persistent, strong, upwelling. During three cross-shelf cruises conducted at each location, larvae of 21 species remained on the inner shelf at both sites by occurring beneath seaward-flowing surface currents while larvae of other species migrated to midshelf (four species) or offshore (14 species) by initially developing near the surface. Postlarvae apparently returned to shore either deep in landward-flowing upwelled water or near the surface where behavior allows them to be transported shoreward by internal waves, diel wind cycles or wind relaxation events. Thus, recruitment limitation in upwelling regimes does not appear to be caused by larval mortality from offshore transport, requiring new research directions to advance our understanding of population dynamics, structure and connectivity.

Keywords: larval transport, behavior, population connectivity, recruitment limitation, upwelling

OPEN ACCESS

Edited by:
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Gorka Bidegain, University of Southern Mississippi, United States

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Specialty section:
This article was submitted to Marine Ecosystem Ecology, a section of the journal Frontiers in Marine Science

Received: *24 January 2018*
Accepted: *23 April 2018*
Published: *15 May 2018*

Citation:
Morgan SG, Miller SH, Robart MJ and Largier JL (2018) Nearshore Larval Retention and Cross-Shelf Migration of Benthic Crustaceans at an Upwelling Center. Front. Mar. Sci. 5:161. doi: 10.3389/fmars.2018.00161

INTRODUCTION

Variation in larval recruitment often determines population and community dynamics in the sea. Both larval dispersal and mortality have been challenging to measure rendering estimates of population connectivity uncertain. Moreover, the ability of larvae to regulate transport could have a large impact on dispersal and population connectivity and has been debated for decades. We recently determined that larvae occurred close to shore in persistent, strong upwelling on the Pacific Coast of the USA—rather than lost offshore as was widely expected (Morgan et al., 2009b,c, 2011; Morgan and Fisher, 2010; Fisher et al., 2014; Hameed et al., 2018)—and that larval mortality in the nearshore retention zone was much lower than previous estimates of larval mortality anywhere (White et al., 2014). We then demonstrated that larval behaviors enabling larvae to remain close to shore throughout development also enable them to settle near natal populations (Drake et al., 2013; Hameed et al., 2016). We now investigate whether larvae also completed larval development close to shore at one of the strongest upwelling centers further reducing the scale of population connectivity.

On the west coasts of continents, strong wind and Coriolis generate seaward-flowing surface currents (Ekman transport) dropping sea level along the coast while upwelling deep, cold water (Hickey, 1998). It has been suggested that larvae of nearshore species are lost to offshore transport

by persistent, strong upwelling conditions (Parrish et al., 1981; Roughgarden et al., 1988; Menge and Menge, 2013), especially at the apex of headlands and immediately equatorward, where wind stress is most intense (Winant et al., 1988; Koracin et al., 2004) as well as at headlands where alongshore flow separates forming an offshore-directed jet (Barth et al., 2000; Kaplan and Largier, 2006). Meanwhile, flow may curve shoreward on the downstream of headlands resulting in onshore flow (Shannon et al., 1981; Halle and Largier, 2011) or forming a separation eddy where larvae may be accumulated (Wing et al., 1995, 1998; Graham and Largier, 1997; Roughan et al., 2005; Mace and Morgan, 2006a; Morgan et al., 2011; Ryan et al., 2014). Thus, larvae are widely expected to be most prone to offshore transport in upwelling centers and immediately downstream of headlands, limiting recruitment and enhancing dispersal away from this source, whereas farther downstream of headlands, they may be entrained in an eddy or transported onshore increasing recruitment and reducing dispersal away from this source.

Larval behavior may reduce transport at headlands and upwelling centers just as it does elsewhere along the coast. The characteristic vertical circulation in wind-driven upwelling areas enables invertebrate larvae and other zooplankters to reduce transport by regulating depth in vertically sheared currents (reviewed by Peterson, 1998; Morgan, 2014), as they do in other places where vertical shear occurs for different reasons (Epifanio and Garvine, 2001; Queiroga and Blanton, 2005; Morgan, 2006, in press; Epifanio and Cohen, 2016). Most species of larvae and copepods in upwelling regimes complete development close to shore within a coastal boundary layer, where Ekman transport is weak and alongshore currents are slow (Peterson et al., 1979; Morgan et al., 2009a; Shanks and Shearman, 2009; Morgan and Fisher, 2010; Nickols et al., 2013; Fisher et al., 2014; Hameed et al., 2018). They remain below a shallow Ekman layer or undertake diel vertical migrations, ascending near the surface to forage at night when offshore flow slows (Peterson et al., 1979; Peterson, 1998; Batchelder et al., 2002; dos Santos et al., 2008; Morgan et al., 2009a; Shanks and Shearman, 2009; Morgan and Fisher, 2010; Miller and Morgan, 2013). By avoiding upward transport into the seaward-flowing surface layer, they are subject to onshore flow and experience a flux convergence at the coast (Genin et al., 2005; Shanks and Brink, 2005). Different species are transported away from shore by occurring in the Ekman layer early in development and toward shore deep late in development, known as an ontogenetic vertical migration (OVM; Peterson et al., 1979; Grantham, 1997; Peterson, 1998; Mace and Morgan, 2006b; Papastephanou et al., 2006; Tapia and Pineda, 2007; Morgan et al., 2009a,b; Morgan and Fisher, 2010; Morgan, 2014). In some places or seasons, larvae late in development rise near the surface, known as a reverse ontogenetic vertical migration (ROVM), where behavior can allow internal waves, diel wind cycles or wind relaxations to transport them toward shore (Hobbs et al., 1991; Shanks, 1995a; Pineda, 1999; Poulin et al., 2002; Marta-Almeida et al., 2006; Morgan et al., 2009a; Morgan and Fisher, 2010).

We tested whether larval behavior effectively regulates transport at upwelling centers, as elsewhere, or whether it is overwhelmed by the intensity of wind forcing and currents. We compared cross-shelf and depth distributions of larvae of inshore benthic crustaceans along two transects near one of the strongest upwelling centers on the west coast of North America during the peak upwelling season. If larval behavior is overwhelmed, then (1) larvae should occur farther offshore at the upwelling center or (2) interspecific differences in larval behavior should render weak species more prone to offshore transport than others. If larval behavior effectively regulates larval transport, then cross-shore transport should be similar among species along the coast and to previous years. We also sampled beyond the shelf break to determine how many species are observed far offshore and potentially transported to the open ocean.

MATERIALS AND METHODS

Study System

We conducted the study within the perennial upwelling center of Point Arena in northern California (**Figure 1**), which is the windiest region along the Pacific Coast of North America (Koracin et al., 2004; Dorman et al., 2005). Prevailing northwesterly winds last for weeks in the spring-summer upwelling season, and near-surface waters (<50 m) flow equatorward and seaward (Hickey, 1998; Roughan et al., 2006). Shallow depths and coastline topography slow flow <10 km from shore (Lentz and Chapman, 1989; Largier et al., 1993; Kaplan et al., 2005; Kirincich et al., 2005; Nickols et al., 2012). This coastal boundary layer widens south of Bodega Bay where flows impinge on the upstream shores of Point Reyes (Robart, 2013) as equatorward flow is deflected offshore, separating from the apex of Point Reyes (Kaplan and Largier, 2006; Vander Woude et al., 2006). Upwelled water and plankton are entrained in an upwelling shadow in the lee of Point Reyes until winds weaken and alongshore flow reverses, transporting larvae poleward and onshore in less than a day (Wing et al., 2003; Roughan et al., 2006; Vander Woude et al., 2006; Morgan et al., 2011, 2012). This occurs about every 4 to 10 days (Send et al., 1987; Largier et al., 1993). Reversing flows result in little net alongshore transport (Largier et al., 1993; Kaplan et al., 2005).

Approach

We sampled stations across the shelf along transects off Bodega Head and in the upwelling center off Stewarts Point (**Figure 1**) toward the end of prolonged upwelling events when larvae are expected to be farther from shore, if simply advected by near-surface currents. We targeted three distinct upwelling events to sample different larval pools. We planned cruises using marine weather forecasts and offshore conditions at National Data Buoy Center 46013 (38° 13′ 30″ N, 123° 19′ 00″ W; http://www.ndbc.noaa.gov; **Figure 1**). We considered upwelling conditions to be northwesterly wind >5 m/s and water <10°C or decreasing. We surveyed vertical distributions of larvae at six stations along two cross-shelf transects on consecutive days on 28 and 29 May, 24 and 25 June, and 14 and 15 July 2009. The Bodega Head transect extended farther from shore as the continental shelf is wider. Stations at Bodega Head were located 1, 6, 11, 32, 42, and 63 km from shore at ∼20, 25, 80, 90, 100, and 120 m depth,

respectively. Stations at Stewarts Point were located 1, 3, 10, 20, 30, and 49 km from shore at ∼20, 25, 80, 90, 100 and 120 m depth, respectively.

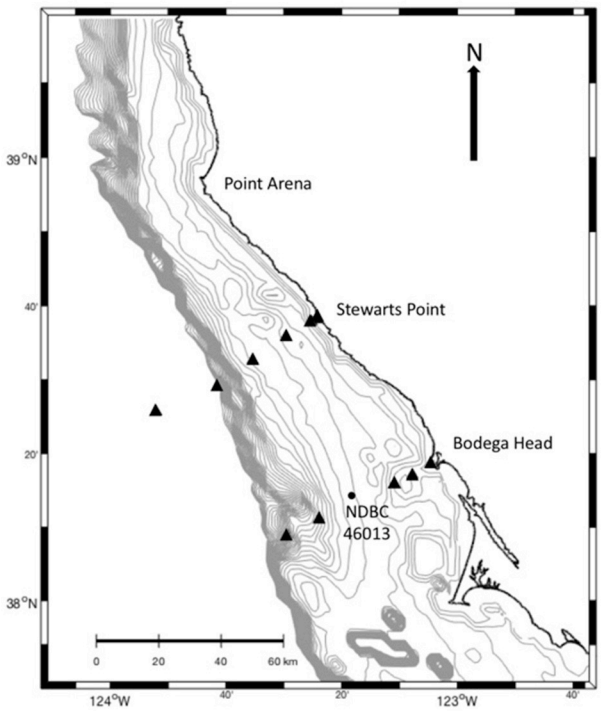

FIGURE 1 | Map of the study area depicting locations of stations along cross-shelf transects off Bodega Head and Stewarts Point in northern California. Location of NDBC buoy 46013 (•) is also shown.

We obtained wind velocity data from NDBC Buoy 46013 and calculated alongshore wind stress by converting it to true north and rotating it to 320° at an air density of 1.3 kg m^{-3} and a drag coefficient of 1.4×10^{-3} to place cruises in the context of upwelling conditions. We obtained water temperature and salinity from a Sea-Bird MicroCAT and chlorophyll-a fluoresence from a WET Labs EcoFluorometer, both at 4 m below the surface on moorings placed on the 15 m isobaths off Bodega Head and Stewarts Point from mid-May through July (**Figure 1**). In addition, temperature 1 m deep and 1 m above the seafloor was recorded with Onset Tidbit thermistors. We measured current using an acoustic Doppler current profiler (ADCP, 1,200 kHz; Teledyne RD Instruments, Poway, California, USA), which were bottom-mounted at moorings off Bodega Head and Stewarts Point at 30 m depth (**Figure 1**). We also mapped surface currents hourly across the study area using high-frequency (HF) radar.

We conducted three pairs of cruises along the two transects near the end of upwelling events, observed as periods of equatorward wind stress, cold water and low chl-a at the moorings off Bodega Head and Stewarts Point (**Figure 2**). Sampling on 28–29 May occurred at the onset of relaxation following a short upwelling event, with rising water temperature and chl-a and poleward flow (**Figure 3**). Sampling on 24–25 June occurred at the end of the strongest prolonged upwelling with temperatures still very low, even with the onset of relaxation on 25 June. Sampling on 14–15 July occurred at the end of a more moderate but prolonged upwelling event with winds and cold temperatures showing that relaxation had not yet started.

We collected plankton in daylight using an electronically tripped Tucker Trawl (0.5 or 1 m^2 mouth) with four nets (335-μm mesh) and temperature and depth sensors to take one sample above the thermocline and two samples below it. We sampled the

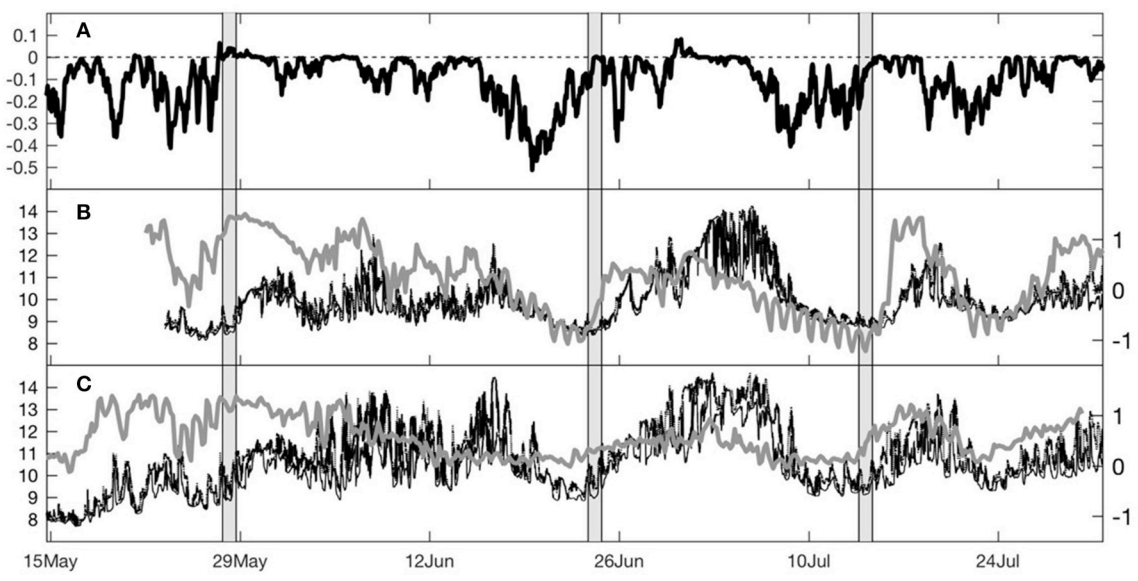

FIGURE 2 | Time series data from 15 May through 26 July 2009: **(A)** alongshore wind stress at NDBC buoy 46013, **(B)** Bodega Head temperature and chlorophyll-a fluorescence and **(C)** Stewarts Point temperature and chlorophyll-a fluorescence. Surface temperature shown as black line and bottom temperature as thin gray line, with chlorophyll-a fluorescence as thick gray line. Survey timing is indicated by vertical gray bars.

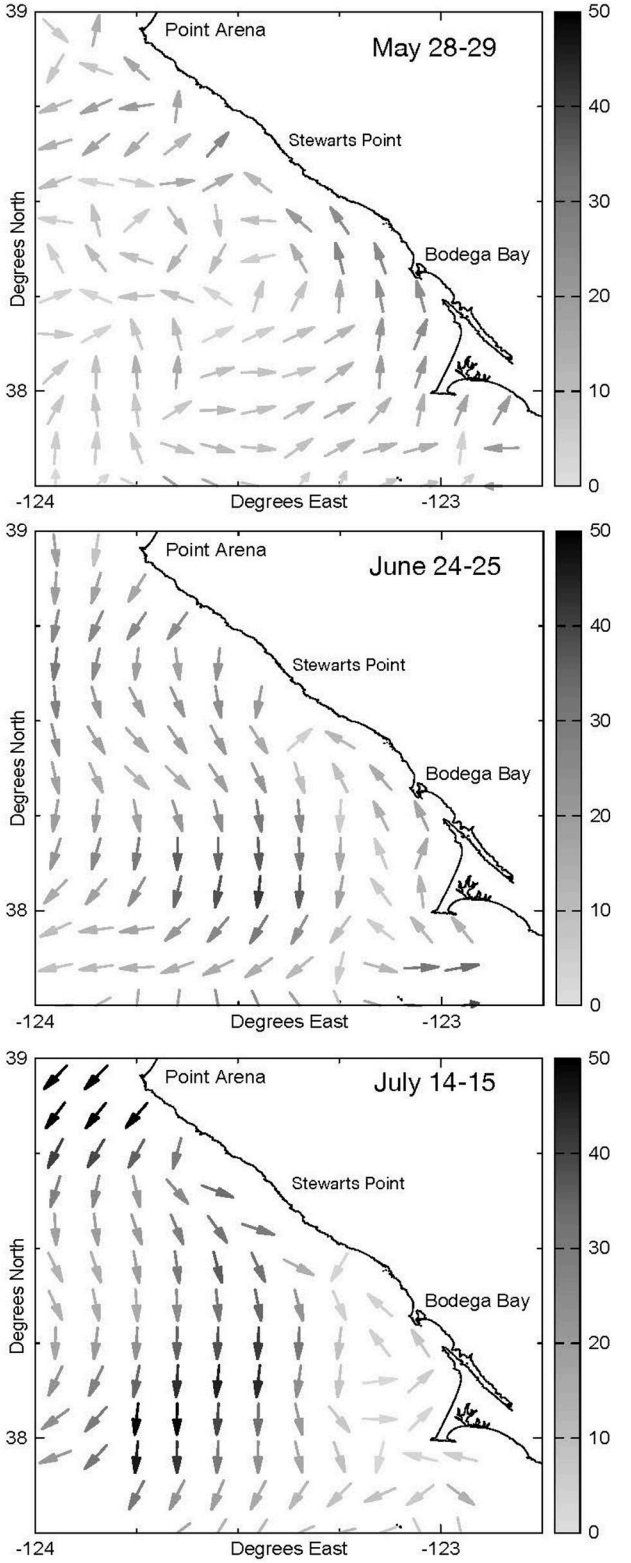

FIGURE 3 | Two-day mean surface current velocity recorded by high-frequency radar across the study region during cruises conducted on 28–29 May, 24–25 June, and 14–15 July 2009. Arrow orientation shows direction while darkness of shading represents speed (cm/s).

surface of the water column using a neuston net (0.5 m^2 mouth, 335-μm mesh). We profiled temperature and salinity with depth at the beginning and end of plankton tows using a conductivity, temperature and depth profiler (Sea-Bird 19-Plus).

We determined cross-shelf distributions for the 42 species of nearshore benthic crustaceans following our previous approach (Morgan et al., 2009b). Larval concentrations per m^2 standardized for the depth of the water column. We determined the cross-shelf and depth distributions of the 39 most abundant species over the six cruises with a nonparametric analysis of similarity (ANOSIM) and a hierarchical cluster analysis and ordination. After averaging depths at each station for the cruises, we determined that cross-shelf distributions of larvae were similar among dates (Bodega: ANOSIM $R = 0.054$, $p = 0.035$; Stewarts: ANOSIM $R = 0.045$, $p = 0.049$), so we averaged dates before conducting analyses on cross-shelf and depth distributions. We tested the resulting dendrogram for differences among groups with a similarity profile test (SIMPROF) and the percent contribution of each species and stage to significant clusters with (SIMPER) to classify cross-shelf and depth distributions for each combination of species and stage. Nonmetric Multidimensional Scaling (nMDS) revealed the separation of larval assemblages by distance from shore and depth. Contours of cross-shore and depth distributions of species by stage were plotted to evaluate whether depth regulation maintained different cross-shelf distributions. We combined species with similar depth distributions during development to simplify presentation and reported the mean depth center of mass (ZCM) and standard error for each species or group.

RESULTS

CTD profiles of temperature and chl-a revealed water column structure across the shelf along the two transects (**Figure 4**). On 28 and 29 May, a warm surface layer was observed, strongest nearshore and consistent with poleward flow–this layer was also characterized by high chl-a concentrations. On June 25 and 24 following a strong, prolonged upwelling event, cold waters shoaled nearshore with weak stratification off Stewarts Point on 24 June, but evidence of poleward flow and an incipient warm surface layer inshore occurred off Bodega Head on 25 June. Chl-a was generally low across the shelf, representative of newly upwelled waters, although a subsurface chlorophyll maximum was observed well offshore of Stewarts Point, beneath a warmer layer of oceanic water. Again on 14 July, active upwelling conditions were observed off Stewarts Point, with cold water shoaling to the surface nearshore and very low chl-a concentrations. At Bodega Head, farther from the upwelling center and a day later, some nearshore stratification and significant chl-a concentration was observed as well as weak surface currents (**Figure 3**).

Surface currents measured by HF radar showed that during the first pair of cruises on 28–29 May flow was poleward nearshore at Bodega Head and Stewarts Point; while offshore flow was observed at Point Arena, onshore flow of surface waters

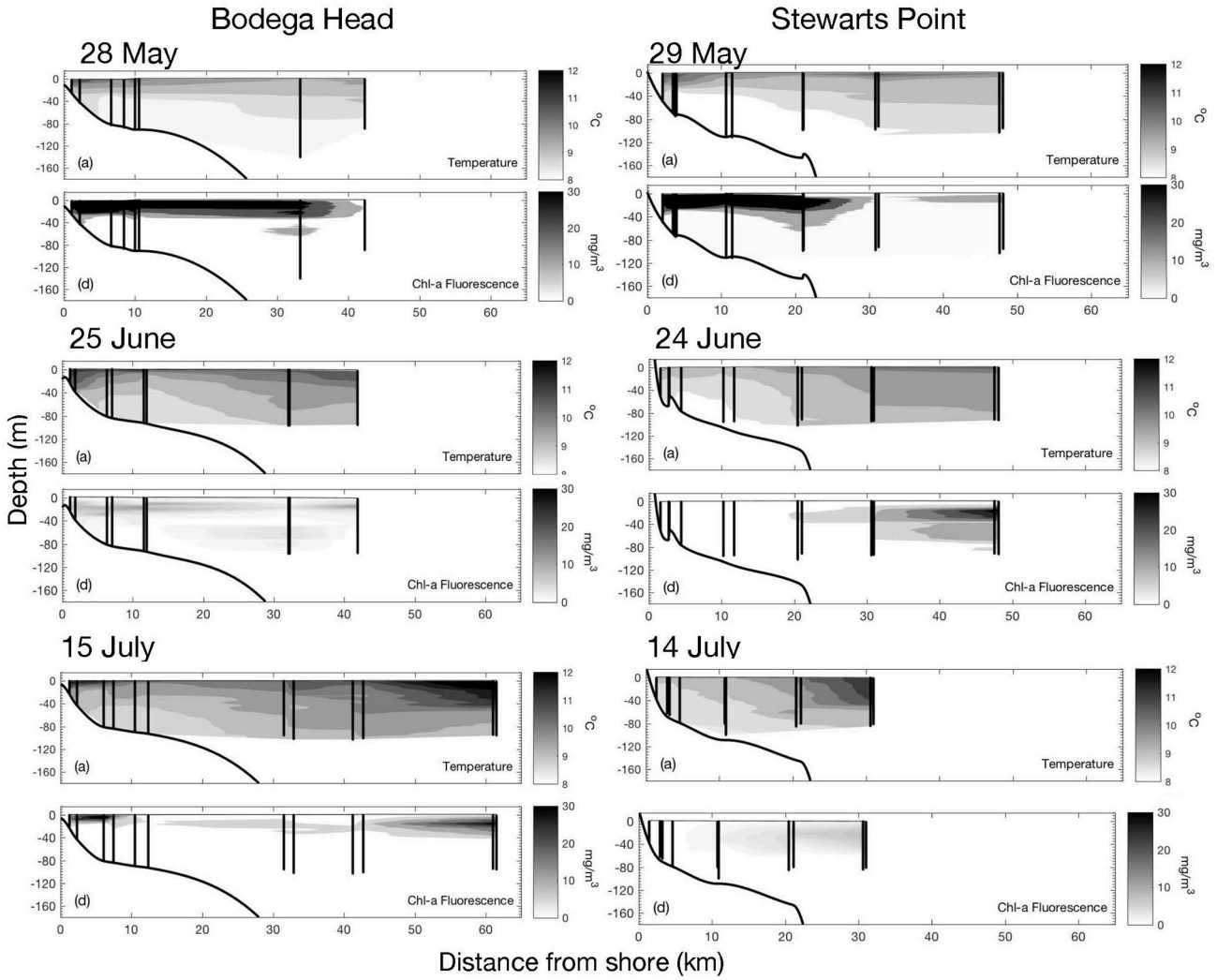

FIGURE 4 | Contours of temperature (°C) and chlorophyll-a from vertical profiles at six stations along transects off Bodega Head and Stewarts Point on 28–29 May, 24–25 June, and 14–15 July 2009. Profile locations at the beginning and end of plankton tows at each station are depicted by black vertical lines.

was observed south of Bodega Head (**Figure 3**). On June 24–25, nearshore flow was poleward from Bodega Head to Stewarts Point and equatorward from Point Arena to Stewarts Point where these currents converged, deflecting alongshore flow offshore. On July 14–15, nearshore flows were very weak in the vicinity of Bodega Head, but equatorward and offshore flow was well developed from Point Arena to south of Stewarts Point.

The progressive vector diagrams showed net poleward transport near-bottom and near-surface at both nearshore sites (**Figure 5**). Transport was shoreward near-surface and seaward near-bottom off Bodega Head, whereas it was seaward near-surface and near-zero near-bottom off Stewarts Point. At both sites, near-surface transport exhibited greatest excursions during upwelling and relaxation events, indicating that larvae remaining deep in the water column would travel the shortest distance.

Larvae of 42 species of benthic crustaceans generally did not occur farther offshore at the upwelling center at Stewarts Point than Bodega Head (**Figure 6**). Larvae largely occurred; l98.7989 $<$ 11 km from shore at both sites, and early larval stages were abundant inshore where larvae are released. All stages of 22 species occurred on the inner shelf $<$11 km from shore off Bodega Head (99.8%) with the large majority of them occurring just 1 km from shore and most of the rest of them occurring 6 km from shore (**Figure 6**), revealing larval retention. Similarly off Stewarts Point, all stages of these species occurred on the inner shelf $<$10 km from shore (98.5%; **Figure 6**) with most of the rest of them occurring 3 km from shore. All stages of four more species occurred $<$11 km from shore off Bodega Head (96.1%) with the large majority of them occurring 1 km from shore and most of the rest of them occurring 6 km from shore while late stages occurred $<$32 km from shore (**Figure 6**). Similarly off Stewarts Point, all stages of these species occurred $<$10 km from shore (95.4%) with the large majority of them occurring just 1 km from shore and most of the rest of them occurring 3 km from shore while late

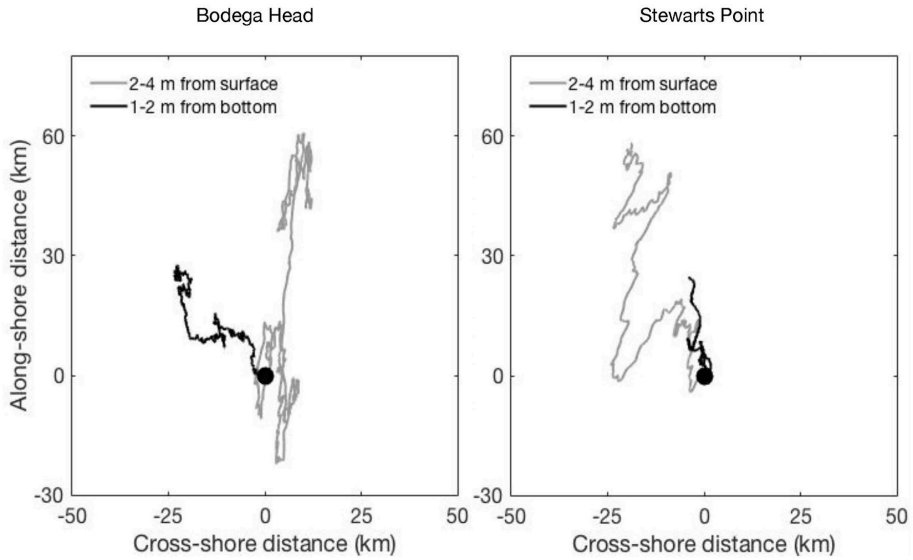

FIGURE 5 | Progressive vector diagrams of potential alongshore and cross-shore displacement due to currents measured near-surface (gray line) and near-bottom (black line) from mid 24 May through 26 July 2009 at Bodega Head and Stewarts Point. Current velocity was measured by a bottom-moored ADCP at 30-m depth at each site. Positive alongshore distances are poleward and positive cross-shore distances are shoreward.

stages occurred <30 km from shore (**Figure 6**). Early stages of 16 more species occurred <11 km from shore (81.8%) and late stages occurred far offshore in much lower abundance off Bodega Head (18.2 %, **Figure 6**). Similarly off Stewarts Point, early stages of these species occurred <10 km from shore (70.6%) and late stages occurred far offshore in low abundance (**Figure 6**). Thus, along both transects, larvae of most species were retained on the inner shelf while late stages other species ranged to the midshelf or offshore.

The 39 most abundant species differed primarily across stations (Bodega Head: ANOSIM $R = 0.439$, $p = 0.001$; Stewarts Point: ANOSIM $R = 0.373$, $p = 0.002$) but also among depths (Bodega Head: ANOSIM $R = 0.107$, $p = 0.096$; Stewarts Point: ANOSIM $R = 0.145$, $p = 0.055$), indicating that depth regulation contributed to interspecific differences in cross-shelf transport at both sites. Cluster analysis and nMDS showed pronounced spatial structure in larval assemblages along both transects grouping taxa into inner, mid and offshore categories for both transects with an outlier (neuston at Station 3) for the offshore group at Stewarts Point (**Figure 7**).

A nearshore cluster of all stages of 21 species largely occurred <6 km from shore (**Figures 7**, **8**), five species of porcelain crabs (*Petrolisthes cinctipes, Pet. eriomerus, Pet. manimaculus, Pachycheles rudis, Pac. pubescens*), a mud shrimp (*Neotrypaea californiensis*), five species of barnacles (*Balanus crenatus B. glandula, Semibalanus cariosus, Chthamalus dalli/fissus*), three hermit crabs (*Pagurus samuelis, P. hirsutiusculus, P. granosimanus*) and seven pea crabs *(Pinnixa faba, P. tubicola, Pinnotheres pugettensis, Scleroplax granulata, Fabia subquadrata*, two unidentified species). However, postlarvae of the three barnacles, three hermit crabs and seven pinnotherids occurred in very low concentrations to ∼18 km from shore during the cruise off Bodega Head on 28 May (**Figure 8**). Pinnotherid postlarvae occurred in low concentrations <30 km off Bodega Head and <20 km off Stewarts Point, because one of the species (*F. subquadrata*) disperses midshelf (Morgan et al., 2009c). Off Bodega Head, all stages of these species composed 12.9% of all larvae along the transect contributing 11.26% of the similarity to the cluster, and off Stewarts Point, all stages of these species composed 2.4% of all larvae collected along the transect and contributed 3.11% of the similarity to the cluster (**Figure 7**). Larvae of these species occurred below the shallow Ekman layer (**Figure 8**). Porcelain crabs undertook a ROVM (**Figure 8**) with similar ZCMs of larvae at the shallow stations inshore off Bodega Head (11.9 ± 3.0 m) and Stewarts Point (9.7 ± 4.6 m) and postlarvae ascending to the neuston (0.5 m) at both sites. In contrast, pinnotherid crabs undertook an OVM (**Figure 8**) with similar ZCMs of larvae inshore off Bodega Head (17.2 ± 3.2 m) and Stewarts Point (16.5 ± 3.5 m) and postlarvae descending much deeper in the water column (Bodega 49.0 m; Stewarts 37.4 ± 2.3 m). The rest of these species mostly occurred below the Ekman layer throughout development while perhaps undertaking an OVM with postlarvae occurring deeper than larvae on one or more cruises along both transects (**Figure 8**). *Neotrypaea californiensis* larvae occurred higher in the water column (14.5 ± 5.7 m) than postlarvae (24.0 ± 0.7 m) off Stewarts Point, though not off Bodega Head where both larvae (32.4 ± 15.0 m) and postlarvae (26.7 ± 8.9 m) occurred deeper than off Stewarts Point. Late-stage barnacle larvae were shallower (5.1 ± 2.3 m) than postlarvae (12.9 ± 1.0 m) off Bodega Head, though postlarvae were deeper on only one cruise off Stewarts Point. Similarly, hermit crab larvae were shallower (17.7 ± 0.6 m) than postlarvae off Bodega Head (46.8 ± 24.4 m), though postlarvae were deeper on only one cruise off Stewarts Point

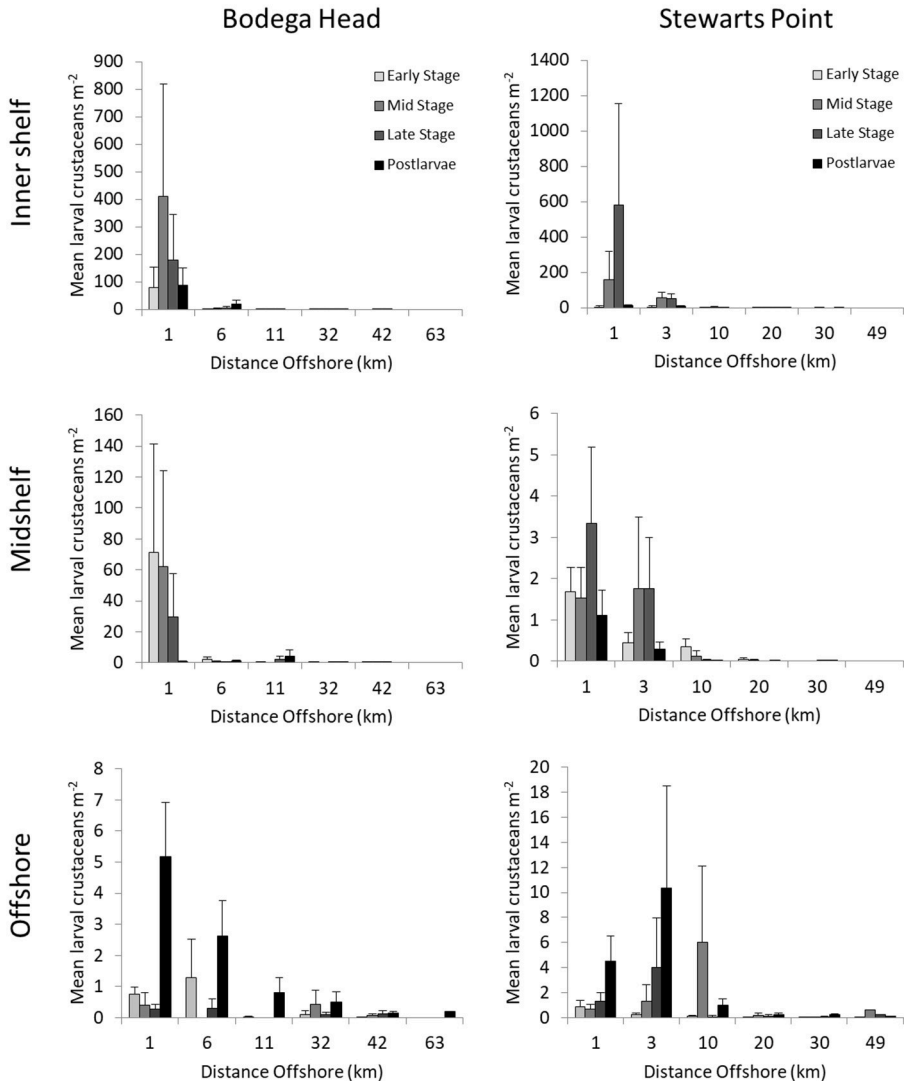

FIGURE 6 | Densities (mean/m^2 + 1 SE) of larval stages of 42 species of benthic crustaceans relative to distance from shore for all depths and cruises combined at Bodega Head and Stewarts Point on 28–29 May, 24–25 June, and 14–15 July. Twenty-two species largely remained on the inner shelf off Bodega Head (<11 km from shore) and Stewarts Point (<10 km from shore) throughout development. Four species primarily occurred on the inner shelf and ranged across the midshelf late in development off Bodega Head (<32 km from shore) and Stewarts Point (<30 km from shore). Sixteen species primarily occurred on the inner shelf and ranged offshore late in development off Bodega Head (>32 km) and Stewarts Point (>30 km). Note scale changes.

A midshelf cluster of all stages of four species largely occurred <6 km from shore with late stages occurring <32 km at both sites, including the xanthid crab *Lophopanopeus bellus*, two grapsid crabs (*Hemigrapsus oregonensis*, *H. nudus*) and *Romaleon* (*Cancer*) *antennarius* (**Figures 7**, **9**). Off Bodega Head, all stages of these species composed 85.1% of all larvae along the transect contributing 38.10% of the similarity to the cluster. Off Stewarts Point, all stages of these species composed 93.7% of all larvae collected along the transect and contributed 31.16% of the similarity to the cluster (**Figure 7**). The vertical distributions of *L. bellus* and the grapsid crabs were similar throughout development (**Figure 9**). ZCMs of *L. bellus* off Bodega Head were 14.0 ± 2.4 m for early larvae and 16.0 m for postlarvae (late stages were not collected), and ZCMs off Stewarts Point were 23.8 ± 5.5 m for early larvae, 27.9 m for late larvae and for 27.9 m postlarvae. Off Bodega Head, ZCMs of grapsid larvae were 13.1 ± 3.1 m for early stages, 14.6 ± 2.6 m for late stages and 12.6 m for postlarvae, and off Stewarts Point, ZCMs were 11.1 ± 1.0 m for early stages, 10.8 ± 1.8 m for late stages and postlarvae were not collected (**Figure 9**). Vertical distributions also were similar throughout development for *R. antennarius* off Bodega Head (early 23.3 ± 10.9 m, late 19.0 ± 3.0 m, postlarvae 17.8 ± 0.8 m), but there was evidence of a possible OVM off Stewarts Point with larvae occurring shallower (early 14.3 ± 5.5 m, late 15.2 ± 6.8 m) than postlarvae on two cruises (31.8 ± 6.8 m).

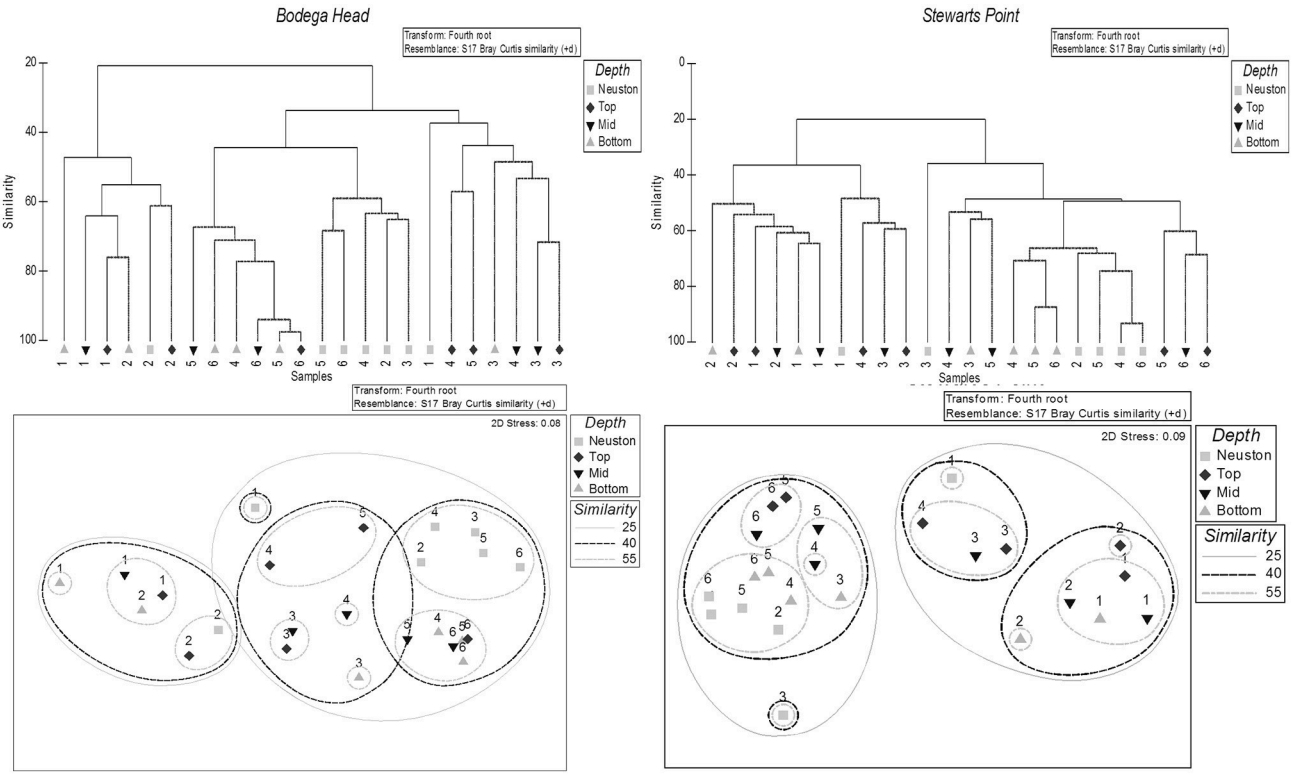

FIGURE 7 | Top panels. Hierarchical clustering dendrogram (using group-average linking) of 48 samples taken from four depths at six sampling stations across the continental shelf: 1, 6, 11, 32, and 63 km from shore off Bodega Head and 1, 3, 10, 20, 30, and 49 km from shore off Stewarts Point. Samples were categorized based on 25 and 40% similarities. Solid black lines indicate significant group structure at the 1% level. Sample distances offshore are reported beneath each group. **Bottom** panels: Nonmetric multidimensional scaling plots (2D stress: 0.08 for Bodega Head and 0.09 for Stewarts Point) from the 48 samples with superimposed significant clusters at similarity levels of 25% (solid lines) and 40% (dashed lines) off Bodega Head and Stewarts Point.

An offshore cluster composed of 14 species with early larval stages largely occurring <11 km from shore and late stages occurring >30 km from shore (**Figures 7**, **10**). Off Bodega Head, all stages of these species composed 1.9% of all larvae collected along the transect and contributed 49.36% of the similarity to the cluster, and off Stewarts Point, all stages of these species composed 3.4% of all larvae along the transect contributing 65.73% of the similarity to the cluster (**Figure 7**). Larvae of seven majiids (*Pugettia richii, P. producta, P. gracilis, Scyra acutifrons, Mimulus foliatus, Oregonia gracilis,* unidentified species) primarily completed development <1l km from shore, whereas larvae of three species of cancrid crabs [*Metacarcinus* (*Cancer*) *magister, Cancer productus, Glebocarcinus* (*Cancer*) *oregonensis*], two barnacles (*Balanus nubilus*, *Pollicipes polymerus*), *Emerita analoga* and an unidentified porcellanid occurred in low concentrations beyond 11 km (**Figures 7**, **10**). Larvae of these species commonly occurred in the Ekman layer midshelf and offshore (**Figure 10**). Cancrid postlarvae even were prevalent in the neuston at Station 3 off Stewarts Point (**Figure 10**), being reflected as an outlier for the offshore group off Stewarts Point in the dendrogram (**Figure 7**). The barnacles appeared to undertake an OVM (**Figure 10**); ZCMs were shallower for late-stage barnacle larvae (Bodega 15.3 ± 0.1 m; Stewarts 15.6 ± 2.8 m) than postlarvae (Bodega 30.5 ± 3.6 m; Stewarts 27.2 ± 4.5 m). Majiids may have undertaken an OVM (**Figure 10**). Off Bodega Head, ZCMs of majiid larvae were shallower (early 11.7 ± 1.6 m, late 11.1 ± 1.1) than postlarvae (21.9 ± 15.8 m), and off Stewarts Point, early-stage larvae also were shallower (15.8 ± 5.3 m) than late-stage larvae (20.6 ± 13.4) and postlarvae (22.1 ± 2.3 m). Cancrids may have undertaken a ROVM (**Figure 10**). Cancrid larvae off Bodega Head were deeper (early 12.0 ± 0.4 m) than postlarvae (0.5 m), and this also was the case off Stewarts Point (early 22.2 ± 10.9 m, late 13.8 ± 1.0 m), except during one cruise when postlarvae occurred in low concentrations ∼45 m deep resulting in a ZCM of 20.2 ± 13.1 m. *Emerita analoga* larvae commonly occurred in the surface layer across the shelf (**Figure 10**) with ZCMs off Bodega Head of 6.7 ± 2.2 m for early larvae and 12.5 m for late larvae and ZCMs off Stewarts Point of 15.0 m for late larvae. Unidentified porcellanid larvae also occurred in the surface layer across the shelf off Stewarts Point with ZCMs of 0.5 m for early larvae and 10.0 m for late larvae, but early stages were deep in the water column during the one cruise that they were collected off Bodega Head with a ZCM of 59.4 m (**Figure 10**). We did not detect ontogenetic changes in vertical distributions of *E. analoga*

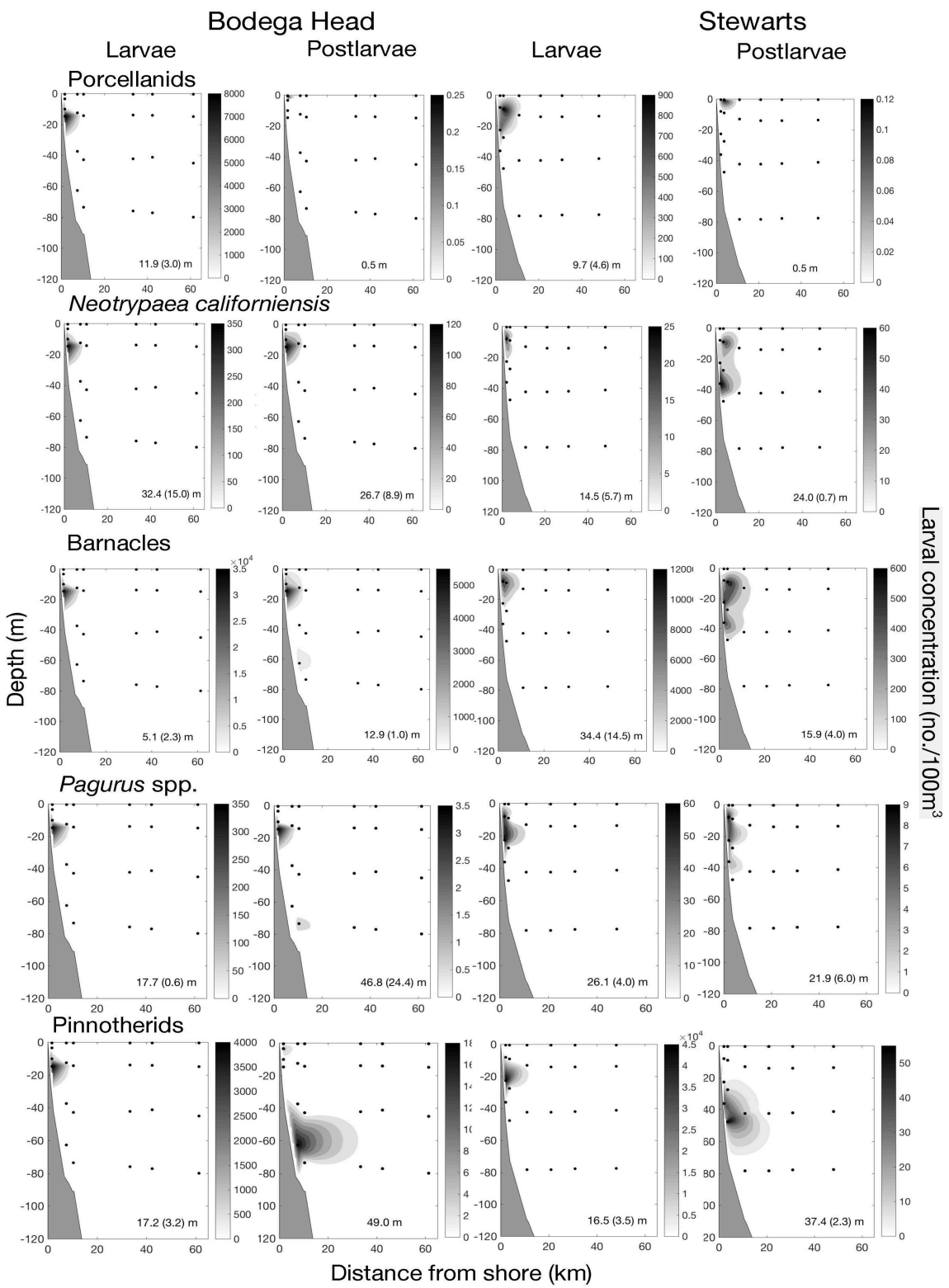

FIGURE 8 | Inner-shelf larval development of 21 species in relation to distance from shore and depth off Bodega Head and Stewarts Point for larvae that largely occurred <6 km. First row of panels for five species of porcelain crabs (*Petrolisthes cinctipes, Pet. eriomerus, Pet. manimaculus, Pachycheles rudis, Pac. pubescens*); second row of panels for a mud shrimp (*Neotrypaea californiensis*); third row of panels for five species of barnacles (*Balanus crenatus B. glandula, Semibalanus cariosus, Chthamalus dalli/fissus*); fourth row of panels for three hermit crabs (*Pagurus samuelis, P. hirsutiusculus, P. granosimanus*); and fifth row of panels for seven

(Continued)

FIGURE 8 | pea crabs *(Pinnixa faba, P. tubicola, Pinnotheres pugettensis, Scleroplax granulata, Fabia subquadrata*, two unidentified species). The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. ZCM with no variation shown in parentheses indicates species were collected during a single cruise, and separate groups of larvae within panels were collected during different cruises. Missing panel indicates that small larvae passed through nets.

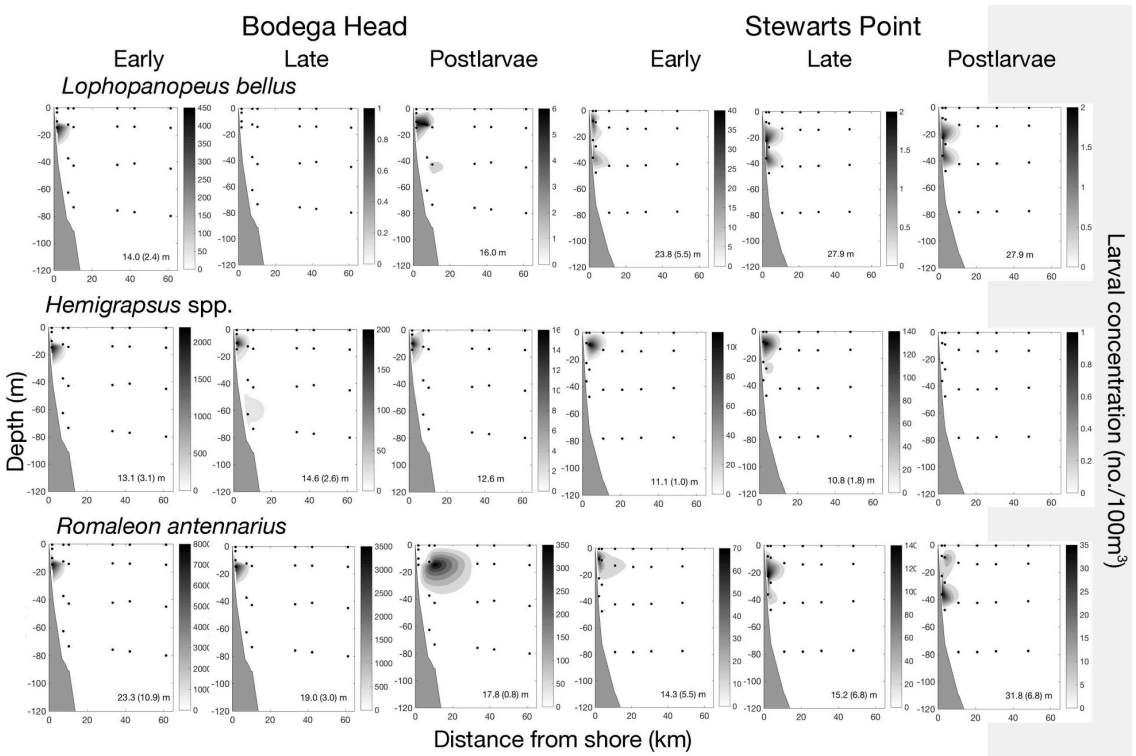

FIGURE 9 | Midshelf larval development of four species in relation to distance from shore and depth off Bodega Head and Stewarts Point where larvae largely occurred <11 km from shore with late stages primarily occurring <32 km. First row of panels for the xanthid crab *Lophopanopeus bellus;* second row of panels for two grapsid crabs (*Hemigrapsus oregonensis, H. nudus*); and third row panels for a rock crab *Romaleon* (*Cancer) antennarius*. The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. ZCM with no variation shown in parentheses indicates species were collected during a single cruise, and separate groups of larvae within panels were collected during different cruises. Missing panel indicates that small larvae passed through nets.

or the unidentified porcellanid because we did not collect postlarvae.

DISCUSSION

We have shown that larvae of nearshore benthic crustaceans are retained nearshore or reliably migrate different distances from shore during the season of peak upwelling and in the core of an upwelling center within the region of the most persistent, strongest upwelling along the Pacific Coast of North America. In this work and previous studies, we have repeatedly sampled larval assemblages during many cruises over multiple locations and years (Morgan et al., 2009b,c; Morgan and Fisher, 2010; Hameed et al., 2018). In this work, we focused on the time and place of maximum upwelling, showing that larvae were not transported farther offshore at this region of strong, persistent upwelling, contrary to widespread expectations. During the present study, we sampled larvae of 42 nearshore benthic crustaceans and 99; l98.7989% of all larvae were collected over the inner shelf, <11 km from shore along both transects. Larvae were most concentrated within a few kilometers of the shoreline, in the coastal boundary layer where offshore Ekman transport and alongshore currents are weak (Lentz and Chapman, 1989; Largier et al., 1993; Kaplan et al., 2005; Kirincich et al., 2005; Roughan et al., 2006; Morgan et al., 2009c; Morgan and Fisher, 2010; Nickols et al., 2012, 2013; Hameed et al., 2018). Not only was this characteristic coastal-boundary-layer circulation (Pettigrew and Murray, 1986; Shanks, 1995a; Largier, 2002, 2003) persistent, but it is expected to contribute to nearshore larval retention of diverse benthic crustaceans in other upwelling regions worldwide (Morgan, 2014).

All larval stages of 21 species occurred in high concentrations primarily in the coastal boundary layer <6 km offshore, including the five species of porcelain crabs, mud shrimp, five species of barnacles, three hermit crabs and seven pea crabs. The three species of barnacles, three species of hermit crabs and six of the seven species of pinnotherids in this nearshore group also completed development in high concentrations <6 km from

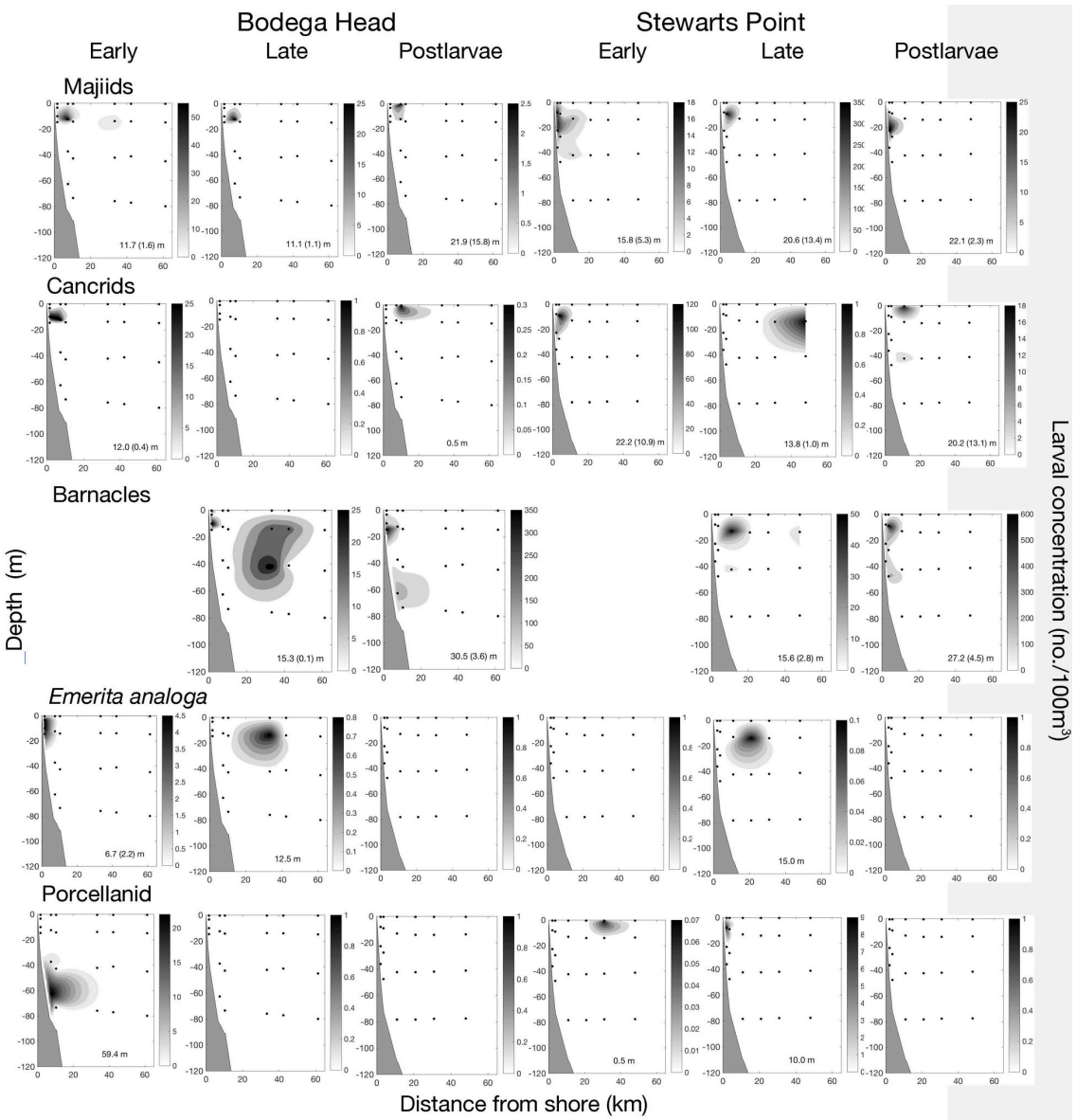

FIGURE 10 | Offshore larval development of 14 species in relation to distance from shore and depth off Bodega Head and Stewarts Point where larvae largely occurred <11 km from shore with late stages occurring >32 km from shore. First row of panels for seven majid crabs (*Pugettia richii, Pugettia producta, Pugettia gracilis, Scyra acutifrons, Mimulus foliatus, Oregonia gracilis,* unidentified species); second row of panels for three cancrid crabs (*C. magister, C. productus, C. oregonensis*); third row of panels for two barnacles (*Balanus nubilus, Pollipes polymerus*); fourth row of panels for the mole crab (*Emerita analoga*); and fifth row of panels for an unidentified porellanid. The depth center of mass (ZCM; mean with SE in parentheses) is given at the bottom of each panel. ZCM with no variation shown in parentheses indicates species were collected during a single cruise, and separate groups of larvae within panels were collected during different cruises. Missing panel indicates that small larvae passed through nets.

shore off Bodega Head in our previous studies (Morgan et al., 2009b,c; Morgan and Fisher, 2010; Nickols et al., 2013; Hameed et al., 2018). In our present study, these barnacles and hermit crabs completed development close to shore in five of the six cruises, but in the 28 May cruise off Bodega Head their postlarvae were found in very low concentrations up to ∼18 km from shore. This survey was conducted during a relaxation event when a poleward flow from the Gulf of Farallones can transport plankton offshore north of Point Reyes, unlike during prevailing upwelling conditions (Kaplan and Largier, 2006; Morgan et al., 2012). In addition, one of the seven pinnotherids (*F. subquadrata*) developed farther from shore than the other six species in our previous study off Bodega Head, but we did not distinguish it from the other pinnotherids during the present study.

Of the species that did not complete their larval life nearshore, many occurred in high concentrations <11 km early

in development and in lower concentrations farther from shore late in development. The four species that occurred midshelf (*L. bellus*, *Hemigrapsus* spp., *R. antennarius*) or the 14 species that occurred offshore (seven majiids, three cancrids, two barnacles, mole crab, unidentified porcellanid) late in development had similar distributions in our previous studies (Morgan et al., 2009b,c; Morgan and Fisher, 2010; Nickols et al., 2013; Hameed et al., 2018). Postlarvae of all of these species spanned the continental shelf while recruiting onshore. Crustacean larvae had similar cross-shelf distributions off Oregon (Lough, 1974; Fisher et al., 2014), indicating that these interspecific differences are maintained in time and space.

Distinctive vertical distributions of larval stages were related to horizontal distributions likely contributing to maintaining the three cross-shelf patterns. Larvae in the nearshore group occurred deep in a shallow water column early in development and most species either descended (*N. californiensis*, *B. crenatus*, *B. glandula*, *Pagurus* spp., pinnotherids) or ascended (porcellanids) late in development apparently undertaking an OVM or ROVM, respectively. Similar ontogenetic changes in vertical distributions were evident in our previous study off Bodega Head, and in addition, *Chthamalus* spp. underwent a ROVM (Morgan et al., 2009c). The subsurface vertical distributions of all these larvae and postlarvae undertaking an OVM (in this and prior studies) placed them in onshore and weak alongshore flow (Largier et al., 1993; Dever et al., 2006; Roughan et al., 2006; Nickols et al., 2012), likely facilitating retention nearshore (Peterson, 1998; Batchelder et al., 2002; Papastephanou et al., 2006; Morgan et al., 2009c; Morgan and Fisher, 2010; Nickols et al., 2013; Hameed et al., 2018). Barnacle and pinnotherid larvae typically stay deep, whereas *N. californiensis* and *Pagurus* spp. larvae rise near the surface at night (Morgan and Fisher, 2010) after winds subside and are often onshore reducing transport (Peterson et al., 1979; Hobbs et al., 1991; Peterson, 1998; Batchelder et al., 2002; Poulin et al., 2002; Marta-Almeida et al., 2006; dos Santos et al., 2008; Bonicelli et al., 2016). By undertaking a ROVM, postlarvae of the porcellanids and *Chthamalus* spp. could be transported shoreward by winds and internal tides in the neuston (Pineda, 1994, 1999; Shanks, 1995a), which occur in our region during relaxation periods in a stratified water column (Rosenfeld, 1990).

Early stages of the rest of the species were transported farther from shore by spending more time in surface currents (Morgan et al., 2009c; Morgan and Fisher, 2010), as do copepods (Peterson et al., 1979; Peterson, 1998; Batchelder et al., 2002; Papastephanou et al., 2006). Ten species (*R. antennarius*, two barnacles, seven majiids), generally descended into deeper onshore flow late in development during our present or previous study (Morgan et al., 2009c). Onshore transport of late stages limits cross-shelf displacement and returns postlarvae to shore (Peterson et al., 1979; Grantham, 1997; Peterson, 1998; Papastephanou et al., 2006; Morgan et al., 2009c). The three species of cancrids transported offshore returned to shore as postlarvae by ascending to the neuston. Ontogenetic vertical migrations either were not apparent (*L. bellus*) or indeterminate without all larval stages being collected (*E. analoga*, unidentified porcellanid) in this or our previous study (Morgan et al., 2009c). Even without ontogenetic changes in vertical distributions, crabs in this region generally rise near the surface at night (Morgan and Fisher, 2010) facilitating onshore transport by internal tides and winds (Jamieson and Phillips, 1988; Shenker, 1988; Hobbs et al., 1991; Shanks, 1995b; Rasmuson and Shanks, 2013).

As we discussed previously (Morgan et al., 2009c; Fisher et al., 2014; Morgan, 2014), passive advection and eddy diffusion alone cannot explain the differences in cross-shelf distributions among so many species, because (1) these larvae are released inshore and encounter the same physical processes, (2) distances larvae migrate from shore are not related to larval durations, (3) larval densities were adjusted to account for increasing depth across the shelf to ensure that high larval concentrations after hatching were not simply reduced by dilution due to vertical mixing as the water column deepened offshore and (4) late stages were as abundant or increased midshelf and offshore instead of decreasing. Thus, behavior is common across larval taxa and many species exhibit behaviors that reduce offshore transport in upwelling regions elsewhere on the Pacific Coast, including in the weaker upwelling off Oregon (Peterson et al., 1979; Shanks and Shearman, 2009; Fisher et al., 2014) and central through southern California (Grantham, 1997; Tapia and Pineda, 2007), as well as worldwide, including Chile (Poulin et al., 2002; Bonicelli et al., 2016) and the Iberian Peninsula (Marta-Almeida et al., 2006; dos Santos et al., 2008; Bartilotti et al., 2014).

If larvae remain close to shore, why are populations recruitment limited in persistent, strong upwelling regions? Presumably, there is a constraint between the larval availability in the plankton over the inner shelf and the settlement of benthic larvae in shoreline habitats. Recent work has shown that the ability of postlarvae to enter the surf zone largely depends on temporal and spatial variation in surfzone hydrodynamics, which is determined by breaking waves interacting with alongshore changes in coastal morphology, yielding a spectrum of surf zones from dissipative to reflective (Wright and Short, 1984). Broad surf zones along mildly sloping shorelines usually have far more larvae and other plankton and much greater settlement onshore (Shanks et al., 2010, 2017, 2018, in press; Morgan et al., 2016, 2017, 2018). These dissipative surfzones have bathymetric rip currents, which concentrate plankton by recirculation in a series of rip currents alongshore, unlike narrow reflective surf zones at steep shores (Shanks et al., 2010, 2017, 2018, in press; Morgan et al., 2016, 2017, 2018). Individual based biophysical models revealed that Stokes drift and benthic boundary layer streaming coupled with downward swimming in response to turbulence from waves facilitated onshore larval delivery beaches (Fujimura et al., 2013, 2014, 2017, 2018). The striking differences in surfzone oceanography at dissipative and reflective shores predictably affect larval recruitment and productivity of inshore communities (Morgan et al., 2016, 2017, 2018; Shanks et al., 2017, in press) and appear to explain recruitment limitation at many sites in California (Morgan et al., 2016, 2017; Shanks et al., 2017; Shanks and Morgan, 2018). Together with the above results on larval distributions in upwelling areas, this suggests a shift in paradigms from the past idea that upwelling necessarily limits recruitment to new ideas that recruitment limitation and population connectivity may be better explained by alongshore

differences in surfzone circulation (Shanks et al., 2017; Shanks and Morgan, 2018; Morgan, in press).

Larval retention evidently occurs all along coasts in upwelling regions, rather than primarily occurring in bays and eddies in the lee of headlands. This implies that alongshore transport and the scale of connectivity in benthic metapopulations in upwelling areas is less than previously suggested. Larval transport would be reduced even further if postlarvae effectively navigate onshore in upwelling regimes. Elsewhere, postlarvae can navigate onshore to suitable settlement sites using hierarchies of cues that are effective over different spatial scales, including celestial bodies, polarized light, magnetic and electric fields, waves and tides, and acoustic, chemical and visual cues (Kingsford et al., 2002; Montgomery et al., 2006; Arvedlund and Kavanagh, 2009; Morgan, in press). Adding onshore navigation into individual based biophysical models in upwelling regions (Pfeiffer-Herbert et al., 2007; Carr et al., 2008; Petersen et al., 2010; Domingues et al., 2012; Drake et al., 2013; Nolasco et al., 2013) should reduce the scale of population connectivity even further, but onshore navigation remains to be documented for species in upwelling regimes (Morgan, in press). The ultimate goal is to determine realized population connectivity, reconciling evidence from studies of circulation, plankton, genetics and microchemistry. Next steps should also include incorporating documented reproductive outputs of a metapopulation (Hameed et al., 2016), larval behaviors documented here and previously (Morgan et al., 2009b; Morgan and Fisher, 2010) and larval mortality rates (White et al., 2014) into the numerical circulation model (Regional Ocean Modeling System; Drake et al., 2013). This would provide one of the first reliable estimates of realized population connectivity (Burgess et al., 2014). Clearly, a fresh look at the underlying processes responsible for spatial and temporal patterns of recruitment and population connectivity for diverse taxa and locations across upwelling coasts is needed to better understand the regulation of marine populations and communities (Shanks et al., 2017; Morgan et al., 2018; Shanks and Morgan, 2018).

In conclusion, larval retention is likely commonplace all along upwelling coasts with larvae recruiting closer to home and more abundantly than has been widely appreciated. Here, we demonstrated that this is even true at locations and times when upwelling is strongest, such as in the Point Arena upwelling center. This deeply affects the ecology, evolution and management of species in upwelling regimes. More larval retention should increase coupling between stock and recruitment, local adaptation and local benefits of marine protected areas as well as vulnerability of marine protected areas to overfishing and other disturbances (Strathmann et al., 2002; Sanford and Kelly, 2011; Burgess et al., 2014, 2016).

AUTHOR CONTRIBUTIONS

SGM: Conceived of the research; SGM and JL: Were awarded funding to conduct the study; SHM, SGM, and MR: Conducted the study; SHM and MR: Processed, analyzed and graphed the data with SGM; SGM: Wrote the ms with input by all.

ACKNOWLEDGMENTS

We thank the crew of the R/V Mussel Point, and M. Sheridan, S. Hameed, W. White, D. Dann, and J. Herum for assisting with sample collection. We also thank M. Losekoot for the HF Radar plots. This research was funded by California Sea Grant (R/FISH-2018) and is a contribution of the Bodega Marine Laboratory.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.