

UC Davis

UC Davis Previously Published Works

Title

Behaviorally Mediated Larval Transport in Upwelling Systems

Permalink

<https://escholarship.org/uc/item/44k130qc>

Author

Morgan, Steven G

Publication Date

2014-07-17

DOI

10.1155/2014/364214

Peer reviewed

Review Article

Behaviorally Mediated Larval Transport in Upwelling Systems

Steven G. Morgan

Bodega Marine Laboratory, Department of Environmental Science and Policy, University of California, Davis, Bodega Bay, CA 94923, USA

Correspondence should be addressed to Steven G. Morgan; sgmorgan@ucdavis.edu

Received 26 March 2014; Accepted 6 June 2014; Published 17 July 2014

Academic Editor: Fengyan Shi

Copyright © 2014 Steven G. Morgan. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Highly advective upwelling systems along the western margins of continents are widely believed to transport larvae far offshore in surface currents resulting in larval wastage, limited recruitment, and increased population connectivity. However, suites of larval behaviors effectively mediate interspecific differences in the extent of cross-shelf migrations between nearshore adult habitats and offshore larval habitats. Interspecific differences in behavior determining whether larvae complete development in estuaries or migrate to the continental shelf are evident in large estuaries, but they sometimes may be disrupted by turbulent tidal flow or the absence of a low-salinity cue in shallow, low-flow estuaries, which are widespread in upwelling systems. Larvae of most species on the continental shelf complete development in the coastal boundary layer of reduced flow, whereas other species migrate to the mid- or outer shelf depending on how much time is spent in surface currents. These migrations are maintained across latitudinal differences in the strength and persistence of upwelling, in upwelling jets at headlands, over upwelling-relaxation cycles, and among years of varying upwelling intensity. Incorporating larval behaviors into numerical models demonstrates that larvae recruit closer to home and in higher numbers than when larvae disperse passively or remain in surface currents.

1. Introduction

Eastern boundary upwelling systems have been studied intensively, because they are one of the most productive marine ecosystems producing ~20% of the fish catch from less than 1% of the global ocean [1]. Strong equatorward winds drive broad, slow eastern boundary currents that attain maximum velocities 50 to 200 km from shore (Figure 1). Wind together with rotation of the earth (Coriolis) along the coastal boundary generates a shallow offshore flow at the surface (Ekman transport) and a drop in sea level, which draws cold, nutrient-rich, bottom water to the surface where sunlight fuels high primary production and fisheries for sardines and anchovies. Spatially varying wind velocity (wind stress curl) and increasing wind offshore also generate upwelling (Ekman pumping).

Larval transport may be affected by differences in the strength of prevailing winds, which are highly dynamic in space and time. At lower latitudes, Ekman transport is greater generating a wider band of persistent upwelling, the thermocline is shallower, oxygen is lower, mixing by weather systems is less, and river discharge is greater [1, 2].

Coastal topography strongly modifies wind, currents, and upwelling. Wind intensifies along the windward side of headlands producing a jet that may transport plankton far from shore, and wind diminishes in the lee of headlands forming retentive eddies (upwelling shadows) [3]. The width of the continental shelf also varies potentially affecting transport into the open ocean. The intensity of upwelling-favorable winds varies throughout the day (sea breeze), throughout the season (weather events), interannually (e.g., El Niño Southern Oscillation), and over decades (e.g., North Atlantic Oscillation, Pacific Decadal Oscillation, and North Pacific Gyre Oscillation). Winds are strongest in the California Current System (CCS) followed by the Iberian Current System (ICS) and Humboldt Current System (HCS), but the order is reversed for the strength of upwelling, which varies inversely with Coriolis. Variance is greatest interannually in the HCS and seasonally in the ICS, whereas it is similar at interannual, seasonal, and intraseasonal time scales in the CCS.

Larvae of nearshore species in upwelling systems must avoid being swept downstream and offshore to replenish adult populations, and behaviors regulating transport could

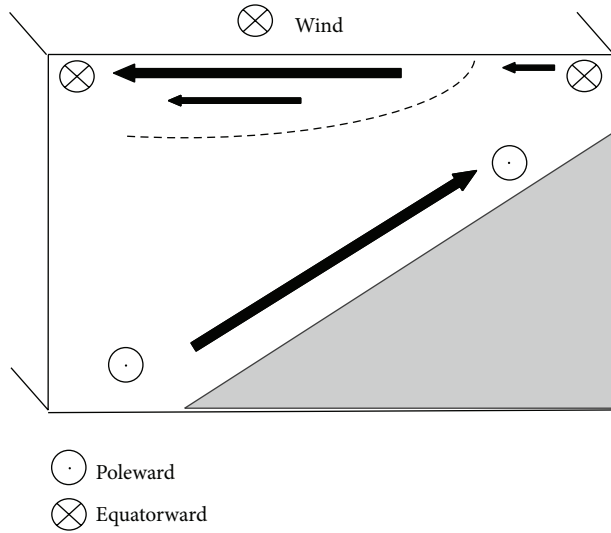


FIGURE 1: Schematic block diagram of generalized circulation. Prevailing winds blow equatorward toward the south with brief periods of relaxation or reversal. Surface waters flow offshore in the Ekman layer, which is weak and a few meters deep nearshore and stronger and about 15 to 30 m deep offshore. Cold, deep waters flow onshore and upwell to the surface often forming a front with warmer surface waters. Nearshore, prevailing currents flow poleward, as indicated by the circle with a dot in middle. Offshore, currents flow equatorward near the surface, as indicated by the circle with a cross in middle, and poleward at depth. Cross-shelf and alongshore transport is regulated by the amount of time larvae spend near the surface and bottom in stratified currents.

be overwhelmed by strong upwelling conditions [4, 5]. Depth regulation by larvae in shallow, low-flow estuaries in the Mediterranean and arid climates of upwelling systems also may be challenging due to mixing or the absence of low-salinity to cue behaviors [6]. Rainfall is insufficient to stratify estuaries during much of the year [7]. These estuaries may be hypersaline with the density of water being similar to that of the ocean, and tidal diffusion rather than two-layer estuarine circulation controls exchange between the estuary and open coast [7, 8].

Despite the important implications for the ecology and evolution and conservation and management of species in upwelling regimes, these hypotheses have been difficult to test for mobile species, such as fishes, which have received the most attention due to their commercial importance. However, insights have come from studying more tractable sedentary intertidal and shallow-water benthic species. Because adults are fairly fixed along a narrow ribbon of shoreline, the starting and ending points of the planktonic phase of the life cycle are more restricted than for species inhabiting dynamic currents. Surveys of cross-shore distributions of progressively later larval stages indicate the extent of offshore transport. Surveys of the vertical distributions of progressively later larval stages over diel and tidal cycles coupled with concurrent profiles of current velocity and water column structure indicate how vertical swimming behavior may mediate cross-shore distributions. Complementary approaches, such as numerical oceanographic models, are needed to determine

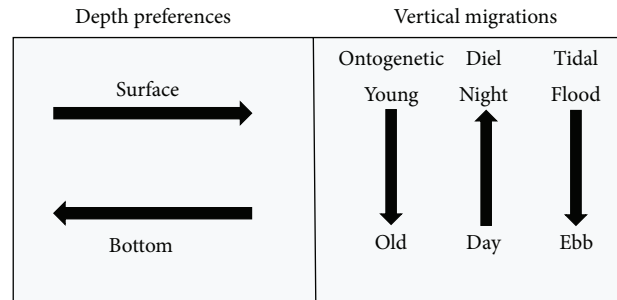


FIGURE 2: Depth regulation by larvae mediating cross-shore transport: depth preferences and vertical migrations. Larvae of some species prefer to occur in surface waters, and larvae of other species prefer to occur in bottom waters. Larvae also may undertake three types of vertical migrations: ontogenetic (descend late in development), diel (ascend at night and descend during the daytime), and tidal (descend during ebb tide and ascend during flood tide). Larvae of other species undertake reverse vertical migrations in the opposite directions.

alongshore transport because larvae could have originated from many locations along the coast.

I review evidence for the behavioral regulation of larval transport of nearshore and estuarine benthic species in upwelling systems. I begin by summarizing generalized larval behaviors that are known to mediate transport in diverse systems. I then briefly review similarities and differences in the characteristics of the three upwelling systems where larval surveys of nearshore benthic species have been conducted: CCS, HCS, and ICS. With this background, I briefly characterize circulation in each upwelling system before reviewing the evidence for the behavioral mediation of larval transport by nearshore benthic species. I focus on evidence from the horizontal and vertical distributions of larvae in the water column rather than inferences drawn from the extensive literature on larval settlement onshore, which is beyond the scope of this review. Next, I synthesize this evidence to characterize shared physical and behavioral processes mediating larval transport across upwelling systems. I conclude by highlighting future directions for investigating larval transport in upwelling systems in an era of climate change.

2. Behavioral Mediation of Larval Transport

The extent of larval transport is largely determined by the vertical distributions of larvae in flow [11, 12]. Current velocity changes throughout the water column, and the time that larvae spend at various depths affects the rate and direction of transport. For example, larvae may be transported from adult habitats by occupying seaward surface waters and toward adult habitats by occupying landward bottom currents in compensatory return flow. Species may complete development in one portion of the water column (depth preferences) or undertake ontogenetic vertical migrations (OVM), descending from surface to bottom waters late in development (Figure 2). Larvae also may vertically migrate periodically relative to tidal and diel cycles (TVM and DVM, resp.), cued by changes in light intensity, salinity, temperature,

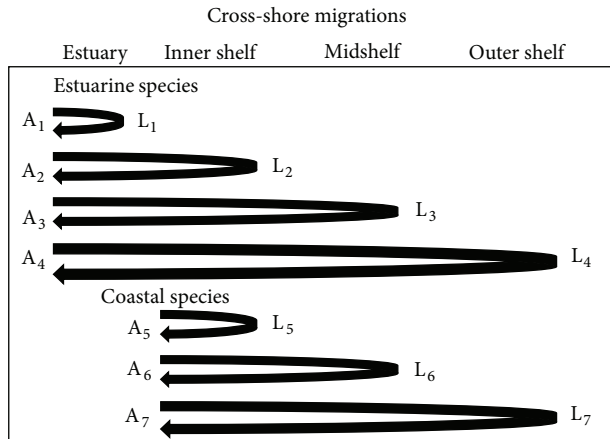


FIGURE 3: Behaviorally mediated cross-shore migrations by larvae (L) of estuarine and coastal species from adult populations (A; subscripts represent different species). Larvae of some estuarine species may complete development in the estuary while other species migrate to the inner, mid-, or outer shelf (or open ocean). Larvae of intertidal and shallow-water coastal species may complete development on the inner shelf or migrate either to the mid- or outer shelf (or beyond).

or hydrostatic pressure. The opposite patterns also have been documented and are known as reverse ontogenetic (ROVM), tidal (RTVM), and diel (RDVM) vertical migrations. Larvae of nearshore species rely on one or more of these behaviors to mediate cross-shore transport between adult and larval habitats [13–15]. Cross-shore larval migrations span a continuum from short-distance migration remaining in nearshore or estuarine habitats to long-distance migration to the outer shelf and open ocean, depending on the time spent in surface currents (Figure 3).

3. California Current System

3.1. Circulation. The California Current can be ~1000 km wide flowing from the North Pacific Current off Washington, USA (~20°N to ~50°N), to the subtropical waters off Baja California, Mexico (~15°N to ~25°N), where it turns westward as the North Equatorial Current (Figure 4). Four regions have been identified in reviews of the CCS [16–22]. Upwelling in the Pacific Northwest is weak, intermittent and largely confined to the wide continental shelf. Strong, persistent upwelling occurs along the narrower shelf in northern and central California. Upwelling weakens in the Southern California Bight (32°N to 35°N), and off the biogeographic break at Point Conception, the California Current flows equatorward along the west side of the Channel Islands forming the Southern California Eddy. The complex geography of the bight and variable winds produce many small eddies that persist from several days to weeks. The California Current turns east to the coast near the border with Mexico, and it bifurcates with some flow returning poleward to the Southern California Bight and the remainder flowing equatorward along the coast of Baja. High-pressure systems generating prevailing northwesterly, upwelling-favorable winds are

interrupted by local low-pressure systems ~2–6 days during the year and ~4–10 days during the peak upwelling season. These interruptions vary from 2–20 days across the CCS, ranging from rare interruptions off California and Baja to frequent interruptions in the Pacific Northwest. Mixing intensifies and surface flow either slows or reverses for several days, with reversals being far more common during the peak upwelling season in the Pacific Northwest than in California.

3.2. Impact of Regional Variation in Advection on Eggs and Larvae. A review of the spawning “strategies” of fishes provides keen insights into the potential losses of eggs and larvae from advection across three regions of the CCS [5]. In the Pacific Northwest, where strong upwelling occurs during spring and summer, spawning of positively buoyant eggs occurs during winter when prevailing downwelling-favorable winds transport eggs in surface waters onshore. In northern and central California, where strong upwelling prevails most of the year, spawning of positively buoyant eggs is uncommon and is replaced by spawning demersal eggs, brooding eggs in benthic nests, and bearing juveniles. In southern California and Baja, where weak upwelling occurs throughout most of the year, spawning of positively buoyant eggs is common with eggs being entrained into many small eddies that form due to the complex geography of the region.

This review helped set the stage for benthic ecologists to focus on the importance of upwelling in regulating populations for the next several decades by monitoring spatial and temporal variation in larval settlement of nearshore species [23]. Yoshioka [24] proposed that upwelling played a major role in reducing larval settlement of a bryozoan (*Membranipora membranacea*) in kelp forests in southern California by correlating settlement with wind speed. A seminal paper by Roughgarden et al. [25] was highly influential in establishing the importance of upwelling in regulating intertidal communities in upwelling systems. Strong upwelling in central California was proposed to limit larval recruitment to infrequent wind relaxation events and reduce subsequent competition for space, whereas larval recruitment would be much greater in the weaker upwelling of the Pacific Northwest, resulting in high larval recruitment and the preeminence of postsettlement interactions in regulating populations and communities [23, 26]. Larvae would be transported offshore in surface waters until they were concentrated at a front separating newly upwelled, cold, nearshore water and warmer, offshore water during sustained upwelling [25, 27–29]. Hence, the distance of the upwelling front from shore would provide a good indicator of larval settlement across the CCS [30]. These conclusions were based on correlations of barnacle settlement and upwelling-relaxation cycles [31, 32], three years of barnacle settlement and upwelling strength [25] and an 11-year record of the seaward limit of barnacle larvae relative to upwelling strength [24]. Subsequent studies have confirmed latitudinal differences in larval settlement and adult densities of intertidal barnacles and mussels in the CCS [33–36].

Upwelling also affects alongshore transport of larvae raising the fundamental question of how populations persist in prevailing equatorward flow. Shanks and Eckert [37]

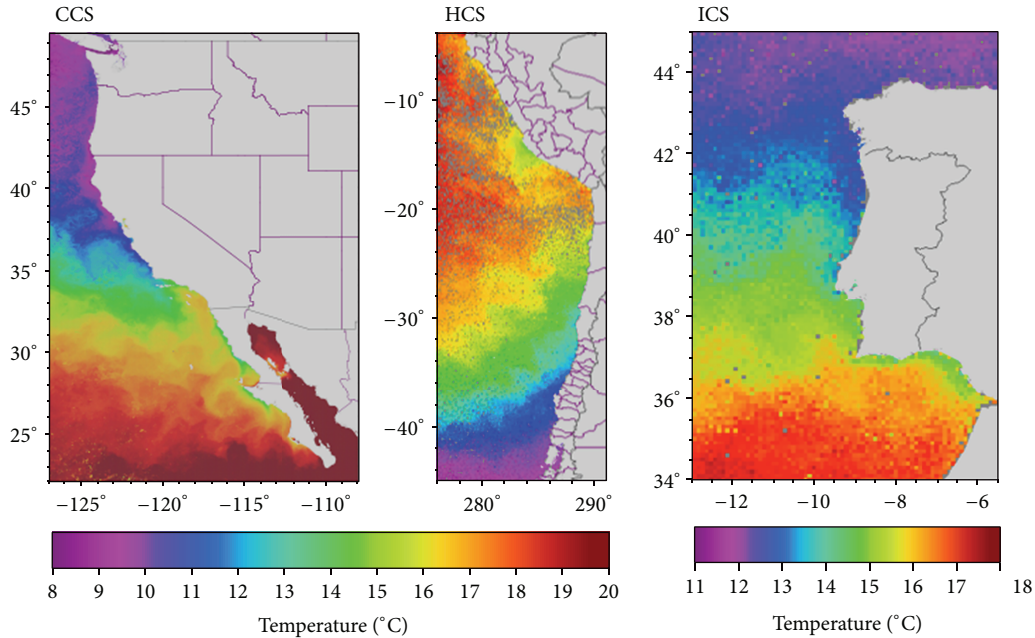


FIGURE 4: Satellite images of sea surface temperature during the peak upwelling season in three upwelling regions: California (CCS), Humboldt (HCS), and Iberia Current Systems (ICS). Images are for 1 month during the peak upwelling season and were obtained from the National Oceanic and Atmospheric Administration Coastwatch website (<http://coastwatch.pfeg.noaa.gov>).

addressed this question by extending the review by Parrish et al. [5] to include the life history traits of both benthic crustaceans and fishes. Nearshore species from the Pacific Northwest to central California have relatively short larval durations (~ 45 d) with strongly swimming larvae developing during peak upwelling (spring-summer). Larval advection is reduced by developing close to shore where currents slow, especially during relaxation events. Nearshore species in southern California and Baja also have short larval durations, strongly swimming larvae and develop during strong upwelling (spring-fall). Larvae develop farther from shore, but eddies and countercurrents may reduce larval advection. Species in this region are longer-lived and more fecund with more broods per year, suggesting a bet-hedging strategy to compensate for larval losses from advection. In contrast to nearshore species, offshore species produce weakly swimming larvae from winter to summer and have long larval durations (~ 136 d). Alongshore displacement may be reduced by offsetting poleward transport in winter with equatorward transport in spring, when larvae develop below the mixed layer in slower, poleward flow. These species are long-lived and highly fecund employing a bet-hedging strategy. A model by Byers and Pringle [38] later showed that many invertebrate species may release larvae in April because large-scale current fluctuations associated with the spring transition would minimize mean dispersal distances and maximize the diffusive spread of settling larvae, allowing diffusion to counteract advective downstream transport.

3.3. Impact of Mesoscale Variation in Upwelling on Larval Transport. Coastal topography generates mesoscale variation in circulation, thereby affecting larval transport and

recruitment. Urchin recruitment is consistently less at four headlands (Cape Blanco, Cape Mendocino, Point Arena, and Point Reyes) than elsewhere along the coast suggesting that many larvae are swept offshore by jets [39]. Subsequent studies on barnacles and mussels also indicated that recruitment is limited at headlands [34, 40]. Larvae and other plankton also may be transported equatorward in the plume of newly upwelled water at these upwelling centers [41–43]. Some of the upwelled water and larvae are entrained into recirculation features in the lee of the headlands forming retentive, recruitment hotspots along otherwise recruitment-limited coasts in California [44, 45].

Retentive recruitment hotspots also occur in the lee of small headlands [46, 47]. Regardless of behavior, larvae of all species are entrained in the recirculation feature in the lee of Bodega Head in northern California during upwelling conditions [48]. The recirculation feature occurs at depth, because the headland is too low to block the prevailing wind resulting in equatorward surface currents on the leeward side [46]. Therefore, retention in the recirculation feature may depend on larvae staying in the lower water column or undertaking DVM between surface and bottom currents [46].

The variation in coastline topography and bathymetry generates fronts, which concentrate phytoplankton and invertebrate larvae, at scales of approximately 50 m across the CCS during the upwelling season [49]. Larvae that swim upward to maintain surface distributions are most likely to concentrate at these shallow frontal convergences [50]. Faster swimming fish larvae aggregate at fronts to exploit the concentrated plankton [28, 29, 51, 52]. Consequently, larval recruitment of nearshore invertebrates and rockfishes is greater where fronts

occur [48]. Fronts also serve as conduits funneling neustonic Dungeness crab (*Cancer magister*) postlarvae to intertidal habits in estuaries [53].

At a smaller scale, coves may form retentive hotspots during the peak upwelling season [54, 55]. Fronts form across the mouths of coves during prevailing upwelling conditions with eggs and early stage larvae of intertidal species primarily concentrated on the landward side and late stage larvae on the seaward side. Fronts persist about 80% of the time in Oregon, breaking down and increasing settlement when winds relax or reverse about every 6 days.

3.4. Behavioral Mediation of Larval Transport on the Shelf

3.4.1. Larval Surveys. It is now clear that offshore transport of larvae is not the cause of the well-documented latitudinal gradients in larval recruitment across the CCS. Characteristic circulation of upwelling regions enables invertebrate larvae to limit cross-shelf and alongshore transport by regulating their depth in stratified flow (offshore transport near the surface and onshore return flow at depth) to maintain their position over the continental shelf, as first shown for copepods [4, 56]. Indeed, consistent patterns occurred in the cross-shelf distances of larvae of 45 species of benthic shallow-water crustaceans in the strong, persistent upwelling of northern California [9, 57]. Larvae of most species occur in high densities throughout development in waters below the surface mixed layer and within 6 km of the coast in a coastal boundary layer of reduced offshore Ekman transport and slow alongshore currents, whereas larvae of other species migrate to the mid- or outer shelf [9, 57, 58]. The interspecific differences in cross-shelf distributions are maintained even at Point Arena and Point Reyes where larvae and eggs are widely expected to be advected offshore [9, 57].

Suites of behaviors maintain the interspecific differences of crustacean larvae in the vertically stratified, opposing flows over the shelf (Figure 5) [9, 59, 60]. Larvae completing development in the coastal boundary layer remain below a shallow Ekman layer (barnacles and pinnotherid crabs) during the daytime or undertake DVM (other species of crabs), only rising into productive surface waters to forage at night when offshore flow is weakest (Figure 5(a)). They avoid being carried to the surface in upwelled waters and are trapped in an onshore flow convergence near the coast [61, 62]. Furthermore, larvae of some species undertake an OVM descending deeper into upwelled bottom waters, whereas larvae of other species undertake a ROVM ascending into the neuston as postlarvae (Figure 5(b)), where internal waves or infrequent wind relaxations may transport them shoreward [63, 64]. Larvae of species that migrate to the middle of the shelf spend more time in the Ekman layer early in development than those that develop in the coastal boundary layer (Figures 5(c) and 5(d)). Like larvae of species that complete development in the coastal boundary layer, larvae of species that migrate to midshelf return onshore by descending deeper in the water column late in development or ascending into the neuston as postlarvae. Larvae of other species migrate to the outer shelf by remaining in the Ekman layer throughout development (Figure 5(e)), and postlarvae

may return onshore by ascending into the neuston where infrequent wind relaxations may transport them shoreward [65]. Crab larvae that migrate to the mid- or outer shelf undertake DVM, rising to the surface at night after winds subside [6, 59, 66]. Interestingly, a lens of low-salinity water (gradient < 1) from local runoff or transported poleward from San Francisco Bay suppresses DVM by all crab larvae except *Cancer* spp. larvae [6, 66].

Similar cross-shelf distributions of the same species of crustacean larvae occur elsewhere in the CCS, indicating that behavior may effectively mediate transport across different upwelling regimes. In the intermittent upwelling regime off the coast of Oregon, interspecific differences in cross-shelf distributions of benthic crustaceans are similar to those off northern California: the highest densities of larvae occur within 5 km of the coast and larvae are rare beyond 18 km [67, 68]. Several species of crustaceans as well as weaker swimming echinoderm and mollusc larvae also complete development almost entirely within 4.5 km of shore by rarely occurring near the surface during the daytime (0–10 m deep) [69]. Sampling was not conducted below 30 m, and, consequently, it remains to be determined whether species that migrate offshore in the upper water column return onshore by spending time deep in the water column late in development, as they do in northern California [9].

In the comparatively weak upwelling in the southern California Bight, barnacle larvae (*Balanus glandula*, *Chthamalus* spp.) are retained close to shore [70], as they are off northern California and Oregon [9, 59, 68, 69]. During a 48-hour survey nearshore [71], the mean depth of nauplii of several barnacle species (*Chthamalus* spp., *Balanus nubilus*, and *Pollicipes polymerus*) was ~5 m, and cyprids of two of these species (*Balanus nubilus*, *Pollicipes polymerus*) occurred deeper in the water column, indicating an OVM (cyprids of *Chthamalus* spp. were not collected). Barnacle nauplii did not undertake DVM, as previously found [59]. Interestingly, barnacle nauplii occurred closer to the surface than they did in northern California and Oregon [9, 59, 69]. This difference was attributed to using a smaller mesh size to capture the earliest naupliar stages [71]. However, the difference in mesh sizes does not explain why later naupliar stages of the same species were not abundant below 5 m, as in northern California and Oregon. One possibility is that lighter winds during the brief study period in southern California may generate less turbulence cuing larvae to rise into productive surface waters to forage [60].

The interspecific differences in cross-shelf distributions do not appreciably shift in response to variability in upwelling intensity. Larvae are not swept farther offshore during upwelling than during relaxation conditions in either the persistent upwelling regime off northern California [9, 57] or the intermittent upwelling regime off Oregon [68, 69]. The interspecific differences in cross-shelf migration also are reliably maintained during years of strong upwelling in both upwelling regimes [9, 57, 68].

Although interspecific differences in cross-shelf distributions do not appear to change appreciably in response to upwelling intensity, alongshore distributions do. European green crabs (*Carcinus maenas*) recruit to Oregon and

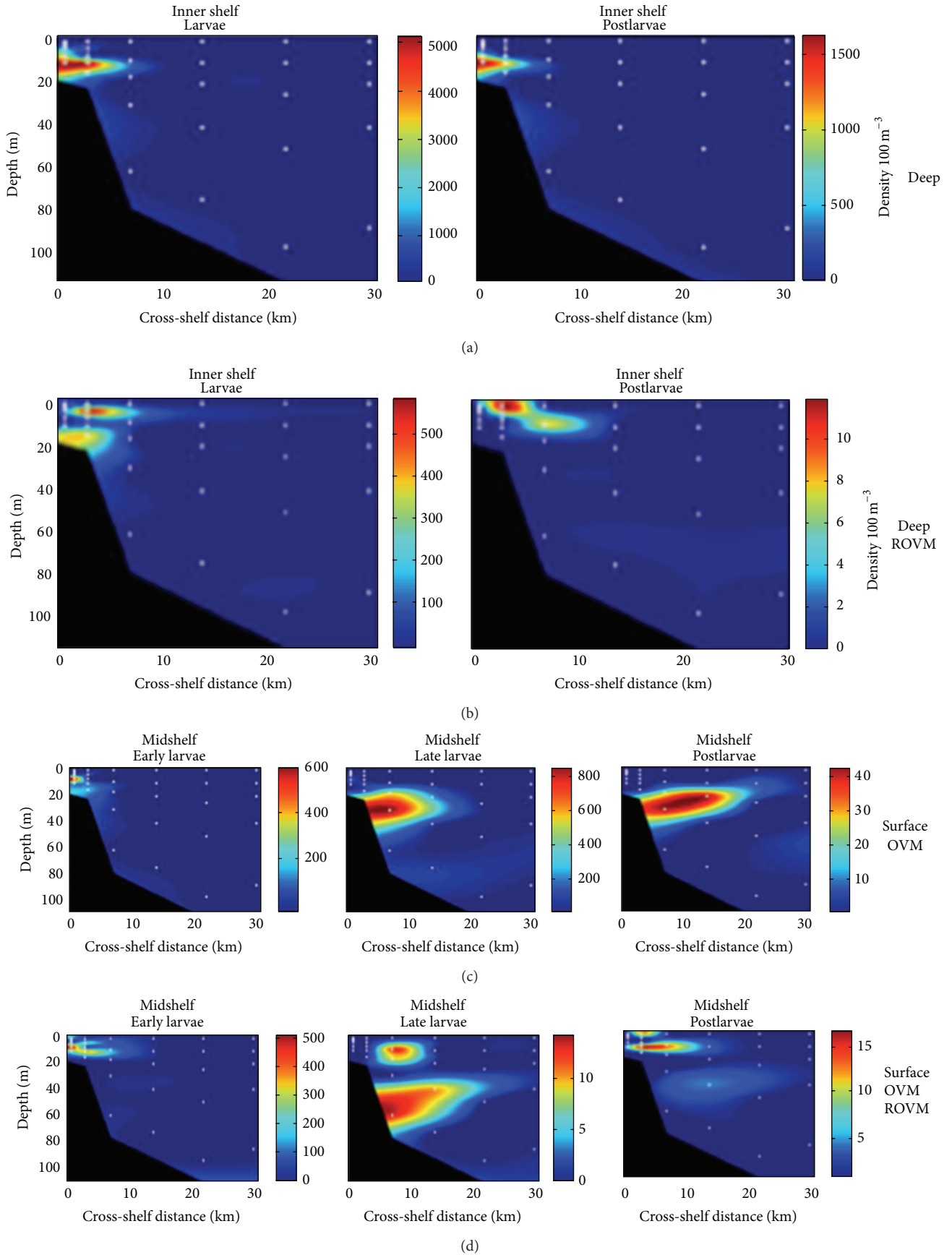


FIGURE 5: Continued.

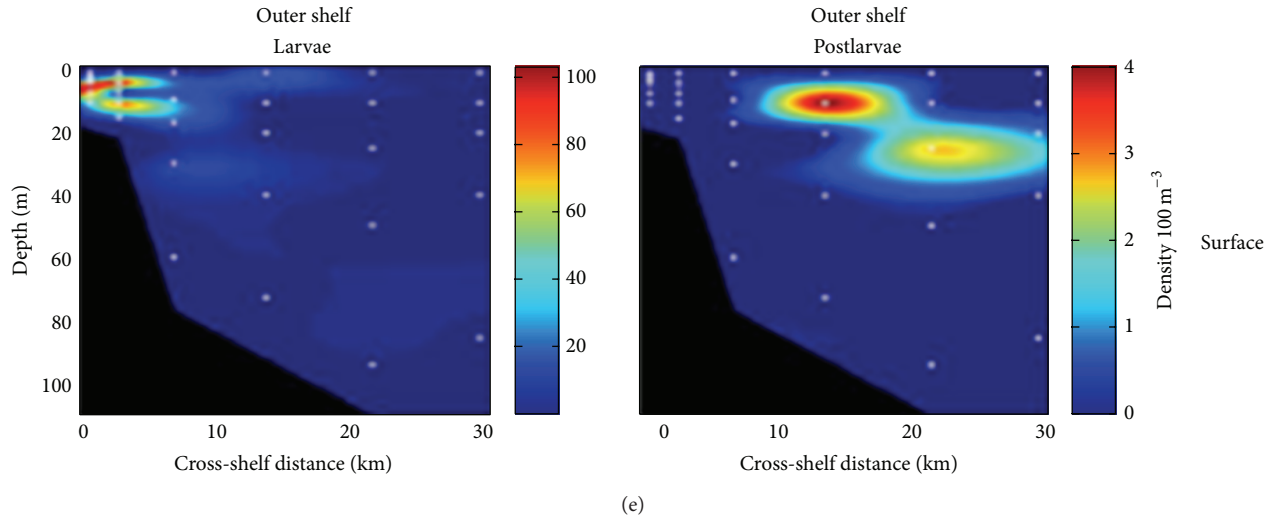


FIGURE 5: Representative horizontal and vertical distributions of larvae of nearshore benthic crustaceans during the daytime off Bodega Bay, northern California. (a) Barnacle larvae (*Balanus glandula*, *B. crenatus*, and *Semibalanus cariosus*) completed development <6 km from shore by occurring deep in the water column throughout development, (b) porcelain crab larvae (*Petrolisthes cinctipes*, *Pet. eriomerus*, *Pet. manimaculus*, *Pachycheles rudis*, *Pac. pubescens*) completed development <6 km from shore by occurring deep in the water column early in development and rising to the surface as postlarvae (ROVM), (c) pea crab larvae (*Fabia subquadrata*) mostly completed development on the inner shelf (<13 km) with early larval stages occurring near the surface close to shore and later stages descending in the water farther from shore (OVM), (d) shore crab larvae (*Pachygrapsus crassipes*, *Hemigrapsus nudus*, *H. oregonensis*) mostly completed development on the inner shelf (<13 km) with early larval stages occurring in the upper water column close to shore, late stages descending in the water farther from shore (OVM), and postlarvae rising to the surface (ROVM), and (e) *Cancer* crab larvae (*C. productus*, *C. oregonensis*, and *C. magister*) migrated to the outer shelf late in development by primarily remaining in the upper water column throughout development. Different patches of larvae in a plot either represent different species or the same species collected on different cruises. Mean sample depths are depicted by white dots. Modified from Morgan et al. [9].

Washington from California during El Niño years when southward flow is weak, the Pacific Decadal Oscillation phase is warm (positive), and water is warm [72]. After initially being introduced to San Francisco Bay in 1989, green crabs spread north in three years of anomalously strong poleward flow reaching Bodega, Tomales, and Humboldt Bays in 1993, Oregon in 1995 or 1996, and Washington and Vancouver Island, British Columbia, in 1998. Poleward expansion during El Niño years has been documented in the CCS for diverse invertebrates and fishes establishing either new populations or pseudopopulations that do not reproduce successfully [73–78].

Evidence for the behavioral regulation of cross-shelf distributions of fish larvae during the peak upwelling season is limited, but consistent cross-shelf structure in larval fish assemblages occurs. Larvae of sculpins, lingcod, and flatfishes with short larval durations occur on the inner shelf (<28 km from shore) and larvae of rockfishes, myctophids, and flatfishes with very long larval durations occur on the outer shelf [79–83]. A distinct larval fish assemblage occurs in the coastal boundary layer by residing close to the substrate in reduced flow, including *Gobiesox maeandricus*, *Clinocottus acuticeps*, *Apodichthys flavidus*, *Anoplarchus purpureus*, *Xiphister mucosus*, *Xiphister atropurpureus*, *Artedius* spp., and *Synchirus gilli* [84]. Farther from shore, fish larvae are most abundant 20–50 m deep [82], suggesting that they may limit offshore transport by avoiding the uppermost water column where Ekman transport is strongest. Larvae of several species

of sole that reside on the inner shelf as adults (butter, English, sand, and slender) appear to avoid surface layers reducing offshore transport [82, 85, 86]. Larvae of several species do reside in the neuston, such as cabezon and sablefish [87, 88], where internal waves and wind relaxations may propel them shoreward. Larvae of other species occur below 50 m, such as slender sole [27, 82, 86], where they may be transported onshore by upwelling. In addition, several species of rockfishes appear to occupy deeper layers as pelagic juveniles [89, 90], suggesting that OVMs may facilitate cross-shelf migrations. Although clear evidence of vertical migrations by fish larvae is limited, DVM has been described in some species of flatfishes [86] and perhaps in some species of rockfishes [83].

3.4.2. Models. Transport was shown to be inherently unpredictable due to the chaotic nature of coastal circulation, especially eddy dynamics, by using numerical particle tracking models of passive larval dispersal during one year of idealized circulation [91–93]. Models also have been developed to evaluate the ability of zooplankton to regulate transport in upwelling regimes, as first proposed for copepods off the coast of Oregon [4] and later extended to other upwelling regimes around the world [56]. Batchelder et al. [94] used a two-dimensional hydrodynamic ecosystem model to show that zooplankton off the coast of Oregon would be transported offshore by remaining in the surface layer, whereas they would complete development nearshore either by remaining

near the bottom or by undertaking DVM. Offshore upwelling flow at the surface is balanced by strong onshore return flow in a relatively thin benthic boundary layer retaining zooplankton nearshore. For DVM, daytime onshore transport of zooplankton compensated for nighttime offshore transport resulting in nearshore retention.

A three-dimensional ROMS model coupled with particle tracking for Monterey Bay showed that simulated zooplankton remaining below the surface throughout the day had high levels of self-recruitment even in this advective region [95]. However, DVM into poleward and onshore subsurface currents during the day does not fully compensate for equatorward and offshore transport in the surface Ekman layer at night failing to retain simulated zooplankton in the region. Alongshore pressure gradients spread onshore return flow more evenly in the lower water column rather than being restricted to a bottom boundary layer, as in the two-dimensional model used by Batchelder et al. [94]. Hence, onshore return flow below the surface is weak relative to offshore Ekman transport at the surface, so that onshore transport of zooplankton at depth during the daytime does not compensate for their offshore transport near the surface at night.

In a second study for Monterey Bay, larval dispersal by the barnacle, *Balanus glandula*, was investigated by incorporating larval development as a function of temperature and chlorophyll concentration and OVM in a ROMS model [96]. Settlement increases during relaxation events consistent with previous studies in the area [31, 32], and more larvae are delivered nearshore poleward than equatorward of the bay. Larvae disperse farther from sites located poleward than equatorward of the bay, and they travel only tens of kilometers despite the potential for them to disperse much farther. The effect of OVM on dispersal was not explored by contrasting it with passive movement or depth preferences.

Several studies have been conducted using ROMS models to investigate the effect of the depth of larval release or subsequent depth preferences on larval dispersal and connectivity. Kim and Barth [97] compared passive larval dispersal and connectivity at six depths (1–75 m) off the Oregon coast for 120 days during the summer upwelling season of 2001. Cape Perpetua is a retention zone, and the Heceta Bank is both a source and destination. Larvae are retained nearshore after prevailing upwelling winds relax or reverse for 6 to 8 days.

Petersen et al. [98] simulated depth preferences (1, 7, 20, 40, and 70 m deep) of rockfish (*Sebastes* spp.) larvae along 730 km of the central California coast. Simulated larvae were released within 75 km from shore at 2-day intervals for currents averaged across 4 years (2000–2003). During the upwelling season, near-surface larvae originating nearshore are transported offshore, whereas deeper larvae are transported poleward. During winter, most larvae are transported poleward at all depths. Larvae remaining nearshore are transported ~50 km compared to ~150 km for those over the midshelf and slope. High rates of larval retention on the shelf occur for releases at ≥ 20 m during summer and at all depths during winter across this highly advective region.

Drake et al. [99] examined the effect of the depth of larval release on dispersal and connectivity by releasing simulated

larvae within 10 km of the coast from Palos Verde, southern California, to Heceta Bank, Oregon, and either remaining in surface waters (≤ 20 m deep) or at depth (40–60 m deep) for 30–60 days or 120–180 days over 7 years (2000–2006). For larvae released near the surface with moderate larval durations, mean dispersal distances range from ~10–230 km (± 130 –220 km SD). Dispersal is poleward throughout the year in southern California, and it generally is poleward from summer through winter farther north; however, dispersal is equatorward during spring in northern California. Larval connectivity generally is similar among years and is strongly influenced by major geographic features, such as the Gulf of the Farallones and Cape Mendocino. Point Conception does not act as a barrier to dispersal for source regions in the Southern California Bight, as is often proposed [100]. Larvae released at 40–60 m with moderate larval durations shift mean dispersal distances poleward by 50–250 km, increase settlement by as much as 100% during spring and summer, and result in less patchy settlement across the region, even though larvae are quickly redistributed vertically following release due to the three-dimensional currents and random walk of the model. These patterns are strengthened when larvae complete development at depth, as found by Petersen et al. [98]. Upon release, these larvae are transported onshore and poleward in upwelled bottom waters of the inshore countercurrent and poleward transport by the upper portions of the California undercurrent before being mixed into the surface layer, thereby reducing dispersion and increasing settlement.

To examine the effect of larval behavior on transport and connectivity, Drake et al. [10] incorporated a full suite of idealized larval behaviors into their high-resolution circulation model yielding the first comprehensive connectivity model. Passive dispersal was contrasted with simulated depth preferences (5 m versus 30 m deep), DVM, OVM, ROVM, and OVM plus DVM during the peak upwelling season (spring) for a larval duration of 30–60 days. Vertical swimming greatly affects cross-shelf and alongshore dispersal with each behavior resulting in a unique structure of alongshore settlement relative to passive larvae (Figure 6). For depth preferences, larvae are 500 times more likely to be retained adjacent to the coast and 145 times more likely to settle along the coast when they swim below the surface layer. Consequently, avoiding the surface boundary layer increases settlement almost everywhere throughout the CCS by at least an order of magnitude, whereas remaining in the surface boundary layer reduces settlement catastrophically from Point Conception to Point Arena with a weaker effect poleward of Cape Mendocino. OVM increases settlement by ~30%, especially between Monterey Bay and Bodega Bay. ROVM increases settlement over most of the study area (Point Conception to Monterey Bay) with nominal equatorward dispersal equatorward of Monterey Bay. Two to three times fewer larvae settle when undertaking ROVM than OVM, because they are near-surface and are swept offshore when competent to settle. DVM increases settlement in regional hotspots without greatly altering overall settlement in the CCS, because both DVM and passive larvae spend similar amounts of time near the surface.

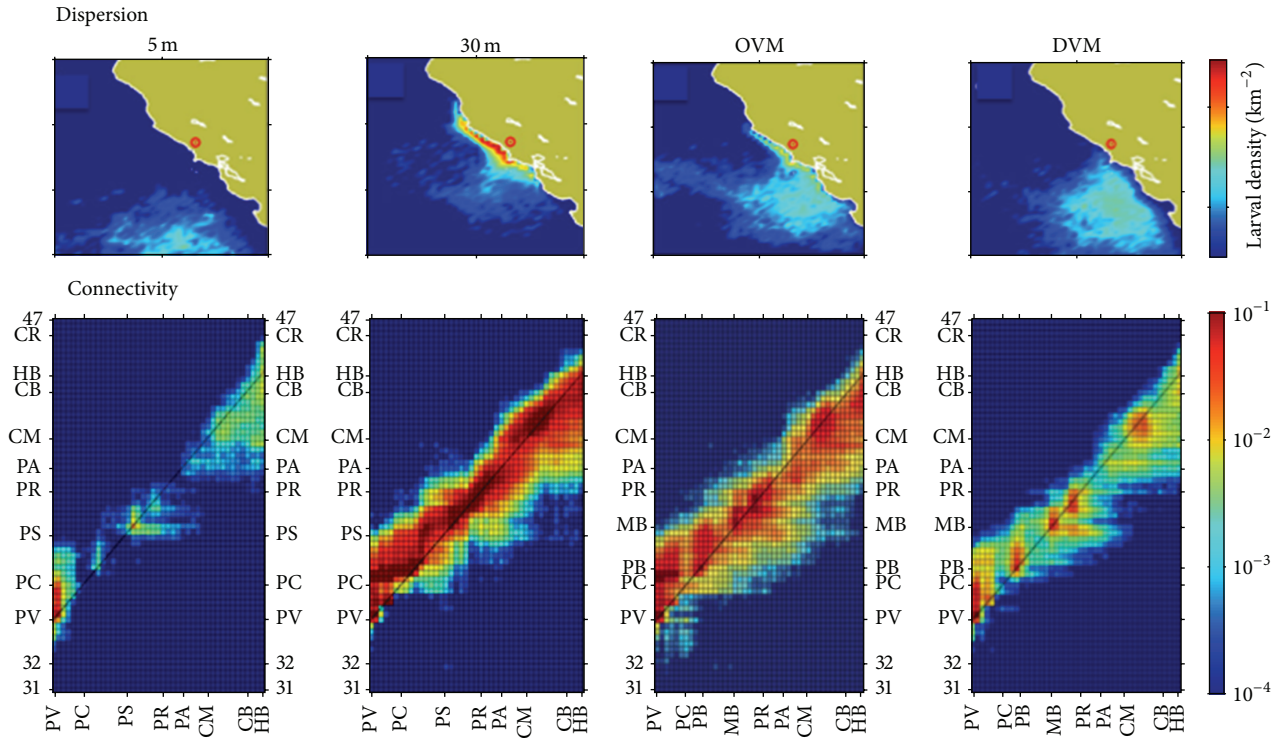


FIGURE 6: Numerical model of larval dispersion and connectivity for larvae (\log_{10} density color scale) regulating depth in four ways during the peak upwelling season (spring) in the California Current System: maintaining a depth of 5 m, maintaining a depth of 30 m, undertaking an ontogenetic vertical migration (OVM) from 5 to 30 m deep, and undertaking a diel vertical migration (DVM) from 5 to 30 m deep. Dispersion after 30 days for larvae released near Bodega Head, California (\square) and connectivity after 30 to 60 days for larvae released and recruiting at sites from Palos Verdes, California, to Heceta Bank, Oregon. Diagonal line in connectivity matrices represents local recruitment with intensity above it representing poleward dispersal and intensity below it representing equatorward dispersal. Palos Verdes (PV), Point Conception (PC), Point Buchon (PB), Monterey Bay (MB), Point Reyes (PR), Point Arena (PA), Cape Mendocino (CM), Cape Blanco (CB), and Heceta Bank (HB). Modified from Drake et al. [10].

3.5. Behavioral Regulation of Larval Transport in Estuaries.

Larvae regulate depth effectively in San Francisco Bay, California, which is the largest estuary on the west coast of the USA [101]. OVM, TVM, or RDVM are displayed by four species of larval and young juvenile fishes in the low-salinity zone of the upper estuary. OVM occurs in three species (native longfin smelt (*Spirinchus thaleichthys*), native delta smelt (*Hypomesus transpacificus*), and exotic yellowfin goby (*Acanthogobius flavimanus*)), TVM occurs in three species (longfin smelt yellowfin goby and exotic striped bass (*Morone saxatilis*)) and RDVM occurs in three species (longfin smelt, delta smelt and striped bass). OVM and TVM occur in the ship channel, facilitating retention, whereas RTVM occurs beyond the ship channel, which may enhance dispersion among shallow bays. Thus, behavioral plasticity in vertical migration occurs at the two locations.

Larvae also regulate depth effectively in San Diego Bay, California, and Willapa Bay, Washington, where RTVM occurs in several species [102, 103]. However, larvae often do not regulate depth effectively in small, low-inflow estuaries typical of the West Coast [6]. In Bodega Harbor, only two (barnacles and pinnotherids) of eight taxa of benthic crustacean larvae displayed depth preferences, even though all of them did so in adjacent coastal waters or the laboratory

[6, 9, 59, 60, 66]. Furthermore, none of them undertook TVM or DVM even though they do in adjacent coastal waters [6, 9, 59, 66]. Vertical mixing and turbulence by tidal flows in the estuary may largely overwhelm larval behaviors. It is unlikely that the sampling design failed to detect vertical migrations in the estuary, because sampling spanned the water column, including the sediment-water interface. Low freshwater inflow into the estuary also may not have cued RTVM, because an endogenous RTVM was apparent for one of these species (*H. oregonensis*) from neighboring fresher San Francisco Bay [104].

Interspecific differences in cross-shore distributions occur in low-flow estuaries along the West Coast even though larval behaviors can be disrupted by turbulent tidal flows or the lack of a low-salinity cue. In Bodega Harbor, barnacle and pinnotherid larvae complete development in nearshore coastal waters by either remaining below the shallow Ekman layer throughout development (barnacles) or rising to the surface at night after winds have subsided (pinnotherids) [9, 48, 57, 59, 66]. By remaining nearshore, larvae can persist in low-inflow estuaries even in the absence of effective depth regulation in the estuary itself [9, 48, 57, 59, 66, 69]. Larvae are exchanged between the estuary and bay over tidal cycles; they are transported from

the estuary during ebb tides and transported back into the estuary during flood tides with an overall net exchange into the estuary [6]. Longitudinal tidal exchange is slow in the upper estuary enhancing larval retention [105–107], including retention of at least early stage pinnotherid larvae in Bodega Harbor [6]. Later larval stages of the six other taxa are absent or rare in Bodega Harbor, because they are passively transported offshore, precluding transport back into the estuary by flood tides [6, 9, 48, 57, 59, 66].

4. Humboldt Current System

4.1. Circulation. The Humboldt Current can be ~1000 km wide flowing from southern Chile (~45°S) to northern Peru (~4°S; Figure 4), and it has been classified into three regions [108–111]. Upwelling occurs during the austral summer (January–March) off southern Chile (~30–40°S) and year-round elsewhere in the HCS. A biogeographic boundary occurs at Coquimbo. In the second region, the Humboldt Current bifurcates off southern Peru as fresher, cooler, sub-Antarctic water mainly flows offshore while less flow continues equatorward alongshore until being subducted beneath saline, warm subtropical water of northern Chile. A surface countercurrent sometimes forms, and an intense oxygen minimum zone occurs. In the third region, frequent eddies occur south of 15°S and off Chimbote (9°S), and a biogeographic boundary occurs at San Juan, Peru. Upwelled water meets fresher, warmer tropical water forming the Equatorial Front at the northern limit of the HCS. Like the CCS, the HCS is highly dynamic interannual variation which is especially important off the coast of Peru [1].

4.2. Larval Transport. Depth regulation by larvae determines transport in the HCS with the same or congeneric species showing the same larval transport patterns as in the CCS. RDVM was found to play a role in nearshore larval retention by conducting complementary larval surveys at different spatial and temporal scales on the central coast of Chile [112, 113]. Competent larvae of shallow water gastropod, *Concholepas concholepas*, only occur in the coastal boundary layer <6 km from shore even during strong upwelling by undertaking a RDVM. They occur in the neuston during the daytime while onshore winds are strongest, and they descend at night during the weaker offshore land breeze.

A brief study on the assemblage of decapod larvae in the Gulf of Arauco during the upwelling season indicates that interspecific differences in vertical distribution in two-layer flow facilitate nearshore retention or offshore export [114]. One group of larvae enhances export by occupying seaward-flowing surface waters during the daytime, including *Cancer* spp. and the mole crab, *Emerita analoga*. A second group of larvae enhances retention by remaining deep in the water column or descending during ebb tides, including porcelain crabs (Porcellanidae), pea crabs (*Pinnixa* spp.), hermit crabs (*Pagurus* spp.), and mud shrimp (*Neotrypaea uncinata*). *N. uncinata* undertakes an OVM favoring seaward transport early in development and landward transport late in development. A third group of larvae are imported from offshore larval release sites by undertaking an OVM, including the

spider crabs *Pleuroncodes monodon* and *Libinia clava*. An offshore species of copepod (*Rhincalanus nasutus*) also migrates onshore by undertaking OVM and DVM, and recirculation in the bay facilitates retention [115].

The distribution and abundance of decapod larvae were surveyed at six stations along each of 11 transects across the continental shelf (35 to 37°S) during the upwelling and downwelling seasons [116]. Stations were mostly located beyond the coastal boundary layer, and consequently only larvae of shallow-water species that disperse offshore (*E. analoga*, *Blepharipoda spinimana*, *N. uncinata*, and *Pagurus* spp.) or shelf species (*L. granaria*) were abundant. The water column was evenly partitioned to determine vertical distributions (0–50, 50–100, 100–150, and 150–250 m) at equatorward stations and every 25 m to 100 m and then every 50 m at shallower depth stations. Consequently fine-scale depth preferences in the surface layer and vertical migration may not have been detected. Larvae of the four shallow-water species disperse offshore in the surface layer, and possible DVM and OVM by two of the taxa (*N. uncinata* and *Pagurus* spp.) may return late stages closer to shore. Larvae of the shelf species (*L. granaria*) occur deepest in the water column.

Larvae of the squat lobster (*Pleuroncodes monodon*) also were collected during these cross-shelf cruises [117]. Larvae do not appear to undertake DVM but postlarvae and juveniles do. A numerical model indicated that passive larvae are advected equatorward from the study area, and <1% of simulated larvae recruit to local nursery grounds. DVM increases recruitment to nursery grounds. Larvae released by a population equatorward of the study area recruit late in the upwelling season.

In a follow-up study of larval dispersal and connectivity along the coast of central Chile, Aiken et al. [118] explored the effect of larval behavior and climate change using numerical ocean simulations of present and future winds. Projected future winds intensify upwelling circulation, which results in mean surface cooling of 1°C over much of the domain, an increase in the strength of the poleward undercurrent and a more energetic mesoscale eddy field. Simulated larvae that sink from the surface Ekman layer into the onshore flow beneath settle much more than passive larvae.

5. Iberia Current System

5.1. Circulation. The Portugal Current flows equatorward along the Iberian Peninsula (Figure 4), and weak upwelling occurs during the peak upwelling season (spring to summer) along the narrow continental shelf [119, 120]. The Iberian Peninsula is divided into northwestern and southwestern regions at Cape Mondego. Substantial runoff in these two regions forms the Western Iberian Buoyant Plume, which typically flows poleward and spreads farther from shore during strong upwelling. Upwelling-relaxation cycles last 10 to 15 days, and flow sometimes reverses along the inner shelf. During the peak upwelling season (spring and summer), upwelling along the coast broadens and upwelling jets form at capes, such as Cape Roca (~38°N). At the end of the peak upwelling season in September, the jets are no longer persistent and subsurface flow along the continental shelf

surfaces as the meandering, warm, saline Iberian Poleward Current, sometimes forming anticyclonic eddies. In the third region, the Azores Current flows into the Gulf of Cadiz, where a change in the orientation of the coastline at Cape Saint Vincent and exchange with the Mediterranean Sea interrupt the continuity of the upwelling system. The Azores Current usually flows eastward into the Gulf along the southern shelf break; however, it sometimes continues equatorward or rarely turns westward to form a cold filament. Following the spring transition, weak intermittent westerly winds generate weak local upwelling alternating with a warm coastal countercurrent that sometimes turns poleward along the Atlantic shelf.

5.2. Larval Transport. Behaviorally mediated larval transport has been well studied off the coast of the Iberian Peninsula. Barnacles and some species of decapods complete development on the inner shelf, whereas green crabs and other species of decapods migrate farther onto the shelf [121–124]. Investigators have focused on the importance of DVM between the surface and the bottom undercurrent in maintaining these distributions [121–123], but OVM also was recently found to play an important role in regulating cross-shelf transport of decapod larvae [124]. Further, residing in landward flowing bottom waters and rising to the surface at night retains *Octopus vulgaris* close to shore [125].

Numerical modeling studies of the Iberian Shelf indicate that DVM contributes to retaining green crab larvae on the shelf and establishing population connectivity [121, 126, 127]. Most of the larvae undertaking simulated DVM are retained within the shelf and advected alongshore during upwelling-relaxation cycles. In contrast, larvae that do not undertake DVM are swept offshore [121, 126]. In the most recent version of the model [127], larval recruitment was monitored daily at the Aveiro estuary, Portugal, during the reproductive season for 2 years and coupled with DVM, temperature-dependent growth, and mortality. Larval recruitment was compared with model predictions using a stepwise approach to test different behavioral, growth, and mortality scenarios that progressively constrained potential dispersal distance. Without DVM, simulated larvae are advected a mean distance of 200 km offshore, whereas with DVM, larvae are concentrated within 22 km from shore and few are advected beyond the shelf break, matching results from cross-shelf surveys [123, 128]. The location of larval pools along the coast and the delivery of postlarvae to estuarine settlement habitats depend on local larval production from estuaries, growth, and alternating alongshore advection. Postlarvae recruiting onshore encounter estuarine plumes, whereupon dissolved chemical cues may stimulate sinking to bottom waters and facilitate transport into the estuary via gravitation circulation and TVM [129]. Average realized dispersal distances are 75 km and 275 km (for larvae supplied from equatorward and poleward estuaries, resp.), reflecting the prevailing equatorward flow during the reproductive season. Examining the entire Iberian coast for 8 years revealed spatial patterns of connectivity and interannual variation in alongshore transport, including the North Atlantic Oscillation [130].

Both larvae and postlarvae of green crabs effectively regulate depth in small estuaries. Newly hatched larvae

undertake RTVM upon hatching during spring tides, thereby expediting transport onto the shelf, whereas the nocturnal TVM by postlarvae expedites transport up the estuary [131–133]. Larvae of other decapods also behaviorally mediate larval transport to and from the estuary via depth preferences, RTVM, and DVM [134].

Sole (*Solea solea* and *Solea senegalensis*) spawn offshore and migrate up estuaries by undertaking TVM [135]. The effect of river drainage, the North Atlantic Oscillation index, and alongshore wind velocity on larval recruitment of these species to the Tagus estuary, Portugal, was investigated from 1988 to 2006, but only river drainage increases larval recruitment. Larger estuarine plumes during wet years increase the probability that sole will locate estuaries.

6. Larval Behavior Mediates Transport in Upwelling Regimes Worldwide

The long-standing view that larvae are transported offshore in upwelling conditions has become entrenched even though it was based on the results of a single larval survey coupled with settlement studies and its intuitive appeal [25]. Although interannual variation in upwelling was correlated with the seaward larval limit of one species of barnacle off central California (with notable outliers), larvae were not surveyed within 8 km of shore, where barnacles and most other nearshore species complete development.

Subsequent larval surveys have demonstrated that larval behavior effectively regulates cross-shelf transport in upwelling regimes as it does elsewhere in the world. Similar interspecific differences in the extent of cross-shelf transport have been documented for many species across the CCS, including the strong persistent upwelling regime off northern California, the intermittent upwelling regime off Oregon, and the weaker upwelling regime off southern California. Furthermore, interspecific distances of cross-shelf transport have been maintained off northern California and Oregon over the years despite interannual differences in the intensity of upwelling. Moreover, larvae do not appear to be advected farther offshore by the upwelling jet from major headlands. Interspecific differences in the extent of cross-shelf transport also are evident in both persistent and intermittent upwelling regimes in the ICS and HCS. Although cross-shelf larval surveys of nearshore benthic species have yet to be conducted in the Benguela Current System, it is highly likely that consistent interspecific differences in cross-shelf larval transport will be found there too.

Passive larval advection and diffusion alone cannot account for the interspecific differences in cross-shelf distributions. Behavior must be important in mediating these migrations, because larvae of different species and different stages of the same species migrate in opposite directions at the same time. Concentrations offshore are dramatically lower than those onshore right after hatching, even when corrected for vertical mixing into the higher volume of a deepening water column. Further, larval concentrations of later larval stages of some taxa remain similar or increase on the middle and outer shelf rather than diminishing offshore (Figure 5).

Interspecific differences in cross-shelf distributions of post-larvae are not simply related to differences in larval duration. For example, crustacean species that develop offshore pass through as few as two larval stages while those developing nearshore may have five or more larval stages. Thus, currents alone cannot explain the observed horizontal distributions of larvae, and behavior must be regulating migrations between adult and larval habitats in upwelling regions.

Copepods and larvae of nearshore benthic species share the same basic behaviors (depth preference, OVM, and DVM) for regulating cross-shelf transport. Reverse vertical migrations (ROVM, RDVM) and additional combinations of behaviors mediating transport have been identified for larvae regulating transport of nearshore benthic species (Figure 5). There is a limited number of ways to regulate depth in two-layer circulation to mediate the extent of transport across the shelf, and these suites of behaviors may be widespread in diverse plankton. Because two-layer flow is a characteristic of upwelling regimes, larvae and other plankton should be able to effectively regulate transport across species' ranges in all upwelling regimes. Thus, circulation in upwelling regions is fundamentally similar worldwide and may have selected for simple larval behaviors that enable them to exploit these consistent circulation patterns.

Models exploring larval transport and connectivity usually assume passive dispersal or dispersal in surface currents. These models have provided valuable insights into the role of stochasticity in larval transport as well as a first order approximation of potential dispersal and connectivity. However, neither passive dispersal nor simple dispersal in surface currents adequately characterizes larval dispersal in upwelling regions. The recent inclusion of selected behaviors into models for the CCS and ICS is now showing that larval behavior greatly reduces the alongshore and cross-shore extent of dispersal resulting in more realistic estimates of dispersal and connectivity matrices.

The same interspecific differences in larval behavior mediating larval retention and export in estuaries occur in both the CCS and ICS. However, larval behaviors are best defined in larger, stratified estuaries in the CCS and in small estuaries in the ICS where low-salinity may cue larvae to regulate depth. The lack of a low-salinity signal or turbulent mixing in shallow, low-flow estuaries in the CCS appears to disrupt depth regulation by larvae. In these low-flow estuaries, RTVM facilitating seaward transport requires migration to the bottom boundary layer (next to the seabed) to be effective, and TVM facilitating larval retention has not been detected. Therefore, larval retention in low-inflow estuaries may occur primarily at the head of estuaries, where tidal exchange is weak and longer retention times are observed [102, 105, 106].

7. Future Directions

Considerable progress has been made in understanding the behavioral mediation of larval transport, recruitment, and connectivity in upwelling systems. However, there are

number of areas that would benefit from more attention, and I briefly highlight seven of them below.

Diverse Species. Interspecific differences in cross-shelf distributions and the vertical swimming behaviors that regulate the extent of these horizontal migrations have primarily been conducted for crustaceans. Crustaceans are especially good model organisms, because larvae can be readily identified morphologically and molting through successive larval stages makes it easy to determine the extent of cross-shelf transport and OVM. However, more studies should be conducted on weakly swimming ciliated larvae and strongly swimming fish larvae. Even ciliated larvae regulate depth in the water column, but it remains to be determined how many of the suites of behaviors are used by them to regulate cross-shelf transport. Surprisingly little is known about depth regulation of cross-shelf transport of nearshore fishes in upwelling regimes. This may be partly due to the focus on less tractable commercial shelf species.

Coastal Topography. More studies are needed to understand the effect of coastal topography on larval transport of nearshore benthic species. Limited evidence suggests that larvae of these species may not be displaced far offshore by upwelling jets at headlands. A better understanding of the effect of recirculation features on transport also is needed to determine the extent of retention throughout development as well as entrainment and retention for a portion of the developmental period.

Coastal Boundary Layer. The coastal boundary layer is a pervasive feature that may facilitate nearshore larval retention in upwelling regimes, and it merits far more attention. The effect of spatial and temporal variation in the width of the coastal boundary layer on larval retention has only recently been explored [136]. The coastal boundary layer often is not sampled by ships that cannot safely sample close to shore, and smaller boats are needed to sample this treacherous area. It is even more difficult to sample the area immediately adjacent to rocky shores, where diver propelled plankton tows or pumps from shore are used.

Depth Regulation in Low-Flow Estuaries. Shallow, low-flow estuaries are widespread in upwelling regimes, but the ability of larvae to regulate depth is unclear. Are larvae overcome by strong vertical mixing or are larvae unable to undertake RTVM without low salinity to cue vertical swimming?

Latitudinal Gradient in Recruitment. If the latitudinal gradient in the intensity and persistence upwelling does not affect larval losses to offshore advection, then what is regulating larval recruitment in the CCS, HCS, and ICS? Possibilities include a latitudinal gradient in (1) the frequency and duration of wind reversals forcing larvae onshore, (2) productivity affecting larval production or survival, and (3) the ability to cross the surf zone [137–139].

Realistic Models. Modeling dispersal and connectivity would become more realistic and informative by incorporating the coastal boundary layer into high-resolution models, given

that larvae of most nearshore benthic species complete development there. Investigators also should incorporate more comprehensive suites of larval behaviors mediating transport into these models.

Climate Change. Effective behavioral regulation of larval transport has far reaching consequences for our understanding of the ecology and evolution and conservation and management of marine life in an era of climate change. However, the effect of global climate change on upwelling systems is uncertain. Upwelling may increase concomitantly with intensifying winds or decrease with increasing stratification [140–145]. The extent to which depth regulation compensates for such changes should use realistic models of behaviorally mediated larval transport coupled with numerical ocean simulations of present and future winds and stratification [118]. Changing precipitation and runoff also may affect transport in estuaries by altering the intensity of stratification, mixing, and salinity cues.

Conflict of Interests

The author declares that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

The author thanks of all his co-authors working on larval transport in the CCS over the years for their contributions to the development of the research summarized here (see cited references). This research was funded by the National Science Foundation (Biological Oceanography OCE-0326110) and California Sea Grant (R/FISH-2018) and is a contribution of the Bodega Marine Laboratory.

References

- [1] F. P. Chavez and M. Messié, “A comparison of Eastern Boundary Upwelling Ecosystems,” *Progress in Oceanography*, vol. 83, no. 1–4, pp. 80–96, 2009.
- [2] P. Fréon, J. Aristegui, A. Bertrand et al., “Functional group biodiversity in Eastern Boundary Upwelling Ecosystems questions the wasp-waist trophic structure,” *Progress in Oceanography*, vol. 83, no. 1–4, pp. 97–106, 2009.
- [3] W. M. Graham and J. L. Largier, “Upwelling shadows as near-shore retention sites: the example of Northern Monterey Bay,” *Continental Shelf Research*, vol. 17, no. 5, pp. 509–532, 1997.
- [4] W. T. Peterson, C. B. Miller, and A. Hutchinson, “Zonation and maintenance of copepod populations in the Oregon upwelling zone,” *Deep Sea Research A*, vol. 26, no. 5, pp. 467–494, 1979.
- [5] R. H. Parrish, C. S. Nelson, and A. Bakun, “Transport mechanisms and reproductive success of fishes in the California current,” *Biological Oceanography*, vol. 1, no. 2, pp. 175–203, 1981.
- [6] S. G. Morgan, J. L. Fisher, S. T. McAfee et al., “Larval transport and flux in a low-inflow estuary,” *Estuaries and Coasts*, 2014.
- [7] J. L. Largier, “Low-inflow estuaries: hypersaline, inverse and thermal scenarios,” in *Contemporary Issues in Estuarine Physics*, A. Valle-Levinson, Ed., pp. 247–271, Cambridge University Press, Cambridge, UK, 2010.
- [8] N. J. Nidzieko and S. G. Monismith, “Contrasting seasonal and fortnightly variations in the circulation of a seasonally inverse estuary, Elkhorn Slough, California,” *Estuaries and Coasts*, vol. 36, no. 1, pp. 1–17, 2013.
- [9] S. G. Morgan, J. L. Fisher, S. H. Miller, S. T. McAfee, and J. L. Largier, “Nearshore larval retention in a region of strong upwelling and recruitment limitation,” *Ecology*, vol. 90, no. 12, pp. 3489–3502, 2009.
- [10] P. T. Drake, C. A. Edwards, S. G. Morgan, and E. P. Dever, “Influence of behavior on larval dispersal and population connectivity in a realistic simulation of the California current system,” *Journal of Marine Research*, vol. 34, pp. 317–350, 2013.
- [11] C. M. Young, “Behavior and locomotion during the dispersal phase of larval life,” in *Ecology of Marine Invertebrate Larvae*, L. McEdward, Ed., CRC Press, Boca Raton, Fla, USA, 1995.
- [12] H. Queiroga and J. Blanton, “Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae,” *Advances in Marine Biology*, vol. 47, pp. 107–214, 2004.
- [13] C. E. Epifanio, “Transport of invertebrate larvae between estuaries and the continental shelf,” in *Proceedings of the American Fisheries Society Symposium*, vol. 3, pp. 104–114, 1988.
- [14] C. E. Epifanio and R. W. Garvine, “Larval transport on the Atlantic continental shelf of North America: a review,” *Estuarine, Coastal and Shelf Science*, vol. 52, no. 1, pp. 51–77, 2001.
- [15] S. G. Morgan, “Larval migration between the Hudson River estuary and New York Bight,” in *The Hudson River Estuary*, J. Levinton, Ed., pp. 157–170, Oxford University Press, 2006.
- [16] B. M. Hickey, “The California Current system—hypotheses and facts,” *Progress in Oceanography*, vol. 8, pp. 191–270, 1979.
- [17] B. Hickey, “Coastal oceanography of Western North America from the tip of Baja California to Vancouver Island,” in *The Sea: Ideas and Observations on Progress in the Study of the Seas*, A. Robinson and K. H. Brink, Eds., pp. 10339–10368, John Wiley and Sons, New York, NY, USA, 1998.
- [18] A. Huyer, “Coastal upwelling in the California current system,” *Progress in Oceanography*, vol. 12, no. 3, pp. 259–284, 1983.
- [19] A. Huyer, J. H. Fleischbein, J. Keister et al., “Two coastal upwelling domains in the northern California current system,” *Journal of Marine Research*, vol. 63, no. 5, pp. 901–929, 2005.
- [20] D. L. Mackas, “Interdisciplinary oceanography of the western north American continental margin: Vancouver Island to the tip of Baja California,” in *The Sea*, A. R. Robinson and K. Brink, Eds., vol. 14, pp. 441–501, Harvard University Press, Cambridge, Mass, USA, 2006.
- [21] B. M. Hickey and N. S. Banas, “Why is the northern end of the California Current System so productive?” *Oceanography*, vol. 21, no. 4, pp. 90–107, 2008.
- [22] D. M. Checkley Jr. and J. A. Barth, “Patterns and processes in the California Current System,” *Progress in Oceanography*, vol. 83, no. 1–4, pp. 49–64, 2009.
- [23] S. G. Morgan, “The larval ecology of marine communities,” in *Marine Community Ecology*, M. D. Bertness, S. D. Gaines, and M. E. Hay, Eds., pp. 159–181, Sinauer, Sunderland, Mass, USA, 2001.
- [24] P. M. Yoshioka, “Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*,” *Ecology*, vol. 63, no. 2, pp. 457–468, 1982.
- [25] J. Roughgarden, S. Gaines, and H. Possingham, “Recruitment dynamics in complex life cycles,” *Science*, vol. 241, no. 4872, pp. 1460–1466, 1988.

- [26] B. A. Menge and J. P. Sutherland, "Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment," *American Naturalist*, vol. 130, pp. 730–757, 1987.
- [27] E. P. Bjorkstedt, *Remote sensing and ichthyoplankton ecology of coastal upwelling fronts off central California [Ph.D. thesis]*, Stanford University, 1998.
- [28] E. P. Bjorkstedt, L. K. Rosenfeld, B. A. Grantham, Y. Shkedy, and J. Roughgarden, "Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region," *Marine Ecology Progress Series*, vol. 242, pp. 215–228, 2002.
- [29] A. Sadrozinski, *Cross-shelf ichthyoplankton distributions in relation to hydrography off Northern California, with special attention to larval rockfishes [M.S. thesis]*, Humboldt State University, 2008.
- [30] Y. Shkedy and J. Roughgarden, "Barnacle recruitment and population dynamics predicted from coastal upwelling," *Oikos*, vol. 80, no. 3, pp. 487–498, 1997.
- [31] T. M. Farrell, D. Bracher, and J. Roughgarden, "Cross-shelf transport causes recruitment to intertidal populations in central California," *Limnology & Oceanography*, vol. 36, no. 2, pp. 279–288, 1991.
- [32] J. Roughgarden, J. T. Pennington, D. Stoner, S. Alexander, and K. Miller, "Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations of central California," *Acta Oecologica*, vol. 12, no. 1, pp. 35–51, 1992.
- [33] S. R. Connolly and J. Roughgarden, "A latitudinal gradient in northeast pacific intertidal community structure: Evidence for an oceanographically based synthesis of marine community theory," *American Naturalist*, vol. 151, no. 4, pp. 311–326, 1998.
- [34] S. R. Connolly, B. A. Menge, and J. Roughgarden, "A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean," *Ecology*, vol. 82, no. 7, pp. 1799–1813, 2001.
- [35] B. A. Menge, C. Blanchette, P. Raimondi et al., "Species interaction strength: testing model predictions along an upwelling gradient," *Ecological Monographs*, vol. 74, no. 4, pp. 663–684, 2004.
- [36] B. R. Broitman, C. A. Blanchette, A. Menge et al., "Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States," *Ecological Monographs*, vol. 78, no. 3, pp. 403–421, 2008.
- [37] A. L. Shanks and G. L. Eckert, "Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox," *Ecological Monographs*, vol. 75, no. 4, pp. 505–524, 2005.
- [38] J. E. Byers and J. M. Pringle, "Going against the flow: retention, range limits and invasions in advective environments," *Marine Ecology Progress Series*, vol. 313, pp. 27–41, 2006.
- [39] T. A. Ebert and M. P. Russell, "Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands," *Limnology & Oceanography*, vol. 33, no. 2, pp. 286–294, 1988.
- [40] S. E. Alexander and J. Roughgarden, "Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model," *Ecological Monographs*, vol. 66, no. 3, pp. 259–275, 1996.
- [41] J. A. Barth, S. D. Pierce, and R. L. Smith, "A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California current system," *Deep-Sea Research II*, vol. 47, no. 5–6, pp. 783–810, 2000.
- [42] F. P. Wilkerson, A. M. Lassiter, R. C. Dugdale, A. Marchi, and V. E. Hogue, "The phytoplankton bloom response to wind events and upwelled nutrients during the CoOP WEST study," *Deep-Sea Research Part II: Topical Studies in Oceanography*, vol. 53, no. 25–26, pp. 3023–3048, 2006.
- [43] C. M. Halle and J. L. Largier, "Surface circulation downstream of the Point Arena upwelling center," *Continental Shelf Research*, vol. 31, no. 12, pp. 1260–1272, 2011.
- [44] S. R. Wing, L. W. Botsford, J. L. Largier, and L. E. Morgan, "Spatial structure of relaxation events and crab settlement in the northern California upwelling system," *Marine Ecology Progress Series*, vol. 128, no. 1–3, pp. 199–211, 1995.
- [45] S. R. Wing, L. W. Botsford, S. V. Ralston, and J. L. Largier, "Mero-planktonic distribution and circulation in a coastal retention zone of the northern California upwelling system," *Limnology and Oceanography*, vol. 43, no. 7, pp. 1710–1721, 1998.
- [46] M. Roughan, A. J. Mace, J. L. Largier, S. G. Morgan, J. L. Fisher, and M. L. Carter, "Subsurface recirculation and larval retention in the lee of a small headland: a variation on the upwelling shadow theme," *Journal of Geophysical Research C: Oceans*, vol. 110, no. 10, 2005.
- [47] A. J. Mace and S. G. Morgan, "Larval accumulation in the lee of a small headland: implications for the design of marine reserves," *Marine Ecology Progress Series*, vol. 318, pp. 19–29, 2006.
- [48] S. G. Morgan, J. L. Fisher, and J. L. Largier, "Larval retention, entrainment, and accumulation in the lee of a small headland: recruitment hot spots along windy coasts," *Limnology and Oceanography*, vol. 56, no. 1, pp. 161–178, 2011.
- [49] C. B. Woodson, M. A. McManus, J. A. Tyburczy et al., "Coastal fronts set recruitment and connectivity patterns across multiple taxa," *Limnology and Oceanography*, vol. 57, no. 2, pp. 582–596, 2012.
- [50] P. J. S. Franks, "Sink or swim: accumulation of biomass at fronts," *Marine Ecology Progress Series*, vol. 82, pp. 1–12, 1992.
- [51] C. B. Woodson and M. A. McManus, "Foraging behavior can influence dispersal of marine organisms," *Limnology and Oceanography*, vol. 52, no. 6, pp. 2701–2709, 2007.
- [52] L. E. Woodson, B. K. Wells, C. B. Grimes, R. P. Franks, J. A. Santora, and M. H. Carr, "Water and otolith chemistry identify exposure of juvenile rockfish to upwelled waters in an open coastal system," *Marine Ecology Progress Series*, vol. 473, pp. 261–273, 2013.
- [53] D. B. Eggleston, D. A. Armstrong, W. E. Elis, and W. S. Patton, "Estuarine fronts as conduits for larval transport: hydrodynamics and spatial distribution of Dungeness crab postlarvae," *Marine Ecology Progress Series*, vol. 164, pp. 73–82, 1998.
- [54] A. Mcculloch and A. L. Shanks, "Topographically generated fronts, very nearshore oceanography and the distribution and settlement of mussel larvae and barnacle cyprids," *Journal of Plankton Research*, vol. 25, no. 11, pp. 1427–1439, 2003.
- [55] A. L. Shanks, A. Mcculloch, and J. Miller, "Topographically generated fronts, very nearshore oceanography and the distribution of larval invertebrates and holoplankters," *Journal of Plankton Research*, vol. 25, no. 10, pp. 1251–1277, 2003.
- [56] W. Peterson, "Life cycle strategies of copepods in coastal upwelling zones," *Journal of Marine Systems*, vol. 15, no. 1–4, pp. 313–326, 1998.
- [57] S. G. Morgan, J. L. Fisher, A. J. Mace, L. Akins, A. M. Slaughter, and S. M. Bollens, "Cross-shelf distributions and recruitment of crab postlarvae in a region of strong upwelling," *Marine Ecology Progress Series*, vol. 380, pp. 173–185, 2009.

- [58] K. J. Nickols, S. H. Miller, B. Gaylord, S. G. Morgan, and J. L. Largier, "Spatial differences in larval supply within the coastal boundary layer impact availability to shoreline habitats," *Marine Ecology Progress Series*, vol. 494, pp. 191–203, 2013.
- [59] S. G. Morgan and J. L. Fisher, "Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast," *Marine Ecology Progress Series*, vol. 404, pp. 109–126, 2010.
- [60] S. H. Miller and S. G. Morgan, "Interspecific differences in depth preference: regulation of larval transport in an upwelling system," *Marine Ecology Progress Series*, vol. 476, pp. 301–306, 2013.
- [61] A. Genin, J. S. Jaffe, R. Reef, C. Richter, and P. J. S. Franks, "Swimming against the flow: a mechanism of zooplankton aggregation," *Science*, vol. 308, no. 5723, pp. 860–862, 2005.
- [62] A. L. Shanks and L. Brink, "Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis," *Marine Ecology Progress Series*, vol. 302, pp. 1–12, 2005.
- [63] J. Pineda, "An internal tidal bore regime at nearshore stations along western U.S.A.: predictable upwelling within the lunar cycle," *Continental Shelf Research*, vol. 15, no. 8, pp. 1023–1041, 1995.
- [64] A. L. Shanks, "Mechanisms of cross-shelf dispersal of larval invertebrates and fishes," in *Ecology of Marine Invertebrate Larvae*, L. McEdward, Ed., pp. 323–367, CRC Press, Boca Raton, Fla, USA, 1995.
- [65] R. C. Hobbs and L. W. Botsford, "Diel vertical migration and timing of metamorphosis of larvae of the Dungeness crab *Cancer magister*," *Marine Biology*, vol. 112, no. 3, pp. 417–428, 1992.
- [66] S. G. Morgan, J. L. Fisher, S. T. McAfee, J. L. Largier, and C. M. Hallea, "Limited recruitment during relaxation events: larval advection and behavior in an upwelling system," *Limnology and Oceanography*, vol. 57, no. 2, pp. 457–470, 2012.
- [67] R. Lough, *Dynamics of crab larvae (Anomura, Brachyura) off the Central Oregon Coast, 1969–1971 [Ph.D. thesis]*, OSU, Corvallis, Ore, USA, 1974.
- [68] J. L. Fisher, W. T. Peterson, and S. G. Morgan, "Does latitudinal variation in the intensity and persistence of upwelling regulate larval advection and supply?" *Marine Ecology Progress Series*, vol. 503, pp. 123–137, 2014.
- [69] A. L. Shanks and R. K. Shearman, "Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling," *Marine Ecology Progress Series*, vol. 385, pp. 189–204, 2009.
- [70] F. J. Tapia and J. Pineda, "Stage-specific distribution of barnacle larvae in nearshore waters: potential for limited dispersal and high mortality rates," *Marine Ecology Progress Series*, vol. 342, pp. 177–190, 2007.
- [71] F. J. Tapia, C. DiBacco, J. Jarrett, and J. Pineda, "Vertical distribution of barnacle larvae at a fixed nearshore station in southern California: Stage-specific and diel patterns," *Estuarine, Coastal and Shelf Science*, vol. 86, no. 2, pp. 265–270, 2010.
- [72] S. B. Yamada and P. M. Kosro, "Linking ocean conditions to year class strength of the invasive European green crab, *Carcinus maenas*," *Biological Invasions*, vol. 12, no. 6, pp. 1791–1804, 2010.
- [73] R. K. Cowen, "Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications," *Journal of Marine Research*, vol. 43, no. 3, pp. 719–742, 1985.
- [74] A. Schoener and D. L. Fluharty, "Biological anomalies off Washington in 1982-83 and other major Niño periods," in *El Niño North: Niño Effects in the Eastern Subarctic Pacific Ocean*, W. S. Wooster and D. L. Fluharty, Eds., pp. 211–225, University of Washington, Washington Sea Grant, Seattle, Wash, USA, 1985.
- [75] W. G. Pearcy and A. Schoener, "Changes in the marine biota coincident with the 1982-1983 El Nino in the northeastern subarctic Pacific Ocean," *Journal of Geophysical Research*, vol. 92, no. C13, pp. 14417–14428, 1987.
- [76] C. Petersen, "Range expansion in the Northeast Pacific by an estuary mud crab—a molecular study," *Biological Invasions*, vol. 8, no. 4, pp. 565–576, 2006.
- [77] C. J. Sorte, W. T. Peterson, C. A. Morgan, and R. L. Emmett, "Larval dynamics of the sand crab, *Emerita analoga*, off the central Oregon coast during a strong El Niño period," *Journal of Plankton Research*, vol. 23, no. 9, pp. 939–944, 2001.
- [78] S. E. Dudas, B. A. Grantham, A. R. Kirincich, B. A. Menge, J. Lubchenco, and J. A. Barth, "Current reversals as determinants of intertidal recruitment on the central Oregon coast," *ICES Journal of Marine Science*, vol. 66, no. 2, pp. 396–407, 2009.
- [79] S. L. Richardson and W. G. Pearcy, "Coastal and oceanic larvae in an area of upwelling off Yaquina Bay, Oregon," *Fishery Bulletin*, vol. 75, pp. 125–145, 1977.
- [80] S. L. Richardson, J. L. Laroche, and M. D. Richardson, "Larval fish assemblages and associations in the north-east Pacific Ocean along the Oregon coast, winter-spring 1972–1975," *Estuarine and Coastal Marine Science*, vol. 11, no. 6, pp. 671–699, 1980.
- [81] M. J. Doyle, K. L. Mier, M. S. Busby, and R. D. Brodeur, "Regional variation in springtime ichthyoplankton assemblages in the northeast Pacific Ocean," *Progress in Oceanography*, vol. 53, no. 2–4, pp. 247–281, 2002.
- [82] T. D. Auth and R. D. Brodeur, "Distribution and community structure of ichthyoplankton off the coast of Oregon, USA, in 2000 and 2002," *Marine Ecology Progress Series*, vol. 319, pp. 199–213, 2006.
- [83] T. D. Auth, R. D. Brodeur, and K. M. Fisher, "Diel variation in vertical distribution of an offshore ichthyoplankton community off the Oregon coast," *Fishery Bulletin*, vol. 105, no. 3, pp. 313–326, 2007.
- [84] J. B. Marliave, "Lack of planktonic dispersal of rocky intertidal fish larvae," *Transactions of the American Fisheries Society*, vol. 115, pp. 149–154, 1986.
- [85] H. M. Ureña, *Distribution of the eggs and larvae of some flatfishes (Pleuronectiformes) off Washington, Oregon, and northern California, 1980–1983 [M.S. thesis]*, Oregon State University, 1989.
- [86] K. M. Sakuma, S. Ralston, and D. A. Roberts, "Diel vertical distribution of postflexion larval *Citharichthys* spp. and *Sebastes* spp. off central California," *Fisheries Oceanography*, vol. 8, no. 1, pp. 68–76, 1999.
- [87] J. M. Shenker, "Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon," *Fishery Bulletin*, vol. 86, no. 2, pp. 299–317, 1988.
- [88] J. J. Grover and B. L. Olla, "Food habits of larval sablefish *Anoplopoma fimbria* from the Bering Sea," *Fishery Bulletin*, vol. 88, pp. 811–814, 1990.
- [89] W. H. Lenarz, R. J. Larson, and S. Ralston, "Depth distributions of late larvae and pelagic juveniles of some fishes of the California Current," *CalCOFI Report* 32:41-46, 1991.
- [90] J. R. M. Ross and R. J. Larson, "Influence of water column stratification on the depth distributions of pelagic juvenile rockfishes off central California," *California Cooperative Oceanic Fisheries Investigations Reports*, vol. 44, pp. 65–75, 2003.

- [91] S. Mitarai, D. A. Siegel, and K. B. Winters, "A numerical study of stochastic larval settlement in the California Current system," *Journal of Marine Systems*, vol. 69, no. 3-4, pp. 295-309, 2008.
- [92] D. A. Siegel, S. Mitarai, C. J. Costello et al., "The stochastic nature of larval connectivity among nearshore marine populations," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 105, no. 26, pp. 8974-8979, 2008.
- [93] C. S. Harrison, D. A. Siegel, and S. Mitarai, "Filamentation and eddy-eddy interactions in marine larval accumulation and transport," *Marine Ecology Progress Series*, vol. 472, pp. 27-44, 2013.
- [94] H. P. Batchelder, C. A. Edwards, and T. M. Powell, "Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention," *Progress in Oceanography*, vol. 53, no. 2-4, pp. 307-333, 2002.
- [95] S. D. Carr, X. J. Capet, J. C. McWilliams, J. T. Pennington, and F. P. Chavez, "The influence of diel vertical migration on zooplankton transport and recruitment in an upwelling region: estimates from a coupled behavioral-physical model," *Fisheries Oceanography*, vol. 17, no. 1, pp. 1-15, 2008.
- [96] A. S. Pfeiffer-Herbert, M. A. McManus, P. T. Raimondi, Y. Chao, and F. Chai, "Dispersal of barnacle larvae along the central California coast: a modeling study," *Limnology and Oceanography*, vol. 52, no. 4, pp. 1559-1569, 2007.
- [97] S. Kim and J. A. Barth, "Connectivity and larval dispersal along the Oregon coast estimated by numerical simulations," *Journal of Geophysical Research*, vol. 116, no. 6, Article ID C06002, 2011.
- [98] C. H. Petersen, P. T. Drake, C. A. Edwards, and S. Ralston, "A numerical study of inferred rockfish (*Sebastes* spp.) larval dispersal along the central California coast," *Fisheries Oceanography*, vol. 19, no. 1, pp. 21-41, 2010.
- [99] P. T. Drake, C. A. Edwards, and J. A. Barth, "Dispersion and connectivity estimates along the U.S. west coast from a realistic numerical model," *Journal of Marine Research*, vol. 69, no. 1, pp. 1-37, 2011.
- [100] B. Gaylord and S. D. Gaines, "Temperature or transport? Range limits in marine species mediated solely by flow," *American Naturalist*, vol. 155, no. 6, pp. 769-789, 2000.
- [101] W. A. Bennett, W. J. Kimmerer, and J. R. Burau, "Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low-salinity zone," *Limnology and Oceanography*, vol. 47, no. 5, pp. 1496-1507, 2002.
- [102] C. DiBacco, D. Sutton, and L. McConnico, "Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange," *Marine Ecology Progress Series*, vol. 217, pp. 191-206, 2001.
- [103] J. K. Breckenridge and S. M. Bollens, "Vertical distribution and migration of decapod larvae in relation to light and tides in Willapa Bay, Washington," *Estuaries and Coasts*, vol. 34, no. 6, pp. 1255-1261, 2011.
- [104] S. H. Miller and S. G. Morgan, "Phenotypic plasticity in larval vertical migrations in estuarine and coastal populations," *Journal of Experimental Marine Biology and Ecology*, vol. 449, pp. 45-50, 2013.
- [105] D. B. Chadwick and J. L. Largier, "Tidal exchange at the bay-ocean boundary," *Journal of Geophysical Research*, vol. 104, no. 12, pp. 29901-29924, 1999.
- [106] C. DiBacco and D. B. Chadwick, "Assessing the dispersal and exchange of brachyuran larvae between regions of San Diego Bay, California and nearshore coastal habitats using elemental fingerprinting," *Journal of Marine Research*, vol. 59, no. 1, pp. 53-78, 2001.
- [107] L. Rasmussen, J. L. Largier, and M. Carter, *Circulation study of Bodega Harbor*, Sonoma County Department of Health Services, Environmental Health Division, 2004.
- [108] P. T. Strub, J. Mesías, V. Montecino, J. Rutllant, and S. Salinas, "Coastal ocean circulation off western South America. Coastal segment," in *The Sea*, K. H. Brink and A. R. Robinson, Eds., pp. 273-313, John Wiley & Sons, New York, NY, USA, 1998.
- [109] M. Thiel, E. C. Macaya, E. Acuña et al., "The Humboldt Current System of northern and central Chile—oceanographic processes, ecological interactions and socioeconomic feedback," *Oceanography and Marine Biology*, vol. 45, pp. 195-344, 2007.
- [110] A. Bertrand, R. Guevara-Carrasco, P. Soler, J. Csirke, and F. Chavez, "The Northern Humboldt Current System: ocean dynamics, ecosystem processes, and fisheries," *Progress in Oceanography*, vol. 79, pp. 95-412, 2008.
- [111] V. Montecino and C. B. Lange, "The Humboldt current system: ecosystem components and processes, fisheries, and sediment studies," *Progress in Oceanography*, vol. 83, no. 1-4, pp. 65-79, 2009.
- [112] E. Poulin, A. T. Palma, G. Leiva et al., "Temporal and spatial variation in the distribution of epineustonic competent larvae of *Concholepas concholepas* along the central coast of Chile," *Marine Ecology Progress Series*, vol. 229, pp. 95-104, 2002.
- [113] E. Poulin, A. T. Palma, G. Leiva et al., "Avoiding offshore transport of competent larvae during upwelling events: the case of the gastropod *Concholepas concholepas* in Central Chile," *Limnology and Oceanography*, vol. 47, no. 4, pp. 1248-1255, 2002.
- [114] B. Yannicelli, L. R. Castro, A. Valle-Levinson, L. Atkinson, and D. Figueroa, "Vertical distribution of decapod larvae in the entrance of an equatorward facing bay of central Chile: implications for transport," *Journal of Plankton Research*, vol. 28, no. 1, pp. 19-37, 2006.
- [115] L. R. Castro, P. A. Bernal, and V. A. Troncoso, "Coastal intrusion of copepods: Mechanisms and consequences on the population biology of *Rhincalanus nasutus*," *Journal of Plankton Research*, vol. 15, no. 5, pp. 501-515, 1993.
- [116] B. Yannicelli, L. R. Castro, W. Schneider, and M. Sobarzo, "Crustacean larvae distribution in the coastal upwelling zone off Central Chile," *Marine Ecology Progress Series*, vol. 319, pp. 175-189, 2006.
- [117] B. Yannicelli, L. Castro, C. Parada, W. Schneider, F. Colas, and D. Donoso, "Distribution of Pleuroncodes monodon larvae over the continental shelf of south-central Chile: field and modeling evidence for partial local retention and transport," *Progress in Oceanography*, vol. 92-95, pp. 206-227, 2012.
- [118] C. M. Aiken, S. A. Navarrete, and J. L. Pelegrí, "Potential changes in larval dispersal and alongshore connectivity on the central Chilean coast due to an altered wind climate," *Journal of Geophysical Research: Biogeosciences*, vol. 116, no. G4, Article ID G04026, 2011.
- [119] J. Aristegui, X. A. Álvarez-Salgado, E. D. Barton et al., "Oceanography and fisheries of the Canary Current/Iberian Region of the Eastern North Atlantic," in *The Global Coastal Ocean, Interdisciplinary Regional Studies and Syntheses*, A. R. Robinson and K. H. Brink, Eds., vol. 2, pp. 879-933, Harvard University Press, Cambridge, Mass, USA, 2006.
- [120] J. Aristegui, E. D. Barton, X. A. Álvarez-Salgado et al., "Sub-regional ecosystem variability in the Canary Current

- upwelling,” *Progress in Oceanography*, vol. 83, no. 1–4, pp. 33–48, 2009.
- [121] M. Marta-Almeida, J. Dubert, Á. Peliz, and H. Queiroga, “Influence of vertical migration pattern on retention of crab larvae in a seasonal upwelling system,” *Marine Ecology Progress Series*, vol. 307, pp. 1–19, 2006.
- [122] A. D. Santos, A. M. P. Santos, and D. V. P. Conway, “Horizontal and vertical distribution of cirripede cyprid larvae in an upwelling system off the Portuguese coast,” *Marine Ecology Progress Series*, vol. 329, pp. 145–155, 2007.
- [123] A. Dos Santos, A. M. P. Santos, D. V. P. Conway, C. Bartilotti, P. Lourenço, and H. Queiroga, “Diel vertical migration of decapod larvae in the Portuguese coastal upwelling ecosystem: implications for offshore transport,” *Marine Ecology Progress Series*, vol. 359, pp. 171–183, 2008.
- [124] C. Bartilottii, A. dos Santos, M. Castro, Á. Pelizand, and A. M. P. Santos, “Decapod larval retention within distributional bands in a coastal upwelling ecosystem: a random episode or the rule?,” *Marine Ecology Progress Series*. In Press.
- [125] J. Otero, X. A. Álvarez-Salgado, Á. F. González, M. Gilcoto, and Á. Guerra, “High-frequency coastal upwelling events influence octopus vulgaris larval dynamics on the NW Iberian shelf,” *Marine Ecology Progress Series*, vol. 386, pp. 123–132, 2009.
- [126] A. Peliz, P. Marchesiello, J. Dubert, M. Marta-Almeida, C. Roy, and H. Queiroga, “A study of crab larvae dispersal on the Western Iberian Shelf: physical processes,” *Journal of Marine Systems*, vol. 68, no. 1–2, pp. 215–236, 2007.
- [127] C. P. Domingues, R. Nolasco, J. Dubert, and H. Queiroga, “Model-derived dispersal pathways from multiple source populations explain variability of invertebrate larval supply,” *PloS ONE*, vol. 7, no. 4, Article ID e35794, 2012.
- [128] H. Queiroga, “Distribution and drift of the crab *Carcinus maenas* (L.) (Decapoda, Portunidae) larvae over the continental shelf off northern Portugal in April 1991,” *Journal of Plankton Research*, vol. 18, no. 11, pp. 1981–2000, 1996.
- [129] R. B. Forward Jr. and D. Rittschof, “Photoresponses of crab megalopae in offshore and estuarine waters: Implications for transport,” *Journal of Experimental Marine Biology and Ecology*, vol. 182, no. 2, pp. 183–192, 1994.
- [130] R. Nolasco, J. Dubert, C. P. Domingues, A. Cordeiro Pires, and H. Queiroga, “Model-derived connectivity patterns along the western Iberian Peninsula: asymmetrical larval flow and source-sink cell,” *Marine Ecology Progress Series*, vol. 485, pp. 123–142, 2013.
- [131] H. Queiroga, “Vertical migration and selective tidal stream transport in the megalopa of the crab *Carcinus maenas*,” *Hydrobiologia*, vol. 375–376, pp. 137–149, 1998.
- [132] H. Queiroga, J. D. Costlow, and M. H. Moreira, “Larval abundance patterns of *Carcinus maenas* (Decapoda, Brachyura) in Canal de Mira (Ria de Aveiro, Portugal),” *Marine Ecology Progress Series*, vol. 111, no. 1–2, pp. 63–72, 1994.
- [133] H. Queiroga, J. D. Costlow Jr., and M. H. Moreira, “Vertical migration of the crab *Carcinus maenas* first zoea in an estuary: implications for tidal stream transport,” *Marine Ecology Progress Series*, vol. 149, no. 1–3, pp. 121–132, 1997.
- [134] F. Pereira, R. Pereira, and H. Queiroga, “Flux of decapod larvae and juveniles at a station in the lower Canal de Mira (Ria de Aveiro, Portugal) during one lunar month,” *Invertebrate Reproduction and Development*, vol. 38, no. 3, pp. 183–206, 2000.
- [135] C. Vinagre, M. J. Costa, and H. N. Cabral, “Impact of climate and hydrodynamics on sole larval immigration towards the Tagus estuary, Portugal,” *Estuarine, Coastal and Shelf Science*, vol. 75, no. 4, pp. 516–524, 2007.
- [136] K. J. Nickols, B. Gaylord, and J. L. Largier, “The coastal boundary layer: Predictable current structure decreases alongshore transport and alters scales of dispersal,” *Marine Ecology Progress Series*, vol. 464, pp. 17–35, 2012.
- [137] G. Rilov and D. R. Schiel, “Seascape-dependent subtidal-intertidal trophic linkages,” *Ecology*, vol. 87, no. 3, pp. 731–744, 2006.
- [138] A. L. Shanks, S. G. Morgan, J. MacMahan, and A. J. H. M. Reniers, “Surf zone physical and morphological regime as determinants of temporal and spatial variation in larval recruitment,” *Journal of Experimental Marine Biology and Ecology*, vol. 392, no. 1–2, pp. 140–150, 2010.
- [139] A. Fujimura, A. J. H. M. Reniers, C. B. Paris, A. L. Shanks, J. H. MacMahan, and S. G. Morgan, “Numerical simulations of larval transport into a rip-channeled surf zone,” *Limnology and Oceanography*, vol. 59, no. 4, pp. 1434–1447, 2014.
- [140] A. Bakun, “Global climate change and intensification of coastal ocean upwelling,” *Science*, vol. 247, no. 4939, pp. 198–201, 1990.
- [141] D. Roemmich and J. A. McGowan, “Climatic warming and the decline of zooplankton in the California current,” *Science*, vol. 267, no. 5202, pp. 1324–1326, 1995.
- [142] M. A. Snyder, L. C. Sloan, N. S. Diffenbaugh, and J. L. Bell, “Future climate change and upwelling in the California Current,” *Geophysical Research Letters*, vol. 30, no. 15, 2003.
- [143] A. Bakun and S. J. Weeks, “Greenhouse gas buildup, sardines, submarine eruptions and the possibility of abrupt degradation of intense marine upwelling ecosystems,” *Ecology Letters*, vol. 7, no. 11, pp. 1015–1023, 2004.
- [144] G. Auad, A. Miller, and E. di Lorenzo, “Long-term forecast of oceanic conditions off California and their biological implications,” *Journal of Geophysical Research C*, vol. 111, no. 9, Article ID C09008, 2006.
- [145] G. A. Vecchi, B. J. Soden, A. T. Wittenberg, I. M. Held, A. Leetmaa, and M. J. Harrison, “Weakening of tropical Pacific atmospheric circulation due to anthropogenic forcing,” *Nature*, vol. 441, no. 1, pp. 73–76, 2006.