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Authors
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Edwards, Christopher A
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Shoreward swimming boosts modeled nearshore larval supply and pelagic connectivity in a coastal upwelling region

Patrick T. Drake[a,*], Christopher A. Edwards[a], Steven G. Morgan[b,c], Erin V. Satterthwaite[b,c]

[a] Ocean Sciences Department, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA
[b] Bodega Marine Laboratory, University of California Davis, P. O. Box 247, Bodega Bay, CA 94923, USA
[c] Department of Environmental Science and Policy, University of California Davis, One Shields Avenue, Davis, CA 95616, USA

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ABSTRACT

Larval transport by marine organisms is regulated by a combination of vertical swimming behavior and seasonal reproductive timing, but recent studies suggest horizontal swimming behaviors may also be important. Larvae in highly productive coastal upwelling regions are especially vulnerable to offshore transport and must employ effective dispersal "strategies" to return onshore to suitable settlement sites. Using a primitive-equation numerical model, we investigate how horizontal swimming affects nearshore larval supply and potential settlement and connectivity during climatological spring and summer in central California, a region of persistent coastal upwelling within the California Current System. The addition of shoreward swimming with speeds of 1–7 cm s^{-1} increases nearshore larval supply by a factor of 1.4–13, depending on the speed, timing of its onset, and the vertical swimming behavior of the larvae, which included both diel and ontogenetic vertical migrations. Nearshore larval supply increases approximately linearly with swimming speed integrated over the pelagic larval duration. While pelagic connectivity increases with shoreward swimming for all vertical behaviors investigated, spatial patterns of connectivity, when standardized by nearshore larval supply, are similar with and without horizontal behavior. Onshore swimming broadens the alongshore extent of areas that can act as effective source regions in central California, increasing potential dispersal distances 11–26%. A related statistic, the reverse pelagic connectivity, reveals Monterey Bay and the Gulf of the Farallones as important source regions that should be considered when adaptively managing California's network of marine protected areas.

1. Introduction

For many marine organisms with a sessile or demersal adult phase, dispersal during the larval or pelagic phase is one of the primary determinants of recruitment of new individuals into populations and can be an important driver of population dynamics and community structure (Cowen and Sponaugle, 2009; Hjort, 1914; Roughgarden et al., 1988; Sale, 1991; Thorson, 1964). Without adequate dispersal, species are unable to colonize new areas, share genetic material between subpopulations, or repopulate lost areas after local extinctions or crashes (Jablonski, 1986; Metaxas and Saunders, 2009; Strathmann et al., 2002). Conversely, excess dispersal or "export" away from natal sites may leave many local populations dependent on recruits from elsewhere for survival or maintenance of a minimal population size (Caley et al., 1996; Hastings and Botsford, 2006; Sponaugle et al., 2002). Because of its importance to population dynamics, understanding the magnitude of dispersal, its spatial patterns, and connectivity between subpopulations is critical for the effective design of networks of marine protected areas, or MPAs (Botsford et al., 2001; Burgess et al., 2014; White et al., 2014).

Both biological and physical processes can affect dispersal, defined as the movement of propagules, larvae, spores or eggs, from a release location to a settlement site (Pineda et al., 2007; Sponaugle et al., 2002). Ocean currents have long been presumed to be the dominant driver of marine dispersal (Bradbury and Snelgrove, 2001; Johnson, 1960; Leis, 2006; Metaxas, 2001; Metaxas and Saunders, 2009; Queiroga and Blanton, 2005; Roberts, 1997; Scheltema, 1988). Even larger benthic larvae are generally assumed to have little, if any, effective swimming ability over dispersive space and time scales, acting simply as passive passengers of currents. These effectively passive larvae influence dispersal only indirectly, either (1) through the amount and timing of larval release, potentially capitalizing on different seasonal oceanic advective regimes (Parrish et al., 1981; Shanks and Eckert, 2005), or (2) through the total time spent in the pelagic

* Corresponding author.
E-mail address: pdrake@ucsc.edu (P.T. Drake).

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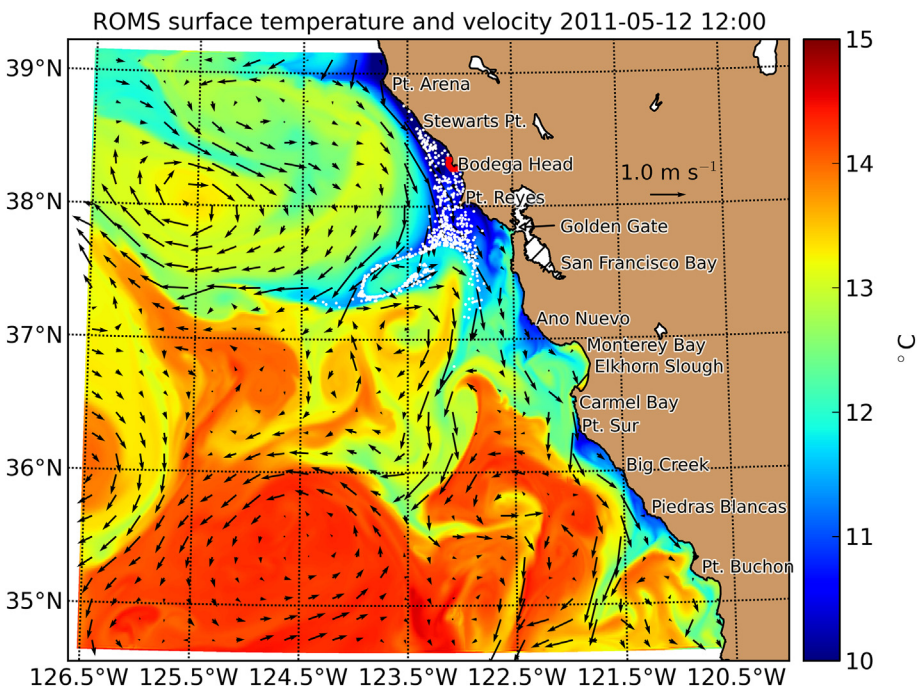

Fig. 1. Daily-averaged model surface temperature and velocities over inner domain on 12 May 2011. White dots show locations of 655 DVM (diel vertical migration) larvae with no horizontal swimming ability released 10 days earlier near Bodega Head (red dots). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Vertical and horizontal swimming behavior scenarios (i.e. vertical-horizontal pairings).

Vertical behavior	Horizontal behavior
In-SBL:	None
Larvae remain in the SBL (surface boundary layer (near 5 m depth)) throughout development until settlement or death	5 cm s^{-1} shoreward beginning day 30
Below-SBL:	None
Larvae remain below the SBL (near 30 m depth) throughout development until settlement or death	5 cm s^{-1} shoreward beginning day 30
DVM:	None
Larvae exhibit diel vertical migration, spending 12 h below the SBL during the day and 12 h in the layer at night, until settlement or death	1 cm s^{-1} shoreward beginning day 10
	1 cm s^{-1} shoreward beginning day 30
	5 cm s^{-1} shoreward beginning day 10
	5 cm s^{-1} shoreward beginning day 30
	Shoreward, linearly increasing from 0 cm s^{-1} at day 0 to 7.5 cm s^{-1} at day 45
OVM:	None
Larvae ontogenetically migrate, staying within the SBL for the first 30 days of development, then descending and remaining below the layer until settlement or death	5 cm s^{-1} shoreward beginning day 30
OVM-DVM:	None
Larvae undergo diel vertical migration for the first 30 days of development, then remain below the SBL until settlement or death	5 cm s^{-1} shoreward beginning day 30
ROVM:	None
Larvae undergo a reverse ontogenetic migration, remaining below the SBL for the first 30 days of development, then staying in the SBL until settlement or death	5 cm s^{-1} shoreward beginning day 30

environment, or pelagic larval duration (PLD), with longer PLDs leading to greater dispersal distances (Shanks, 2009). More recently, larval behavior, or directed swimming in response to a cue (Metaxas and Saunders, 2009), has been recognized as a factor that profoundly affects the distances larvae travel, and hence dispersal and connectivity (Epifanio, 1988; Kingsford et al., 2002; Leis, 2006; Morgan, 2014, in press; Queiroga and Blanton, 2005; Staaterman and Paris, 2014; Swearer et al., 2002).

Many decades of surveying larval distributions, endemism on isolated islands, and the spread of introduced species indicated that larval retention or migrations between adult habitat may be common. However, recent advances in determining dispersal distances, such as parentage analysis and natural elemental markers, have provided more persuasive evidence that larvae stay closer to home than is widely believed (Burgess et al., 2014, 2016; Levin, 2006; Morgan, 2014, in press; Swearer et al., 2002; Thorrold et al., 2002, 2007).

The vertical distribution of larvae in the water column greatly affects dispersal, as vertically stratified currents can transport larvae different distances, and often in different directions. Sustained oceanic vertical velocities are typically orders of magnitude less than horizontal velocities. It is therefore traditionally assumed that larvae can more easily control their vertical rather than horizontal position. Larvae swim or migrate vertically to help regulate their retention or dispersal, either continuously or through diel or ontogenetic vertical migrations (Bradbury and Snelgrove, 2001; Epifanio and Cohen, 2016; Epifanio and Garvine, 2001; Morgan, in press; Queiroga and Blanton, 2005). Larvae can swim vertically to find favorable horizontal currents (Paris and Cowen, 2004), or swim against vertical velocities to maintain their depth, often resulting in aggregations at fronts (Bjorkstedt et al., 2002; Franks, 1992; Graham et al., 1992; Ryan et al., 2014; Shanks et al., 2000; Shanks et al., 2003a) or the coast (Genin et al., 2005; Shanks and Brink, 2005). Modeling studies show relatively small changes in depth

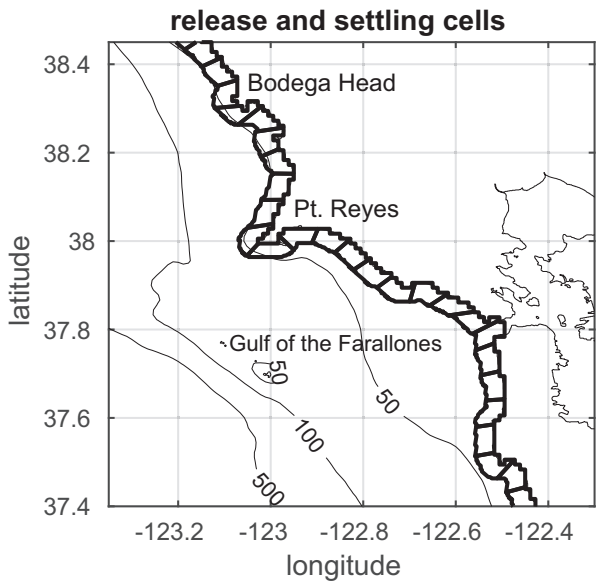

Fig. 2. Bodega Head and Gulf of the Farallones area, showing release and destination cells (heavy curves). The 25 km^2 cells extend 3.5 km offshore and continue along the entire model coastline, for a total of 100 cells. Fine curves are the 50, 100 and 500 m isobaths.

of tens of meters can lead to dramatic changes in horizontal transport, retention and connectivity (Bonhommeau et al., 2009; Corell et al., 2012; Domingues et al., 2012; Drake et al., 2013; Marta-Almeida et al., 2006; Paris et al., 2007; Petersen et al., 2010).

Horizontal swimming, known to be important for adults of many species, is increasingly invoked as a method to regulate retention and dispersal by allowing larvae to navigate toward suitable settlement sites near the end of the larval phase (Kingsford et al., 2002; Cowen and Sponaugle, 2009; Leis, 2006; Staaterman et al., 2012; Staaterman and Paris, 2014). The effective in situ swimming ability of larvae over their total larval development period is unknown for most species (Giangrande et al., 2017; Leis, 2010; Queiroga and Blanton, 2005). In the laboratory, pre-settlement stage fish larvae typically swim less than 5 cm s^{-1} (Blaxter, 1986) and can maintain swimming speeds of 1 cm s^{-1}. Porch (1998) reports few species of these larvae swim faster than 10 cm s^{-1} for more than a few minutes at a time. Swimming ability of fish larvae typically increases with size or age. For example, in the northern Pacific Ocean, rockfish larvae have critical speeds of 0.5–2 cm s^{-1} at parturition, whereas newly settled juveniles are capable of swimming 9–50 cm s^{-1} (Kashef et al., 2014). In the tropics, settlement stage larvae of reef fishes typically swim about 20 cm s^{-1}, maintaining speeds of 8–24 cm s^{-1} for hours at a time (with some species sustaining 65 cm s^{-1} for 194 h covering 94 km) (Sponaugle et al., 2002; Leis, 2006).

Larvae of many invertebrates pass through a series of morphological stages, each with its own swimming ability and depth preference, if any. Swimming speeds range from 0.01–5 cm s^{-1} (Chia et al., 1984), with most observations ranging from 0.5–2 cm s^{-1} (Queiroga and Blanton, 2005). In the northern Pacific Ocean, porcelain crab zoeae are relatively fast, attaining speeds of 5 cm s^{-1} for short periods in the laboratory (Smith and Jensen, 2015). Crab megalopae, such as *Pachygrapsus crassipes*, *Lophopanopeus bellus bellus*, *Cancer oregonensis* and *C. gracilis*, are directional swimmers with estimated speeds of 5–20 cm s^{-1} (Shanks, 1985, 1995a). It is unclear how well larvae and postlarvae can maintain these speeds over the relevant time and space scales of dispersal (Queiroga and Blanton, 2005). Lobster postlarvae have been observed swimming toward shore for 40–60 km at velocities reaching 30 cm s^{-1} (Phillips and Sastry, 1980; Cobb et al., 1989). Several modeling studies have found it necessary to include horizontal swimming to predict observed adult densities and recruitment (Porch, 1998; Staaterman and Paris, 2014; Wolanski et al., 1997). For example, shoreward swimming at 4–10 cm s^{-1} was needed to match observed distributions of lobster postlarvae off New Zealand, whereas passive entrainment by eddies best described the distributions of mid-stage larvae (Chiswell and Booth, 1999). Autocorrelated directional horizontal swimming can also increase settlement and the extent of connectivity (Berenshtein et al., 2018). Despite these results, there is general uncertainty in the role that horizontal swimming plays in regulating retention and dispersal (Leis, 2006, 2010; Metaxas, 2001).

Even when horizontal currents can easily overwhelm the typical swimming speeds of larvae, horizontal swimming may still have a large impact on settlement. Oceanic currents are highly variable in space and time (Brink et al., 2000), and it is unlikely larvae would experience a "typical" unidirectional current for more than a few days (Sponaugle et al., 2002; Wing et al., 2003). Larvae are often aggregated near clines and fronts and display highly structured nonuniform distributions (Le Fèvre, 1986; McManus and Woodson, 2012). In contrast, some form of directed swimming may be maintained, however, for most, if not all, of their PLD. The combined effects of ocean advection and vertical and horizontal swimming on dispersal are unclear, as they may interact in the variable pelagic environment in unpredictable ways (Leis, 2010; Metaxas, 2001).

Larvae in highly productive coastal upwelling regions along eastern boundaries should be especially susceptible to transport away from home populations (Parrish et al., 1981; Roughgarden et al., 1988; Menge and Menge, 2013; Morgan, 2014; Shanks and Eckert, 2005). In

Table 2
Representative nearshore CCS species with a spring or summer larval release and PLD close to or overlapping the modeled PLD (30–45 days). Swimming speed and vertical behavior are given if available from the literature.

Family	Species	Common name	Spawning period (day of year)	PLD	Swimming speed (cm s^{-1})	Vertical behaviors
Serranidae	*Paralabrax clathratus*	Kelp bass	167–272	30	8–30[a]	
Sciaenidae	*Atractoscion nobilis*	White seabass	61–244	35	6–11[a]	
Labridae	*Oxyjulis californica*	Senorita	121–303	39	14–26[a]	
Balanidae	*Balanus glandula*	Acorn barnacle	32–152	21	1.4–6[b]	Below-SBL, ROVM
Grapsidae	*Hemigrapsus oregonensis*	Shore crab	122–274	32		Below-SBL, OVM, DVM
Grapsidae	*Hemigrapsus nudus*	Purple shore crab	122–182	32		Below-SBL, OVM, DVM
Xanthidae	*Lophopanopeus bellus bellus*	Black-clawed crab	122–274	35	~5[c]	Below-SBL, DVM
Porcellanidae	*Petrolisthes cinctipes*	Flat porcelain crab	1–365	46	3–7[d]	Below-SBL, DVM, ROVM
Pinnotheridae	*Pinnixa faba*	Pea crab	214–182	47		Below-SBL, OVM
Pinnotheridae	*Pinnixa littoralis*	Gaper pea crab	245–152	47		Below-SBL, OVM
Thalassinidae	*Neotrypaea californiensis*	Bay ghost shrimp	153–182	49		Below-SBL, OVM, DVM
Cancridae	*Cancer gracilis*	Graceful rock crab	92–274	49	5[c]	

Spawning and PLD values are taken from Shanks and Eckert (2005). Swimming speeds from: [a]Webber (2011); [b]Lamont (2018); [c]Shanks (1995a); [d]Smith and Jensen (2015). Vertical behaviors are inferred from Morgan and Fisher (2010), Morgan et al. (2009a, 2009b) and Morgan (in press). End spawning date is the date on which spawning ends plus the pelagic larval duration (PLD).

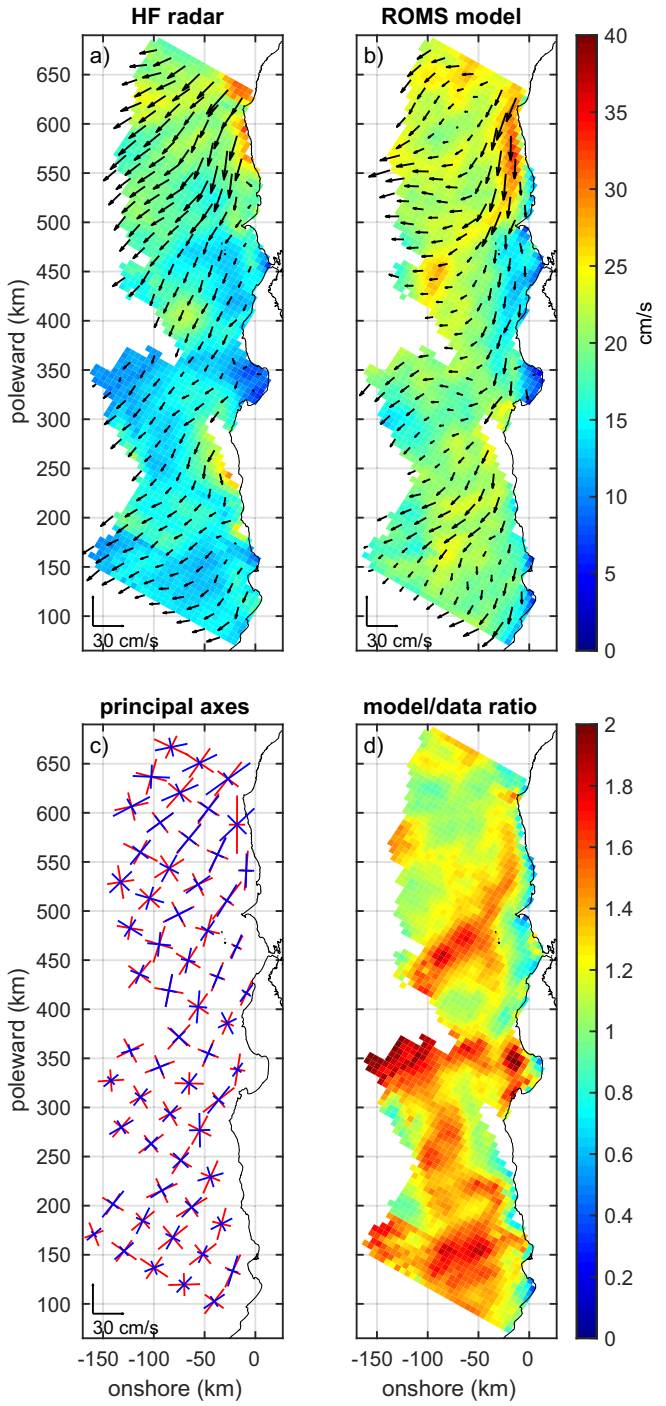

Fig. 3. Time-mean velocities (arrows) and eddy speeds (color intensity) for HF radar-derived (a) and ROMS modeled (b) estimates of surface currents. c) Principal axes of variance for radar-derived (blue) and modeled (red) surface currents. Length of each axis from its origin gives standard deviation of current velocity. d) Ratio of modeled to radar-derived mean eddy speed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

these regions, predominantly equatorward winds together with the Coriolis force drive Ekman transport away from the coast (Brink, 1983; Smith, 1981) in the surface boundary layer (Lentz, 1992). The resulting drop in sea level near the coast is associated with an alongshore, equatorward surface jet, often with substantial speeds, embedded within a chaotic eddy field (Strub et al., 1991; Strub and James, 2000; Kurian et al., 2011). The combined near-surface currents should flush larvae from the shelf and away from their home populations in several days (Carr et al., 2008; Mitarai et al., 2008; Drake et al., 2013). Nevertheless, benthic larvae in these regions are consistently retained near the coast, typically within a few kilometers of shore. These larval distributions are observed along the US west coast (Fisher et al., 2014; Hameed et al., 2018; Morgan and Fisher, 2010; Morgan et al., 2009a, 2009b, 2012; Morgan, in press; Nickols et al., 2013; Shanks and Shearman, 2009), as well as upwelling regimes off Chile (Bonicelli et al., 2016; Poulin et al., 2002) and the Iberian Peninsula (Bartilotti et al., 2014; dos Santos et al., 2008; Domingues et al., 2012; Marta-Almeida et al., 2006). Larvae may avoid offshore transport by residing subsurface, where currents are weaker or onshore. Depth regulation in stratified flow determines interspecific differences in the distances that larvae migrate from shore (Domingues et al., 2012; Marta-Almeida et al., 2006; Miller and Morgan, 2013; Morgan, 2014; Morgan et al., 2009b, 2012; Morgan, in press; Morgan and Fisher, 2010; Poulin et al., 2002; Shanks and Shearman, 2009). Whether and how postlarvae navigate to suitable settlement sites is unknown. The inherent advective nature of these coastal regions suggests that benthic species must use larval behavior to remain nearshore or return to natal populations. The methods and degree to which larvae are able to regulate their transport and eventual dispersal in these areas is key to understanding the connectivity, dynamics and structure of populations in coastal regions worldwide.

We use a dynamical model of the California Current System (CCS) to study the interplay between spatially and temporally variable ocean circulation and sustained vertical and horizontal larval swimming along the central California coast. The region experiences persistent coastal upwelling (Checkley and Barth, 2009; García-Reyes and Largier, 2012), and larval behavior should be critical for successful dispersal and recruitment. Sustained winds are the strongest on the west coast of North America (Halliwell and Allen, 1987), and the region's wind-driven circulation is relatively well understood (Dever et al., 2006; Largier et al., 1993; Lentz, 1994). Previous modeling studies in this region have shown that larval supply to settlement areas is largely determined by the total amount of time larvae spent in the surface boundary layer, with more time in the layer leading to exponentially less retention and supply (Drake et al., 2013, 2015). In our present study, we combine six vertical swimming behaviors, including diel and ontogenetic vertical migration, with a variety of shoreward-directed swimming speeds to explore the importance of larval behavior to the supply of larvae to the nearshore and their potential settlement and connectivity.

Our model's 1/90° (< ~1.2 km) horizontal resolution grid resolves the large-scale CCS structure (equatorward mean flow of the California Current, the poleward-flowing California Undercurrent and its associated inshore countercurrent (sometimes called the Davidson Current, when present)), mesoscale variability, and submesoscale features, including nearshore filaments and fronts. We do not resolve very nearshore and high-frequency processes (e.g., surface wave-driven motion, small-scale fronts, the seabreeze), choosing instead to investigate how submesoscale and larger ocean circulation patterns during the pelagic larval phase influence alongshore larval redistribution and supply to nearshore regions.

2. Data, models and methods

2.1. Hydrodynamic model

To estimate the currents of the CCS, we used an implementation of the Regional Ocean Modeling System (ROMS) (Shchepetkin and McWilliams, 2005), a widely-used, primitive-equation hydrodynamic model. The model implementation has been described and evaluated in previous studies (Drake et al., 2011, 2013). Here we extend the model with a higher-resolution nest. The outer domain (not shown) is identical to that used previously and covers most of the U.S. portion of the CCS, from 30–48°N and 134–115.5°W. The nested domain used in the

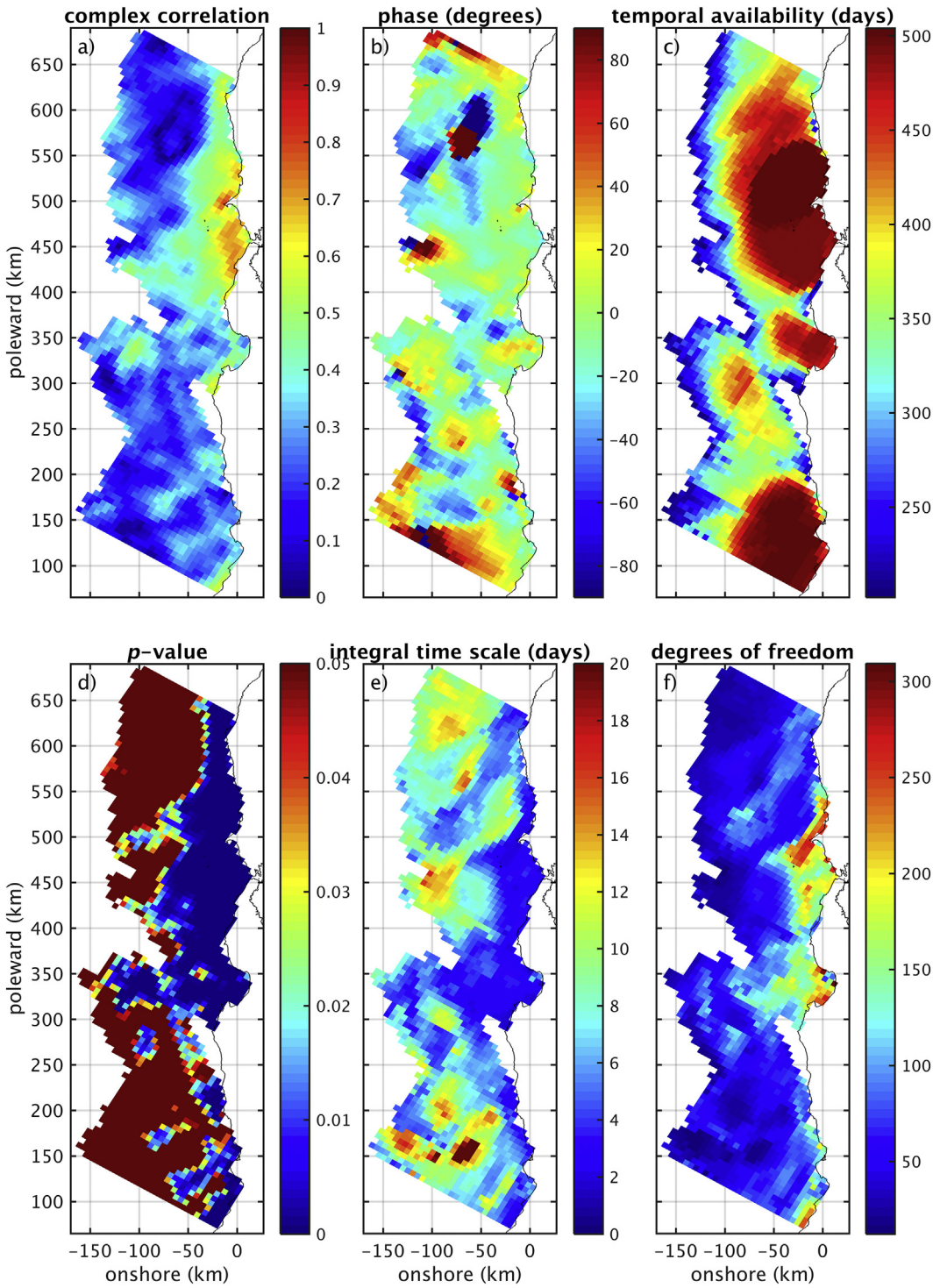

Fig. 4. Complex correlation (a) and phase (b) between radar-derived and modeled surface currents. c) Temporal coverage of radar-derived currents (days) (maximum possible 504). d) Probability of obtaining correlation by chance. e) Integral time scale (days). f) Degrees of freedom used in probability estimates (d).

present study is centered on central California, extending approximately from Pursima Point (near Point Conception) northward to Point Arena (Fig. 1). It employs a 1/90th degree horizontal resolution (~1 km) with 42 terrain-following vertical levels in an s-coordinate scheme. It was forced by daily-averaged fields from the Coupled Atmospheric Mesoscale Prediction System (COAMPS) (Hodur et al., 2002). The model did not contain San Francisco Bay, tides, a seabreeze, high-frequency surface waves or freshwater riverine input.

2.2. Larval trajectories, swimming and nearshore larval supply

Larval trajectories were calculated hourly from daily-averaged modeled Eulerian velocity fields using an Euler-trapezoidal, predictor-corrector particle tracking scheme described in Drake et al. (2013). In this scheme, each larva at each hourly time step swam vertically toward a fixed target depth with a speed of 0.5 cm s^{-1}, plus a random perturbation chosen to give normal distributions of larvae about the target depths. As discussed in Drake et al. (2013), most modeled particle

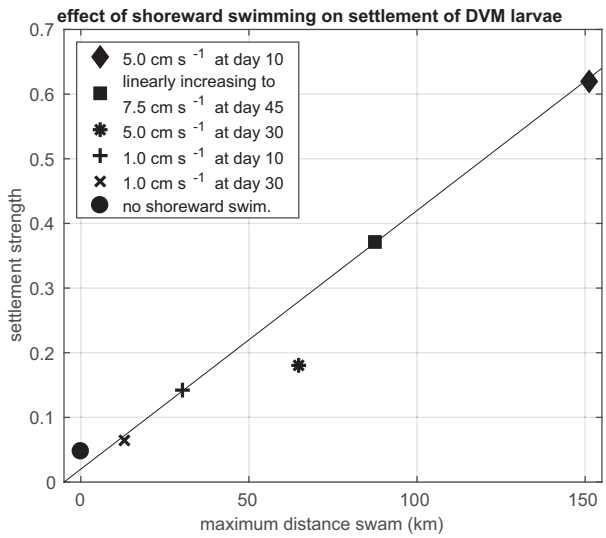

Fig. 5. The effect of various shoreward swimming behaviors on normalized nearshore larval supply of DVM (diel vertical migration) larvae. Normalized nearshore larval supply (see Data, models and methods) increases approximately linearly with "maximum distance swam" (the maximum possible distance larvae could have swam if swimming continued uninterrupted until death at age 45 days). Solid line is a least squares, simple linear regression.

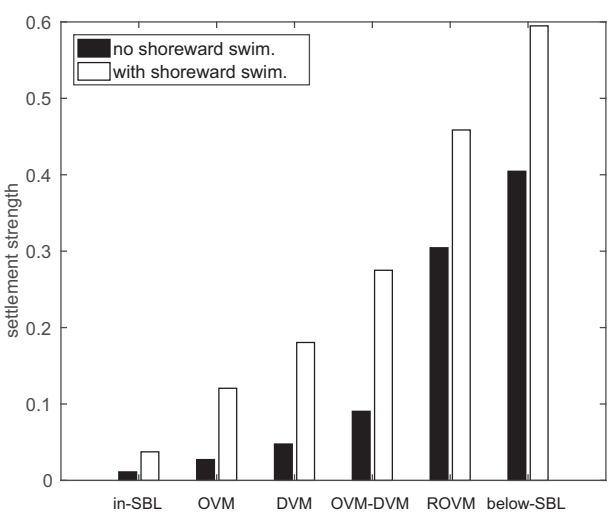

Fig. 6. The effect of shoreward swimming (5 cm s^{-1} beginning on day 30 of development) on normalized nearshore larval supply for various vertical swimming behaviors. Values of supply are for the entire coastline as a whole and not weighted per cell. Vertical behaviors: in-SBL (in surface boundary layer); OVM (ontogenetic vertical migration); DVM (diel vertical migration); OVM-DVM (combined ontogenetic and diel vertical migration); ROVM (reverse ontogenetic migration); below-SBL (below surface boundary layer). For vertical behavior descriptions see Table 1.

transport away from the central California coast in spring is confined to a surface layer approximately 20 m thick, the nominal surface boundary layer. To allow the influence or avoidance of this transport, larvae were assigned mean (target) depths of 5 or 30 m. The random swimming perturbations were chosen to give a standard deviation of 2.5 m about these depths. These distributions ensured 95% of larvae would be confined to a 10 m thick layer either within or below the nominal surface boundary layer. Because the ocean model did not contain tides, the horizontal mixing realized by nearshore tides was simulated with a random walk. Larvae were given a random, normal horizontal displacement when in water depths less than 800 m, corresponding to a nearshore tidal velocity of 5 cm s^{-1} (Drake et al., 2013). To minimize the effects of model errors at the northern, southern and eastern boundaries, larvae moving within 0.2° of these boundaries were assumed lost and not permitted to contribute to larval supply or potential dispersal, but still contributed to the number released in larval supply and connectivity statistics.

We investigated six vertical swimming behaviors (Table 1) that commonly occur in upwelling regions (Peterson, 1998; Morgan, 2014) and elsewhere (Epifanio and Cohen, 2016; Epifanio and Garvine, 2001; Queiroga and Blanton, 2005). Because all larvae in this study were assumed to have at least some control of their vertical position at all times, we did not investigate the case of purely passive propagules. In addition to vertical swimming, larvae were assigned horizontal swimming speeds of 0–7.5 cm s^{-1} toward a fixed compass direction of 60° (i.e., 60° east of north, or approximately east-northeastward). Given the overall strike of the central California coastline, this direction was approximately onshore for most larvae most of the time. This simple model of horizontal orientation was inspired by the solar compass used by some crab larvae (Shanks, 1995a), but here we have fixed the swimming direction a priori to maximize larval supply to the inner shelf. Real larvae may orient themselves using a combination of solar, magnetic or olfactory cues (Kingsford et al., 2002; Queiroga and Blanton, 2005; Staaterman and Paris, 2014). Horizontal swimming was initiated after 10 or 30 days of development with speeds of 1 or 5 cm s^{-1}, simulating the start of an invertebrate larval stage with new swimming abilities. In addition to these step-changes in swimming ability, we also considered a scenario where the swimming speed increased linearly with time, or age, mimicking a larval fish or invertebrate, which may experience a gradual increase in ability throughout development. The linear increase was applied to larvae exhibiting diel vertical migration (DVM), and the speed was increased from 0 at release to 7.5 cm s^{-1} at day 45 (corresponding to 5 cm s^{-1} at day 30). For this case, we also examined random horizontal swimming designed to simulate errors in orientation. In addition to swimming toward a fixed onshore direction, larvae were given a random perturbation in swimming velocity at each particle time step. Normal perturbations were applied separately to each larva's eastward and northward velocity component. Perturbations had zero mean and standard deviation equal to the component's instantaneous value. Although these random fluctuations had a magnitude equal to the nonrandom, linearly increasing swimming speed, they did not affect the results. Pelagic connectivity matrices (defined below) with and without random swimming were almost identical, and nearshore larval supply (defined below) differed by less than 0.2%.

Larvae were released during months of seasonally strong upwelling, March–June, from 2009 to 2013. For each vertical-horizontal behavior pairing, approximately 30,000 larvae were released every other day, for a total of 8.3 million larvae per swimming case. Larvae were released within 3.5 km of shore with an approximately random uniform horizontal distribution. Each larval release was tracked for 45 days. The shoreline was divided into 100 equally sized, 25 km^2 polygons, each extending 3.5 km offshore (Fig. 2) and acting as both a release and destination cell. As our model lacks the spatial resolution necessary to model many of the very nearshore (Shanks et al., 2003a) processes affecting settlement, we measure nearshore larval supply, defined as the total number of larvae found within any destination cell anytime after 30 days of development. Each larva could only contribute to this quantity once for any given release scenario. The fraction of all released larvae contributing to this quantity (i.e., the fraction of released larvae supplied to the nearshore) is referred to as normalized nearshore larval supply. We note that our definition of supply does not necessarily represent actual settlement or recruitment back to subtidal and intertidal communities, but rather the supply of competent larvae to the inner shelf. Larvae older than 45 days were assumed dead and not allowed to settle, giving a PLD of 30–45 days. This PLD overlaps the reported range of many vertebrates and invertebrates found in central California (Shanks and Eckert, 2005), including the porcelain crab *Petrolisthes*

Table 3
Alongshore dispersal statistics for different vertical swimming behaviors with and without shoreward swimming of 5 cm s^{-1} beginning on day 30 of development. For the mean, median and standard deviation, each of 100 release cells contributes equally to statistics, regardless of number of settlers per cell. Values of nearshore larval supply are for the entire coastline as a whole and not weighted per cell. Positive alongshore was defined as the compass direction of 330°, approximately north-northwestward along the general strike of the central California coastline.

Behavior	Nearshore larval supply	Mean (km)	Median (km)	Standard deviation (km)
In-SBL without shoreward swimming	0.0111	−37.2	−22.0	98.9
In-SBL with shoreward swimming	0.0374	−52.4	−42.5	111
Below-SBL without shoreward swimming	0.405	27.1	20.5	83.0
Below-SBL with shoreward swimming	0.595	26.6	20.3	91.8
DVM without shoreward swimming	0.0476	−27.1	−17.8	94.1
DVM with shoreward swimming	0.180	−44.0	−35.8	118
OVM without shoreward swimming	0.0272	−52.0	−38.3	116
OVM with shoreward swimming	0.121	−52.3	−47.4	134
OVM-DVM without shoreward swimming	0.0904	−34.6	−25.1	108
OVM-DVM with shoreward swimming	0.275	−34.4	−30.0	125
ROVM without shoreward swimming	0.304	25.9	19.7	75.9
ROVM with shoreward swimming	0.459	20.8	17.0	87.2

cinctipes and the demersal reef fish *Oxyjulis californica* (Shanks et al., 2003b). Several additional CCS species with similar life history traits are given in Table 2. As noted above, the exact pelagic behaviors of most larvae are unknown. We list these species as a brief representation of the types of CCS organisms for whom this study may be relevant. When available from the literature, swimming speeds and behaviors are included.

Horizontal larval densities were calculated with a 10 km × 10 km resolution. When calculating densities, larvae were not allowed to settle, but could exit the domain through the open boundaries. Pelagic connectivity was quantified as the matrix, $C(i, j)$, giving the fraction of larvae released from coastal cell i that are eventually supplied to coastal cell j. Each larva is assigned to the first destination cell it encounters during its competency window (30–45 days). We emphasize the pelagic connectivity represents the net effects of physical oceanic transport resolved by the model and larval swimming, but does not capture the many processes affecting larvae as they traverse the very nearshore zone toward subtidal and intertidal populations.

An important and largely unanswered question in marine ecology is identifying the probable source locations of incoming recruits. Although the pelagic connectivity reveals important oceanic pathways between subpopulations, it is designed to show the relative importance of destinations or "sinks" for a given source. An equally important question is what are the dominant sources of recruits to a given destination population, or sink. To examine this relationship, we calculated an additional statistic, the reverse pelagic connectivity matrix, $C_R(i, j)$, defined as the fraction of larvae supplied to coastal cell j that originate from coastal cell i. The reverse pelagic connectivity is normalized so that all the values for a given destination cell sum to one. For normalized nearshore larval supply, larval density, pelagic connectivity and other statistics, all releases from all years were combined to create climatological estimates. To focus on swimming behavior, no biological factors (e.g., starvation, foraging, predation, etc.) other than swimming ability were considered in the model.

2.3. HF radar velocities

The availability of high frequency (HF) radar-derived surface velocity estimates along the California coast (Terrill et al., 2006) allows for an evaluation of modeled velocities. Radar-derived velocities were downloaded from the Coastal Observing Research and Development Center website (http://cordc.ucsd.edu/projects/mapping) at a 6 km spatial resolution, the highest resolution for which substantial temporal and spatial coverage was available. To produce the most direct model-data comparison, the hourly HF radar data was daily averaged, and daily-averaged ROMS surface velocities were spatially averaged onto the HF radar's 6 km grid. Simultaneous data and model coverage was only readily available from 2011 to 2013, and the offshore extent of coverage was limited to ~100–150 km. The periods from these years for which virtual larvae were in the water column (March 1–August 15) were concatenated to form one extended, faux-continuous upwelling season. Only grid cells with at least 40% temporal coverage (Kaplan et al., 2009) over this extended season of 504 days were included in the model-data comparison (below). Mean eddy speeds were calculated as the square root of twice the eddy kinetic energy (√2EKE), where $EKE = 0.5[u'^2 + v'^2]$, and u' and v' are deviations from the time mean fields of eastward and northward velocity (Drake et al., 2011). The complex correlation between radar-derived and modeled velocities was calculated (Kundu, 1976), and significance levels were computed assuming perfect covariance between the alongshore and cross-shore components of the currents (i.e., by treating the complex correlation as a correlation of two scalar variables). This approach is more conservative than assuming imperfect covariance (Kaplan et al., 2005). To account for temporal autocorrelation, the effective degrees of freedom for significance levels was determined using the integral time scale, as suggested by Emery and Thomson (2001, Chapter 3). The integral was truncated at the first zero crossing.

3. HF radar-derived and modeled velocity comparison

Measured and modeled mean surface velocity fields show similar spatial structure (Fig. 3a, b). Both fields reveal an overall pattern of primarily southwestward flow with larger mean velocities in the northeastern corner of the domain near Point Arena. Mean eddy speeds present a similar pattern of increased intensity in the northeastern portion of the domain near Point Arena, and reduced speed in the Gulf of the Farallones and Monterey Bay. An intense alongshore jet is present in the model between Point Arena and Point Reyes. Although this jet is frequently observed in nature (Halle and Largier, 2011), it is not a well-defined feature in the radar-derived mean. Principal axes of current variance in the model in places resemble and at other locations differ from those of the data (Fig. 3c). Spatial patterns of standard deviation are similar. The model overestimates the eddy speed over many portions of the domain (Fig. 3d), but the degree of overestimation is highly variable. The complex correlation between radar-derived and modeled velocities is highest in the Gulf of the Farallones and significant over a large nearshore region (50–100 km from shore) north of Point Sur (Fig. 4). An alternative measure of vector correlation and significance proposed by Crosby et al. (1993) (not shown) gives almost identical results, with similar spatial patterns of significant correlation.

4. Horizontal swimming and nearshore larval supply

We use DVM (Table 1) as a baseline vertical swimming behavior to

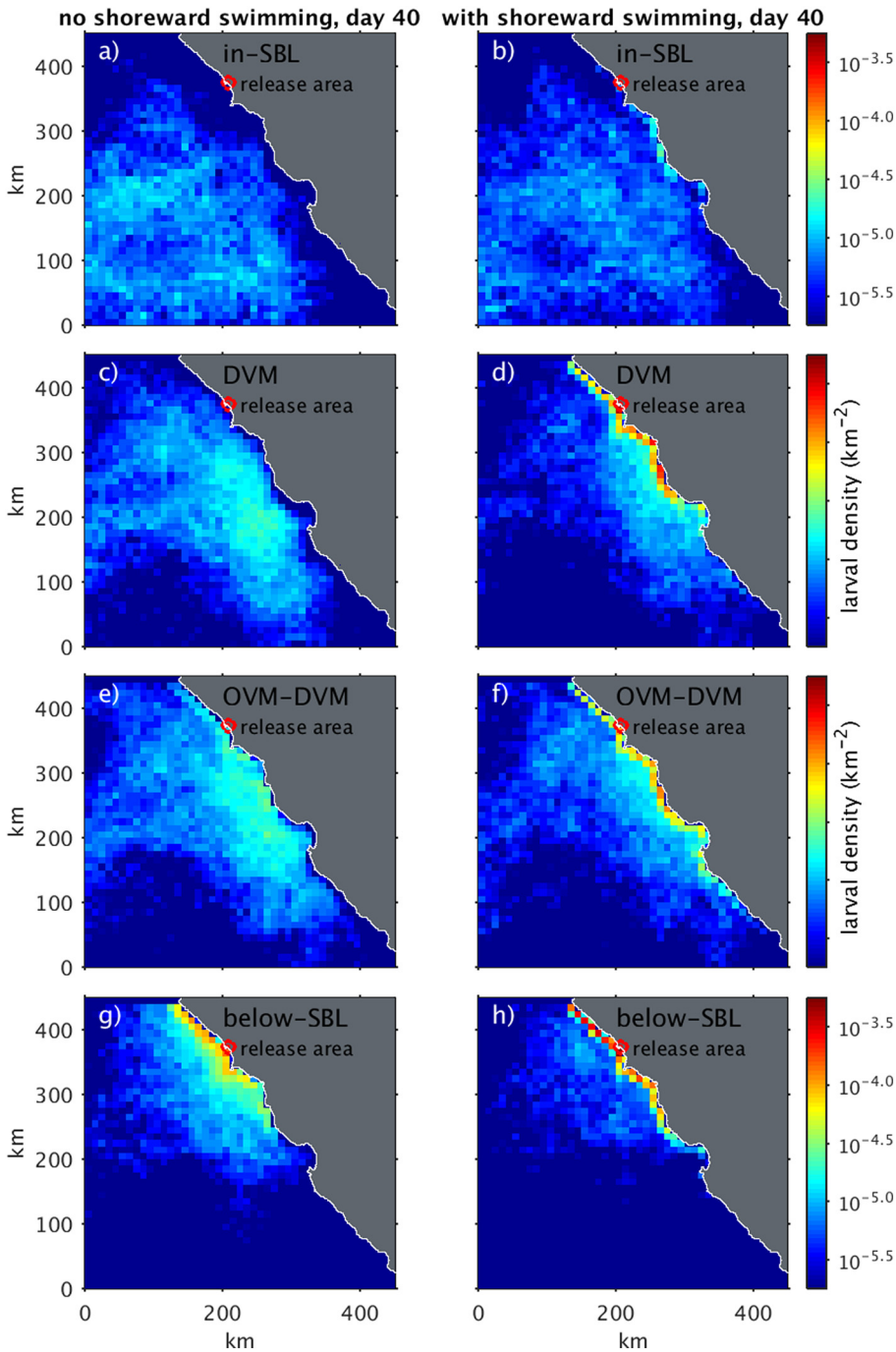

Fig. 7. Climatological larval densities for various vertical swimming behaviors at 40 days after release given a Bodega Head release, both without horizontal swimming (left panels), and with shoreward swimming (5 cm s^{-1} beginning on day 30 of development) (right panels). Vertical behaviors: a),b) in-SBL; c),d) DVM; e),f) OVM-DVM; g),h) below-SBL. When calculating horizontal densities, larvae were not allowed to settle. For abbreviations see Fig. 6.

explore a range of horizontal swimming scenarios. Directed onshore swimming dramatically increases normalized nearshore larval supply (nearshore supply) for DVM larvae (Fig. 5). Nearshore supply increases approximately linearly with "maximum distance swam," the maximum possible distance larvae could have swum if swimming continued uninterrupted from onset until death at 45 days. This distance is similar to the endurance statistic reported for laboratory measurements of fish larvae (Leis, 2010). A least squares, simple linear regression yields: *normalized-nearshore-larval-supply* = 0.02 + 0.004 ∗ *maximum-distance-swam*, with distance in km. In the cases examined, nearshore supply is greatest when larvae start swimming on day 10 at 5 cm s^{-1}. These larvae experienced a 13-fold increase in nearshore supply relative to the non-swimming case. The larvae given the weakest horizontal swimming ability, 1 cm s^{-1} starting on day 30, experienced the smallest increase in nearshore supply, as expected, with 35% more settling relative to the horizontally passive case. Swimming 5 cm s^{-1} starting on day 30 almost quadruples nearshore supply for DVM larvae.

This horizontal swimming scenario increases nearshore supply for all vertical behaviors, but affects each behavior differently (Fig. 6, Table 3). The increase is greatest for the OVM and DVM cases, which increased by factors of 4.4 and 3.8, respectively, and least for the ROVM and below-SBL behaviors, which both increased by a factor of 1.5. These same effects can also be easily seen in the horizontal larval densities, which are all shifted shoreward relative to non-swimming

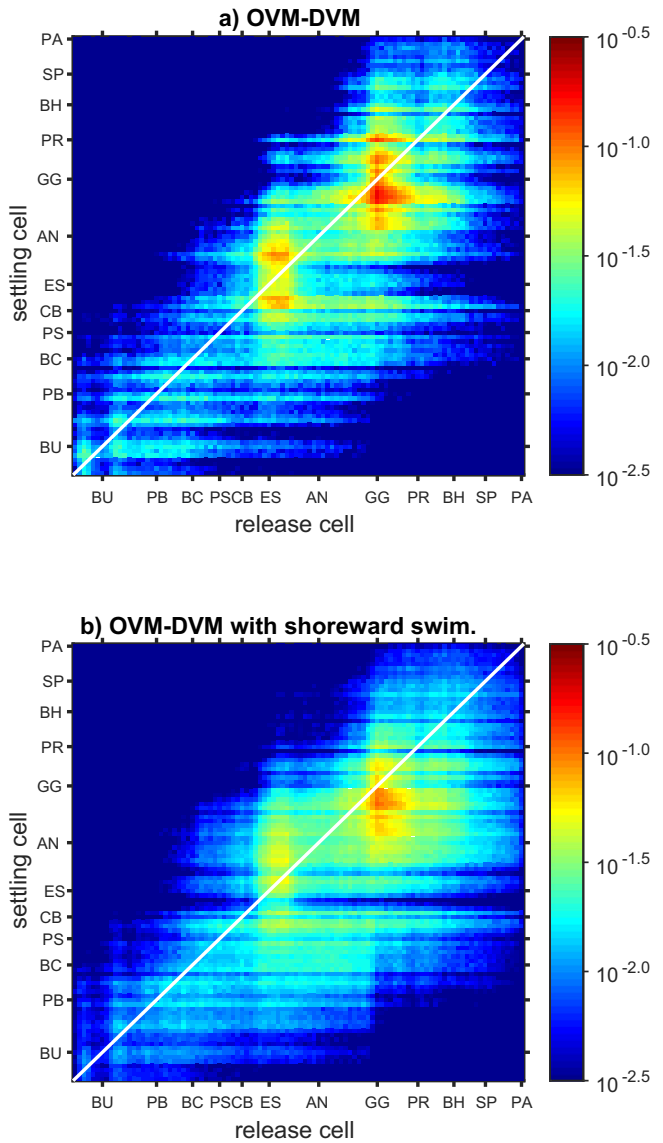

Fig. 8. Pelagic connectivity for OVM-DVM larvae a) without horizontal swimming and b) with shoreward swimming (5 cm s^{-1} beginning on day 30 of development), standardized by overall settlement strength, displayed with a log_{10} color scale. Color intensity above the diagonal line indicates northward transport and nearshore larval supply, and intensity below the line indicates southward transport and supply. BU: Point Buchon; PB: Piedras Blancas; BC: Big Creek; PS: Point Sur; CB: Carmel Bay; ES: Elkhorn Slough; AN: Año Nuevo; GG: Golden Gate; PR: Point Reyes; BH: Bodega Head; SP: Stewarts Point; PA: Point Arena. For additional abbreviations see Fig. 6. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

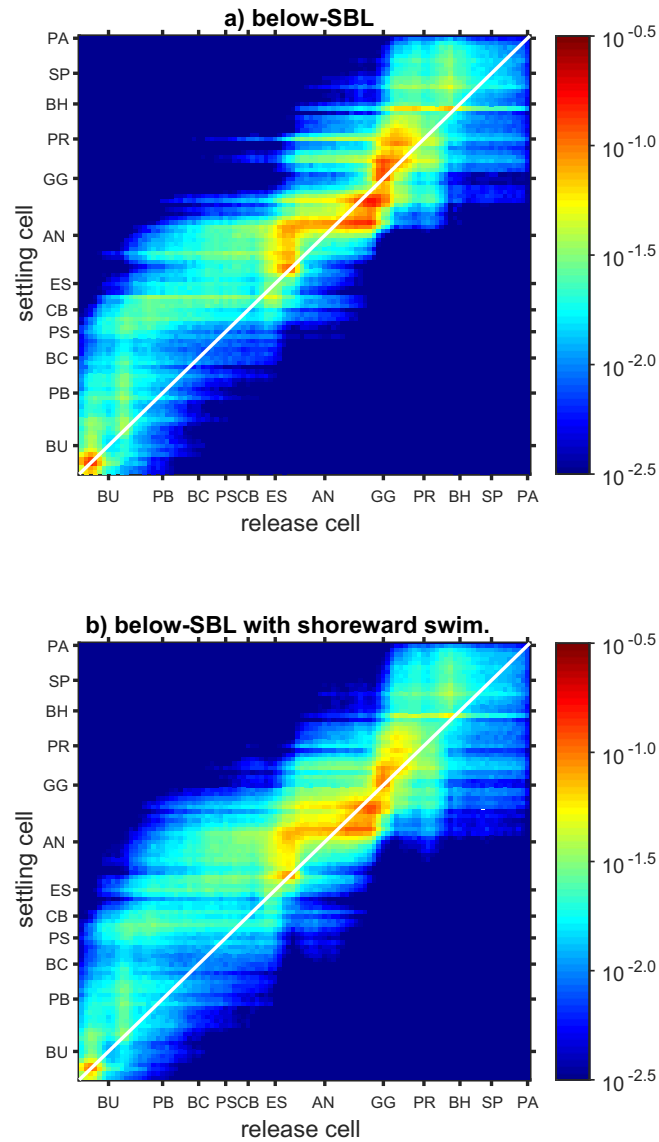

Fig. 9. Pelagic connectivity for below-SBL larvae a) without horizontal swimming and b) with shoreward swimming (5 cm s^{-1} beginning on day 30 of development), standardized by overall settlement strength, displayed with a log_{10} color scale. For abbreviations see Figs. 6 and 8. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

larvae, as expected (Fig. 7). The shift is most noticeable for the DVM case and least noticeable for below-SBL larvae. The relatively small increase in nearshore supply for the below-SBL behavior is likely related to its high retention of larvae nearshore (Fig. 7e), which allows 40% of larvae to be supplied to the nearshore without horizontal swimming.

5. Horizontal swimming and pelagic connectivity

We now concentrate on the two behaviors most likely employed by benthic invertebrate larvae in central California, the OVM-DVM and below-SBL cases (Morgan et al., 2009b). Pelagic connectivities for the non-swimming OVM-DVM and below-SBL behaviors differ (Figs. 8a and 9a). Here we have standardized (divided) the pelagic connectivities by the normalized nearshore larval supply. This standardization elucidates differences in spatial patterns, rather than the absolute magnitude of nearshore supply and potential settlement (Watson et al., 2010). Color intensity above the diagonal line indicates northward transport, supply and possible settlement, and intensity below the line indicates southward transport, supply and possible settlement. Relative to the OVM-DVM behavior, standardized connectivity and nearshore supply is generally much more northward for the below-SBL case, especially from source locations south of Año Nuevo (AN). In general, a narrower band of release regions contribute to any given destination cell for the below-SBL larvae.

We focus on one horizontal behavior, the 5 cm s^{-1}, day 30 scenario, motivated by larvae of the porcelain crab *Petrolisthes cinctipes*. On the US west coast, these larvae are most abundant close to shore (1.8–5.5 km from the coast) (Smith and Jensen, 2015), likely as a result of their behavior. This swimming scenario increases non-standardized

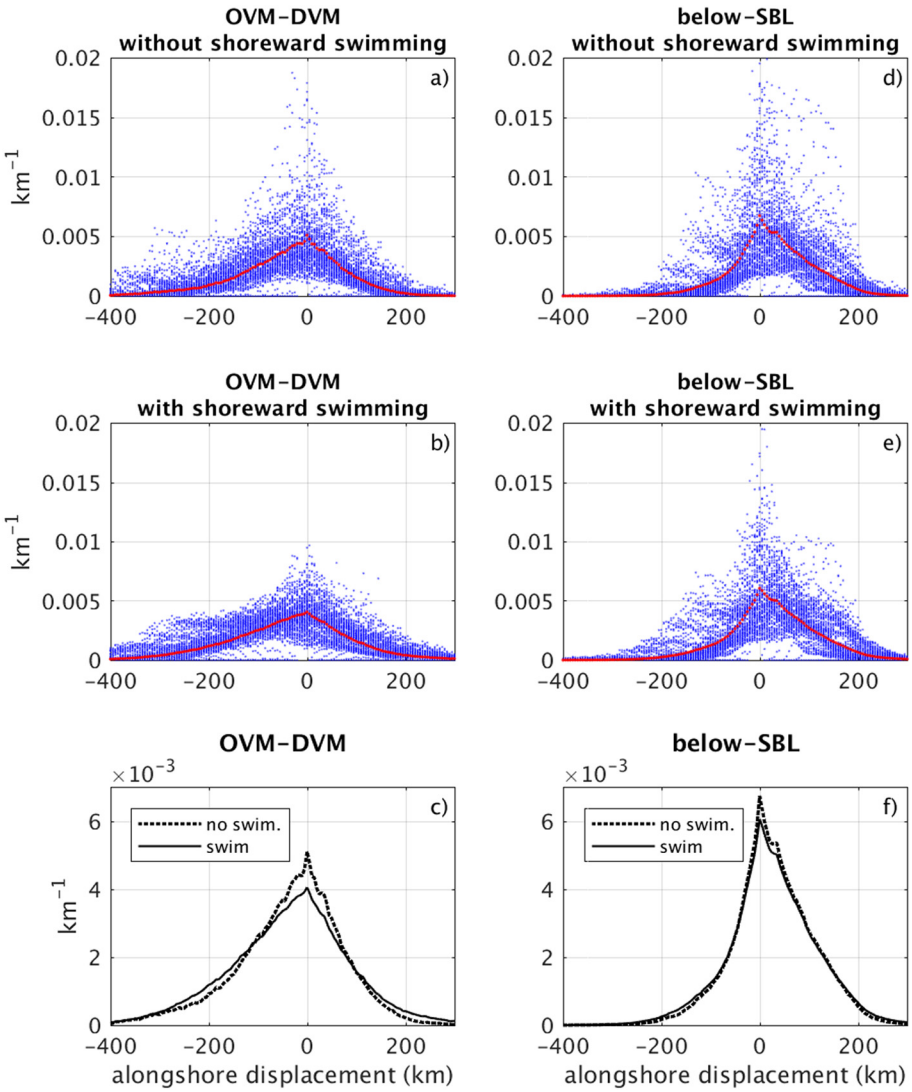

Fig. 10. Distribution of potential dispersal (i.e., the potential dispersal kernel) as a function of alongshore displacement both with and without shoreward swimming of 5 cm s^{-1} beginning on day 30 of development. a) OVM-DVM larvae without and b) with shoreward swimming. Blue dots show the individual distributions of each of 100 release cells. Red curves show the mean of all distributions, weighted equally per cell. All curves are normalized to contain unit area. c) Red curves from a) and b) shown together for direct comparison. d) Below-SBL larvae without and e) with shoreward swimming. f) Red curves from d) and e) shown together for direct comparison. Positive alongshore was defined as a compass direction of 330°, approximately north-northwestward along the general strike of the central California coastline. For relevant statistics see Table 3. For abbreviations see Fig. 6. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

pelagic connectivity relative to non-swimming larvae almost everywhere for all vertical behaviors (not shown). However, the overall spatial patterns of standardized connectivity for both OVM-DVM (Fig. 8a and b) and below-SBL (Fig. 9a and b) larvae are relatively unchanged with horizontal swimming, and local "hot spots" of pelagic connectivity are preserved. This preservation likely reflects the choice of swimming direction, directly onshore.

The effects of the imposed horizontal swimming on the standardized connectivity are to reduce local maxima slightly and to make values more diffuse overall. These effects are associated with a slight broadening of the north-south extent of release cells that contribute to any given settlement cell. The broadening can be seen more directly in the distribution of normalized nearshore larval supply as a function of alongshore displacement from source to inner-shelf destination location (Fig. 10). This distribution is related to the dispersal kernel (Cowen et al., 2007; Hameed et al., 2016), which represents the probability density of a larva dispersing from a natal site to any settling location, ignoring mortality and post settlement processes. As our model does not well-resolve settlement and the inner shelf, we refer to the distribution of larval supply as the potential dispersal kernel. Mean potential dispersal kernels were calculated by averaging distributions of individual release cells, weighting each cell equally regardless of the number of larvae it eventually supplies to the inner shelf, and assuming all larvae are supplied where they first encounter a destination cell during competency. Horizontal swimming increases the probability that an OVM-DVM larva will potentially disperse greater than ~100 km from its natal site (Fig. 10c), at the expense of more local supply and potential settlement. But the overall shapes of the non-swimming and swimming distributions are remarkably similar. Both curves have a maximum at zero, are negatively skewed, and have similar statistics (Table 3), with the standard deviation of potential dispersal increasing 17 km (16%) with horizontal swimming. The respective curves for the below-SBL case also show a maximum at zero, but are positively skewed (Fig. 10f). They are almost identical to each other, with the standard deviation increasing 11% with horizontal swimming (Table 3).

For the behaviors where larvae spend time in the surface boundary layer during their competency window (in-SBL, DVM and ROVM), shoreward swimming results in slightly more southward potential dispersal (Table 3). Potential dispersal curves (not shown) have a maximum at zero and are negatively skewed, similar to the OVM-DVM shape. Given east-northeastward swimming, the ~5–17 km southward shift in the mean of potential dispersal represents an apparent paradox. It can be resolved by realizing that with shoreward swimming beginning late in development, larvae that have been advected offshore and southward in near-surface waters of the California Current and which would otherwise not be supplied to the inner shelf, can be, but with a more equatorward displacement from their release site. See, for example, the large patch of DVM larvae offshore of Monterey Bay in Fig. 7c, and their implied settlement near Año Nuevo (Fig. 7d), south of their Bodega Head release site. We note that the displacement in the

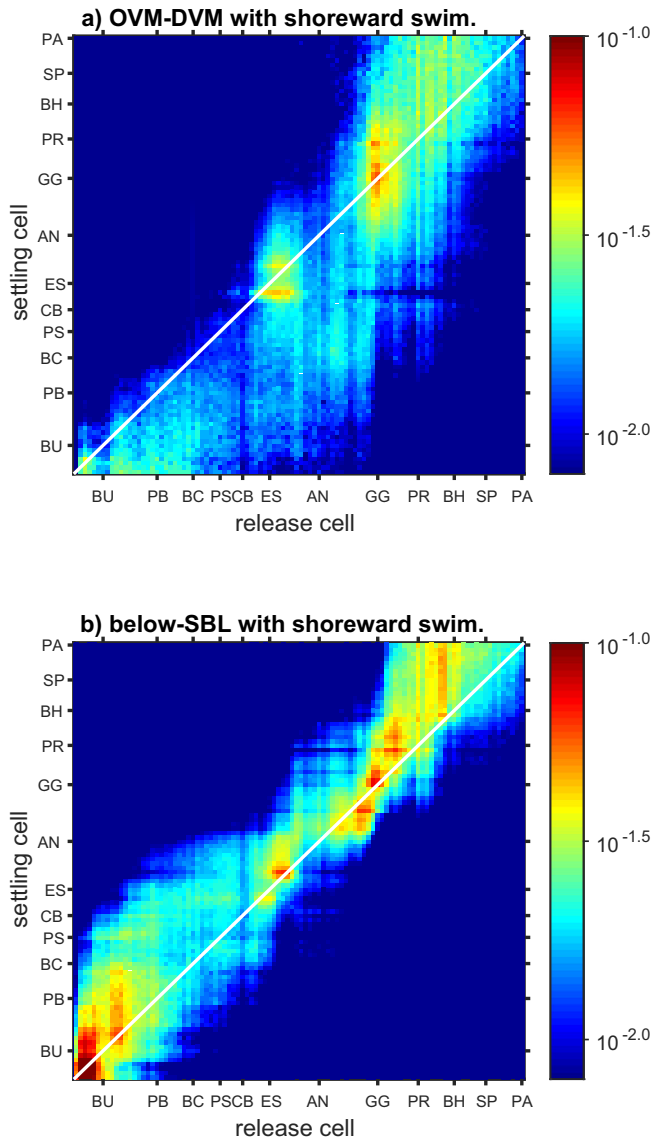

Fig. 11. Reverse pelagic connectivity matrices for a) OVM-DVM and b) below-SBL larvae, both with shoreward swimming of 5 cm s^{-1} beginning on day 30 of development, displayed with a log_{10} color scale. As with the standard connectivity, color intensity above the diagonal line indicates northward transport and nearshore larval supply, and intensity below the line indicates southward transport and supply. For abbreviations see Figs. 6 and 8. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mean with horizontal swimming is still quite small compared to the standard deviations in all cases.

Reverse connectivity matrices for the OVM-DVM and below-SBL behaviors given horizontal swimming (Fig. 11) reveal that source areas of contribution to supply and potential settlement are much narrower than implied by a cursory reading of the standard pelagic connectivity. For example, with the OVM-DVM behavior, northward supply of larvae from source cells south of Carmel Bay (CB) is absent in the reverse matrix (compare Figs. 8b and 11a), indicating it is relatively inconsequential to total larval supply. Source cells in northern Monterey Bay, between Elkhorn Slough (ES) and Año Nuevo (AN), have a substantially reduced extent of nearshore larval supply. Much of the southward supply and potential settlement from source cells between the Golden Gate (GG) and Stewarts Point (SP) is also absent for this behavior, as well as for the below-SBL case (compare Figs. 9b and 11b). The southern Point Buchon (BU) area is also revealed to be more important as a source region for destination cells south of Big Creek (BC). A comparison of the reverse pelagic connectivity matrices for horizontal swimming and non-swimming larvae (not shown) reveals that horizontal swimming weakens the intensity of hotspots. When a broader expanse of coastline contributes to supply and potential settlement to any specific region, as it does when shoreward swimming is activated, the relative contribution of the dominant sources is diminished.

6. Discussion

The addition of shoreward horizontal swimming leads to a substantial increase in nearshore larval supply for all combinations of modeled vertical and horizontal larval swimming behaviors. The strength of its effect varies approximately linearly with the speed of swimming integrated over the pelagic duration of the larvae. The general effectiveness of these modest horizontal swimming speeds was somewhat surprising. At first glance, the horizontal currents in our model appear to be easily able to overwhelm the swimming ability of benthic larvae, with instantaneous surface fluctuations of ~25 cm s^{-1} and offshore mean velocities of ~10 cm s^{-1} (Fig. 3b). Larval swimming speeds are just 1–5 cm s^{-1} and only realized for a portion of the PLD. But even modest horizontal swimming abilities acquired very late in development (1 cm s^{-1} at age 30 days) can increase nearshore larval supply 35%. And more robust swimming abilities acquired earlier in development (5 cm s^{-1} at age 10 days) can increase nearshore larval supply by more than an order of magnitude (13×).

The effectiveness of horizontal swimming as a booster of nearshore larval supply likely results from the constant choice of swimming direction and the relatively linear geometry of the coastline. Random perturbations to mean horizontal swimming had a negligible effect on nearshore larval supply and pelagic connectivity, implying the directed nature of swimming was critical. Larvae were programmed, once swimming started, to swim indefatigably until settlement, and they could not "miss" their target, except by exiting the domain. Ocean currents, however, are not so single-minded. Highly variable in space and time, ocean currents have unpredictable effects on transport (Mitarai et al., 2008), especially over shorter, non-seasonal timescales. For example, larvae can be entrained in seaward-growing filaments (Bjorkstedt et al., 2002; Strub et al., 1991) or otherwise transported offshore, but they also can be entrained in transiently stationary eddies or fronts that may result in little net transport (Fig. 1), at least temporarily. For most of the behaviors we explored, larvae experienced flow at two primary depths that were deliberately chosen to sample both offshore and onshore currents, potentially negating any net transport.

Larval interactions with fronts may be a major contributor to the increase in nearshore larval supply with shoreward swimming. Fronts are associated with phytoplankton blooms and aggregate phytoplankton and larvae, and these phenomena are well-documented in central California (Bjorkstedt et al., 2002; Graham et al., 1992; Ryan et al., 2010, 2014; Traganza and Conrad, 1981; Woodson et al., 2009). Fronts are common and persistent in the CCS (Castelao et al., 2006; Shanks et al., 2003a), and are spatially correlated with higher recruitment of both intertidal and subtidal species (Woodson et al., 2012). However, fronts may also inhibit recruitment locally by preventing larval-rich water from reaching shore (Galarza et al., 2009; McCulloch and Shanks, 2003). Aggregation in persistent fronts may help larvae remain close to shore during most of their development, before horizontal swimming abilities become effective. Later in development, when larvae become more powerful horizontal swimmers, they can swim to adult populations. Our study investigated nearshore larval supply probabilistically, combining all resolved processes, and did not identify or examine specific oceanographic features, such as fronts and eddies. The impact of fronts on nearshore retention, larval growth and development, larval supply and potential settlement and connectivity

remains an important area of future research.

The sensitivity of nearshore larval supply to horizontal swimming, for a variety of different vertical behaviors, indicates it should be considered as a possibly important factor in biophysical models of transport in the central California coastal ocean, and likely in upwelling regions more generally. One of the original simplifying assumptions about larval transport is that larvae are purely passive propagules given the dispersive power of the ocean (Leis, 2006; Queiroga and Blanton, 2005). The results of our previous modeling study investigating the effect of vertical swimming behaviors (Drake et al., 2013), and the results of the present study on the effect of horizontal swimming provide additional evidence that this assumption is no longer appropriate. These behaviors can substantially affect nearshore larval supply, potential dispersal and pelagic connectivity.

Pelagic connectivity increases almost everywhere when horizontal swimming behavior of larvae is incorporated into the model; the magnitude of the increase varies with vertical swimming behavior. The vertical swimming behavior with the most nearshore larval supply without horizontal swimming (below-SBL) experiences the least fractional increase with its addition. This is likely due to the high starting value of supply (40%) for this case, which allows less potential for increase. Horizontal swimming may be less important for settlement when larvae already have strong retention mechanisms in the nearshore environment.

Spatial patterns of pelagic connectivity, when standardized by the normalized nearshore larval supply, remain relatively constant with the addition of horizontal swimming for our two primary behaviors, below-SBL and OVM-DVM. For example, the retentive areas the Gulf of the Farallones and Monterey Bay are the most important source and destination regions in central California regardless of vertical swimming behavior or presence of horizontal swimming (Figs. 8 and 9). The persistence of these patterns is likely due to our choice of swimming direction, directly onshore, and the simple, linear geometry of the coastline. For these behaviors, estimates of the mean and median of potential alongshore dispersal (Table 3) are also little changed by the addition of horizontal swimming. Other behaviors experience a southward shift of ~5–17 km. For all behaviors, the standard deviation increases slightly (11–26%), indicating greater overall potential dispersal distances (i.e., a greater north-south extent of coastal habitat contributes to any given potential settling location), and less local larval supply and potential settlement. These statistics can be relatively constant because they do not depend directly on the absolute amount of larval supply, the aspect of larval transport found to be most sensitive to horizontal behavior. Given that direct shoreward swimming did not substantially alter spatial patterns of connectivity, this type of horizontal swimming ultimately may not play a large role in structuring the connectivity of nearshore marine subpopulations. The primary function, when present, may be to increase nearshore larval supply and settlement. Vertical behaviors, other types of horizontal swimming, and settlement behaviors may be the primary ways organisms influence population connectivity during the larval stage.

The more northward mean potential dispersal distance of the below-SBL behavior (27 km vs. −35 km for the OVM-DVM case, Table 3) is likely due to the more poleward currents found below the surface boundary layer in central California (Drake et al., 2013). Our estimates of the horizontal extent of potential dispersal (standard deviations of 76–116 km, Table 3) are smaller but of the same order of magnitude as previous Lagrangian modeling estimates reported by Drake et al. (2011), who found a mean and standard deviation of −88 and 152 km, respectively, for larvae in the central California during spring. The differences are likely due to the different time periods and vertical swimming behaviors studied. The earlier study spanned the springs of 2000–2006, and studied purely passive propagules with a vertical distribution determined by ocean conditions (vertical advection and mixing). In the present study, vertical position is determined by behavior only. The two studies also employed different horizontal resolutions for the underlying Eulerian model, ~3.5 km for the previous case and ~1 km presently. The present study achieves a much better resolution of the coastline and inner shelf.

We note that potential dispersal estimates from both modeling studies are half an order of magnitude greater than those derived for the region by Hameed et al. (2016) for *Petrolisthes cinctipes*, the model species for our 5 cm s^{-1}, day 30 horizontal swimming scenario. These larvae likely employ a ROVM vertical behavior (Morgan et al., 2009b; Morgan and Fisher, 2010). Using inverse statistical methods and field observations of fecundity, population size and settlement, Hameed et al. (2016) report a mean dispersal distance of just 7 km with a standard deviation of 25 km for this species. Our model's slight overestimation of the surface eddy speed (Fig. 3d) may contribute to this discrepancy in estimates of the standard deviation of dispersal, as larger turbulent velocities should disperse particles farther from a point source release, all else being equal (Poulain and Niiler, 1989). However, our numerical estimates of potential dispersal are consistent with simple theoretical models of diffusion and observations of the eddy diffusivity from the real ocean. Under idealized conditions of statistically stationary, isotropic, horizontally homogeneous turbulence and no mean flow, a point source of particles should disperse as a symmetric, two-dimensional Gaussian cloud with standard deviation given by $\sigma = (2Kt)^{1/2}$, where σ is the standard deviation, K is the single-particle eddy diffusivity and t is the time since release (Csanady, 1973; Poulain and Niiler, 1989). Using the above equation, an observed value of the diffusivity for the California Current of ~3000 $m^2 s^{-1}$ (Brink et al., 2000), and a PLD of 30 days yields a rough estimate for the standard deviation of potential dispersal of ~125 km, close to the present results (Table 3).

Our model grid has a horizontal resolution of ~1 km. Although this is a relatively high resolution for a domain of its geographical extent (most of central California), its resolution of the coastal boundary layer, the nearshore region of the coastal ocean where the immediate frictional effects of the coastal boundary are most felt, is relatively poor. This layer is generally just a few kilometers in lateral extent, but experiences reduced mean horizontal velocities that may increase nearshore retention and local settlement (Nickols et al., 2015). Our model also lacked tides, a seabreeze, surface waves and surfzone processes, all mechanisms that can increase mixing and aggregation in the nearshore region and thereby alter dispersal (Shanks, 1995b; Lentz and Fewings, 2012). Surfzone hydrodynamics, in particular, are a key small-scale determinant of larval recruitment to inshore communities. Whether recruiting larvae enter the surf zone depends on alongshore variation in surfzone hydrodynamics caused by the interaction of breaking waves with coastal morphology. Orders of magnitude more larvae occur in surf zones on gently sloping, rather than steep, shores due to the presence of bathymetric rip currents (Morgan et al., 2016, 2017, 2018; Shanks et al., 2017). The substantial inconsistencies between our results and the ecologically based dispersal estimates suggest that a higher-resolution modeling effort, capable of resolving the additional physical processes in the coastal boundary layer and surf zone, is needed to accurately predict the dispersal of benthic larvae, the corresponding connectivity of benthic subpopulations, and the design of MPAs.

Finally, our model showed that horizontal swimming could substantially increase nearshore larval supply in upwelling regimes despite Ekman transport. Empirical tests are now needed to determine how late-stage larvae and postlarvae of species with a range of swimming abilities navigate onshore to suitable settlement sites. Larvae likely use hierarchies of cues that are effective over different spatial scales, including celestial bodies, polarized light, magnetic and electric fields, waves and tides that indicate the general direction of settlement sites, and acoustic, chemical and visual cues that provide specific information on more-exact settlement locations (Arvedlund and Kavanagh, 2009; Kingsford et al., 2002; Leis et al., 2011).

Declarations of interest

None.

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