



Offshore oil production platforms as potential sources of larvae to coastal shelf regions off southern California

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ABSTRACT.—A diverse assemblage of adult reef fishes and invertebrates occurs at offshore oil production platforms in the Southern California Bight (SCB). Coincident with the initiation of the decommissioning of six platforms in the SCB, the goal of this study was to examine how a platform's geographical location plays a role in its potential contribution of larval recruits to natural areas. Using a three-dimensional biophysical model, we quantified the potential connectivity of larvae, particularly relevant to reef fishes, from three offshore platforms to four coastal shelf regions where the majority of rocky settlement habitat occurs in the SCB. The regions cover the shelves of the mainland coast and islands and offshore banks in the southern SCB. The main findings indicate that (1) the potential for larval subsidies from platforms in the southern SCB to populations in the northern SCB are greater than the potential for larval subsidies from platforms in the northern SCB to the southern SCB; (2) there is greater seasonal variability of potential connectivity from platforms to the mainland shelf region of the northern SCB than to the mainland shelf region of the southern SCB or shelves around islands and banks; and (3) there is consistency across years in the relative magnitude of potential connectivity from the platforms to the four shelf regions. We conclude that a platform's function as a larval source should be considered an ecological criterion when evaluating whether a platform is to be converted to an artificial reef and implementing marine spatial planning.

Fishes and invertebrates of oil and
gas platforms off California

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With the passage of the California Marine Resources Legacy Act (CMRLA) of 2010, the State of California and the United States (US) government will consider the option of leaving a decommissioned oil platform partially in place as a permanent artificial reef. This is an alternative to completely removing the structure when oil and gas production ends as was originally mandated when the platform was built. A decommissioned platform has yet to be converted to a natural reef off California. Two platforms in 1988, and four platforms most recently in 1996, all in California State waters, were completely removed (Manago and Williamson 1997).

The US established a federal artificial reef program in 1985 that allowed for decommissioned oil platforms in federal waters to be converted to artificial reefs if the state incorporates the structure into an established state artificial reef program and accepts liability. Louisiana, Texas, Mississippi, Alabama, and Florida have incorporated thousands of decommissioned platform structures as reefs into state artificial reef programs that were established in the 1980s (Scarborough Bull and Love 2018). Most nations require complete removal of obsolete structures. However, platforms have also been converted to artificial reefs in waters offshore Malaysia and Brunei Darussalam (Scarborough Bull and Love 2018). The possibilities of a rig-to-reef policy are being explored by Australia, Thailand and the United Kingdom (Molen et al. 2018, Scarborough Bull and Love 2018). The decision to fully or partially remove a platform off California will be made on a rig-by-rig basis based on specific criteria (Schroeder and Love 2004, Bernstein et al. 2010, Fowler et al. 2014).

Specified in the CMRLA, a decommissioned platform left in place as an artificial reef must provide a “net benefit” to the environment. However, the criteria by which the State will evaluate a platform’s net benefit is yet undefined. Bernstein et al. (2010) provides the California Natural Resources Agency with an expert committee-reviewed report of the scientific and legal information that will frame future state policy discussions on the alternatives for decommissioned platforms. A recommendation in the report is that an assessment of a decommissioned platform’s potential value as an artificial reef should necessarily address the importance of biological production at a platform to the regional ecosystem. One aspect of such an assessment is the degree to which reproduction at a platform contributes to the maintenance and/or recovery of regional populations of species (Bernstein et al. 2010, Fowler et al. 2014). Larval production by reef fishes and invertebrates that spawn at the offshore platforms can benefit regional populations if the young are able to survive through the dispersive phase and contribute to production in natural areas (Thorpe 2012, Molen et al. 2018). Larval dispersal patterns are expected to differ among the platforms that are scattered across a broad region of the Southern California Bight (SCB) that is characterized by highly complex ocean circulation (Bernstein et al. 2010, Simons et al. 2016). The goal of this study is to examine if geographical location plays a role in a platform’s potential contribution of larvae to natural areas in the SCB.

PLATFORMS AS LARVAL SOURCES.—A highly productive food web supports a diversity of fishes and invertebrates at oil platforms. Epifaunal invertebrates, including mussels, rock scallop, anemones, barnacles, sponges, corals, tubeworms, bryozoans and hydroids, cover the platform legs, crossmembers and well conductors (Love et al. 2019b, Page et al. 2019a). Motile invertebrates such as crabs, amphipods and other crustacea, seastars, nudibranchs and polychaetes are abundant. The shellfish and attached epifauna that fall from the structure form a shell mound that serves as low-relief, reef-like habitat for motile invertebrates and reef fishes at the bases of shallow and deep-water platforms (Goddard and Love 2010, Love et al. 2019b, Page et al. 2019a). In regard to fishes, Claisse et al. (2014) showed that California platforms, due to their three-dimensional structure, have the highest secondary production per unit area of seafloor among marine ecosystems in the world for which data exists.

Many of the fish species observed amid the complex structure of offshore oil platforms that rise from the seafloor to the surface are common in rocky-reef habitat and are uncommon or rare on soft bottom habitat (Love et al. 2003, Pondella et al. 2015,

Love et al. 2019a). Rockfishes (genus *Sebastes* Cuvier, 1829) are the most speciose taxa and are among the most abundant taxa on platforms (Love et al. 2019a). Adults of deep-water rockfishes dominate the assemblage at the bottom of the platforms (Love et al. 2019a). Adults of species found at shallower near-shore reefs are regularly observed in the upper portion of the structures (Nishimoto et al. 2019, Love et al. 2019a). Fish assemblages at platforms are both similar to and distinct from those of natural reefs (Love et al. 2019a). These distinctions are due more to differences in species' densities rather than to the presence or absence of certain taxa.

Juvenile recruits of shallow and deep dwelling rockfish species are often observed to be more abundant on platforms than adult fishes (Nishimoto et al. 2019) and account for most of the growth in biomass (Claisse et al. 2014). As at natural reefs, settlement is highly variable both spatially and temporally within and between years (Love et al. 2012, Love et al. 2019a, Nishimoto et al. 2019). In many instances, young reef fish are more abundant at platforms than at many natural sites. Firstly, this may be because platforms encompass the entire water column, and thus pelagic larvae and juveniles are more likely to encounter the tall structure than natural habitats, which have relatively little relief above the seafloor (Love et al. 2019a). Secondly, predation on the small reef fish recruits may often be lower in platform midwaters than on natural habitats because the platform midwaters tend to harbor lower densities of large predatory reef fishes than natural habitats and because pelagic predators (i.e., jacks, sharks, and barracuda) are relatively rare around California platforms (Love et al. 2019a). Scuba surveys at Platform Gail and Platform Gilda indicate that currents from south of the Santa Barbara Channel (SB Channel), rather than from central California, supply recruits to settlement habitat in the eastern SB Channel and that the spatial scale of connectivity for some fish populations in the eastern SB Channel expands well beyond the SB Channel (Nishimoto et al. 2019). Some species that recruit to the platforms, for example bocaccio (*Sebastes paucispinnis* Ayres, 1854) survive and mature (Love et al. 2006), supporting the thriving population on the oil platforms that may produce offspring for natural reefs.

Arguably, the offshore platforms may be attracting some species of sea life or capturing competent ready-to-settle recruits that would otherwise find or intercept natural habitat. However, passive drifter simulations using high-frequency radar surface current mapping indicate that young fish could potentially intercept and settle at one of the platforms at the western entrance of the SB Channel that would otherwise have been transported far offshore and likely perished in the absence of the structure (Emery et al. 2006).

In addition to biomass production at platforms, reproduction can be considered a contribution to a platform's net benefit to the environment. Mature reef fishes are common at the platforms in the SCB (Love et al. 2003, 2005, 2019a). The assemblage of reef fish at platforms include species that are broadcast spawners of planktonic eggs [e.g., *Chromis punctipinnis* (Cooper, 1863)] or planktonic larvae (e.g., *Sebastes* spp.) and benthic spawners of adhesive eggs from which hatch planktonic larvae. Egg nests of cabezon [*Scorpaenichthys marmoratus* (Ayres, 1854)] and garibaldi [*Hypsypops rubicundus* (Girard, 1854)] have been observed on several platforms (Martin and Lowe 2010).

For most benthic marine invertebrates and fishes, planktonic gametes, eggs or larvae produced at a platform are dispersed by currents in the open ocean environment. The larvae of nearly all reef fish species occurring at platforms and nearshore reefs,

with exception of Embiotocidae that bear live fully formed juveniles, are collected in extensive offshore ichthyoplankton surveys (Moser et al. 1993, 1994). Ocean conditions and circulation will impact larval dispersal and survival (Ralston and Howard 1995, Houde 2008, Shulzitski et al. 2016, Wheeler et al. 2017). The ontogenetic pelagic phase varies from minutes to months among species, after which time, individuals that are competent to settle and intercept suitable habitat transition to a benthic phase (Pineda et al. 2007, Love 2011). The duration of the early pelagic phase of reef fish species that are common as adults on platforms in the SCB ranges from 1 to 6 mo. These fishes settle as late stage larvae transitioning to juveniles or juveniles fully formed as adults depending on the species. Newly settled fish have been observed by scuba divers, remotely operated and autonomous underwater vehicles, and in manned submersibles on a variety of rock habitats mostly at depths of about 100 m and shallower ranging from a single cobblestone embedded in mud to as expansive an area as a continuous rock ridge (Love 2011, Love et al. 2019a).

LARVAL DISPERSAL FROM PLATFORMS.—There are 27 oil and gas production platforms off the southern California coast. The platforms are located 2–16 km from the mainland shore in depths 9–365 m and span 270 km of the coastline from Platform Irene north of Point Conception to Platform Eureka offshore Huntington Beach south of Los Angeles (Fig. 1). The platforms were installed between 1963 and 1990 and are all approaching the end of the expected lifetime of useful oil and gas production (Scarborough and Love 2018). As of September 2019, decommissioning has begun for one of four platforms in California state waters (within 3 mi offshore) and five of 23 platforms in federal waters. The remainder will likely be decommissioned sometime before 2030 (Bernstein et al. 2010).

The platforms are distributed across much of the SCB, which has been described as a broad biogeographic transition zone between marine communities with affinities for cooler northerly waters of the Oregon Province and warmer southerly waters of the San Diego Province (Harms and Winant 1998, Pondella et al. 2005, Blanchette et al. 2008). The SCB is part of the US west coast upwelling current system, but the general circulation pattern in the SCB is very different from the coastal region north of the SCB where year-round, wind-induced coastal upwelling and cold waters from the California Current are the predominant drivers of variability in coastal circulation (Hickey 1979, Harms and Winant 1998). The northern and southern regions of the SCB display distinctly different circulation and temperature profiles. The oceanographic regime in the southern SCB is defined by warm equatorial waters, which are driven north by the Southern California Counter Current (SCCC; Hickey 1993, Winant et al. 2003). In contrast, the northern SCB, which includes the SB Channel and the northern Channel Islands, is a mixing zone where the cold waters from the northern California Current and the warm waters from the SCCC meet, creating its own distinct circulation and temperature patterns (Otero and Siegel 2004, Simons et al. 2015). The high marine biodiversity in the SCB region is due to the mixing of these warm- and cold-water regimes (Horn and Allen 1978, Murray and Littler 1981, Hickey 1993, Hamilton et al. 2010). Due to the shape of the coastline, the SCB is sheltered from the strong northerly wind north of Point Conception, and thus the wind in the SCB is relatively weak, especially nearshore. In the southern SCB, a domain-scale gyre called the Southern California Eddy manifests from two distinct currents (Fig. 2), the California Current and the SCCC. The California Current is a meandering

offshore current, which carries cooler, fresher water from the northern Pacific equatorward. The eastern boundary of this broad current is located to the west of the SB Channel and the Santa Rosa ridge and extends southeastward from the northern Channel Islands, which form the southern border of the SB Channel. Near the US/Mexico border, the California Current bifurcates, and part of the flow turns inshore and converges with the poleward flow (towards the north pole) of the SCCC, which carries warmer, saltier water from the tropics. The complex bathymetry within the SCB steers standing eddies within topographic basins: the Santa Barbara Channel Eddy, the Central Southern California Bight Eddy, and the Catalina-Clemente Eddy (Fig 2.; Harms and Winant 1998, Dong et al. 2009).

This study is intended to be a broad generic study aimed at determining whether different platforms potentially contribute different quantities of larvae to natural reefs purely based on their location and ocean circulation. We use a three-dimensional biophysical model to assess the potential connectivity from oil platforms to areas over the continental shelf, shelves around islands, and the crests of offshore banks that encompass the majority of suitable habitat for newly settled reef fishes in the SCB. Following methods from Mitarai et al. 2009 and Watson et al. 2010, we define potential connectivity as the probability of passive larval dispersal from a source to destination areas via currents. We opted to focus on potential connectivity, as opposed to realized connectivity as defined by Watson et al. (2010), because it does not include species specific data such as larval production, larval behavior and mortality, and yet meets the goal of our project.

METHODS

We examined the dispersal of larvae and potential connectivity from three offshore platforms [C (34°19'N, 119°37'W; bottom depth of 58 m), Gail (34°07'N, 119°24'W; bottom depth of 224 m), and Eureka (33°33'N, 118°06'W; bottom depth of 212 m)] to all areas off the mainland coast, islands, and submerged banks in the SCB where bottom depths are 100 m and less (Fig. 1). Most reef fish species in the SCB, including those that occur at the base and amid the vertical structure of the platform, utilize natural areas with rock substrate at depths shallower than 100 m for settlement, and newly recruited fishes are much less abundant at deeper depths (Love 2011, Love et al. 2019a). The three source platforms were selected because they are located a substantial distance away from the boundary of the model domain and the near-field and far-field circulation patterns markedly differ among the three platforms (Hickey 1979, Harms and Winant 1998, Dong et al. 2009). Both Platforms C and Gail are located in the eastern SB Channel, with Platform C standing in relatively shallow water on the mainland shelf and Platform Gail standing in deep water off a steep shelf break. Platform Eureka is in the southern portion of the SCB in a depth comparable to that at Platform Gail.

We divided all areas off the mainland coast, islands, and submerged banks in the SCB where bottom depths are 100 m and less into what we will refer to herein as "settlement regions" (Fig. 1): (1) SBCMAIN (area of 1192 km²), consisting of areas along the mainland shelf of the SB Channel between Point Conception and Hueneme Canyon; (2) SMAIN (area of 1926 km²), consisting of the area along the mainland shelf south of the SB Channel to the southern boundary of the SCB; (3) SBCI (area of 1275 km²), consisting of areas surrounding the four Northern Channel Islands

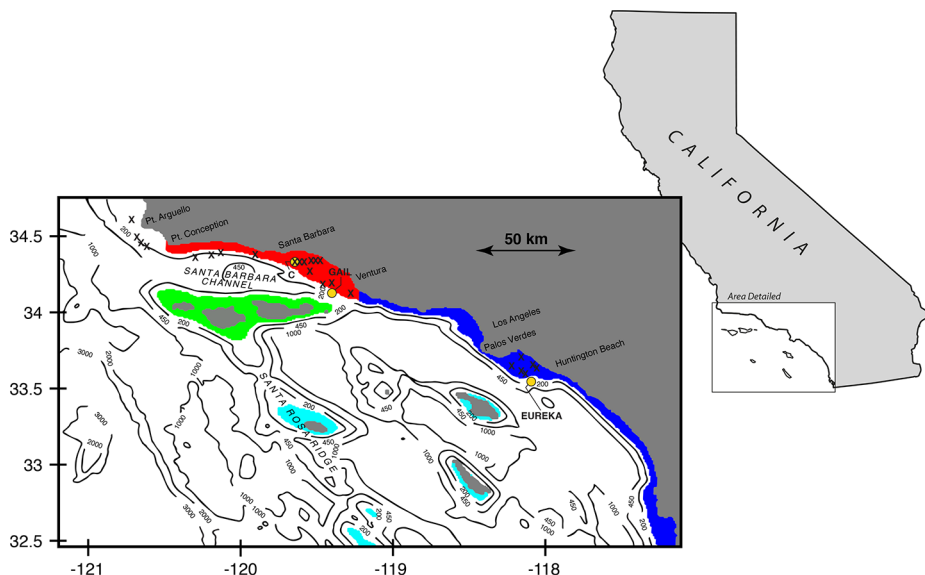


Figure 1. Southern California Bight (SCB) and model domain with bathymetry (m). Four settlement regions encompass all areas < 100 m depth: red zone is the Santa Barbara Channel mainland (SBCMAIN); dark blue zone is the south coast of the SCB (SMAIN); green zone is the Northern Channel Islands (SBCI); and light blue zone is the Southern Channel Islands and offshore banks (SIB). Yellow circles identify Platforms C, Gail, and Eureka, the larval source locations in the study. Xs represent the remaining 24 platforms in the SCB.

that form the southern border the SB Channel; and (4) SIB (area of 879 km^2), consisting of areas surrounding the Southern Channel Islands and the offshore banks in the southern SCB. Figure 2 shows that current patterns distinguish the northern SCB (the SB Channel) from the southern region of the SCB. Settlement regions 1–4 comprise 7.9% of the total surface area of the ocean in the SCB ($66,557 \text{ km}^2$). These are broad in size, but relevant to population dynamics, community structure, and resource management in the SCB (Love et al. 2009).

To estimate larval dispersal from the platforms to the settlement regions, we used a three-dimensional biophysical model, which consists of an ocean circulation model (OCM) coupled with a particle-tracking model. The three-dimensional OCM is a Regional Ocean Modeling System (ROMS) applied to the SCB (Shchepetkin and McWilliams 2005, Dong and McWilliams 2007). The model domain, which contains the SCB, is shown in Figures 1 and 2. The model grid is $258 \text{ km} \times 386 \text{ km}$ with a 1 km horizontal resolution and 40 vertical levels. Detailed information on the lateral and surface boundary conditions and model validation can be found in Dong and McWilliams (2007) and Dong et al. (2009). Following the methods in Carr et al. (2008) and Mitarai et al. (2009), the three-dimensional particle-tracking model is driven by 6-hr averaged three-dimensional velocity fields produced by the ROMS. For this study, the ROMS velocity fields were available for 12 yrs from 1996–2007. Particles are moved forward in time using a fourth-order accurate Adams-Bashforth-Moulton predictor-corrector scheme and a 900 s time step. The particle-tracking model has been validated against observational data from drifter experiments by Ohlmann and Mitarai (2010). The biophysical model accurately reproduced the spread of the

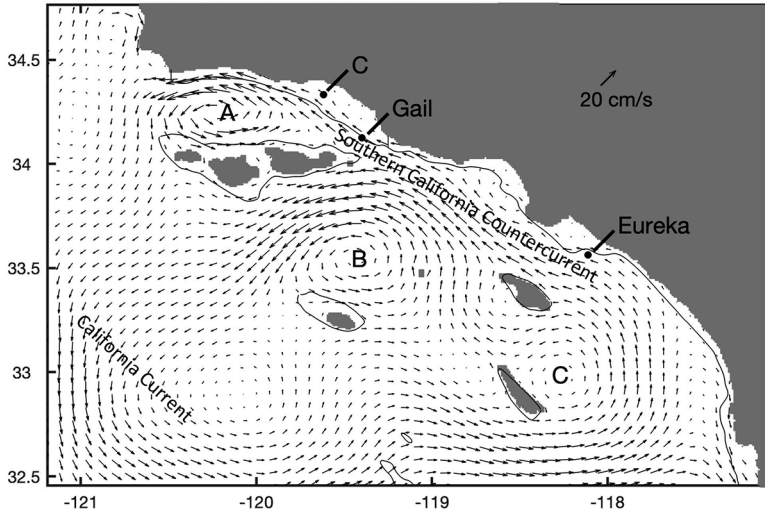


Figure 2. Platforms and mean currents in the SCB model domain, depth-averaged over the uppermost 80 m of water column, generated by the Regional Ocean Modeling System (ROMS). The black lines identify the 100 m isobaths that bound the four settlement regions.

nonnative bryozoan *Watersipora subtorquata* among platforms in the SB Channel (Simons et al. 2016, Page et al. 2019b), and a similar model has been used to estimate larval dispersal from platforms in the west coast of Scotland (Adams et al. 2014).

At each platform, particles were released vertically every 0.25 m from 1 to 80 m below the surface, the depth range where the larvae of most rocky reef dwelling fishes are found based on the following research. Moser and Pommeranz (1999) provided a detailed description of the vertical distribution of ichthyoplankton at two stations in the SCB during March and April 1980, and found that the larvae of both shallow- and deeper-dwelling species were highest between 20 and 80 m and occurred throughout the water column from the surface to 200 m, the deepest depth sampled. Studies generally agree that larvae of northeast Pacific nearshore and deep-water reef fishes tend to occur above 100 m and that distributions roughly are centered within and below the thermocline (e.g., Ahlstrom 1959, Boehlert et al. 1985, Sakuma et al. 1999, Bjorkstedt et al. 2002, Auth et al. 2007). Conservatively, this study can be limited to apply to fish species that reside at the platform and occur in the upper portion of the platform with the depth range where particles are released in the model (Table 1).

Particles were released every 3 hrs from each platform and tracked passively for 30 d over the course of 12 yrs. Justification for the selection of passive particle behavior and 30-d dispersal period can be found in the discussion section. The number of particles released and the particle release frequency was selected to meet the criteria for robustness in particle-tracking models (Simons et al. 2013). For this study, approximately 33 million particle trajectories were simulated from the platforms.

The particle trajectories are transformed into a two-dimensional particle density distribution (PDD). The PDD provides an accounting of the probability of dispersal from a source platform to every 1 km² grid cell of open water (a total of 66,557 km²) within the model domain.

Table 1. Examples of mature reef fishes occurring at all platforms (C, Gail, and Eureka), depth distribution, spawning seasonality, and early life history characteristics (Love 2011; Love et al. 2019a; Nishimoto and Love, unpub. data).

Species	Common name	Common adult depth (maximum)	Spawning mode	Spawning period (peak season)	PLD (days) ¹	Settlement depth (maximum)	Size at settlement
<i>Chromis punctipinnis</i> (Cooper, 1863)	Blacksmith	46 m (91 m) ²	Adhesive egg nests	Apr–Nov (Summer–Fall)		≤15 m ^{2,3}	1 cm TL and larger
<i>Medialuna californica</i> (Steindachner, 1876)	Halfmoon		Gametes released	May–Nov (Summer–Fall)		≤40 m	2.5 cm SL
<i>Ophiodon elongatus</i> Girard, 1854	Lingcod	<100 m (475 m)	Adhesive egg nests ⁴	Nov–June (Winter–Spring)	90–120	≤100 m (200 m)	7–8 cm TL
<i>Paralabrax clathratus</i> (Girard, 1854)	Kelp bass	30 m (61 m)	Gametes released	Apr–Aug (Summer)	25–36		0.9–1.4 cm TL
<i>Scorpaenichthys marmoratus</i> (Ayres, 1854)	Cabezon	≤73 m (231 m)	Adhesive egg nests	All year (Winter)		≤30 m	3–5 cm TL
<i>Sebastes atrovirens</i> (Jordan and Gilbert, 1880)	Kelp rockfish	82 m	Larval parturition	Feb–Aug (Spring–Summer)	60–90		2.0–4.6 cm TL ⁵
<i>Sebastes caurinus</i> Richardson, 1984	Copper rockfish	86 m	Larval parturition	Jan–Apr		≤40 m	1.2–1.8 cm SL
<i>Sebastes hopkinsi</i> Cramer, 1895	Squarespot rockfish	55–115 m (305 m)	Larval parturition	Jan–Apr	105–120	≥21 m	4.3 cm SL
<i>Sebastes miniatus</i> (Jordan and Gilbert, 1880)	Vermillion rockfish	105 m (439 m)	Larval parturition	All year (Fall)		≤40 m	1.3–3 cm SL
<i>Sebastes mystinus</i> (Jordan and Gilbert, 1881)	Blue rockfish	55 m (549 m)	Larval parturition	Oct–Mar (Winter)	90–180	≤40 m (63 m)	3.1 cm SL and larger
<i>Sebastes semicinctus</i> (Gilbert 1897)	Halfbanded rockfish	60–125 m (402 m)	Larval parturition	Nov–Apr (Winter–Spring)		≥30 m	2 cm TL and larger
<i>Bodianus pulcher</i> (Ayres, 1854)	California sheephead	60 m	Gametes released ⁶	Apr–Sept (Summer–Fall)	35–78		1.3 cm SL

¹ Pelagic larval duration (PLD) is the phase before settlement and includes a pelagic juvenile stage for some species

² Limbaugh 1964

³ Nishimoto et al. 2019

⁴ Nests observed at 30–92 m

⁵ Ammann 2004

⁶ Spawning observed at 3–4 m below sea surface

Using the three-dimensional distribution of particles at 30 d released over a month from a single platform, a monthly PDD was produced by summing the number of 30-d old particles within a grid cell over depth and then dividing by the total number of particles released (Mitarai et al. 2009). Herein, we will refer to the particles as “larvae” and the 30-d old larvae as “prerecruits”. An assumption is that reef fish prerecruits are able to remain in the settlement region to complete the ontogenetic pelagic phase and “settle” or transition to the benthic phase where suitable rocky habitat is found. The monthly PDDs were treated as sample units from each platform. We use the monthly PDDs to statistically examine the expected locations of prerecruits within the domain 30 d after release. Potential connectivity from a platform to a settlement region is measured as the fraction of larval trajectories released from a platform that end in a settlement region standardized per km² of that region (fraction of particles km⁻²). Based on the methods followed in Mitarai et al. (2009) and Simons et al. (2013), these fractions produced are small but within the same order of magnitude of similar studies that estimate larval connectivity using biophysical models (e.g., Cowen et al. 2006, Siegel et al. 2008, Mitarai et al. 2009, Costello et al. 2010, White et al. 2010). The fractions represent the relative probability of potential connectivity and are only meaningful when compared to each other. Monthly potential connectivity per settlement region was calculated by averaging the PDD values of the grid cells within that region. Seasonal estimates of connectivity within each year were calculated as 3-mo averages. We defined the four seasons as November–January for winter, February–April for spring, May–July for summer, and August–October for fall.

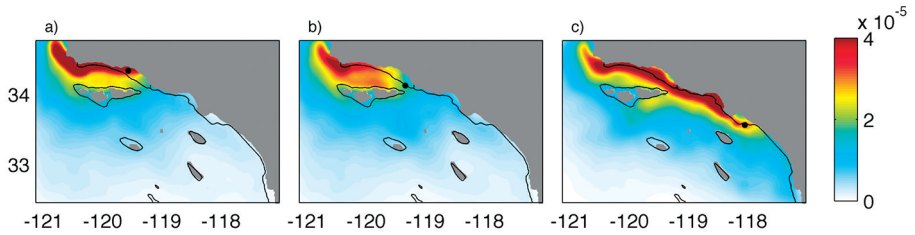


Figure 3. Probability density distributions (PDDs) averaged over all months and years for (a) Platform C, (b) Platform Gail and (c) Platform Eureka. The solid black circles identify the platforms. The black lines identify the 100 m isobaths that bound the four settlement regions.

RESULTS

The PDDs averaged over all months and years show that larval dispersal from each of the three platforms is extensive throughout the SCB, and display features that distinguish Platform Eureka in the southern SCB from Platforms C and Gail in the SB Channel (Fig. 3). Overall, prerecruits (i.e., 30 d old larvae) had been advected poleward from the three platforms by the prevailing SCCC over the shelf and slope (Fig. 2). For the PDDs displayed in Figure 3, 55%, 53%, and 72% of the larvae released remain within the model domain for Platforms C, Gail, and Eureka, respectively. Since the dominant flow pattern along the coast is poleward forced by the SCCC, the majority of larvae lost from the model domain is through the northern boundary. Platforms C and Gail have lost more larvae from the model domain than Platform Eureka because they are much closer to the northern boundary. Of the prerecruits remaining within the model domain, 14%, 11%, and 14% are contained within the four regions for Platforms C, Gail, and Eureka, respectively (Fig. 3). This implies that although more larvae are lost from the model domain for Platforms C and Gail than Platform Eureka, the total percentage of prerecruits from each platform that land in the four regions is similar. The prerecruits are predominantly found in the SB Channel and on the shelf north of the SB Channel for all three platforms and on the shelf south of the SB Channel for Platform Eureka. Based on a comparison of long-term average PDDs in Figure 3 and flow fields in Figure 2, the prevailing SCCC appears to restrict the equatorward dispersal of prerecruits along the coast, thus substantially limiting the dispersal of prerecruits from the platforms to the southern part of the SCB. Cyclonic eddy circulation in the SB Channel also appears to retain prerecruits from Platforms C and Gail within the SB Channel and Platform Eureka in the southern part of the SCB (Figs. 2 and 3).

The degree of potential connectivity to each of the four settlement regions differs among the three platforms (Fig. 4). Prerecruits from Platforms C and Gail are about five times more likely to be delivered to the SBCMAIN and SBCI than to SMAIN and SIB. The potential connectivity of Platform Eureka to SBCMAIN is greater than the potential connectivity of Platform Gail. As shown in Figures 1 and 2, Platforms Gail and Eureka are both in open deep water, at 224 m and 212 m depth, respectively, and fully exposed to the strong poleward flows of the SCCC. Forced by the SCCC, the PDDs in Figure 3 show that the prerecruits released from both Platforms Gail and Eureka are primarily distributed along the coast north of the platforms. As Platform

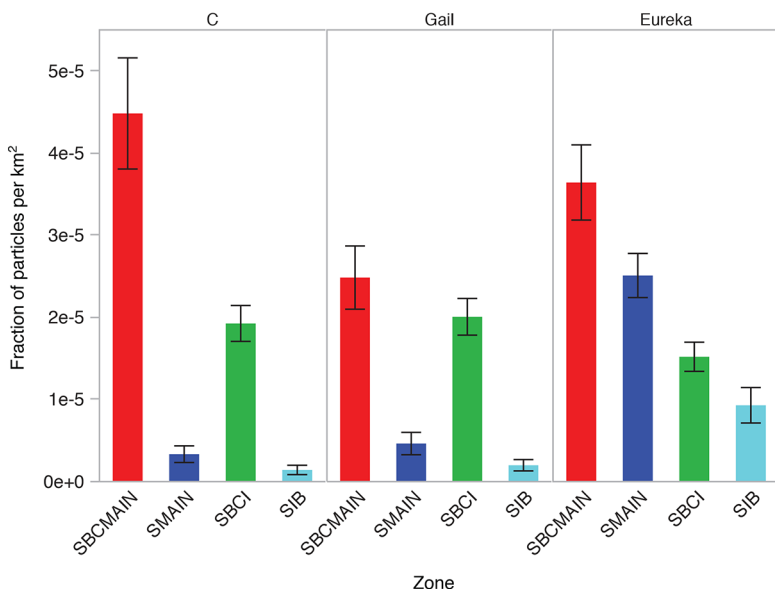


Figure 4. Potential connectivity from Platforms C, Gail and Eureka (source sites) to the four settlement regions averaged over all months and years. Potential connectivity is measured as the average fraction of released particles from a source per km² within a settlement zone 30 d after release. Error bars are 95% confidence intervals of the mean. Colors correspond with the four regions mapped in Figure 1.

Eureka is located about 100 km south of the SB Channel, the high potential connectivity, shown in red in Figure 3, from Platform Eureka stretches out along the coast from Platform Eureka and into the SB Channel and SBCMAIN. In contrast, although the high connectivity from Platform Gail has also been driven poleward by the SCCC, most of the prerecruits released from Platform Gail have been driven away from SBCMAIN and into the offshore waters of the western SB Channel. Thus even though Platform Gail is closer to SBCMAIN than Platform Eureka, the strong advection of the SCCC and the 30 d tracking time of the prerecruits results in higher connectivity from Platform Eureka to SBCMAIN than from Platform Gail. The potential connectivity of Platform Eureka to SMAIN and SIB is about four times greater than from either Platforms C or Gail in the SB Channel.

Seasonal variability in the PDDs for each platform and in the SCB-wide and subregion scale circulation is evident in Figures 5 and 6. In the PDDs for all three platforms, winter marks the peak prerecruit densities in SB Channel (Fig. 6). These high prerecruit densities are driven by the strongest poleward currents of the year along the shelf and slope from the SCCC along with cyclonic recirculation in the SB Channel (Fig. 6). During the spring transition, both cyclonic recirculation and upwelling-favorable winds strengthen in the SB Channel and the SCCC weakens. In the SB Channel, waters from the mainland shelf and slope are advected out the western entrance or recirculated eastward and out the eastern entrance or the gaps between the Northern Channel Islands (Fig. 5). Consequently, prerecruit densities from Platforms C and Gail decrease in SBCMAIN from winter to spring and are at their lowest during the summer (Fig. 7). In comparison, seasonal PDDs for Platform Eureka show

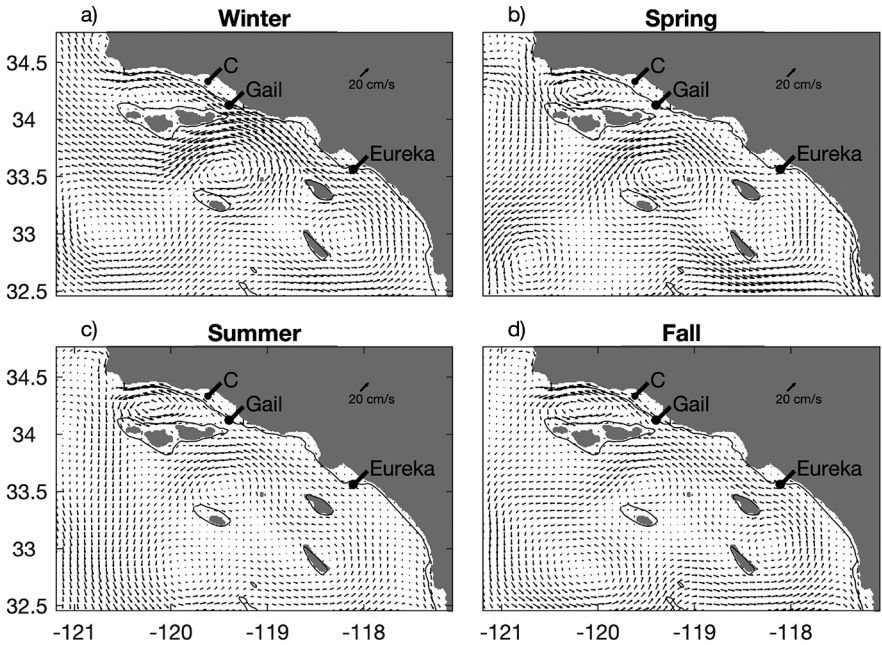


Figure 5. Mean currents in the SCB model domain, depth-averaged over the uppermost 80 m of water column, generated by the ROMS for (a) Winter, (b) Spring, (c) Summer and (d) Fall.

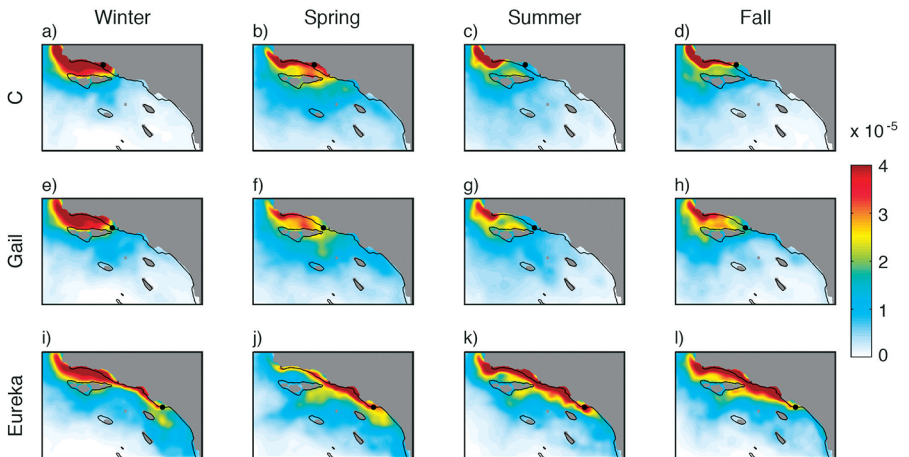


Figure 6. Probability density distributions (PDDs) averaged over four seasons for (a–d) Platform C, (e–h) Platform Gail and (i–l) Platform Eureka. The solid black circles identify the platforms. The black lines identify the 100 m isobaths bounding the four settlement regions mapped in Figure 1.

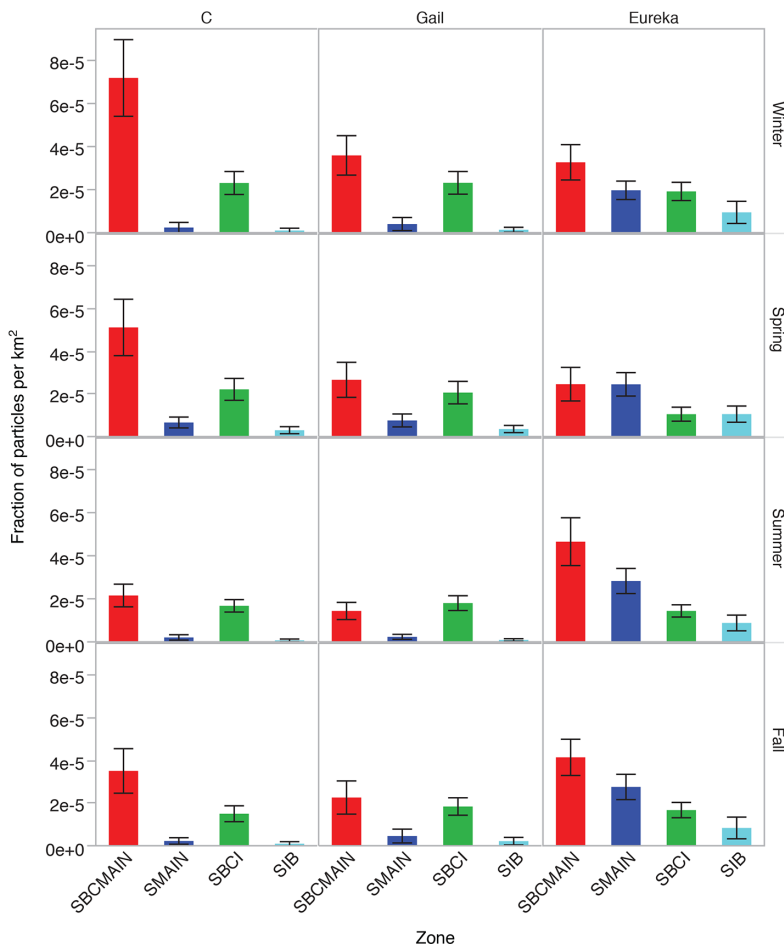


Figure 7. Seasonal potential connectivity from Platforms C, Gail and Eureka (source sites) to the four settlement regions averaged across months and years. Error bars are 95% confidence intervals of the mean. Colors correspond with the regions mapped in Figure 1.

that prerecruit densities are at the lowest in SBCMAIN in the SB Channel during the spring when poleward flow from the SBCC is weakest (Fig. 7). However, as poleward flow strengthens across the eastern entrance of the SB Channel during the summer and fall, prerecruit densities from Platform Eureka increase in SBCMAIN (Fig. 7).

The potential connectivity of platforms to the settlement regions is variable across seasons. However, there is some consistency across seasons in the relative magnitude of potential connectivity to the four regions from each platform (Fig. 7). Consistent with the long-term averages shown in Figure 4, potential connectivity of the platforms for all four seasons show that prerecruits from Platforms C and Gail are far more likely to be found in SBCMAIN and SBCI within the SB Channel than in SMAIN and SIB south of the SB Channel. The potential connectivity from Platform Gail to the SBCMAIN is consistently less than from Platform C, indicating that prerecruits from Platform C are more likely to be retained on the shelf than transported offshore compared to Platform Gail. Furthermore, the potential connectivity of

Platform Eureka to the SMAIN and to SIB exceeds the potential connectivity from either of the two platforms, C and Gail, in the SB Channel.

The potential connectivity from the platforms to the settlement regions is generally consistent across years (Fig. 8). Similar to the long-term and seasonal averages shown in Figures 4 and 7, annual estimates of potential connectivity show that prerecruits from Platforms C and Gail are far more likely to be delivered to SBCMAIN and SBCI than to the regions south of the SB Channel, SMAIN and SIB. The potential connectivity from Platform Gail to SBCMAIN is consistently less than from Platform C. Furthermore, the potential connectivity from Platform Eureka to SMAIN and to SIB exceeds the potential connectivity from either of the two platforms, Platforms C and Gail, in the SB Channel. Results in Figure 8 show that only a few years in the time series exhibit an anomalous pattern of potential connectivity from a platform to a settlement zone. For example, in 1999, the potential connectivity from Platform Eureka to SBCMAIN was substantially lower compared to other years, while potential connectivity to SIB was markedly elevated.

DISCUSSION

Results from our simulation show that the relative contribution of larval prerecruits from three source localities (platforms) to four settlement regions off the mainland, islands, and banks reflects the subdomain scale eddy circulation of the northern and southern SCB. The main findings indicate that (1) the potential for larval subsidies from platforms in the southern SCB to populations in the northern SCB are greater than the potential of larvae subsidies from platforms in the northern SCB to the southern SCB; (2) there is greater seasonal variability of potential connectivity from the three platforms to the mainland shelf region of the SB Channel (SBCMAIN) than to the mainland shelf of the southern SCB (SMAIN) and the offshore shelves of the southern islands and banks (SBCI and SIB); and (3) there is consistency across years in the relative magnitude of potential connectivity from the platforms to the four settlement regions.

Year-round cyclonic eddy recirculation within the SB Channel and the poleward SCBC along the mainland coast and shelf of the SCB restricts the dispersal of larvae into the southern SCB through the eastern entrance of the SB Channel (Figs. 2 and 3; Nishimoto and Washburn 2002, Simons et al. 2015). Thus, the potential connectivity from Platform Eureka to settlement regions in the SB Channel is greater than the potential connectivity from Platforms C or Gail to settlement regions in the southern SCB (Fig. 4). Watson et al. (2011) utilizes the SCB ROMS in a biophysical metapopulation model to estimate patterns of larval connectivity and demonstrates that key subpopulations are located around the offshore islands in the southern SCB and are the major sources of recruits for the population at large within the SCB. According to Watson et al. (2011), removing these subpopulations would theoretically increase the risk for domain-wide metapopulation collapse. In contrast, the SB Channel was found to be lacking key subpopulations. Watson et al. (2011) pointed out that the southern SCB island subpopulations must have high potential connectivity to other subpopulations and a relatively high carrying capacity that is dependent on the suitability of habitat for recruitment and replenishment. We surmise that Platform Eureka may function like key subpopulations around offshore islands in the southern SCB that Watson et al. (2011) identified. In addition to our finding that potential

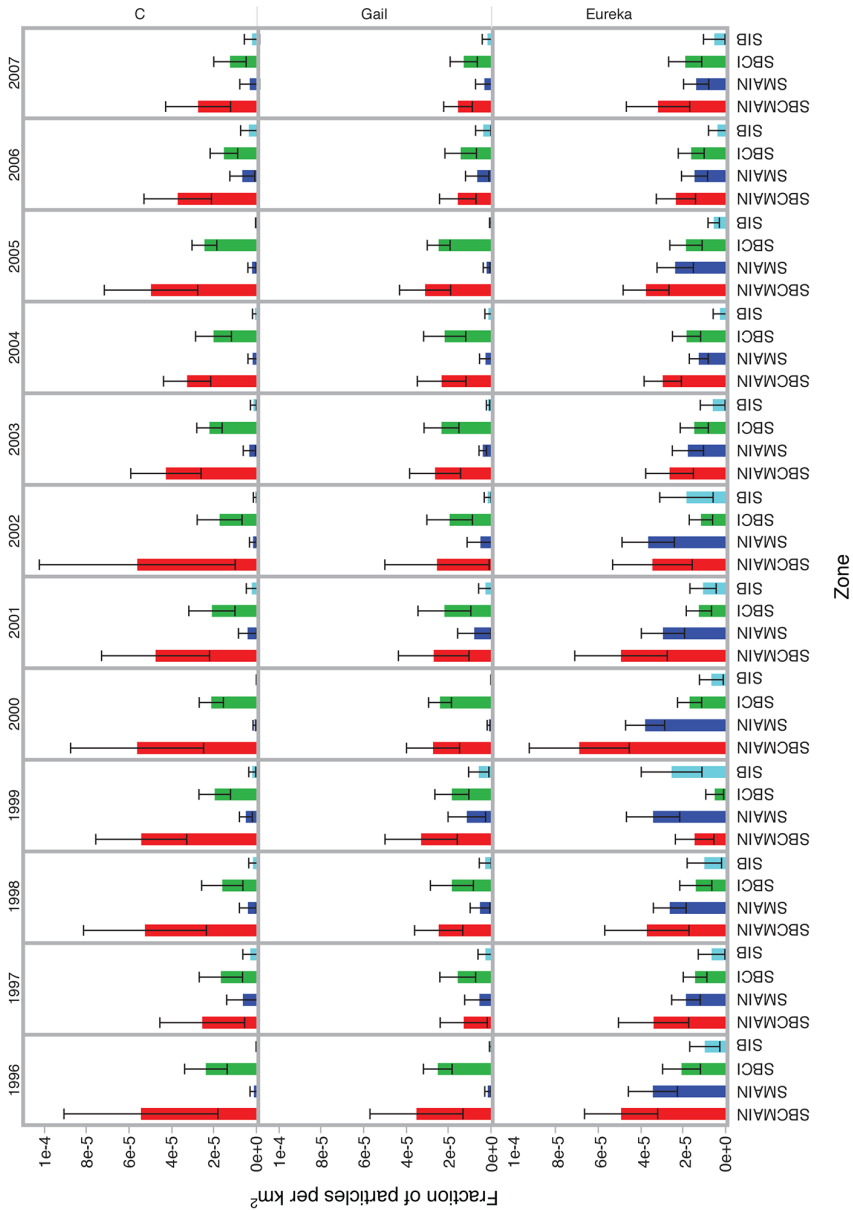


Figure 8. Annual potential connectivity from Platforms C, Gail and Eureka (source sites) to the four settlement regions averaged across all months within each year. Error bars are 95% confidence intervals of the mean. Colors correspond with the regions mapped in Figure 1.

larval connectivity of Platform Eureka was higher than that of Platform Gail to the SBCMAIN region, Love et al. (2019a) shows that although recruits are abundant at both platforms, the spawning population is more abundant at Platform Eureka than at Platform Gail in the SB Channel. Platform Eureka and the other offshore platforms in the southern SCB may provide critical larval subsidies to natural reefs throughout the SCB.

Although the mean potential connectivity to SBCMAIN from Platform Eureka is greater than from Platform Gail (Fig. 2), the relative importance of the two platforms as potential sources of prerecruits to SBCMAIN varies seasonally. Furthermore, the species assemblage of the egg/larval pool dispersed from a platform is expected to be seasonally variable (Table 1). The potential connectivity of winter and spring spawners from Platform C to SBCMAIN is twice that from Platforms Gail and Eureka. Oppositely, summertime spawners at Platform Eureka are twice as likely as those at Platforms C and Gail in the SB Channel to contribute prerecruits to the SBCMAIN. Thus, the degree of seasonal variability in potential connectivity may contribute to differences in community structure, including species and genetic diversity, among settlement regions.

We employed a null model of larval behavior in which dispersal is solely driven by three-dimensional ocean circulation. Modeling the dispersal of passive particles contrasts with the growing trend in recent years of incorporating one or several larval behaviors and traits in addition to pelagic larval duration such as spawning frequency, directional swimming, sensory cueing, growth rate, condition and mortality into biophysical models (Huret et al. 2007, Paris et al. 2013, Paris et al. 2013, Staaterman and Paris 2014, Wolanski and Kingsford 2014, Vaz et al. 2016, Drake et al. 2018, Molen et al. 2018). Vertical migration was the first trait to be identified as a retention mechanism that increased settlement near natal habitat (Paris and Cowen 2004, Paris et al. 2007). The addition of horizontal swimming into biophysical models has been more recent and significantly affects settlement success, as many fish species prove to be fast swimmers in laboratory experiments (Staaterman and Paris 2014).

It is important to recognize that most specimens in “larval fish” swimming speed experiments are best described as presettlement juveniles in transition from the pelagic to benthic habitat and most are observations of tropical species (Koumoundouros et al. 2009, Faillettaz et al. 2018). Fisher et al. (2005) showed that body morphology, particularly in relation to caudal fin development, accurately predicts swimming speed based on published Ucrit swimming speed data from 100 tropical fish species and 26 different families that are described mostly as largely developed into the adult body form. Ucrit is the maximum speed at which a fish specimen can maintain its position against a current for 2 min while visually cuing to a marker in an experimental flume. The specimens ranged from an average of 0.64 cm to 3.73 cm among families and were smaller or near the size of newly settled temperate reef fishes like those listed in Table 1. Leis et al. (2013) provides a review of how larval dispersal differs among tropical and temperate reef fishes in relation to biology and the ocean environment. Reef species that occur in temperate waters tend to have slower larvae (5–10 body lengths s^{-1}) while most tropical reef taxa have fast swimming larvae (15–20 body lengths s^{-1}) through the early pelagic phase before settlement. This is attributed to most temperate taxa morphologically transitioning more slowly from the larval to juvenile form than tropical taxa, and the hydrodynamic limitation of

greater viscosity and drag on the preflexion and flexion larval form swimming in a colder water environment (Leis et al. 2013).

We chose a dispersal period of 30-d during which larvae of many temperate reef fish species, including rockfishes (Petersen et al. 2010, Kashef 2014), have not yet developed the skeleton, musculature and fins of older larvae transitioning to the juvenile form. Small larvae at hatching or parturition, as is the case for live bearing rockfishes, do swim, but in using a passive dispersal model, we make the assumption that the repertoire of behaviors of larvae less than 30-d old will not statistically affect the estimate of a platform's potential larval connectivity to the settlement regions. Eggs, clearly subject to passive dispersal, and small larvae of temperate taxa have been found to have similar patterns of spatial heterogeneity (i.e., patchiness in ichthyoplankton surveys) indicating that the preflexion larvae are effectively passive propagules in the open ocean (Stanley et al. 2012). Kashef (2014) observed that swimming ability increases throughout ontogeny for rockfish species, including kelp rockfish and blue rockfish that occur as adults at all three platforms and potentially reproduce at the structures (Table 1). Based on an average U_{crit} ranging from 0.76 to 1.36 cm s^{-1} for six species of rockfish larvae at the preflexion stage, it is unlikely that larvae at this stage would be able to swim against current speeds of the scale of 10 cm s^{-1} or greater, which characterize the alongshore flow over the outer shelf and slope in the SCB. In contrast to tropical taxa, it is not until 1–2 mo of age that the larvae of rockfishes, at a size of 0.7–0.8 cm total length, undergo notochord flexion and caudal-fin formation. At this postflexion stage, the larvae attain the capability to swim faster than typical water motions in their natural habitat. For this reason, we defined the end of the passive dispersal period as 30 d.

Several studies suggest some generality among cool temperate species in swimming ability and size at comparable ontogenetic stages (Bradbury et al. 2003, Guan et al. 2008, Leis 2010, Stanley et al. 2012). These studies identify a critical ontogenetic benchmark of 1.0 cm for larval length in terms of functional morphology, swimming behaviors, and spatial pattern observed in the field for multiple temperate species including redfish (*Sebastes* sp.) in the Atlantic. As the larvae approach this size, they morphologically transition from the preflexion to flexion stage, the viscous drag of the hydrodynamic swimming environment decreases, and the swimming efficiency and speed increase (Leis et al. 2010). Comparatively, tropical larvae in warmer and therefore less viscous waters experience an earlier transition at 5–8 mm from a viscous to an inertial hydrodynamic environment.

We assume that prerecruits arriving in a settlement region at age 30 d are at the terminal end of their pelagic period, transitioning from the preflexion stage to the postflexion stage, undergoing notochord flexion and caudal-fin formation, and subsequently settling in the region where they were delivered. With this transition that may take weeks to months, growth and morphological developments contribute to more effective swimming capabilities (Montgomery et al. 2001, Leis 2010, Laidig 2010). Larval fish sensory abilities (hearing, olfaction, vision) form early, are well developed, and some species are able to detect cues relevant to orientation (Leis and Carson-Ewart 2001, Kingsford et al. 2002, Montgomery et al. 2006, Leis 2010, Staatterman et al. 2012). Realistically, the age at settlement is variable (see the pelagic duration of species in Table 1) and can be prolonged among individuals within a species, as the rate of the ontological transition to the juvenile form at which most taxa settle may vary. For example, Laidig (2010) found interannual differences in the

duration of the pelagic larval stage and pelagic juvenile stage that ranged 41–100 d and 14–90 d, respectively, of recently settled blue rockfish (*Sebastes mystinus*) determined from otolith analyses. Plasticity in development and in the age at which settlement occurs may reflect a species ability to adapt to variable ocean conditions during the pelagic phase from year to year (Laidig 2010, Moser and Boehlert 1991). Such plasticity in a competency window for settlement may also be dependent on proximity to suitable habitat and swimming ability moderated by parameters such as growth rate and condition (Montgomery et al. 2001, Simpson et al. 2008, Wolanski and Kingsford 2014).

A broad age range for settlement may indicate that although juveniles have the sensory and motor capabilities to actively search for and find settlement habitats, species may have evolved to utilize the pelagic environment in a number of ways until the juveniles encounter settlement habitat or suitable environmental conditions (e.g., temperature, prey resources, biotic structure of a kelp forest for shelter) in settlement habitat (Moser and Boehlert 1991, Sogard and Olla 1998, Ross and Larson 2003). Other species may possess behaviors unrelated to swimming capabilities or orientation to settlement habitat that can shape the potential connectivity of source locations to settlement areas. For example, pelagic juveniles of a number of species are known to utilize offshore drift kelp (Mitchell and Hunter 1970; Moser and Boehlert 1991); consequently, the passive dispersal of drift kelp patches may have a significant role in determining patterns of connectivity for species. When formulating complex biophysical models to estimate connectivity, the realism of behavioral parameters, beyond passive dispersal during the early larval phase, that are assigned to a species of interest should be assessed.

In the scenario after the 30-d terminus of individual trajectories, we assume the prerecruits in the settlement regions have the capability to orient to sensory cues and find and remain in the vicinity of suitable reef habitat in the region. However, it is possible that 30-d old prerecruits may not respond to near-reef stimuli when within a settlement region. Post flexion larvae near the size of 1 cm TL are rarely observed at scuba diving depths (<30 m) in the vicinity or nearshore reefs (Table 1; Nishimoto and Love, unpublished data); however, other survey methods such as near-bottom, oblique, or neuston (surface) net tows designed to target small prerecruits in the settlement environment may be more appropriate (e.g., Gruber et al. 1982, Jahn and Lavenberg 1986, Sponaugle et al. 2003). Postflexion larvae and small juveniles have been collected in these kinds of net surveys in nearshore waters; although abundances and number of species may be underestimated since fast swimmers may be able to avoid nets if they are not specifically designed to be towed at sufficient speeds. Although our model provides a measure of the probability of prerecruits arriving to settlement regions, the probability of prerecruit settling in the four regions is unknown. Speculatively, either many or few of the prerecruits, for example in the SBCMAIN region, that are unable to settle in the region could be transported poleward along the shelf outside of the domain boundary. Thus, the oil platforms could provide larval subsidies for more distant locations.

A bias in our results from modeling a fixed 30 d dispersal phase, particularly given the length of the SBCMAIN and SMAIN regions along the mainland shelf with the predominant poleward alongshore flow, is that the likelihood of being advected out of a settlement region is greater for larvae approaching 30 d that are upstream and near the region's western boundary than for larvae that are further away from the

boundary. For example, larvae dispersing from Platform C are closer to the western boundary of SBCMAIN than larvae from Platform Eureka. Our results indicate that between the spring and summer, the percentage of prerecruits released from Platform C in SBCMAIN decreases and the percentage of prerecruits in SBCMAIN that were released from Platform Eureka increases. Future investigation could explore the sensitivity of the model to this bias, for example, by running the modeling experiment with varying pelagic larval durations that are shorter and longer than 30 d.

Using a broad generic biophysical model, our results reveal that potential connectivity from different platforms to natural habitat varies significantly purely based on location and the spatiotemporal complexity of ocean circulation. When evaluating the options of either removing a platform or leaving part of it in place, we suggest that an individual platform's contribution to recruitment be included as a criterion of its net environmental benefit. PDDs and connectivity estimates from simulations for species of interest with differing spawning seasons and larval durations should be compared. Rather than modeling the potential contribution based on passive dispersal, estimates of the amount of recruits supplied by a platform to targeted settlement sites, such as Marine Protected Areas, can be modeled by including species-specific life history parameters such as spawning stock size, fecundity, larval growth and mortality, and ontogenetic behaviors such as swimming and orientation to environmental cues (Metaxas and Saunders 2009, Pineda et al. 2007, Werner et al. 2007, Watson et al. 2010, Wolanski and Kingsford 2014). However, a caveat is that incorporating larval traits and behaviors into larval dispersal models is challenging because of a limited understanding of the many variables that can influence dispersal outcomes (Sponaugle et al. 2012).

We found that the differences in the relative proportion of prerecruits from a platform to the four settlement regions off the mainland and offshore islands and banks were generally consistent across a 12-yr time series (Fig. 8). However, there are years that deviated from the long-term pattern. The anomalies indicate that it is prudent to utilize long-term datasets, empirical or modeled, when statistically estimating connectivity. Studies are needed to determine the degree to which life history and behavioral parameters are affected by ocean conditions, and how sensitive the biophysical models are to realistic changes in the parameters in the geographic area of interest (Werner et al. 2007, Metaxas and Saunders 2009, Treml et al. 2015). Self-recruitment at the platforms and stepping-stone theories should also be evaluated as part of targeted species-specific modeling studies (Almany et al. 2017). We suggest that verification studies (Sponaugle et al. 2012) are needed to determine how well connectivity models predict not only the spatiotemporal variation of settlement but also the three-dimensional distributions of ontogenetic pelagic stages before settlement as observed in large-scale ocean surveys.

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