OCS Study
BOEM 2019-001

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US Department of the Interior
Bureau of Ocean Energy Management
Pacific OCS Region

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ABOUT THE COVER

The non-native bryozoan *Watersipora subatra* on horizontal support members of Platform B in the Santa Barbara Channel. Photo by Brandon Doheny.

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List of Abbreviations and Acronyms

ANOSIM	Analysis of Similarities
BOEM	Bureau of Ocean Energy Management
BSEE	Bureau of Safety and Environmental Enforcement
CAP	Canonical Analysis of Principal Coordinates
CFR	Code of Federal Regulations
ESP	Environmental Studies Program
ESPIS	Environmental Studies Program Information System
LME	Linear-Mixed Effects
NOAA	National Oceanic and Atmospheric Administration
PERMANOVA	permutational multivariate analysis of variance
PDD	particle density distribution
PLD	planktonic larval duration
POCS	Pacific Outer Continental Shelf
ROMS	Regional Ocean Modeling System
SCB	Southern California Bight
SBC	Santa Barbara Channel
SMB	Santa Maria Basin
SPB	San Pedro Bay
SST	sea surface temperature

1 Executive Summary

Information Needed

The purpose of this study was to survey offshore oil and gas platforms in the Santa Barbara Channel/Santa Maria Basin and San Pedro Basin, other artificial structures, and natural reefs for the non-native species *Watersipora subatra* (previously identified as *Watersipora subtorquata*), measure the reproductive seasonality of this species, and identify potential vectors for dispersal among platforms and between platforms and natural habitat. The need for this information is to elucidate the role that offshore artificial structures may have in affecting biological communities for use by the State of California in evaluating decommissioning options under California legislation AB 2503 (the California Marine Resources Legacy Act) and to comply with the duties of Federal agencies that are outlined in Section 2 of Executive Order 13112 (Invasive Species). BOEM will use study results for environmental reviews pertaining to ongoing operations and decommissioning alternatives of offshore oil and gas platforms and potential marine renewable energy facilities. This study also developed results applicable specifically for BSEE management decisions so that BSEE can specify requirements to industry or other interested parties when decommissioning occurs. Using the results, the State of California can ensure proper evaluation under the California Rigs-to-Reefs Program law AB 2503 (the California Marine Resources Legacy Act) and BSEE can ensure that specified criteria can be properly evaluated during the decommissioning process pursuant to the federal regulations at 30 CFR 250.1730.

Research Summary

Shallow water (< 18 m depth) invertebrate assemblages of 23 offshore oil and gas platforms in the Southern California Bight were found to vary among four geographical regions defined *a priori* by differences in sea surface temperature. Variation in platform assemblages was broadly associated with SST; however, assemblages of platforms in the southeast Santa Barbara Channel were distinct due to the high cover of the non-native bryozoan *Watersipora*. Invertebrate assemblages also varied idiosyncratically among platforms within a region likely due to the vagaries of larval supply and local environmental conditions that includes disturbance from platform maintenance cleaning operations. Surveys also revealed that mussels, often reported as abundant historically, did not consistently dominate shallow water platform invertebrate assemblages. Over smaller spatial scales, the idiosyncratic differences in invertebrate assemblages among platforms within regions indicate that these assemblages would have to be considered on a platform-by-platform basis under various decommissioning scenarios.

Surveys of assemblages of seven offshore oil and gas platforms in the Santa Barbara Channel revealed the spread of *Watersipora* from one platform in 2001 to four platforms in 2013. Modeling suggested that larval dispersal via currents could account for this spread, but also that *Watersipora* is unlikely to spread from these four platforms to the three other surveyed platforms through larval dispersal. In addition, modeling results suggest that taxa with planktonic larval durations (PLDs) of 24 hours or less, such as *Watersipora*, released from offshore platforms can disperse further than larvae with similar PLDs released from nearshore habitat.

Manipulative experiments and field observations revealed that the removal of dense epifaunal invertebrate assemblages attached to offshore platforms in the Santa Barbara Channel creates a disturbance that facilitates the establishment of *Watersipora*. However, one year after an experimental disturbance, sessile invertebrates occupied all available settlement space in the disturbed plots, and there was little recruitment of *Watersipora* into these plots despite the availability of larvae, indicated by larval recruitment onto settlement plates. Similarly, the removal of attached invertebrates from another platform during maintenance cleaning by the operators resulted in the colonization of cleared surfaces by *Watersipora* and the attainment of high cover over time compared to uncleaned surfaces.

We surveyed 61 sites, including natural and artificial habitat, and evaluated the potential dispersal connectivity of *Watersipora* larvae from harbors and oil platforms to natural reefs using survey results and three-dimensional biophysical modeling. *Watersipora* was more widely distributed than expected, occurring on approximately 50% of the oil platforms and mainland reef sites, but only 17% of the island reef sites. Modeling indicated high potential connectivity of *Watersipora* populations from one harbor to a nearby reef, but little to no potential connectivity from this harbor to other more distant reefs. Our results suggest that the successful dispersal of *Watersipora* larvae from harbors and oil platforms to distant reef sites would likely require intermediate stepping stone sites or transport via vessel hull fouling.

Conclusions

Although *Watersipora* is more widespread on natural reefs than expected, there appear to be opportunities to manage current and future invasions through the control of sources of propagules via the application of best management practices in harbors and on offshore oil platforms and potentially through the manual removal or reduction of existing field populations. Our results suggest that the establishment of *Watersipora* on offshore oil platforms can be managed by adjusting the timing of maintenance cleaning to occur shortly after this bryozoan’s peak reproductive period in late summer – fall. This timing could remove newly settled recruits and allow sufficient time for native species to colonize available bare space prior to the bryozoan’s next reproductive period. Even relatively frequent cleaning activities (every 2 – 3 years) could be scheduled to allow adequate time for native species to colonize the bare space before the recruitment period of *Watersipora*. However, these decisions should be made on a case-by-case basis to account for differences in site-specific characteristics, such as species assemblages or physical factors. The biophysical modeling reveals that careful consideration of potential connectivity to source populations in the placement of mariculture infrastructure with respect to harbors and other sources of non-native propagules could also help to reduce the potential for stepwise spread to natural habitat. This consideration would be most impactful in areas of little natural rocky reef habitat, such as the eastern SBC. Our results may also inform decision-making regarding the decommissioning of offshore oil and gas platforms. Some stakeholders prefer decommissioning alternatives that maintain deeper parts (> 26 m) of the platform structure to function as an artificial reef (Schroeder and Love 2004; Smyth et al. 2015). In California, such “rigs-to-reefs” alternatives can be considered if they comply with the National Fishing Enhancement Act (1984) and the California Marine Resources Legacy Act (2010). In the case of platforms with established *Watersipora* populations, the low abundance of this species at 24 m water depth suggests that if a reefing option is selected, removing the shallow portions of the platform may reduce the ability of this non-native species to persist locally. However, more information is needed on the dispersal potential of *Watersipora* at deeper depths to understand the consequences of this decommissioning alternative.

2 Background

The invasion and spread of non-native plant and animal species is considered one of the greatest threats to biological diversity and the functioning of aquatic ecosystems today (Schmitz and Simberloff 1997, Bax et al. 2003). Non-native species can reduce the number and abundance of native species, alter the structure of native habitat, and negatively affect ecosystem processes (Grosholz 2002). Non-native species were found on two of seven offshore oil and gas platforms in the Santa Barbara Channel in previous BOEM funded studies (Page et al. 2006, 2007, 2008). None of these species had been previously reported from platforms. Of these non-native species, the foliose bryozoan, *Watersipora*, is the most invasive because it readily overgrows smaller native species, forms masses several centimeters in thickness, and has the potential to cover 100% of available space on platform support members (Page 2006).

Once established on platforms, *Watersipora* and other non-native species can become dominant members of the invertebrate assemblage to the detriment of native species and serve as a potential source of propagules to natural reef habitats (Page et al. 2006). It has been proposed that offshore oil and gas platforms could facilitate species range expansions and/or the introduction of non-native species into new geographic areas by serving as hard substrate recruitment habitat and thus ‘stepping stones’ of vertical relief across a soft seafloor environment (Gallaway and Lewbel 1982, Sammarco et al. 2004). In addition, the presence of non-native species in invertebrate assemblages may influence the degree to which oil and gas platforms provide the ecological functions (e.g., biodiversity, food chain support) similar to those of natural reefs. The presence of non-native species on platforms also has consequences for the various platform decommissioning options in California and elsewhere, including the removal and transport of platforms for use as artificial reefs, particularly if removals are conducted without regard for the potential transport/dispersal of these species.

The purpose of this study was to survey offshore oil and gas platforms in the Santa Barbara Channel/Santa Maria Basin and San Pedro Basin, other artificial structures, and natural reefs for the non-native species *Watersipora subatra* (previously identified as *Watersipora subtorquata*), measure the reproductive seasonality of this species, and identify potential vectors for dispersal among platforms and between platforms and natural habitat. The need for this information is to elucidate the role that offshore artificial structures may have in affecting biological communities for use by the State of California in evaluating decommissioning options under California legislation AB 2503 (the California Marine Resources Legacy Act) and to comply with the duties of Federal agencies that are outlined in Section 2 of Executive Order 13112 (Invasive Species). BOEM will use study results for environmental reviews pertaining to ongoing operations and decommissioning alternatives of offshore oil and gas platforms and potential marine renewable energy facilities. This study also developed results applicable specifically for BSEE management decisions so that BSEE can specify requirements to industry or other interested parties when decommissioning occurs. Using the results, the State of California can ensure proper evaluation under the California Rigs-to-Reefs Program law AB 2503 (the California Marine Resources Legacy Act) and BSEE can ensure that specified criteria can be properly evaluated during the decommissioning process pursuant to the federal regulations at 30 CFR 250.1730.

The specific objectives of this study were to:

- Characterize the geographic distribution, abundance, and depth distribution of *Watersipora* on oil and gas platforms in the Santa Barbara Channel/Santa Maria Basin, San Pedro Basin, and natural reefs near platforms;
- Quantify the reproductive seasonality (as recruitment) of *Watersipora* that can identify timing of potential dispersal to service vessels, and other artificial and natural habitat;

- Evaluate the role of disturbance, for example from offshore oil and gas platform maintenance cleaning operations, in facilitating the establishment and spread of *Watersipora*;
- Identify potential vector pathways of dispersal of *Watersipora* among oil and gas platforms, and between platforms and natural reefs using ocean circulation and particle tracking models.

This report is divided into four chapters. The first chapter reviews the composition of the “typical” or historically expected shallow water (< 80 feet) invertebrate assemblage of POCS offshore oil and gas platforms as reported in the unpublished and published literature, and the biogeographical patterns in these assemblages on offshore platforms in the Southern California Bight as revealed through the sampling conducted during the present study (Page et al., in press). The second chapter reports the spread of *Watersipora* from its presence on one of seven surveyed platforms in the Santa Barbara Channel in 2001 to three additional platforms in 2013, and modeling results revealing that larval transport via ocean currents, in addition to anthropogenic transport on the hulls of service vessels, could explain its spread (Simons et al. 2016). The third chapter presents the results of field experiments showing that disturbance (e.g., from platform maintenance clean operations) and water depth influence the rate of colonization of offshore platforms by *Watersipora* (Viola et al. 2018). The fourth chapter presents the results of an extensive survey for *Watersipora* in the Santa Barbara Channel of offshore platforms, other artificial habitat, and natural reefs, and modeling that explores potential larval connectivity between harbors, platforms, and natural reefs (Page et al., in review).

3 Regional Patterns in Shallow Water Invertebrate Assemblages on Offshore Oil Platforms Along the Pacific Continental Shelf

3.1 Introduction

Identifying biogeographical patterns in marine communities and their relationships with local physical and biological factors provides a valuable foundation for analyses of temporal and spatial dynamics in marine ecosystems. Much of this research along the California coast has centered on describing spatial variation in the structure and dynamics of algal and invertebrate assemblages in rocky intertidal habitat and of subtidal rocky reef fish assemblages, and the importance of gradients in water temperature, primary productivity, and propagule supply in driving observed patterns (Murray and Littler 1981, Broitman et al. 2005, Holbrook et al. 2007, Blanchette et al. 2006, 2008). Impetus for this research has increased in the face of longer-term climate change that predicts a general warming of the world's oceans (Fields et al. 1993, Harley et al. 2006) and evidence and predictions of shifts in species distributions, including those of non-native species, associated with changes in ocean climate (Barry et al. 1995, Stachowicz et al. 2002, Helmuth et al. 2006, Horn and Stevens 2006, Sorte et al. 2010, 2011).

Manmade structures in the marine environment provide suitable habitat for a variety of marine biota and can serve as a useful study sites for exploring factors driving biogeographic patterns. Considerable oil and gas development has occurred in the Southern California Bight (SCB) over the past 60 years (reviewed in Love et al. 2010) and 26 oil and gas platforms are currently present offshore of California, extending from north of Point Conception in the Santa Maria Basin, south to San Pedro Bay, a coastline distance of > 300 km (Fig. 1). Most of the platforms (16) in the SCB occur in the Santa Barbara Channel (SBC), a biogeographical transition zone between the northern Oregonian and Southern Californian (San Diegan) provinces (Murray and Bray 1993, Horn et al. 2006). Here, strong gradients in surface water temperature occur beginning in late spring, and extending into fall as cool waters from the equatorward flowing California Current enter the SBC through its west entrance at Point Conception and mix with waters of the Southern California Countercurrent entering the channel through its eastern entrance (Hendershott and Winant 1996, Harms and Winant 1998, Otero and Siegel 2004) (Fig. 1). Periodically, the California Current weakens during the El Nino phenomenon, allowing warmer waters from the Equatorial Countercurrent to extend poleward, elevating ocean water temperatures in the SCB by several degrees above normal.

The structure of biotic assemblages has been shown to reflect these oceanographic gradients. For example, Blanchette et al. (2006, 2008) identified clear biogeographic patterns in rocky intertidal invertebrate assemblages that correlated closely with sea surface temperature within the Northern Channel Islands and more broadly along the Pacific coast of North America from south-eastern Alaska, USA, to central Baja California Sur, Mexico. Similarly, the composition and relative abundance of reef fish assemblages reflect gradients in sea temperatures in the SCB (Horn et al. 2006). Love et al. (2010) found that cool-temperate taxa are well represented in the fish assemblages of more northerly offshore oil and gas platforms within the Santa Maria Basin and SBC, whereas warm-temperate taxa dominate assemblages of the southerly platforms. Offshore platforms are discrete islands of hard substrate habitat for assemblages of organisms that might respond to oceanographic gradients; however, biogeographic patterns could also be obscured by local factors, such as water depth and proximity to shore, that have been shown to affect fish assemblages (Love et al. 2010). If invasive species dominate the artificial habitat that platforms provide, this could also alter these communities relative to biogeographic expectations (Page et al. 2008).

To date, studies of local and regional variability in biotic assemblages on offshore platforms and their association with environmental factors are limited in California. A photographic and sampling survey of invertebrate assemblages on six platforms used cluster analysis to identify geographic groups of platforms (CSA 2005). Two platforms in the eastern SBC grouped more closely together than three platforms in the Santa Maria Basin. Page et al. (2008) conducted a multivariate analysis of invertebrate assemblages on shallow portions (< 24 m) of seven platforms distributed along the SBC. This analysis revealed a trend of differences in assemblage structure with coastline distance along the channel if two dominant non-native species on two of these platforms were excluded from the analysis. Platforms in closest proximity to one other tended to have invertebrate assemblages more similar to each other than to platforms located farther away.

In addition to biogeographic differences, platform biotic assemblages may respond to decadal and shorter-term fluctuations in oceanographic conditions such as those noted for fishes on both rocky reefs and platforms (Holbrook et al. 1997, Love et al. 2010). Some southern affinity fish species extend their ranges poleward in warm-regime years associated with the El Niño phenomenon (Holbrook et al. 1997, Horn and Stephens 2006, Love et al. 2010). The period 2014-2015 featured anomalously warm ocean temperatures fueled by a large mass of warm water off the Pacific coast of North America (the "Blob") and the El Niño of 2015-2016 (Bond et al. 2015, Diamond and Schreck 2016), providing an opportunity to monitor changes in platform invertebrate assemblages that might anticipate longer-term changes driven by ocean climate.

In this section, we use published studies and recent data (2013-2016) to: 1) briefly review existing information on the major space-holding taxa found on offshore oil and gas platforms in the SCB, 2) provide new information on regional patterns in the composition of these assemblages in association with prevailing gradients in oceanographic conditions in the SCB, continuing and expanding the analysis of Page et al. (2008), 3) evaluate the importance of factors that could drive regional and local spatial patterns, and 4) identify taxa that could act as potential sentinels of change in ocean climate.

Studies of platform invertebrate assemblages are hampered by logistical considerations and incomplete taxonomic information. As a result, the focus of the present study remains on conspicuous space holding taxa, some of which provide biogenic habitat for other sessile, semi-mobile or mobile species.

3.2 Materials and Methods

3.2.1 Environmental variables

We determined mean annual sea surface temperature (SST) within ~1 km of each platform using daily data published by the Group for High-Resolution Sea Surface Temperature Global Data Assembly Center (https://mur.jpl.nasa.gov/index.php) and compiled using the Marine Geospatial Ecology Toolbox in ArcGIS. An annual mean SST was computed to within 1 km of each platform from the daily values for the years 2010 – 2016. Regional mean SST values were calculated by averaging the annual SST values for each platform within each region. Similarly, mean annual chlorophyll concentrations were acquired from monthly composite satellite images (Aqua MODIS, NOAA, https://coastwatch.pfeg.noaa.gov/erddap/index.html) to within 1 km of each platform in the Southern California Bight and used to compute regional mean annual chlorophyll a concentrations encompassing the period 2010 – 2016.

3.2.2 Geographical setting and platform study sites

The study platforms are located in the Santa Barbara Channel (16) and San Pedro Bay (7) (Fig. 1) in a range of water depths (29–225 m) and distances from shore (2.9–14.4 km, Table 1). We grouped these platforms *a priori* into four regions based on expected differences in annual mean SST and the spatial arrangement of platforms; each region contained from four to seven platforms to provide replication within each region (Table 1, Fig. 1). Four additional platforms in the Santa Maria Basin were grouped into a fifth region, shown for reference in Figure 1, but only qualitatively surveyed and not included in our analysis. The study platforms differ in size, but their general configuration is similar, with a subtidal portion consisting of steel vertical, oblique, and horizontal cross members, together with conductor pipes through which the oil and gas passes. Reef habitat at the water depths of the study platforms is rare in the Southern California Bight.

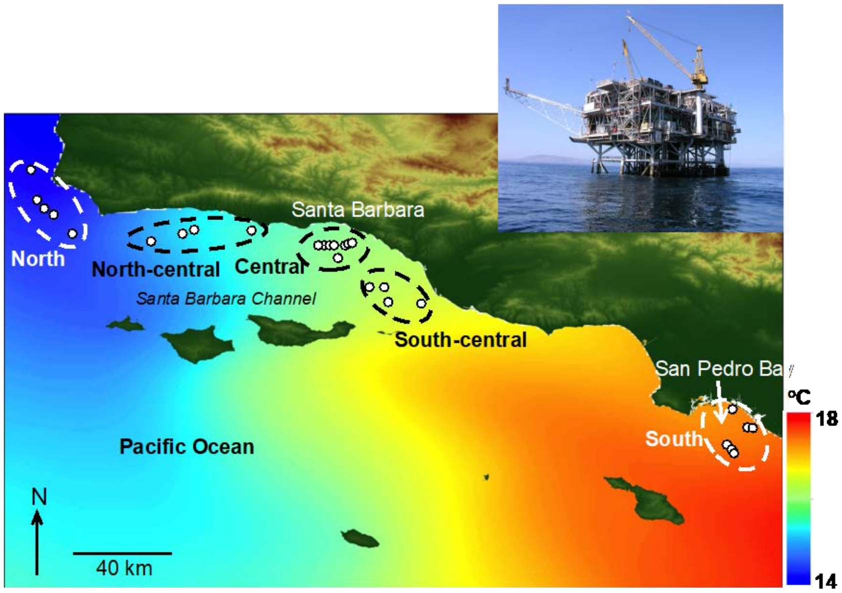

Figure 1. Gradient in sea surface temperature in the Southern California Bight in summer 2014 and locations of platforms and the five regions referenced in Table 1.
Offshore oil platforms shown as white dots. North region is not included in the analysis.

3.2.3 Platform surveys

Invertebrate assemblages were quantitatively sampled once using SCUBA during the spring through fall months of 2013 and 2014 by photographing a 0.25 m^2 quadrat located on the inside and outside of the four corner legs and on four randomly selected conductor pipes at depths of 6, 12, and 18 m. We used a Canon EOS 6D digital camera with a 14 mm wide-angle lens in a waterproof housing, mounted with two strobes on a frame designed to photograph a 0.25 m^2 quadrat following methods modified from Witman and Smith (2003). Quadrats measured 41 x 62 cm internal diameter (0.25 m^2) to accommodate the dimensions of the platform legs and conductor pipes.

From the photographs, we identified and estimated the percent cover of sessile and semi-mobile invertebrate taxa in each plot using point-contact methods. A grid of 100 uniformly spaced points was superimposed onto each digital image, contacts under each point were scored manually within the BisQue online image analysis system (http://bioimage.ucsb.edu/, Rahimi et al. 2014), and the data was subsequently exported for analysis. Invertebrates were identified to the lowest taxon possible. There is a paucity of taxonomic information on platform invertebrates and some sponges, in particular, had to be characterized by color and shape. Because invertebrate assemblages on the platforms may be several centimeters thick, only organisms occupying the visible surface layer were scored. Underlying taxa, for example, mussels and scallops, were thus under sampled in the photoplots because they were often covered by other species (Page et al. 2010). We also recorded data on different categories of non-living substrata (e.g. bare steel), if present. A total of 655 photographs distributed among the 23 platforms were analyzed.

Photographic methods undersample mussels and scallops, two potentially important space-holding taxa. To address this, we measured the densities of mussels and scallops at a subset of seven platforms in the SBC (Gina, Grace, Hogan, Henry, A, C, Holly) within one 13 x 52 cm quadrat on each of four randomly selected conductor pipes at depths of 6, 12, 18, and 24 m in 2015.

Table 1. Offshore oil and gas platforms surveyed in the Southern California Bight in San Pedro Bay (SPB) and the Santa Barbara Channel (SBC).
Four platforms located in the Santa Maria Basin (SMB) assigned to the North region that were not surveyed, and one platform (Esther) in San Pedro Bay not analyzed because of its shallow depth are also included. Distance = distance from shore. Depth = water depth. Size = jacket dimensions on the seafloor. *not included in analysis, n/a = not available.

Region	Platform.	Distance (km)	Depth (m)	Size (m^2)	Year installed
South (SPB)	Esther*	2.2	6.7	n/a	1990
	Eva	3.3	17.4	n/a	1964
	Emmy	2.2	14.3	n/a	1963
	Eureka	16.7	213.4	4590	1984
	Edith	15.7	80.8	2900	1980
	Ellen	15.9	77.7	2520	1980
	Elly	15.9	49.1	2928	1983
South-central (SBC)	Grace	19.4	96.9	3120	1979
	Gilda	16.3	62.5	2340	1981
	Gina	6.9	29.0	560	1980
	Gail	18.3	225.2	5400	1987
Central (SBC)	A	10.7	57.3	1920	1968
	B	10.6	57.9	1920	1968
	C	10.6	58.5	1920	1977
	Hillhouse	10.2	57.9	1960	1969
	Henry	8.0	52.7	1485	1979
	Hogan	6.9	49.7	1444	1968
	Houchin	7.6	46.9	1444	1967
	Habitat	14.4	88.4	2280	1981
North-central (SBC)	Heritage	15.1	327.7		1989
	Harmony	11.9	365.2	10647	1989
	Hondo	9.4	256.6	4624	1976
	Holly	3.3	64.3	1728	1966
North (SMB)	Harvest*	12.4	205.7	5917	1985
	Hermosa*	12.6	183.8	5185	1985
	Hidalgo*	10.9	131.1	4134	1986
	Irene*	7.6	73.8	2632	1985

3.2.4 Data analysis

We evaluated differences in SST and chlorophyll *a* among regions and over time using Linear Mixed-Effects (LME) models that handle temporally correlated data. Region (North-central, Central, South-central, South) and time were treated as fixed factors, individual platforms treated as subjects, and time as a repeated measure. Post-hoc Sidak tests were used to evaluate differences in SST and chlorophyll *a* among regions if the overall model was significant. The Sidak test adjusts *p*-values in multiple pairwise comparisons to reduce Type 1 error (Day and Quinn 1989).

We tested for differences in the composition (as percent cover) of invertebrate assemblages among regions and among platforms within each region using a nested permutational multivariate analysis of variance (PERMANOVA). Platform was treated as a random factor nested within region, which was treated as a fixed factor in the analysis. Analyses were conducted on untransformed data with the resemblance matrix calculated using the Bray-Curtis Similarity Index.

On finding significant differences in invertebrate composition among regions using PERMANOVA, we used Canonical Analysis of Principal Coordinates (CAP) ordination (Anderson et al. 2008) on Bray-Curtis similarity values to visualize patterns in invertebrate assemblages on platforms by region and examine relationships with environmental parameters (SST, chlorophyll *a* concentration, water depth, platform size, distance from shore) and the abundance of the nonnative bryozoan *Watersipora subatra*, a dominant competitor that alters platform communities (Viola et al. in press). CAP is a nonparametric discriminant analysis used to classify groups based on a suite of predictor variables that is suitable if the data do not meet the assumptions required of parametric Multivariate Analysis of Variance (MANOVA) (Anderson et al. 2008). Differences across group (region) centroids were evaluated using a permutation test, and pairwise differences between groups were evaluated using Analysis of Similarities (ANOSIM) (Clarke and Gorley 2001). We used partial correlation analysis to identify the taxa driving observed patterns in the CAP ordination and the relationship of patterns to environmental variables. Environmental data were normalized prior to this analysis. Parametric statistics were run using SPSS 24. PERMANOVA, ANOSIM, and CAP analysis were done using PRIMER v. 6 and PERMANOVA+ for PRIMER. Mobile taxa such as crabs, sea stars, and sea urchins were excluded from statistical analysis.

Platforms are subject to maintenance cleaning that removes attached epifauna to facilitate visual inspection of the structure for damage. This disturbance occurs mainly in the upper 6–8 m of the structure (Page et al. 1999). The cleaning schedule is irregular, varies from platform to platform, and only portions of a platform may be cleaned at any one time. Therefore, data from photoplots taken at 6 m were not included in our analysis.

3.3 Results

3.3.1 Synopsis of platform invertebrate assemblages

Major space-holding invertebrate taxa that compose platform invertebrate assemblages include mussels (*Mytilus californianus* Conrad, 1837, *M. galloprovincialis* Lamarck, 1819), barnacles (e.g. *Megabalanus californicus* (Pilsbry, 1916), *Balanus nubulis* Darwin, 1854), encrusting bivalves (*Crassodoma gigantea* (J. E. Gray, 1825), *Pododesmus cepio* (Gray, 1850), *Chama arcana* F. R. Bernard, 1976), and bryozoans (*Watersipora subatra* (Ortmann, 1890)) attached to primary space (Fig. 2). Sponges (*Sphaeciospongia confoederata* de Laubenfels, 1930, *Haliclona* spp. Schmidt, 1862) and anemones (*Corynactis californica* Carlgren, 1936, *Metridium senile* (= *M. dianthus*) (Linneaus, 1761), *Anthopleura elegantissma* (Brandt, 1835)) are found attached either to primary or hard secondary space (Wolfson et al. 1979, Page et al. 1999, CSA 2005, Page et al. 2008, Page et al. 2010: Fig. 2). In shallower depths on platforms, this assemblage can exceed 15 cm in thickness when undisturbed by storms or maintenance cleaning operations (Wolfson et al. 1979, Page et al. 1999, CSA 2005, Page et al. 2010, this study). Macroalgae are relatively uncommon and, when present, are restricted to shallow depths on the periphery of the structure that receives more light. These algae typically consist of red filamentous or foliose taxa (e.g., *Polysiphonia*, *Rhodymenia*, *Antihamnion*, CSA 2005).

The platform invertebrate assemblage provides habitat and food for commercially and recreationally important fish and macroinvertebrates directly (e.g., Page et al., 1999, Page et al. 2007), and through "faunal litterfall," as organisms slough off the structure and fall to the seafloor where they provide a subsidy of organic and inorganic material to benthic organisms (Page et al. 1999, Bomkamp et al. 2004, Goddard and Love 2010). Native and non-native platform invertebrates are also a source of propagules that can disperse to other artificial and natural habitat (Sammarco et al. 2004, Simons et al. 2016).

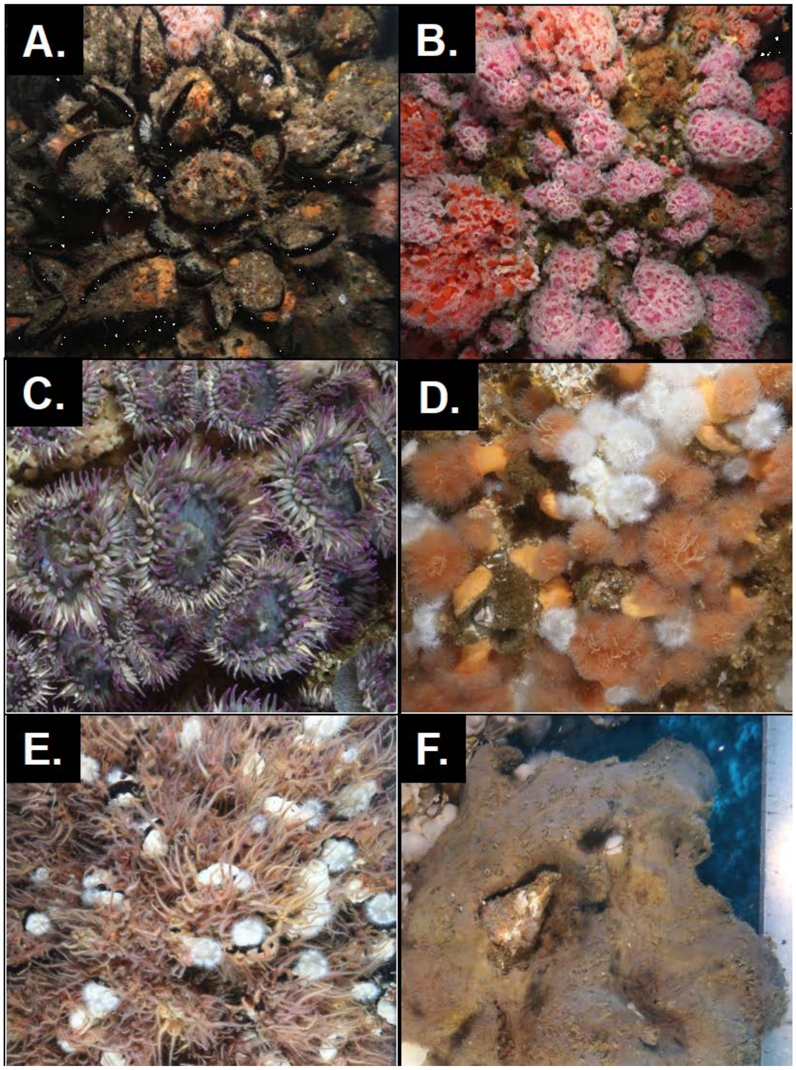

Figure 2. Examples of common native space-holding invertebrate taxa on oil and gas platforms in the Southern California Bight.
A) sea mussel *Mytilus californianus*, B) strawberry anemone *Corynactis californicus*, C) anemone *Anthopleura elegantissima*, D) white and brown color morphs of the anemone *Metridium senile,* E) brittlestar *Ophiothrix spiculata* and *Metridium senile*, and F) sponge *Spheciospongia confoederata*

3.3.2 Environmental parameters

Mean annual surface water temperature (SST) varied significantly among regions and also increased significantly from 2010 through 2016 (region, $F_{3, 19.49} = 386.67$, $p < 0.001$; year, $F_{6, 112.9} = 12478$, $p < 0.001$; year x region, $F_{18, 112.9} = 12478$, $p < 0.001$, LME model) (Fig. 3A). Across years, mean annual SST values ranged from 14.3 ± 0.1° to 17.2 ± 0.1° (x ± 1se) in the North-central region to 16.5 ± 0.1° to 19.1 ± 0.1° in the South, and there was noticeable temporal coherence in temperature values across regions. Satellite data agreed well (average within 0.5°) with temperature data acquired using a continuously recording datalogger deployed *in situ* at 6 m depth at Platform B in 2014 (unpubl data).

Mean annual values of surface chlorophyll concentration varied over time, but not among regions (region, $F_{3, 22.98} = 0.47$, $p = 0.70$; year, $F_{6, 105.0} = 11.94$, $p = 0.001$; year x region, $F_{18, 105.0} = 2.90$, $p = 0.001$, LME model) (Fig. 3B). Chlorophyll *a* concentrations showed a lack of temporal coherence across regions, and high spatial variability among platform sites within a region. The spatial variability was particularly evident in the South, where mean annual values of chlorophyll *a* concentrations at platforms in deeper water (Edith, Elly, Ellen, Eureka) were much lower (0.4 – 1.8 mg/m^3) than values at platforms in shallower water (Esther, Eva, Emmy) (4.0 –26.1 mg/m^3).

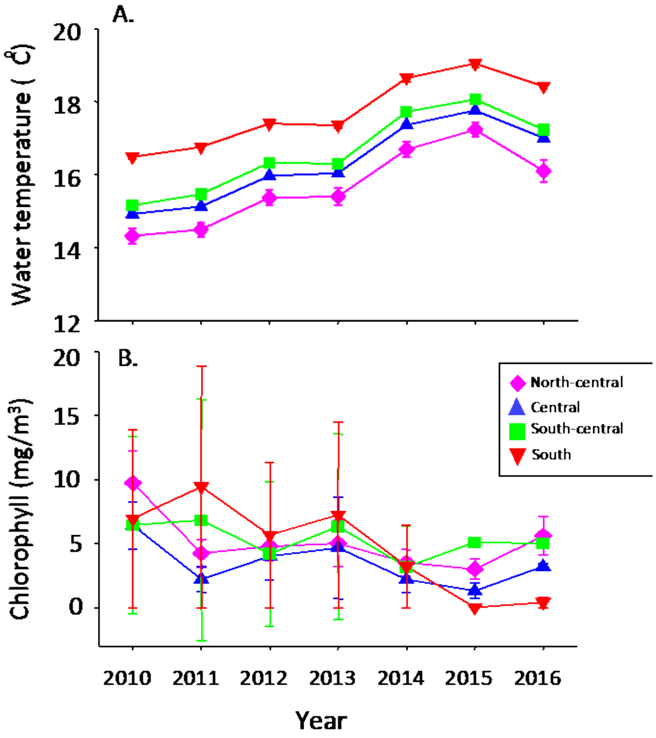

Figure 3. A) Average annual sea surface temperature by study region and B) average annual chlorophyll a concentration by study region for the years 2010 – 2016.

3.3.3 Regional patterns in invertebrate assemblages

Anemones dominated the percent cover of platform invertebrate assemblages with numerous other taxa present at much lower cover (Table 2). PERMANOVA revealed significant differences in invertebrate assemblages among regions (*pseudo*-$F_{3, 18.05} = 3.92$, $p = 0.001$) and among platforms within a region (*pseudo*-$F_{18, 633} = 14.41$, $p = 0.001$). The CAP ordination and pairwise comparison of Global R values from the ANOSIM showed that the composition of assemblages in the North-central, South-central, and South regions were most distinctive, whereas assemblages in the Central region were most similar to those of the other regions (Table 3, Fig. 4). The assemblages of all regions differed significantly from one another in pairwise comparisons ($p = 0.001$, ANOSIM) (Table 3). The North-central assemblage was the most distinct and the Central group the least distinct among the four regions.

Partial correlations of the regional CAP scores with the CAP axes indicated that the South region was distinguished by a higher abundance of amphipod tube complex, an unidentified bryozoan, and *Corynactis californica*, with a relative scarcity of *Metridium senile*, which is abundant in more northerly assemblages (Fig. 4). South-central platforms were most distinguishable by the abundance of an unidentified sponge and the non-native bryozoan *Watersipora subatra* (also identified as *W. subtorquata* in southern California, Vieira et al. 2014)

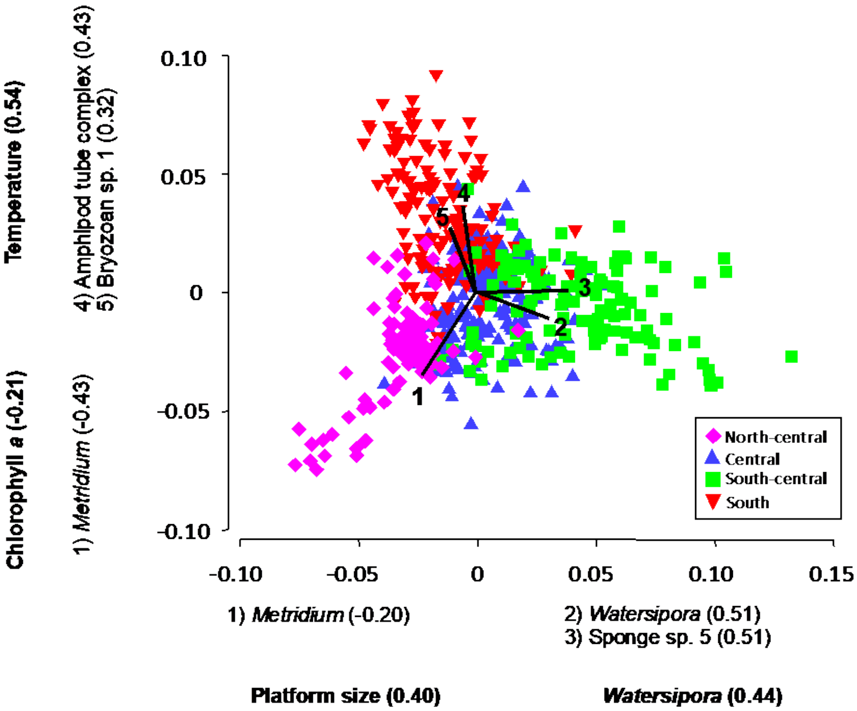

Figure 4. Regional differences in invertebrate assemblage composition visualized using Canonical Analysis of Principle Coordinates (CAP) ordination.

Values in parentheses = partial correlation coefficient of individual taxa with CAP axis, indicating the principal taxa driving observed differences. Values in boldface = partial correlation coefficient of environmental factors with CAP axis. Only most correlated (> 0.2) variables shown. Differences among regions $p = 0.001$, permutation test and pairwise ANOSIM, $n = 655$.

Table 2. Mean percent cover values by region of the most abundant taxa contributing differences in assemblage structure in Figure 2. Zeros represent < 0.5% cover. North-central (N – C), Central (C), South-central (S – C), South (S). Complete list of taxa used in analysis provided in Table 4.

	Region			
Taxa	N - C	C	S - C	S
Metridium senile	61	32	23	14
Corynactis californica	1	32	27	32
Watersipora subatra	0	0	11	0
Sponge sp. 5	0	1	8	0
Hydroid/bryozoan complex	2	2	1	7
Haliclona sp. 1	2	2	1	4
Ophiothrix spiculata	0	6	6	4
Amphipod tube complex	5	7	6	13
Anthropleura elegantissima	0	0	3	0
Bryozoan sp. 2	0	0	0	4
Sponge sp. 3	4	2	0	0
Celleporaria brunnea	0	0	0	1

Table 3. Global R-values from pairwise ANOSIM analysis on Bray-Curtis similarity indices. All pairwise comparisons were significant at $p = 0.001$. Lower values indicate more similarity in assemblage composition. The results reveal that invertebrate assemblages of the North-central group were the most distinct and the Central group least distinct among the four groups.

	South	South-central	Central	North-central
North-central	0.454	0.344	0.227	0
Central	0.117	0.136	0	
South-central	0.154	0		
South	0			

3.3.4 Within region patterns

Pair-wise ANOSIM analysis revealed that platforms within a region generally had statistically distinct invertebrate assemblages ($p < 0.05$) (Fig. 5A-D). This was due to differences in the relative abundance of ubiquitous taxa (e.g., *Corynactis californica*, *Metridium senile*) and in the occurrence and abundance of less common and non-native taxa (e.g., various sponges, *Watersipora subatra*). Within regions, only platforms Eureka and Elly (South region) had assemblages that were not significantly different ($p = 0.5$) from one another. Interestingly, the assemblages at Platforms Ellen and Elly in the South differed significantly ($p = 0.043$) despite being next to each other (connected by a causeway). Two southern platforms, Emmy and Eva, had quite distinct assemblages compared with the other five southern platforms (Fig. 5D). Both are located in much shallower water (14 m and 17 m depths, respectively) than the other platforms (Table 1). The non-native taxon *W. subatra* was present on all four platforms of the South-central region, but the higher abundance of this bryozoan and the brittle star *Ophiothrix spiculata* Le Conte, 1851 distinguished platforms Gina and Gail from Grace and Gilda (Fig. 5C).

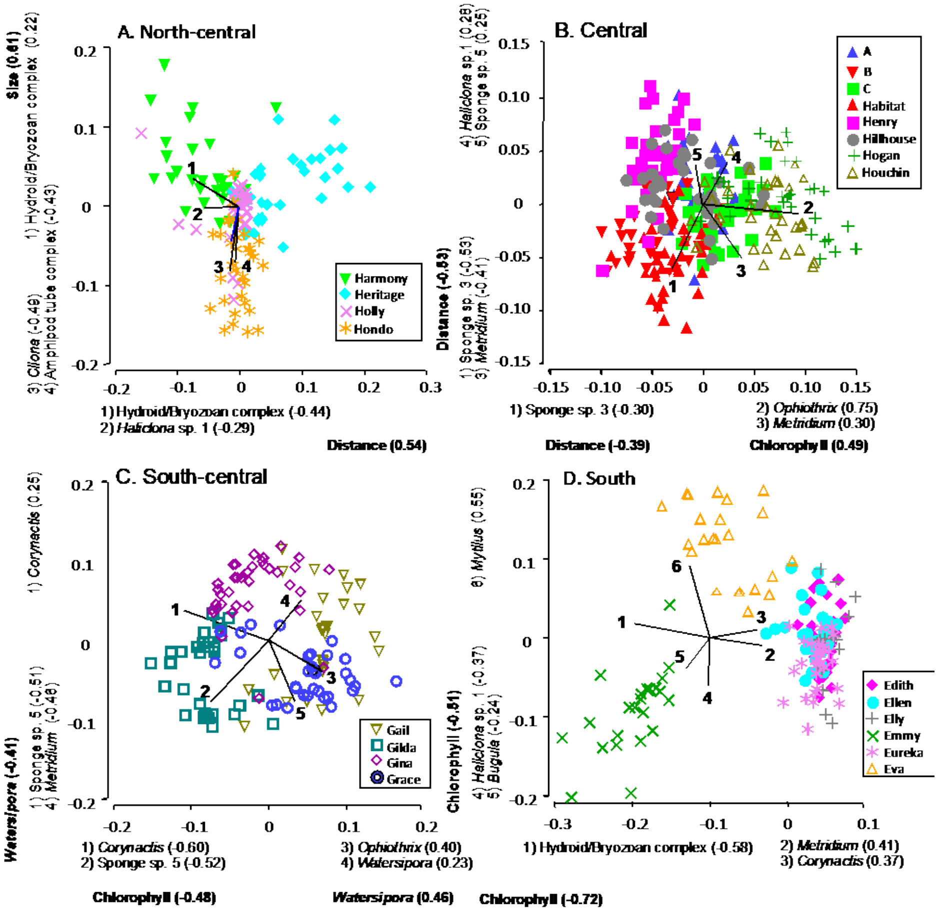

Figure 5. Differences in invertebrate assemblages among platforms within regions visualized using CAP ordination.
Values in parentheses = partial correlation coefficient of individual taxa with CAP axis. Values in boldface = partial correlation coefficient of environmental factors with CAP axis. Only most correlated variables shown. Differences among regions $p = 0.001$, permutation test and pairwise ANOSIM. Sample sizes: North-central, $n = 127$, Central, $n = 257$, South-central, $n = 128$, South, $n = 143$.

3.3.5 Invertebrate assemblages and environmental variables

Regional separation of invertebrate assemblages was most strongly associated with the gradient of annual SST found along the SCB, with more positive scores along the CAP 2 (y) axis distinguishing South and South-central platforms located in warmer waters from the negative scores for North-central platforms located in cooler waters with higher chlorophyll *a* concentration (Fig. 4). The percent cover of *Metridium senile* was negatively correlated with SST (Fig. 6A), whereas the cover of *Corynactis californica* increased with SST (Fig. 6B). Positive scores for assemblages in the South-central region along the CAP 1 (x) axis were most strongly associated with the higher cover of the non-native bryozoan *Watersipora subatra* and an overall greater distance from shore than platforms in the other regions (Table 1, Fig. 4).

Within regions, separation of platform invertebrate assemblages along CAP axes 1 and 2 was most commonly associated with chlorophyll *a* concentration and distance from shore (Fig. 5). An exception were the platforms of the South-central region in which *Watersipora subatra*, along with chlorophyll *a* concentration, contributed to the separation of invertebrate assemblages along the CAP 1 and 2 axes (Fig. 5C). Partial correlation values of SST with CAP scores were low (< 0.25) indicating that this variable was probably not an important driver of assemblage structure within regions as it was between regions (Fig. 4).

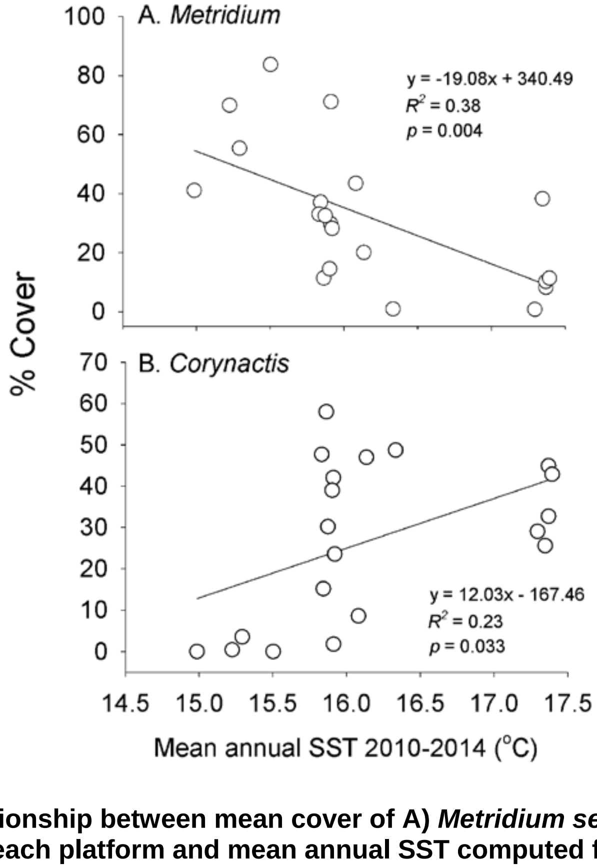

Figure 6. Relationship between mean cover of A) *Metridium senile* and B) *Corynactis californica* for each platform and mean annual SST computed for 2010 – 2014.

3.3.6 Unusual habitat forming and space holding taxa

Non-native and unusual species were locally abundant. These taxa include the non-native Mediterranean mussel, *Mytilus galloprovincialis* Lamarck, 1819 (formerly considered *M. edulis* Linnaeus, 1758 and previously reported as abundant on some platforms in the SBC, Page and Hubbard 1987, Page et al. 1999), the foliose encrusting bryozoan, *Watersipora subatra* (Ortmann, 1890) (also identified as *W. subtorquata* (d'Orbigny, 1852) in the SCB), the anemone *Diadumene* sp., and the hydroid *Tubularia crocea* (Fig. 7). During the period 2015-2016, we detected two nonnative encrusting, habitat forming bryozoan species, *Thalamoporella gothica* Hincks, 1887 and *Conopeum reticulum* Linnaeus, 1767 (or *C. commensale* Kirkpatrick and Metzelaar, 1922, H. Chaney, Santa Barbara Natural History Museum, pers. com.) in platform invertebrate assemblages (Platforms B and Holly, respectively) that had not been recorded previously on platforms in the SBC (CSA 2005, Page et al. 2008).

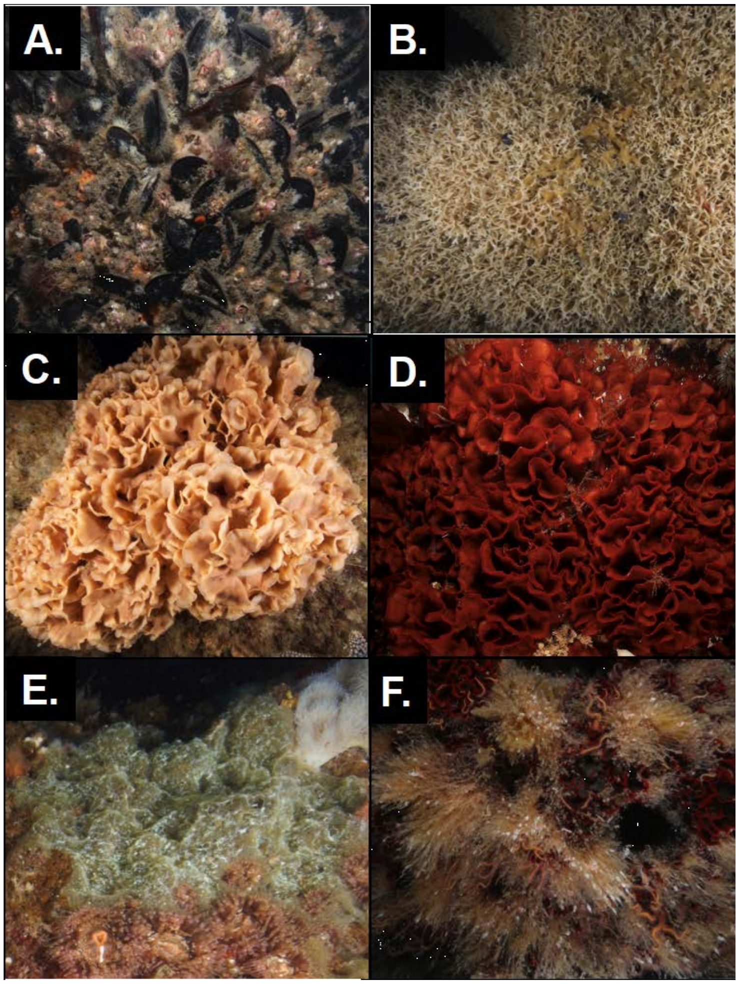

Figure 7. Examples of unusual and nonnative space-holding invertebrate taxa on oil and gas platforms in the Southern California Bight.
A) non-native Mediterranean mussel *Mytilus galloprovinicalis*, B) southern affinity native bryozoan *Thalamoporella gothica*, C) bryozoan *Conopeum reticulum* (or *C. commensale*), D) non-native bryozoan *Watersipora subatra*, E) non-native ascidian *Diplosoma listerianum*, and F) non-native hydroid *Tubularia crocea*

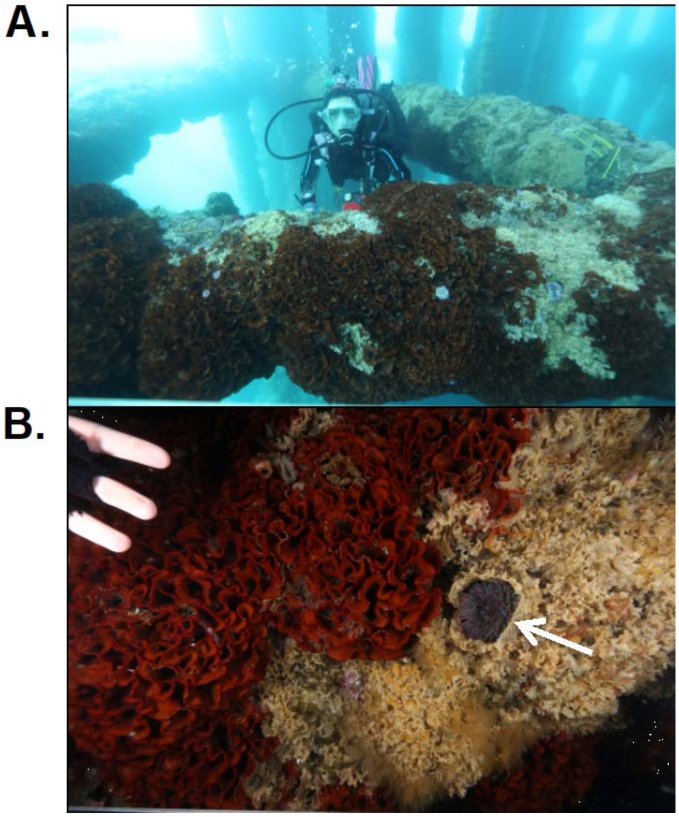

Figure 8. Image taken in April 2017 showing horizontal support members at a depth of 12 m on Platform B.
A) Non-native bryozoan *Watersipora subatra* (dark mass) and native southern affinity bryozoan *Thalamoporella gothica* (light masses) and B) close-up of the two bryozoans and an anemone (*Anthopleura elegantissima*) surrounded by *T. gothica* (white arrow).

3.3.7 Densities and depth distribution of mussels and rock scallops

Of the seven platforms specifically surveyed to assess the densities of mussels and scallops, three (Holly Gina, Grace) had low densities of < 15 and < 4 individuals/0.25m^2, respectively (data not shown). The shallower depths of these platforms had been cleaned during one or more years prior to our survey. Densities of mussels on the remaining four platforms (A, C, Henry, Hogan) were highly variable, ranging up to 308 individuals/0.25m^2 (Fig. 9). As noted on other platforms (CSA 2005), highest mussel densities occurred at the shallowest depths with few individuals recorded deeper than 12 m. In contrast, the densities of scallops increased with depth, ranging between 50 and 100 individuals/0.25 m^2 at depths of 18 and 24 m.

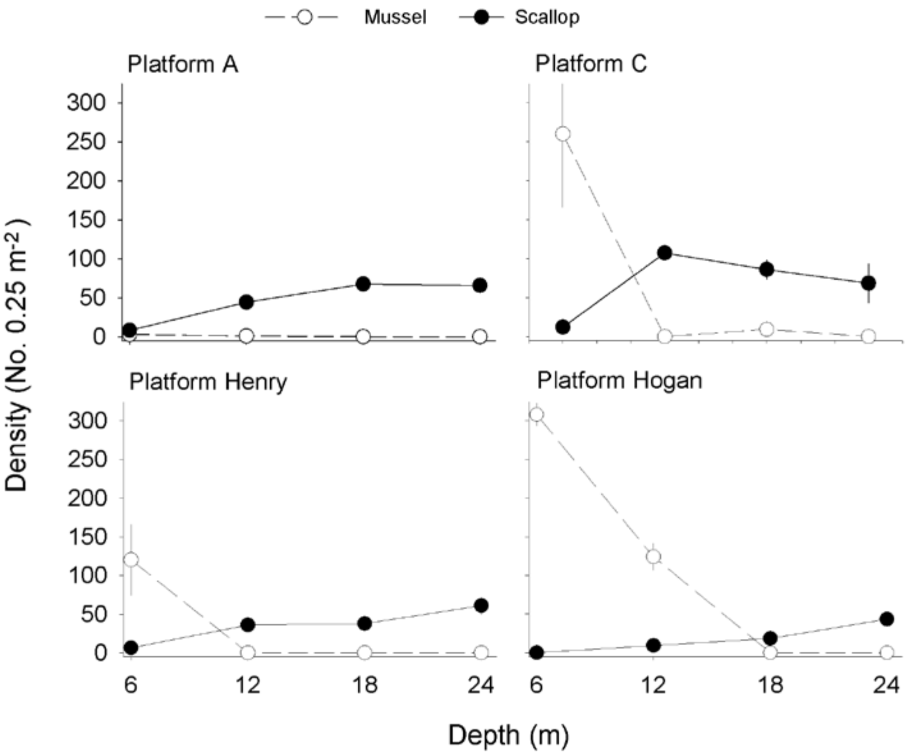

Figure 9. Density and depth distribution of mussels (*Mytilus* ssp.) and rock scallops (*Crassodoma gigantea*) on selected platforms.
Mean values ±1se, n = 4 quadrats per depth. Error bars not visible are within the points.

3.4 Discussion

Our surveys revealed regional differences in the composition of invertebrate assemblages on the shallower portions of offshore platforms across the SCB. These differences were attributable, in part, to variation in the relative abundance of two widely distributed anemones, *Metridium senile* and *Corynactis californica*. Percent cover of these anemones was previously observed to vary with SST among seven platforms in the SBC (Page et al. 2008). We found that this pattern was maintained across the broader SCB, with *M. senile* in highest cover on the more northerly platforms, and *C. californica* in highest cover on those to the south. Other taxa, including sponges, hydroids, and bryozoans, were generally present at much lower cover, more variable in occurrence, and individually lacked a clear relationship with SST or other measured variables.

Although statistically distinct, assemblages on platforms in the Central region showed large overlap with those of the other regions. If platform invertebrate assemblages respond to local oceanographic conditions, this pattern may reflect a greater mixing of water masses that enter the SBC from the east with those of the west here compared with the other regions. This possibility is supported by observations of fish assemblages at platforms in the Central region containing representatives with both northern (e.g., rockfishes, *Sebastes* spp.) and southern (garibaldi, *Hypsypops rubicundus* (Girard, 1854), California sheephead, *Bodianus pulcher* (Ayres, 1854) affinities (Love et al. 2010).

Separation of platform invertebrate assemblages across South, Central, and North-central regions in the CAP ordination was strongly associated in partial correlation analysis with annual mean SST, but the separation of platforms in the South-central region from the other regions was most associated with the abundance of *Watersipora subatra*. This bryozoan was particularly abundant on platforms in the South-central region and has expanded its distribution within this region since it was originally discovered on one platform (Gina) in 2001 (Page et al. 2006, Simons et al. 2016). The higher abundance of *W. subatra* in the South and South-central regions compared with Central and North-central regions suggests that the distribution of this bryozoan may be expanding northward in the SCB.

Within a region, invertebrate assemblages were idiosyncratic in composition and statistically similar in only one pairwise comparison. Partial correlation analysis indicated that separation among platforms within a region could be attributed to variation in mean chlorophyll concentration, water depth, distance from shore, and the abundance of *W. subatra*. Page et al. (2008) documented differences in mussel (*Mytilus galloprovincialis*) growth rate and up to a 6-fold difference in barnacle (*Balanus trigonus*) recruitment among the four platforms within the South-central region. It is likely that platform assemblages within a region are structured by the vagaries of larval supply and physical and biological processes that influence post-settlement growth and survival, such as food availability, competition for space, and disturbance from storm swell and platform maintenance operations.

Mussels are historically considered the dominant space-holding bivalve at shallower depths on California offshore oil and gas platforms (Mearns and Moore 1976, Wolfson et al. 1979, Page et al. 1999, CSA 2005). In this regard, the invertebrate assemblages of Pacific offshore platforms differ from those in the Gulf of Mexico, U.S.A., where barnacles are the dominant epifaunal organism on the coastal platforms, and cementing bivalves predominate on platforms further offshore (Gallaway et al. 1982, Carney 2005). In both regions, however, these hard-shelled taxa provide the physical structure of the assemblage, and secondary substratum for the attachment of macroalgae and other invertebrates such as anemones, sponges, hydroids and bryozoans.

Mussels are under-sampled using photographic methods because anemones, barnacles and other organisms typically cover them. This was dramatically illustrated in a comparison of percent cover to wet biomass obtained through scrape sampling on two platforms (Houchin, Hogan) in the SBC (Page et al. 2010). Mussels (*Mytilus californianus*) comprised only 10 and 14% cover, but 70 and 80% of the wet biomass at a depth of 12 m on these platforms. Our sampling of mussel density on a subset of platforms in this study revealed that, as reported previously (Page et al. 1999, CSA 2005), mussel abundance decreases with depth, but also that mussels are not as widely distributed among platforms as they have been in the past. On some platforms (Platform B, Gina, Gail), the mussel community has been replaced by a high cover of bryozoans that may pre-empt mussel recruitment (Viola et al., i2018), a pattern possibly reflecting a more general shift in the structure of shallow water biotic assemblages on offshore platforms in the SCB.

One mechanism facilitating the shift in invertebrate assemblage structure from mussel-anemone dominated to bryozoan-dominated on some platforms is the periodic manual removal of attached epifauna during platform cleaning operations to allow inspection of the structure and reduce hydrodynamic loading. Cleaning operations can occur anywhere on the structure, but are most typical in shallower depths (< 12 m) that develop the thickest invertebrate assemblage (Page et al. 1999). This anthropogenic disturbance opens up space and facilitates the establishment of *Watersipora subatra*, which has recently attained > 80% cover in shallower depths on some platforms (Viola et al. 2018, Page unpubl data). Nonnative species can become dominant members of invertebrate assemblages on artificial structures to the detriment of native species and these populations can serve as potential sources of propagules to natural reef habitat (Bulleri and Airoldi 2005, Adams et al. 2014). The presence of non-native species on platforms has consequences for various platform decommissioning options in California, including the removal and transport of platforms, particularly if removals are conducted without regard for the potential transport and dispersal of these species (Page et al. 2006, Macreadie et al. 2011).

The rock scallop, *Crassodoma gigantea*, is another space-holding species that provides secondary attachment surface for anemones, barnacles, and other taxa. Rock scallops occur below the putative mussel zone to depths exceeding 30 m (CSA 2005) and are therefore generally not affected by *W. subatra* or cleaning operations. Given the density of *C. gigantea* on the platforms, and a planktonic larval duration of ~5 weeks (Leighton 2001), it seems likely that platforms are a source of rock scallop recruits to natural reefs in the region.

Novel species appeared on SBC platforms following the El Nino of 2015, a period of warm water incursion into the SBC. The bryozoan, *Thalomoporella gothica*, is more typically found in tropical and subtropical regions of the eastern Pacific than in southern California (Chaney et al. 1989). The type locality is Mazatlan, Mexico (Osburn 1950). This encrusting bryozoan aggressively competed for space, overgrowing other native invertebrates and the non-native bryozoan, *Watersipora subatra*, to achieve nearly 100% cover on some horizontal support members during 2015-2016 (unpubl data). The anemone *Diadumene leucolena* is native to the western Atlantic coast, and has been introduced to the eastern Pacific, where it was reported in earlier surveys from coastal embayments (i.e., San Francisco Bay, Elkhorn Slough), but was not reported from southern California (Cohen et al. 2002, CDFG 2008). This anemone also occurred in localized high cover on vertical and horizontal surfaces at some platforms. Another unusual bryozoan, *Conopeum reticulum* (Linnaeus 1767) or *C. commensale* Kirkpatrick and Metezelaar 1922 (H. Chaney, pers. com.), not previously recorded from platforms in the SCB, was observed in isolated clumps on one platform (Holly). Unfortunately, without better taxonomic resolution not much can be said about the possible source of this bryozoan. *Conopeum reticulum* has a cosmopolitan distribution and is widespread in northern Europe and the U.K. and reported from California (Osburn 1950). *C. commensale* is a tropical species; the type locality occurs in Northwest Africa, but it is also widely distributed along the Pacific coast from northern Mexico to Ecuador (Osburn 1950, Cohen and Carlton 1995).

It is puzzling how *Thalomoporella gothica* was able to disperse northward over a relatively short period of time into the SBC from source populations putatively located 100's of kilometers to the south, given the expected short planktonic larval duration of this taxon (10–12 hours, Chaney et al. 1989). Chaney et al. (1989) reported that the Thalamoporellidae have not generally utilized hull fouling as a form of transport unlike other lecithotrophic bryozoans. Other possible mechanisms of dispersal include the use of "stepping stones" whereby taxa progressively expand in distribution through step-wise dispersal onto new habitat away from the original source population (Sammarco et al. 2004, Simons et al. 2016). Another possibility includes the rafting of sexually reproducing colonies into new areas on moveable substrates, such as floating kelp or logs (Chaney et al. 1989). In this scenario, the floating substrate with attached *T. gothica* (or other novel species) becomes lodged on the platform, or travels within dispersal distance of the platform.

Whatever the dispersal mechanism, *Thalomoporella gothica* was able to achieve high cover in localized areas on one platform. As of August 2017, this bryozoan remains in high cover, but its ability to persist into the future is unknown. Although shifts in the composition of fish assemblages on offshore platforms as a result of warm water events have been reported with the movement of subtropical fishes poleward (Love et al. 2010), to our knowledge the present study is the first report of a similar phenomenon occurring for invertebrates on platforms.

Hare and Mantua (2000) suggested that a regime shift in the ocean might best be detected by monitoring marine organisms. Two aspects of our findings support the potential utility of invertebrate assemblages or taxa on offshore structures as sentinels of change in ocean climate (Page et al. 2008). First, a shift in climate regime might be reflected in changes in taxa whose abundance is correlated with SST. The abundance (as cover) of the anemone *Metridium senile* was strongly negatively correlated with SST and this species, in particular, may be sensitive to ocean warming. A decline in the cover of this species and a shift in distribution from shallower to deeper, cooler depths could occur on platforms in the western SBC with ocean warming. Second, a regime shift to warmer waters would likely result in the appearance and persistence of subtropical species not previously present on platforms in the SCB. The southern-affinity bryozoan *Thalmoporella gothica* may be such a species, now rare but capable of dispersing to platforms in the SBC. A general increase in the abundance of subtropical taxa such as *T. gothica* on offshore structures may occur abruptly with warm regime events, as observed during our study, or slowly, as have zooplankton declines in the SCB over two decades of warming (Roemmich and McGowan 1995).

In conclusion, platform invertebrate assemblages were distinguishable across the broader SCB, varying in association with SST and the abundance of the non-native species *Watersipora subatra*. However, assemblages within a region were distinct from one another, a finding that has implications to the decommissioning and disposition of these structures following oil and gas operations. Decommissioning will eventually be implemented for platforms in the SCB; the actual process for any individual platform may take decades to complete. Similar to platform fish assemblages (Love et al. 2010), invertebrate assemblages are distinct enough that the outcome of various decommissioning scenarios will need to be evaluated on a platform-by-platform basis. Invertebrate taxa that will be affected, their productivity and connectivity to other artificial and natural habitat, and the transport and disposition of non-native species, will need to be considered in future decision-making pertaining to the fate of offshore platforms in the SCB and elsewhere (Schroeder and Love 2004, Claisse et al. 2014).

Table 4. List of sessile and semi-mobile taxa recorded during the photographic sampling on offshore oil and gas platforms in the Santa Barbara Channel and San Pedro Bay (2013-2014). Mobile taxa that included crabs, sea urchins, and seastars were recorded but not included in the analysis.

Porifera

Cliona celata? Brant, 1826
Halichondria sp. 1 Fleming 1828
Halichondria sp. 2 Fleming 1828
Haliclona sp.1 Schmidt, 1862 (cream)
Haliclona sp. 2 Schmidt, 1862
Leucilla nuttingi (Urban, 1902)
Spheciospongia confoederata de Laubenfels, 1930
Sponge sp. 1 (orange encrusting)
Sponge sp. 2 (yellow erect)
Sponge sp. 3 (yellow mound)
Sponge sp. 4 (purple)
Sponge sp. 5 (yellow green)

Cnidaria

Aglaophenia sp. Lamouroux, 1812
Anthopleura elegantissima (Brandt, 1835)
Anthopleura sola (Brandt, 1835)
Corynactis californica Carlgren, 1936
Diadumene sp. Stephenson 1920
Hydractinia milleri Torrey, 1902
Metridium senile (= *M. dianthus*) (Linneaus, 1761) (Ellis, 1768)
Obelia sp. Péron and Lesueur, 1810
Paracyathus stearnsi Verrill, 1869 (Cairns 1994)
Plumularia sp. Lamarck 1816
Tubularia crocea (Agassiz, 1862)
Anemone sp. 1 (calico)

Ectoprocta

Bugula californica Robertson, 1905
Bugula neritina (Linneaus, 1758)
Bugula sp. Oken, 1815
Celleporaria brunnea (Hincks, 1884)
Celleporina robertsoniae (Canu and Bassler, 1923)
Crisia sp. 1 Crisiidae, Johnston, 1838
Diaperoforma californica (d'Orbigny, 1853)
Filicrisia sp. d'Orbigny, 1853
Watersipora subatra (Ortmann, 1890)

Ectoprocta (con’t)
Bryozoan sp. 1 (cream)
Bryozoan sp. 2 (peach)

Echinodermata
Cucumaria salma Yingst, 1972
Ophiactis simplex (Le Conte, 1851)
Ophiothrix spiculata Le Conte, 1851

Mollusca
Crassadoma gigantea (J. E. Gray, 1825)
Mytilus galloprovincialis Lamarck, 1819
Mytilus californianus Conrad, 1837
Serpulorbis squamigerus (Carpenter, 1856 or 1857)

Annelida
Eudistylia polymorpha (Johnson, 1901)
Filograna implexa? Berkeley, 1835
Myxicola infundibulum (Montagu, 1808)
Pista elongata Moore, 1909
Serpula columbiana Johnson, 1901
Spiochaetopterus costarum (Claparède, 1869)
Spirobranchus spinosus Moore, 1923
Spirorbid worm sp. 1
Sectioned tube worm (unknown)

Arthropoda
Balanus nubilus Darwin, 1854
Balanus trigonus Darwin, 1854
Megabalanus californicus (Pilsbry, 1916)
Barnacles (unknown)

Chordata
Aplidium solidum (Ritter and Forsyth, 1917)
Botrylloides diegensis Ritter and Forsyth, 1917
Didemnum sp. Savigny, 1816
Diplosoma listerianum Milne Edwards, 1841
Distaplia occidentalis? Bancroft, 1899
Pyura haustor (Stimpson, 1864)
Trididemnum opacum (Ritter, 1907)
Trididemnum sp. Delle Valle, 1881

Chordata (con't)
Tunicate sp. 1 (small orange)
Tunicate sp. 2 (white)

Substrate (misc)
Amphipod tube complex
Hydroid/Bryozoan complex

Macroalgae
Chlorophyta
Filamentous

Rhodophyta
Bladey
Branching
Encrusting coralline spp.
Filamentous

4 The Effects of Anthropogenic Structures on Habitat Connectivity and the Potential Spread of Non-native Invertebrate Species in the Offshore Environment

4.1 Introduction

Connectivity of habitats through the dispersal of reproductive propagules, such as seeds, spores, and larvae, is a major driver of population dynamics, community structure, gene flow, and the distribution of native and non-native species in terrestrial and marine ecosystems (Gallaway and Lewbel 1981, Roberts 1997, Cain et al. 2000; Cowen and Sponaugle 2009, Pergl et al. 2011). For the majority of marine invertebrate species, the principal dispersal stage is a planktonic larva. Connectivity among populations and habitats is related to the duration of this planktonic stage and to physical and biological factors that affect larval transport and survival (Levin 2006, Pineda et al. 2007, Cowen and Sponaugle 2009). Human-mediated activities in the marine environment can increase larval connectivity and introduce non-native species to new habitats. The transport of non-native species as larvae in ballast water or as adults attached to boat hulls are often cited examples of human facilitated dispersal of non-native species to new regions (Carlton and Geller 1993, Ruiz et al. 1997, Verling et al. 2005).

It has been suggested that offshore energy structures, such as oil and gas platforms (Gallaway and Lewbel 1981, Sammarco et al. 2004) and wind farms Adams et al. 2014), can facilitate species range expansions and the introduction of non-native species into new geographic areas. These structures are often situated in a soft seafloor environment, providing vertical and shaded hard substrate habitat where it would not normally exist. As a result, these structures provide patches of habitat or “stepping stones” that could facilitate the dispersal of species into new areas (Gallaway and Lewbel 1981, Sammarco et al. 2004, Mineur et al. 2012, Adams et al. 2014). Such effects are likely to vary with physical and biological factors that include proximity to inshore habitat that could act as a source of propagules, the number and spacing of structures, local and regional current patterns, and species life histories (Adams et al. 2014). However, few studies have explicitly explored potential larval connectivity among existing offshore structures or their possible role in the dispersal of non-native species despite the need for such information (Sheehy and Vik 2010, Macreadie et al. 2011, Miller et al. 2013).

Potential connectivity among offshore platforms can be explored using biophysical models of larval dispersal (Miller 2007, Werner et al. 2007, Cowen and Sponaugle 2009, Metaxas and Saunders 2009). We define potential connectivity as the probability of larval transport from a source site to a destination site via currents (Mitarai et al. 2009, Watson et al. 2010). Biophysical models have been widely used to investigate dispersal patterns and connectivity among habitats for invertebrates and fish with planktonic larval durations (PLDs) ranging from days to months (Metaxas and Saunders 2009). However, larval dispersal of marine invertebrates with PLDs of 24 hours or less has been rarely investigated using biophysical models. Limited field studies have suggested that the larval dispersal distances of species with PLDs of 24 hours or less are on the order of meters to 100s of meters (Siegal et al. 2003, Shanks 2009), which may be one reason why connectivity modeling of these species is uncommon.

Surveys of sessile invertebrates on seven offshore oil and gas platforms in the Santa Barbara Channel (SBC, Fig. 10) in 2001 revealed the non-native encrusting bryozoan *Watersipora subtorquata* (=*W. subatra*, Vieira et al. 2014, hereafter *Watersipora*) on one of the seven platforms (Page et al. 2006). *Watersipora* is now common in the harbors and coastal embayments of central and southern California (Cohen et al. 2005), but rarely reported in more open coastal habitat. Under favorable conditions, *Watersipora* is an aggressive competitor for space (Needles and Wendt 2013), overgrowing and excluding other benthic epifauna during growth (e.g. barnacles and bivalves) and acting as a foundation species or a "bioengineer" by forming large (several decimeter to larger) three-dimensional masses that provide a novel habitat for invertebrate taxa (Needles and Wendt 2013, Sellheim et al. 2010). *Watersipora* has short lecithotropic larval stage with an estimated maximum PLD of 24 hours (Cohen 2011, Ng and Keough 2003).

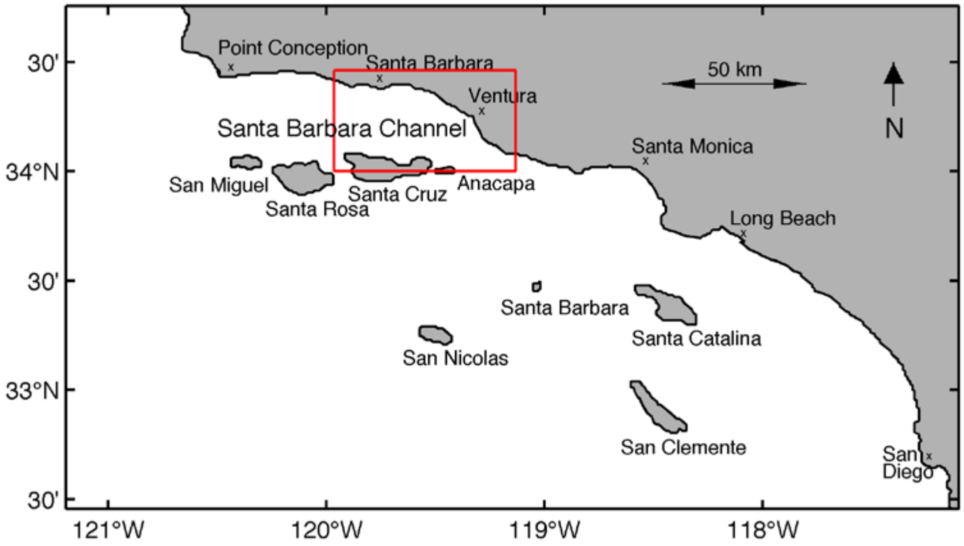

Figure 10. Southern California Bight and model domain.
The study area, shown by the red box, is located in the eastern Santa Barbara Channel.

In this study, we investigated the potential connectivity of *Watersipora* between seven offshore oil and gas platforms in the SBC (Fig. 11). The transport and connectivity of *Watersipora* larvae was estimated using a three-dimensional biophysical model, which consists of an ocean circulation model to simulate flow and a particle tracking model to simulate larval transport. We used the biophysical model to assess whether habitat connectivity via larval dispersal is a plausible mechanism to explain an observed spread of *Watersipora* from one platform in 2001 to four platforms in 2013. Hull fouling is also a possible mechanism for the dispersal of *Watersipora* among habitats (Floerl and Inglis 2005, Davidson et al. 2010). *Watersipora* is widely distributed in the harbors of southern California and has been documented in the four harbors, Santa Barbara, Ventura, Channel Islands, and Port Hueneme, inshore of our study platforms (Anderson and Haygood 2007, Foss 2008, Cohen 2011, Mackie et al. 2012, Santschi 2012). Thus, these four harbors are included as potential sources of *Watersipora* larvae in our modeling. Our study also examines the influence of the offshore hydrodynamic environment on larval dispersal distances for taxa with PLDs of 24 hours or less.

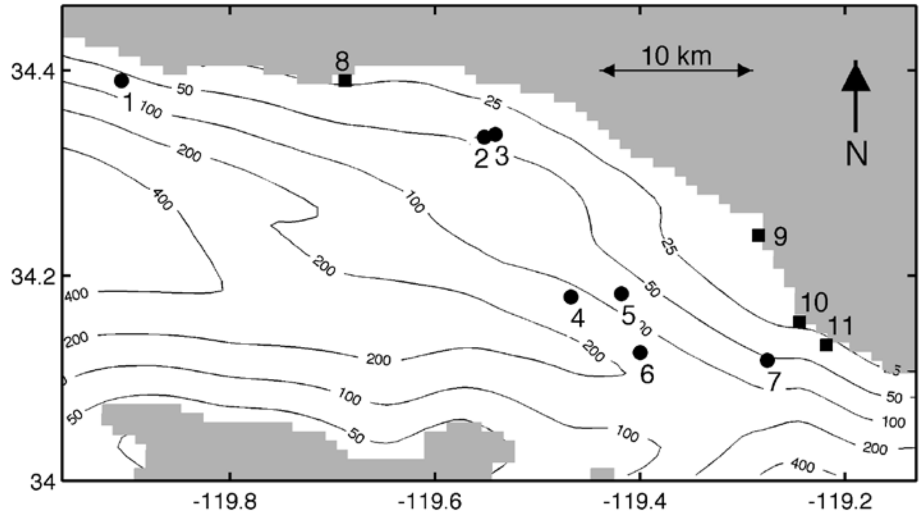

Figure 11. Locations of oil and gas platforms (circles) and harbors (squares): Red symbols identify the locations where *Watersipora* was assumed present or observed in 2001 and 2013. Blue symbols identify the locations where *Watersipora* was present in 2013, but not in 2001. Green symbols identify the locations where *Watersipora* was not present in 2001 or 2013. SBH=Santa Barbara Harbor, VH=Ventura Harbor, CIH= Channel Islands Harbor, and PHH=Port Hueneme Harbor. Bathymetry contours in meters are shown by the black lines.

4.2 Methods

4.2.1 Distribution and abundance of *Watersipora* on platforms

We documented changes in the distribution and abundance of *Watersipora* from 2001 to 2013 using SCUBA surveys of seven offshore oil and gas platforms located in the western SBC (Fig. 11). The following companies issued permission to dive the platforms: Veneco, Inc. (platforms Holly, Grace and Gail), Pacific Operators Offshore, LLC. (platforms Houchin and Hogan), and Nuevo Energy in 2001 and DCOR, LLC. in 2013 (platforms Gilda and Gina). The study platforms encompassed a range of sizes, water depths, and distances from shore (Table 5, Fig. 11, Page et al. 2006, Page et al. 2008). The submerged portion of the platforms consisted of vertical, oblique, and horizontal cylindrical steel support members and vertical conductor pipes through which the wells are drilled. The hard substrate provided by the submerged structure was typically occupied subtidally by a diverse assemblage of sessile and semi-mobile invertebrates, including mussels (*Mytilus californianus*, *M. galloprovincialis*), barnacles (e.g. *Megabalanus californicus*), rock scallops (*Crassodoma gigantea*,), and anemones (*Corynactis californica*, *Metridium senile*) (Page et al. 2008, Page et al. 2010). The support structures and conductor pipes of the platforms are cleaned infrequently, usually years apart, and typically to a depth of ~9 m. *Watersipora* colonies are negatively buoyant and when dislodged from the platforms, the fragments drop to the seafloor (diver observations). Thus, platform cleaning is an unlikely to provide a vector pathway for the spread of *Watersipora*.

Table 5. Characteristics of study platforms.

Variable	Platforms						
	Gina	Gail	Gilda	Grace	Hogan	Houchin	Holly
Year of Installation	1980	1987	1981	1979	1967	1968	1966
Distance from shore (km)	5.0	13.2	11.9	14.4	5.1	7.0	2.9
Water depth (m)	29	225	64	97	46	49	64
Platform size (m^2 on bottom)	560	5,600	2,340	3,120	1,444	1,444	1,728

To measure the distribution and abundance of *Watersipora*, we used a camera enclosed in an underwater housing with two strobes mounted on a quadrapod designed to photograph 0.25 m^2 plots following methods modified from (Coyer et al. 1999). Plots measured 41 cm x 62 cm to accommodate the dimensions of the platform legs and conductor pipes. We photographed one 0.25 m^2 plot on the inside and outside of each of the four corner legs and four randomly selected conductor pipes at depths of 6 m, 12 m, and 18 m for a total of 48 photoplots per platform. Additional qualitative swimming surveys of approximately 30 minutes were done among the conductor pipes at each depth searching for presence of *Watersipora*. Surveys were weather and access dependent and conducted from late August to early November in 2001 and 2013. The time to survey a particular platform varied between 1- 2 days depending on platform size.

We identified and estimated the percentage cover of *Watersipora* within each photoplot using point-contact methods. The image from each photoplot was projected onto 100 uniformly distributed points and points with *Watersipora*, contacts, were recorded to estimate cover. The same plot locations were surveyed in 2001 and 2013. We also consulted previous survey data of some of the platforms conducted by others in October 1999 and 2000 for records of *Watersipora* (CSA 2005).

4.2.2 Biophysical modeling of larval dispersal and connectivity

A three-dimensional biophysical model was used to estimate larval dispersal of *Watersipora* from the seven oil and gas platforms and four harbors in our study area (Fig. 11). The biophysical model combined an ocean circulation model and a particle tracking model, where the particles represent simulated larvae. The three-dimensional ocean circulation model was a high-resolution Regional Ocean Modeling System (ROMS) applied to the Southern California Bight (Dong and McWilliams 2007, Shchepetkin and McWilliams 2005). The model domain covered the southern California coastline including the eight Channel Islands (Fig. 10). The model grid was 258 km by 386 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). The model has been rigorously calibrated against field observations and shown to accurately capture mean, interannual, seasonal, and intraseasonal mesoscale dynamics of the Southern California Bight, which includes the SBC (Dong et al. 2009, Dong et al. 2011, Simons et al. 2015). Thus, the model resolution is adequate to estimate larval dispersal distances of 1 km or larger. The three-dimensional particle tracking model was driven by 6-hour averaged three-dimensional velocity fields produced by the ROMS following the methods in Mitarai et al. (2009) and Carr et al. (2008). For this study, the ROMS velocity fields were available for 12 years from 1996 – 2007. Particles were 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 was validated against observational data from drifter experiments by Ohlmann and Mitarai (2010).

To model the potential connectivity among the platforms and harbors, particles were released from eight source sites in the study area; platforms Grace, Gilda, Gail, and Gina and Santa Barbara, Ventura, Channel Islands, and Port Hueneme harbors (Fig. 11). Following Watson et al. (2010) and Mitarai et al. (2009), potential connectivity is defined as the probability of larval transport from a source to a destination location as estimated by particle tracking simulations. By definition, potential connectivity does not include parameters for larval production and survival.

As the model grid was 1 km^2 in the horizontal direction, the details of the harbor bathymetry could not be included in the model. To release particles from the harbors, the particles were placed at the first water grid cell adjacent to the harbor location near the shoreline. This procedure assumes that *Watersipora* larvae can be transported out of the harbor, which is supported by the presence of *Watersipora* on a wharf near the entrance to Santa Barbara harbor (personal observation). At each source site, particles were released vertically every 0.1 meters from 1 to 18 meters below the surface, the depth range at which *Watersipora* colonies were observed at the platforms (Page et al. 2006). Particles were released every 3 hours and tracked passively for 24 hours, based on the estimated maximum PLD of *Watersipora* (Cohen 2011, Ng and Keough 2003). Typical of other bryozoan taxa, *Watersipora* larvae are small and weak swimmers (Bradbury and Snelgrove 2001, Chia et al. 1984). *Watersipora* larvae initially show positive phototaxis on release (Ryland 1960, personal observation), but due to their size and weak swimming, it is unlikely that they could change their vertical position in the water column to influence their horizontal transport. Due to *Watersipora*'s weak swimming ability and short PLD along with the strong offshore horizontal currents in the SBC, larvae are modeled as passive particles. To address any potential variability in the depth distribution of larvae in the water column, particles were released over the top 18 m of the water column where *Watersipora* was observed on the platforms. The particle release frequency was selected to meet the criteria for robustness in particle tracking models (Simons et al. 2013). Particles were released for June through August, the estimated reproductive season for *Watersipora* (unpublished data, Table 4), for 12 years from 1996 to 2007. For this study, approximately seven million particle trajectories were simulated with 875,000 particles released from each of the eight sources. The number of particles was selected to achieve model robustness following the methods in Simons et al. (2013).

To estimate the extent of larval dispersal, the individual particle trajectories, calculated by the biophysical model, were transformed into two-dimensional particle density distributions (PDDs) for each source site. Since *Watersipora* larvae were assumed to have a PLD of 3-24 hours (Cohen et al. 2005, Ng and Keough 2003), the particle locations from each trajectory were saved every 3 hours up to 24 hours after their release. The three-dimensional distribution of all particles released from a platform or harbor over the reproductive season of June to August for a single year, was used to produce an annual PDD. This involved summing the number of particles within a grid cell over depth and then dividing by the total number of particles released (Mitarai et al. 2009). The annual PDDs for each source were then averaged over the 12 model years from 1996-2007 to obtain a long-term average of particle dispersal. Although the model years of 1996-2007 did not coincide exactly with the years between the surveys of 2001-2013, the model provided a long-term average of particle dispersal, which was applicable to the 12-year period between the surveys. Potential connectivity was quantified in the form of a matrix by sampling the values of the 12-year averaged PDDs from the source platforms and harbors at the seven destination platforms. The values of the connectivity matrix represent the fraction of the total number of particles released from a source site that arrived at a destination site, which can be converted to a percentage by multiplying the matrix by 100. Overall, the connectivity matrix illustrates the relative degree of potential connectivity between the source and destination sites.

4.3 Results

4.3.1 Distribution and abundance of *Watersipora* on platforms

Our 2001 surveys revealed *Watersipora* on only one of the seven study platforms, platform Gilda (Fig. 12) (Page et al. 2006). At platform Gilda in 2001, the mean cover of *Watersipora* decreased with depth from 40.8% ± 9.5% SE at 6 m to 10.6% ± 3.7% SE at 18 m. An independent survey of study platforms Gail and Grace in 1998-2000 using SCUBA divers and remotely operated vehicles also failed to find *Watersipora* (CSA 2005). Our 2013 surveys found that the distribution of *Watersipora* had expanded to include 3 additional platforms, Grace, Gail and Gina, with the cover of *Watersipora* varying among platforms and depths (Fig. 12). The highest mean percent cover occurred on platform Gail (41.1% ± 8.3% SE) at the intermediate depth of 12 m. The mean percent cover was lowest (2.0% ± 0.6% SE) on platform Grace, where only small colonies were found at a depth of 6 m. Platform Gilda, the site of the first record of *Watersipora* on a platform in 2001, had been recently cleaned with the invertebrate assemblage removed to a depth of approximately 12 m and mean coverage at all depths had decreased to less than 6%.

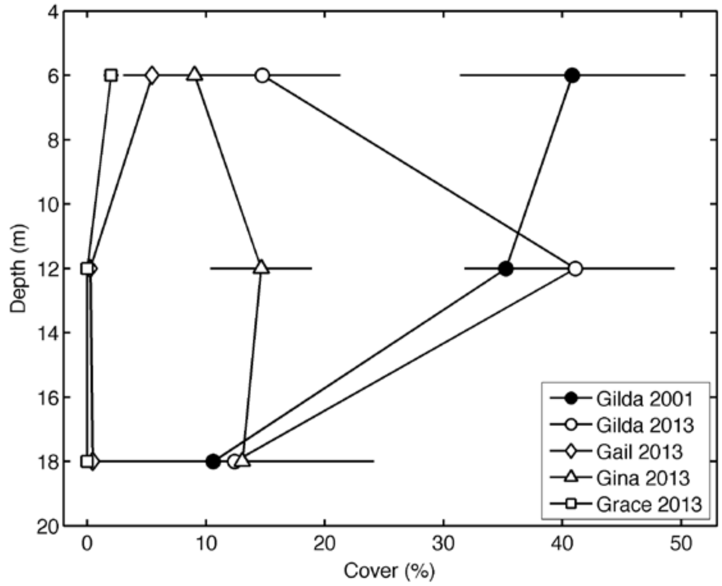

Figure 12. Percent cover of *Watersipora* at depths of 6 m, 12 m, and 18 m on platform Gilda in 2001 and 2013 and on platforms Gail, Gina, and Grace in 2013.
Watersipora was absent from platforms Gail, Gina, and Grace in 2001. The percent cover is displayed as mean values ± one standard error.

4.3.2 Biophysical modeling of larval dispersal and connectivity

Based on our survey results, two modeling scenarios were used to explore the potential dispersal and connectivity of *Watersipora* larvae among seven platforms and four harbors in the SBC. In the first scenario, particles were released from platform Gilda, where *Watersipora* was observed in 2001, and the four harbors and tracked to all seven platforms. In the second scenario, particles were released from platforms Grace, Gilda, Gail, and Gina, where *Watersipora* was observed in 2013, and the four harbors and tracked to all seven platforms.

In order to display the horizontal extent of larval dispersal, the PDDs from the individual source sites for each scenario are added together and displayed in Fig. 13. In scenario 1, the particles released from platform Gilda disperse significantly farther than the particles released from the four harbors. Platform Gilda is centrally located in the SBC (Fig. 11) and is thus exposed to higher flow than the harbor mouths, which are located near the shoreline. As strong currents run along the basin of the eastern SBC (Harms and Winant 1998), the major axis of the elliptical PDD for platform Gilda aligns with these flows as well as the bathymetric contours shown in Fig. 11. The PDD from platform Gilda extends to nearby platforms Grace and Gail, indicating that particles released from platform Gilda can reach these platforms in 24 hours or less. The PDDs from Channel Islands and Port Hueneme harbors also extend to platform Gina, but not to the other six platforms. The PDDs from Ventura and Santa Barbara harbors do no extend to any of the seven platforms. In scenario 2, the PDDs from platforms Gilda, Grace, and Gail overlap such that they are not distinguishable, indicating potential connectivity between these three platforms. The overlapping PDDs from platform Gina, Channel Islands harbor and Port Hueneme harbor suggest potential connectivity between these sources as well. The three northwestern platforms, Holly, Houchin and Hogan, do not display potential connectivity with any of the eight sources in scenario 1 or 2.

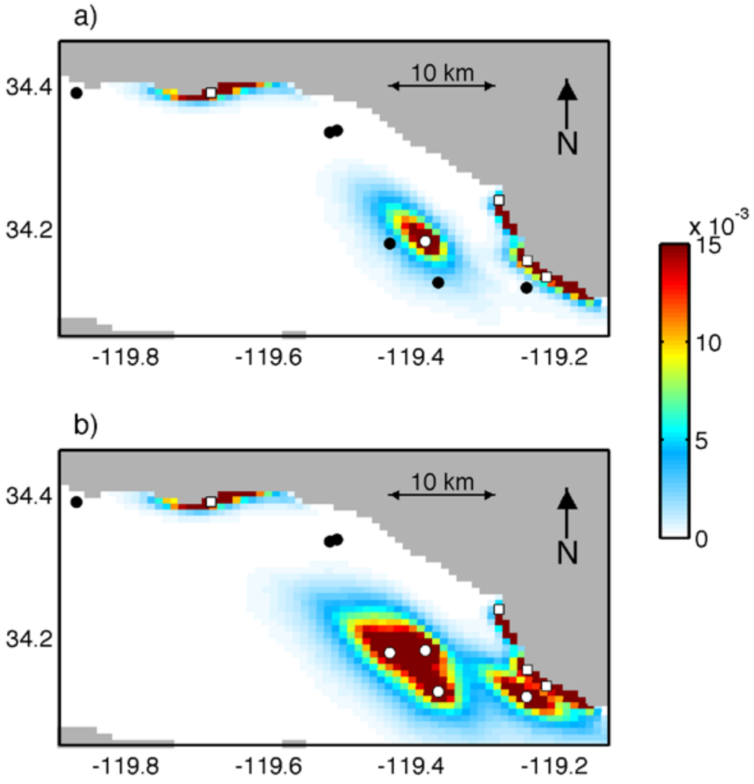

Figure 13. (a) PDDs averaged over 12 years for scenario 1. (b) PDDs averaged over 12 years for scenario 2.

White circles and squares identify the platforms and harbors respectively that are source sites, where particles are released. Black circles identify the platforms that are used only as destination sites.

Table 6. Potential connectivity matrix for scenario 1.
The values represent the percentage of the total number of particles released from a source site that arrived at a destination site.

Source Sites	Destination Sites (Platform)						
	Holly	Houchin	Hogan	Grace	Gilda	Gail	Gina
Platform Gilda	0	6.8×10^{-4}	0	2.3×10^{-1}	4.7	1.7×10^{-1}	3.3×10^{-3}
Port Hueneme Harbor	0	0	0	0	0	0	2.3×10^{-2}
Channel Islands Harbor	0	0	0	0	0	0	2.6×10^{-2}
Ventura Harbor	0	0	0	0	0	0	0
Santa Barbara Harbor	2.1×10^{-3}	1.4×10^{-3}	7.7×10^{-4}	0	0	0	0

For scenario 1, the potential connectivity matrix (Table 6) reveals the highest connectivity from platform Gilda to itself. This self-connectivity indicates high local retention at platform Gilda, which is not unexpected given the short PLD of *Watersipora*. The second highest potential connectivity values in Table 6, on the order of 10^{-1}, are from platform Gilda to platforms Grace and Gail, which are 5 km and 7 km respectively from platform Gilda. The potential connectivity matrix also reveals connectivity from Channel Islands and Port Hueneme harbors to platform Gina. Little or no potential connectivity is detected from platform Gilda to the three northwest platforms, Holly, Houchin, and Hogan, or from Ventura or Santa Barbara harbors to any of the seven surveyed platforms.

Table 7. Potential connectivity matrix for scenario 2.
The values represent the percentage of the total number of particles released from a source site that arrived at a destination site.

Source Sites	**Destination Sites (Platform)**						
	Holly	Houchin	Hogan	Grace	Gilda	Gail	Gina
Platform Gina	0	0	0	1.9×10^{-3}	2.1×10^{-2}	1.7×10^{-2}	4.6
Platform Gail	0	0	0	4.1×10^{-1}	1.2×10^{-1}	2.8	1.0×10^{-2}
Platform Gilda	0	6.8×10^{-4}	0	2.3×10^{-1}	4.7	1.7×10^{-1}	3.3×10^{-3}
Platform Grace	0	0	0	2.9	1.0×10^{-1}	8.1×10^{-2}	1.4×10^{-3}
Port Hueneme Harbor	0	0	0	0	0	0	2.3×10^{-2}
Channel Islands Harbor	0	0	0	0	0	0	2.6×10^{-2}
Ventura Harbor	0	0	0	0	0	0	0
Santa Barbara Harbor	2.1×10^{-3}	1.4×10^{-3}	7.7×10^{-4}	0	0	0	0

For scenario 2, the potential connectivity matrix (Table 7) reveals self-connectivity or high local retention at each of the four source platforms, Grace, Gilda, Gail, and Gina. High potential connectivity is also predicted between platforms Grace, Gilda, and Gail as indicated by the second highest values in Table 7, on the order of 10^{-1}. In addition to Channel Islands and Port Hueneme harbors, platform Gina now shows a similar level of potential connectivity with platform Gail. Even with the additional sources of platforms Grace, Gail, and Gina, the platforms to the northwest, Holly, Houchin, and Hogan, continue to show little to no potential connectivity with the platforms to the southeast, Grace, Gilda, Gail, and Gina.

By calculating the average distance traveled by the particles released from platforms Gilda, Grace, Gina, and Gail over the 12 model years, we explore the relationship between the range of PLDs used for *Watersipora*, 3 – 24 hours, and the average dispersal distance traveled by the particles (Fig. 14). In Fig. 14, the PLD equates to the travel time of the particles. For all four platforms, the average dispersal distance increases linearly with increasing PLD. The average dispersal distances for the four platforms range from 1.1 to 1.4 km at a PLD of 3 hours and from 9.6 to 11.5 km at a PLD of 24 hours. In Fig. 14, the average dispersal distance is greater for platforms Gail and Grace than platforms Gilda and Gina. Platforms Gail and Grace are located farther offshore in deeper water than platforms Gilda and Gina (Fig. 11) and are thus exposed to higher flows, driving a greater dispersal distance.

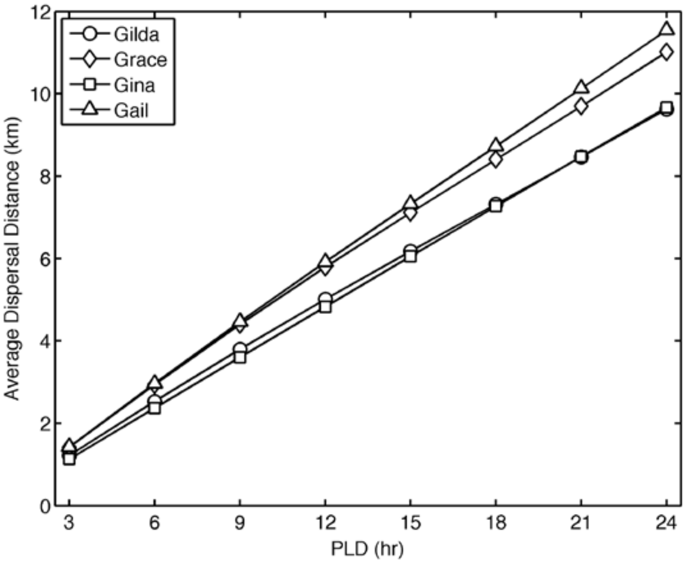

Figure 14. Average dispersal distance of particles (km) versus PLD (hr) for platforms Gilda, Grace, Gina, and Gail.
PLD equates to the travel time of the particles.

4.4 Discussion

4.4.1 Larval connectivity between platforms and harbors

Our modeling study explores whether larval dispersal needs to be considered, along with hull fouling, as a potential pathway for the spread of *Watersipora* among platforms and harbors in the SBC. Estimates of no potential connectivity from the harbors to platform Gilda shown in Table 7 suggest that the colonization of platform Gilda by *Watersipora* prior to 2001 was not due to larval dispersal from the four harbors. Thus, we hypothesize that hull fouling was most likely the initial vector of introduction at platform Gilda. Hull fouling could have occurred via service vessel traffic, including crew boats and barges, or less likely from recreational boats, which are not permitted to tie up or closely approach offshore platforms in the SBC. Multiple commercial boat companies service the platforms in the SBC. One boat company usually provides services to one or two oil companies with specific boats dedicated to specific platforms or sets of platforms owned by the same oil company. However, we have no information on whether *Watersipora* was attached to the boat hulls or on the past frequency and pathways of boat traffic and are thus unable to quantify this potential vector. Since the link between boat traffic and the spread of *Watersipora* in the SBC remains ambiguous, hull fouling must be considered a potential mechanism to explain the spread of *Watersipora* in the SBC.

Our modeling results reveal three distinct patterns of larval dispersal and potential connectivity among platforms and harbors in the SBC. First, the modeling estimates the highest potential connectivity among the four southeastern platforms, Grace, Gilda, Gail, and Gina. These results are consistent with field surveys from 2001 and 2013, which revealed the spread of *Watersipora* from a single platform, Gilda, to three previously uninvaded platforms, Grace, Gail and Gina. Due to *Watersipora*'s short PLD, estimated to be at most 24 hours (Carlton and Geller 1993, Ng and Keough 2003, Anderson and Haygood 2007, Page et al. 2008), the modeling predicts high local retention of *Watersipora* larvae within the vicinity of colonized platforms, which is also consistent with our survey results as *Watersipora* was found on platform Gilda in 2001 and 2013. Although our surveys indicated that the cover of *Watersipora* on platform Gilda varied between 2001 and 2013, this taxon is recognized as a potentially dominant species, capable of monopolizing space once established through the lateral growth of colonies and the high local retention of short-lived larvae (Needles and Wendt 2013). Thus, it is extremely likely that *Watersipora* remained on platform Gilda during the 12-year period between surveys. To illustrate the aggressive nature of *Watersipora* colonization on the platforms, photographs of the same sample plot taken on a conductor pipe at platform Gail at a depth of 9 m show the dramatic change from a barnacle dominated assemblage in 2001 to one dominated by *Watersipora* in 2013 (Fig. 15). Thus, the modeled high potential connectivity among the southeastern platforms along with high local retention of larvae on colonized platforms suggests that *Watersipora* is likely to remain on these platforms into the future.

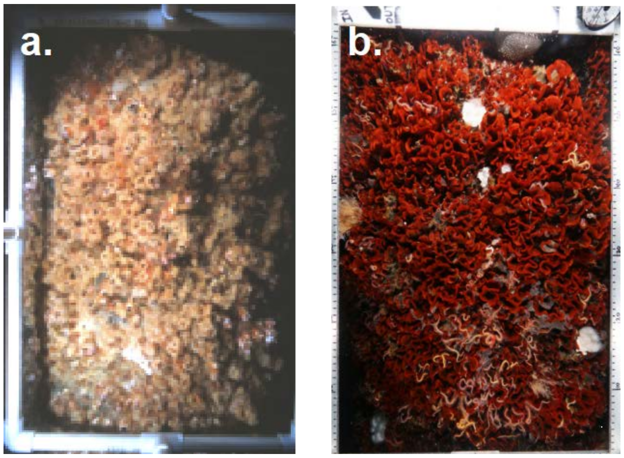

Figure 15. Photographs of the same sample plot on platform Gail (a) in 2001 with plot dominated by barnacles and (b) in 2013 with plot dominated by *Watersipora*.
Sample plot was located on a conductor pipe at 9 m depth and measured 41 x 62 cm internal diameter (0.25 m^2).

Second, the modeling predicts little to no potential connectivity between the four southeastern platforms, Grace, Gilda, Gail, and Gina, and the three northwestern platforms, Holly, Houchin, and Hogan. *Watersipora* was not detected on the three northwestern platforms during the 2001 or 2013 field surveys, despite the expansion in distribution of *Watersipora* among the southeastern platforms during this period. These results suggest that colonization of the three northwestern platforms by *Watersipora* is unlikely to occur via larval dispersal from the four southeastern platforms.

Third, the harbors showed little to no potential connectivity with any of the platforms with the exception of platform Gina. When interpreting the modeled potential connectivity from the harbors, it is important to consider a key assumption. Since the model has a 1-km horizontal grid, the small-scale hydrodynamics of the nearshore, driven by variations in bathymetry, shoreline topography, and other factors, are not included in the model. Thus the coastal flows used to model particle dispersal from harbors are higher and less variable than real nearshore flows. Consequently, the modeling estimates of dispersal from the harbors are likely overestimated. Thus for six of the platforms in the study, Grace, Gilda, Gail, Holly, Houchin, and Hogan, there is likely no potential connectivity with any harbors. Given the uncertainties of modeling the nearshore, the potential spread of *Watersipora* to platform Gina from the harbors may also be overestimated.

The limited potential connectivity of *Watersipora* between platforms in the southeast relative to those in the northwest and between platforms and harbors may have implications for the genetic structure of these populations that can be evaluated in future work. For example, genetic differentiation in coral species was evident between populations in the Flower Garden Banks reefs and colonies on offshore oil and gas platforms in the northern Gulf of Mexico (Atchison et al. 2008, Sammarco et al. 2012). Mackie et al. (2012) observed genetic differentiation in *Watersipora* along the California coastline, including differences between samples collected in two of our study harbors, Port Hueneme and Channel Islands. Because genetic markers are sensitive to exchange between populations (Hellberg et al. 2002), variation in the genetic structure of *Watersipora* between platforms and harbors could further support our conclusions regarding connectivity among habitats developed using the biophysical model.

4.4.2 Nearshore vs. offshore dispersal

Shanks (2009) compiled empirical data on the relationship between PLD and dispersal distance for 67 species and found that species with PLDs of less than one day had dispersal distances on the order of meters to 100s of meters. This relationship was also observed by Siegel et al. (2003) using genetic estimates of dispersal distance for 32 species. These observed dispersal distances are much less than the modeled dispersal distances from the four southeasterly platforms in our study, which range from 1.1-1.4 km at a PLD of 3 hours to 9.6-11.5 km at a PLD of 24 hours (Fig. 14). These modeled dispersal distances are supported by the 2001 and 2013 surveys, which observed the potential spread of *Watersipora* between platforms that are 5-10 km apart.

The hydrodynamic environment (e.g., flow velocity and direction, turbulence) has been identified as an important driver of larval dispersal (Gawarkiewicz et al. 2007, Cowen and Sponaugle 2009, Shanks 2009). Due to shallow water and variable bathymetry, nearshore flows are slower and more complex than offshore flows. Shanks (2009) hypothesized that species with short PLDs may only disperse a short distance in the nearshore simply because they are exposed to slow flows during their brief planktonic stage. Our results suggest that the enhanced dispersal of larvae with short PLDs released from offshore structures is driven, at least in part, by the high, sustained flows of the offshore hydrodynamic environment. Our modeling results show that *Watersipora* larvae could potentially travel up to 10 km to a potential settlement site within 24 hours. However, the probability of successful settlement is likely reduced with increased dispersal distance by high mortality rates in the plankton (Strathmann 1985, Calabrese and Fagan 2004) and by low post-settlement survival and growth due to delayed settlement Woollacott et al. 1989, Wendt 1998, Sams et al. 2015).

Shanks (2009) also hypothesized that organisms with PLDs of 12 hours or less may have short dispersal distances because they exhibit behavior that allows them to remain close to the sea floor, increasing their likelihood of encountering suitable habitat. This behavior is unlikely for *Watersipora* colonizing offshore platforms for two reasons. First, *Watersipora* was found in the top 18 m of the water column on the platforms during the 2001 and 2013 field surveys. This release depth is well above the seafloor as the four platforms where *Watersipora* was found are located in water depths ranging from 30 to 230 m. Second, typical of other bryozoan larvae, *Watersipora* initially show positive phototaxis on release (personal observation and Ryland 1960), which would result in larvae entering the water column. Unless these larvae encounter another part of the platform, this behavior increases the chance that larvae are potentially advected away from the platform by currents. Larval settlement would then depend on a chance encounter with another platform or being transported inshore to suitable habitat.

In conclusion, we hypothesize that the dispersal of *Watersipora* larvae and likely the larvae of other organisms with short PLDs, such as other bryozoans and ascidians (Strathmann 1985), is greater when released in the offshore above the seafloor than when released in the nearshore and that the enhanced dispersal is driven by the high sustained flows of the offshore hydrodynamic environment. Our results further suggest that offshore habitat in general, such as pinnacles, shallow seamounts, and wind farms in addition to oil and gas platforms, could facilitate wider dispersal by sessile invertebrates with short PLDs. Therefore if connectivity between offshore structures is to be minimized, the distance between structures and the hydrodynamic environment should be considered.

Supporting Information

Table 8. Unpublished data from settlement plates at platform Gilda.
Mean number of *Watersipora* colonies on 15 x 15 cm ceramic tile settlement plates deployed and retrieved every three months at platform Gilda from June 2001 through May 2002. Mean number of colonies 1 ±SE, n = 4 plates.

Date	No. *Watersipora* colonies
June - August 2001	28 ± 7
September - November 2001	3 ± 2
December 2001 - February 2002	0
March - May 2002	0

5 Anthropogenic Disturbance Facilitates a Non-Native Species on Offshore Oil Platforms

5.1 Introduction

Non-native species often thrive on artificial structures in the marine environment (Mineur et al. 2012). Offshore energy infrastructure, such as oil or natural gas platforms and renewable energy installations, introduce hard substrate into an offshore environment typically characterized by soft sediments, and consequently provide novel habitat for reef-associated species (Page et al. 2006; Sammarco et al. 2014, De Mesel et al. 2015). These artificial islands may serve as “stepping stones” of habitat that increase regional connectivity via planktonic larval dispersal, thereby facilitating species range expansions (Sheehy and Vik 2010, Adams et al. 2014, Simons et al. 2016). This increase in connectivity may be of concern to managers if offshore infrastructure harbours non-native taxa and are proximate to natural reefs, including Marine Protected Areas (Sheehy and Vik 2010, Adams et al. 2014, Simons et al. 2016), because non-native species can negatively impact community composition and ecosystem function (Levin et al. 2002, Sellheim et al. 2010, Needles and Wendt 2013). Because thousands of offshore energy structures exist worldwide and thousands more are planned (Parente et al. 2006, EWEA 2016), managers need information on the ecology of non-native species to predict and mitigate potential impacts of activities associated with offshore development, such as maintenance operations and decommissioning.

Routine maintenance operations for offshore structures include the manual removal (cleaning) of the dense biogenic layer of epibenthic invertebrates from the subtidal substrate to reduce hydrodynamic loading and enable visual inspection of the structure (Page et al. 2010, van der Stap 2016). These planned mass removals of space-holding invertebrates clear much larger areas than natural storm events and may enhance opportunities for non-native species to colonize offshore structures. Existing epifauna may reduce or inhibit non-native species establishment by consuming or damaging incoming larvae (Mileikovsky 1974, Cowden, Young and Chia 1984; Young and Gotelli 1984), pre-empting space (Osman and Whitlatch 1995 a and b, Levin et al. 2002), or reducing the growth, reproduction, and survival of recruits (Clark and Johnston 2009, Claar et al. 2011). Because some epifaunal invertebrates recruit in seasonal pulses (Stachowicz and Byrnes 2006), restricting the timing of cleaning operations to periods when undesirable species are not reproducing could provide a straightforward and cost-effective mitigation measure that reduces opportunities for non-native species establishment.

In addition to informing maintenance practices, knowledge of a non-native species’ ecology can contribute to decision-making during the decommissioning of offshore infrastructure. Decommissioning typically involves the removal of oil and gas facilities, which in turn eliminates the hard substrate used by many species during the operations phase. However, some jurisdictions allow decommissioning alternatives that preserve deeper parts of the structure to function as an artificial reef (Schroeder and Love 2004, Smyth et al. 2015). Information on the effects of depth and disturbance on the colonization success of non-native species would be useful to managers seeking to predict the ecological consequences of various decommissioning alternatives.

A globally distributed non-native bryozoan species, *Watersipora subatra* (hereafter, *Watersipora*; formerly identified as *W. subtorquata* in Southern California; Vieira et al. 2014) has colonized and spread among several offshore oil and gas platforms in the Southern California Bight (Page et al. 2006, Simons et al. 2016). The genus is widely distributed in harbours of California (Cohen et al. 2005, CDFG 2008). *Watersipora*’s global distribution includes Australia, Brazil, Japan and New

Zealand, and it was recently reported in Europe (Vieira et al. 2014, Bishop et al. 2015). Like other bryozoans, *Watersipora* has a short (< 24 h) nonfeeding larval stage (Wilsely 1958, Ng and Keough 2003) that should limit its dispersal potential. *Watersipora* is a superior competitor for primary space and the three-dimensional structure of its colonies provides microhabitats for other species (Floerl et al. 2004, Sellheim et al. 2010). These characteristics of *Watersipora* could lead to changes in community structure, including the facilitation of other non-native species (Floerl et al. 2004, Stachowicz and Byrnes 2006). Once established, this bryozoan can persist and spread to other artificial and natural habitats (Sorte and Stachowicz 2011, Needles and Wendt 2013, Simons et al. 2016).

We investigated the influence of disturbance in enhancing *Watersipora* colonization on offshore oil platforms in the Southern California Bight. Our goal was to use ecological information to develop potential mitigation measures that may prevent or control the spread of *Watersipora*, and potentially other non-native species, on these and other offshore structures during maintenance and decommissioning activities. We addressed this goal by 1) evaluating the hypothesis that disturbance facilitates the establishment of *Watersipora*, 2) exploring the effect of depth, larval supply and established native epifauna on *Watersipora*'s recruitment and growth, 3) assessing the response of *Watersipora* to a large-scale maintenance cleaning, and 4) outlining a strategy to limit the spread of *Watersipora*, and potentially other non-native species, on offshore structures.

5.2 Materials and Methods

5.2.1 Study sites

We conducted this study on offshore oil and gas production platforms “B” and “Gina” in the eastern Santa Barbara Channel, California (Fig. 16). Platform B (34º19’ N, 119º37’ W), installed in 1968, is located ~9 km offshore in a water depth ~58 m and platform Gina (34º07’ N, 119º16’ W), installed in 1981, is ~6 km offshore in a depth of ~30 m. The two platforms differ in size (platform footprint at the seafloor: B: 48 x 40 m, Gina: 28 x 20 m), but share a general sub-surface structure of vertical, oblique, and horizontal cylindrical steel support members that include the legs, and vertical conductor pipes enclosing additional pipes through which oil and gas flows.

The support members and conductor pipes of offshore platforms in the Santa Barbara Channel are typically covered intertidally and subtidally by a community of sessile and semi-mobile suspension feeding epifaunal invertebrates, including mussels (*Mytilus californianus, M. galloprovincialis*), barnacles (e.g. *Megabalanus californicus*), rock scallops (*Crassodoma gigantea*), and anemones (*Corynactis californica, Metridium senile*) (Page et al. 2010). Macroalgae are relatively sparse and restricted to shallow depths on the periphery of the structure. Herbivorous grazers, such as urchins and snails, are also rare.

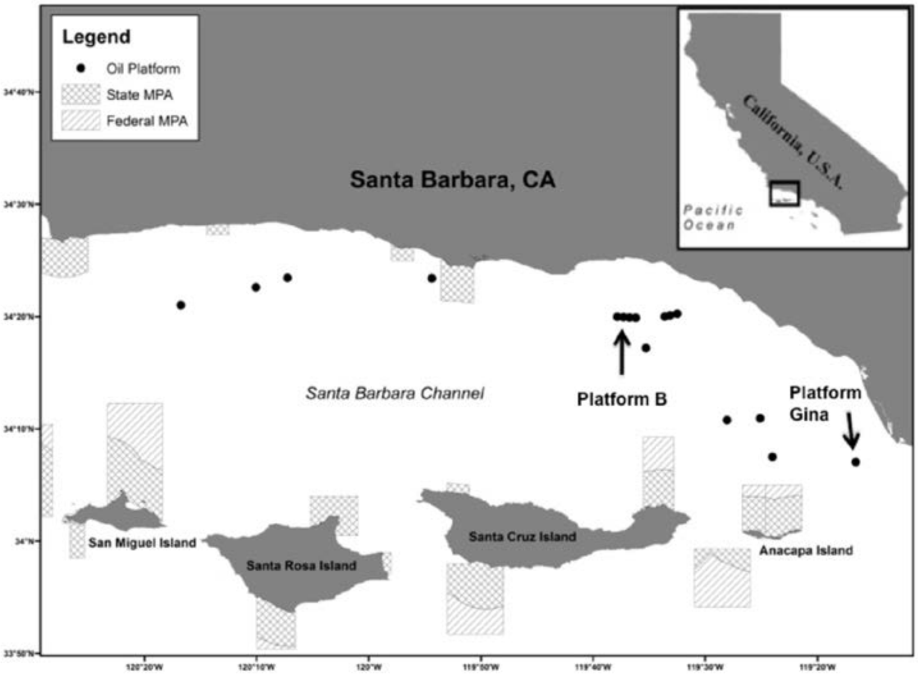

Figure 16. Map showing location of the study platforms in the Santa Barbara Channel.

5.2.2 Disturbance and depth effects on *Watersipora* abundance

To experimentally examine the effect of disturbance and water depth on the establishment of *Watersipora*, we removed the epibenthic community from 0.41 x 0.62 m (0.25 m^2) rectangular experimental plots at three depths (12, 18, and 24 m) on the north sides of the conductor pipes that run east – west across Platform B in August 2014. Divers manually removed epifaunal organisms to expose the bare metal surface in each treatment plot using hammers and chisels. At each depth, four disturbed plots alternated with four undisturbed control plots on adjacent conductor pipes, resulting in 12 disturbed and 12 control plots total. A maintenance cleaning prior to the onset of our experiment removed the epifaunal community from the structure to a depth of 9 m, which prevented a comparison of disturbed to control plots at shallower depths.

After removing epifauna in the disturbed plots, all plots were photographed using a Canon EOS 6D digital camera with a 14 mm wide-angle lens and two strobes mounted on a 0.41 x 0.62 m quadrat frame (Page et al. 2008). The plots were re-photographed approximately every two months from August 2014 until November 2015 to evaluate temporal patterns in *Watersipora* abundance following disturbance. From the photographs, we identified and estimated the percent cover of sessile and semi-mobile epifauna (e.g. anemones, barnacles, bivalves) occupying the visible layer in each plot using the BisQue online image analysis system (http://bioimage.ucsb.edu/, Rahimi et al. 2014). A grid of 100 uniformly spaced points was superimposed onto each digital image and contacts under each point were scored manually, automatically recorded in XML files, and exported for analysis. We also recorded cover of non-living substrata (e.g., bare steel), when present.

We evaluated the effects of disturbance, depth, and time on *Watersipora* abundance (as cover) using Linear Mixed-Effects (LME) models that handle unequal variances and temporally correlated data. Treatment (disturbed vs. control), depth, and time were treated as fixed factors, individual plots treated as subjects, and time as a repeated measure. On finding a significant interaction between treatment and time ($p < 0.001$, Supporting Information, Table 9), the effects of treatment and depth at each time were evaluated (Table 10). Percent cover data were arcsine-transformed ($x' = \text{arcsine}(\sqrt{x})$) prior to analysis.

5.2.3 Spatial and temporal patterns in the abundance of *Watersipora* larvae

We measured monthly recruitment of *Watersipora* onto settlement plates to assess temporal and depth-related variability in abundance of *Watersipora* larvae. Settlement plates consisting of a 225 cm^2 unglazed ceramic tile attached to a 16 x 30 cm PVC frame were suspended on ropes in between the conductor pipes of disturbed and control plots on Platform B (n = 4 plates per depth). From August 2014 through November 2015, settlement plates were removed approximately monthly (25 to 37 days) and replaced with plates that had been pressure-washed and air-dried to remove epifauna. Retrieved plates were returned to the laboratory where *Watersipora* colonies and other attached organisms were identified and counted. Counts of *Watersipora* on the plates were standardized to number of recruits per 30 days to adjust for variations among deployment periods. The effects of depth and time on the density of *Watersipora* recruits were evaluated using a generalized linear model with a Poisson error distribution (O'Hara and Kotze 2010), with depth and time as fixed factors. On finding a significant interaction between depth and time ($p < 0.001$, Table 11), the effects of depth at each time, and time for each depth, were evaluated (Table 12).

5.2.4 Disturbance and depth effects on *Watersipora* colony dynamics

To investigate the effect of the existing epifaunal community on *Watersipora* recruitment and growth, we quantified the number and sizes of *Watersipora* colonies in the images of the disturbed and control plots over time. Colony size was quantified by manually tracing the perimeter of each colony (defined as a continuous area of *Watersipora)* using the area measurement tool in Adobe Acrobat X. Colony area was calculated based on the known area of the quadrat frame in the photos.

To evaluate the effect of disturbance and depth on *Watersipora* recruitment and colony size, we grouped colonies into size classes (small: < 5 mm^2, medium: 5 – 1000 mm^2, large: > 1000 mm^2) and compared densities of colonies separately for each size class between treatments and among depths initially using LME models that incorporated repeated measures on both untransformed and transformed (Box Cox) data. On finding a significant interaction between treatment and time ($p < 0.05$, Table 13), the effects of treatment and depth for each time were evaluated using generalized linear models assuming a Poisson distribution (Table 14). The density of small colonies in disturbed and control plots (a proxy for early recruitment success) was compared to recruitment data from the settlement plates (a proxy for larval availability) using linear regression. To determine if the relationship differed between the two observed reproductive seasons, the data were analysed separately for the first (August 2014 – March 2015) and second (May 2015 – November 2015) halves of the experiment.

5.2.5 Maintenance cleaning and *Watersipora* abundance

To explore the effect of large-scale anthropogenic disturbance on the establishment of *Watersipora*, we sampled conductor pipes and legs of Platform Gina before (September 2013) and after (August 2014, January and July 2015) a cleaning event. In Spring 2014, epifauna attached to the conductor pipes, but not the legs, were removed by platform operators to a depth of ~15 m. The high-pressure discharge "blasters" used in these cleaning operations remove hard and soft epifauna, leaving only the basal plates of barnacles and cemented portions of encrusting bivalves. To evaluate changes in abundance and distribution of *Watersipora* and other space-holding invertebrates over time, we measured invertebrate cover in 0.25 m^2 plots at two depths on the uncleaned legs and the cleaned conductor pipes using the methods described above.

To evaluate possible differences in epifauna between legs and conductor pipes, assemblage composition and cover of *Watersipora* prior to cleaning were compared between these locations with permutational analysis of variance (PERMANOVA) (Anderson, Gorley and Clarke 2008) using either the Bray-Curtis resemblance matrix (multivariate) or Euclidean distance (*Watersipora* alone) in which location and depth were treated as fixed factors. The effects of cleaning disturbance and depth over time on *Watersipora* cover were evaluated using LME models as described above on data collected following the maintenance cleaning (August 2014, January and July 2015). On finding a significant interaction between treatment and time ($p < 0.001$, Table 15), the effects of time for each treatment and treatment at each time were evaluated (Table 16). All analyses were conducted using SPSS 24 (IBM), and PERMANOVA+ for PRIMER (PRIMER-E Ltd).

5.3 Results

5.3.1 Disturbance and depth effects on *Watersipora* abundance

The common invertebrate species in the existing epifaunal community of Platform B occupied over 95% of available space, and included the native anemones *Metridium senile* and *Corynactis californica* (30 – 50% cover), followed by tubiculous amphipods (10 – 20%), hydroids (10 – 20%), barnacles (5 – 10%) and sponges (~9%). Various other native taxa were found at low abundance in the existing community. *Watersipora* was present, but at low cover (< 5%) across all depths (Fig. 17).

Watersipora and native taxa colonized the disturbed plots following the removal of existing epifauna, reducing the availability of bare space at all depths from 100% to < 20% by 2 months and to < 5% after 4 months (Fig. 18A-C). In the control plots, epifaunal invertebrates occupied 100% of the primary space for the duration of the experiment (Fig. 18A-C). *Watersipora* cover increased significantly over time in the disturbed (time, $F_{7,67.538} = 10.378$, $p < 0.001$), but not control (time, $F_{7, 69.332} = 1.724$, $p = 0.118$) plots, and was significantly higher in the disturbed compared to the control plots in all weeks except week 44 ($p < 0.05$, Table 10). *Watersipora* cover also varied consistently with depth beginning at week 35, with no interaction between treatment and depth for any time period ($p > 0.09$, Table 10). At 12 and 18 m, mean cover of *Watersipora* in the disturbed plots ranged from 6 – 20% and 7 – 16%, respectively, compared with 2 – 9% and <1 – 6% in the control plots (Fig. 18D-F). At 24 m, mean cover of *Watersipora* remained low during the experiment in both the disturbed (< 5%) and control plots (< 1%, Fig. 18D-F).

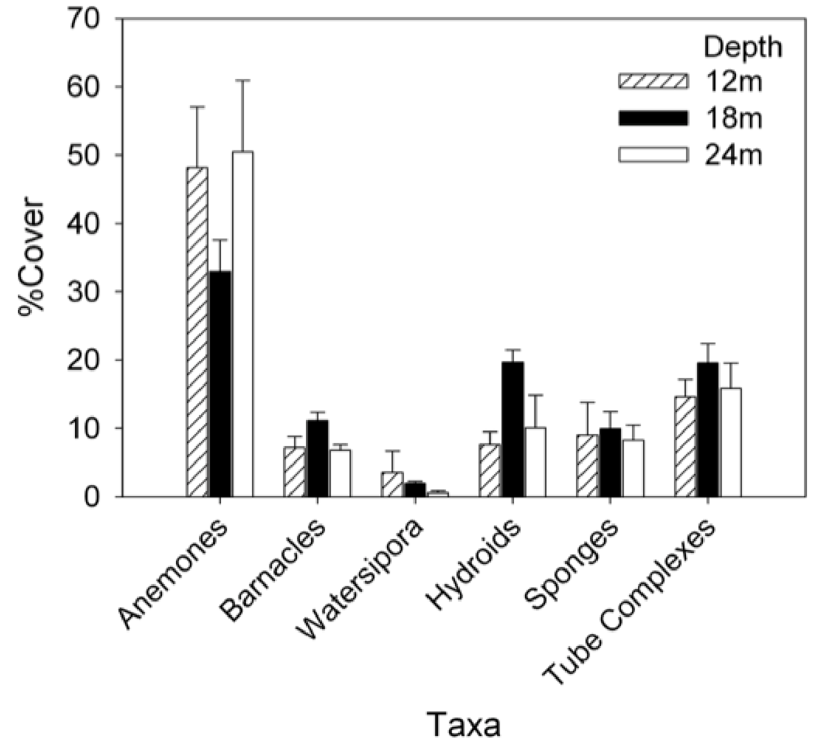

Figure 17. Initial invertebrate community composition on the conductor pipes of Platform B in August 2014 at depths of 12 m, 18 m, and 24 m.
Mean cover ±1SE, n = 4 plots/depth.

5.3.2 Spatial and temporal patterns in abundance of *Watersipora* larvae

Watersipora recruitment onto ceramic tiles varied with time at each depth ($p \leq 0.005$, Table 12A). In both 2014 and 2015, recruitment occurred primarily in late summer – fall, with negligible recruitment during the rest of the year (Fig. 18G-I, 23). The effect of depth on recruitment was only significant in August and September 2015, and higher at 12 and 18 m compared with 24 m depth ($p < 0.05$, Wilcoxon pairwise test, Fig. 18G-I).

5.3.3 Disturbance and depth effects on *Watersipora* colony dynamics

Watersipora recruitment into the experimental plots at Platform B, as estimated by the density of small (< 5 mm^2) colonies, was higher in disturbed compared to control plots up to 19 weeks ($p < 0.001$, Table 14, Fig. 19A-C). In addition to higher densities of recruits, the disturbed plots had a consistently higher density of medium colonies (5 – 1000mm^2) from 9 weeks to the end of the experiment ($p < 0.001$, Table 14AB, Fig. 20D-I). Finally, the densities of large *Watersipora* colonies (> 1000mm^2) were generally higher in the disturbed compared with the control plots from 27 weeks to the end of the experiment ($p \leq 0.03$, Table 14AB, Fig 19D-I), with a significant depth effect from 9 weeks on ($p < 0.05$, Table 14A, Fig. 20D-I).

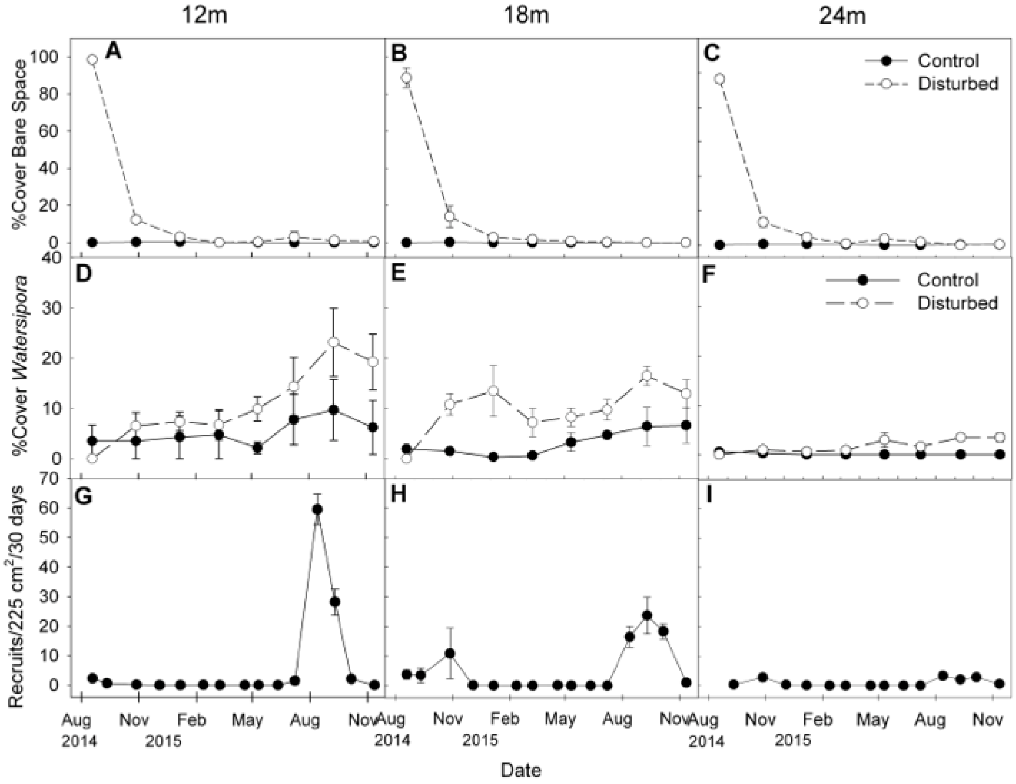

Figure 18. A-C: Availability of bare space over time at depths of 12 m (A), 18 m (B), and 24 m (C) in the disturbed and control plots on Platform B.
Mean cover ±1SE, n = 4 plots/depth. D-F: *Watersipora* cover over time in the disturbed and control plots at 12 m (D) 18 m (E), and 24 m (F) on Platform B. Mean cover ±1SE, n = 4 plots/depth. G-I: *Watersipora* recruitment rate on ceramic plates at 12 m (G), 18 m (H), and 24 m (I) at Platform B. Mean values ±1SE, n = 4 plates/depth.

During the first half of the experiment (August 2014 – March 2015), the density of small colonies in the disturbed plots was significantly correlated with larval supply, measured using settlement plates, across all depths, ($p < 0.001$, $R^2 = 0.31$; Fig. 20A). However, there was no relationship between the density of small colonies in the disturbed plots and larval supply in the second half of the experiment (May 2015 – November 2015) ($p = 0.8$, Fig. 20B). There was no relationship between the density of small colonies and larval supply in the control plots in either the first or second reproductive season ($p > 0.05$; Fig. 20A and B).

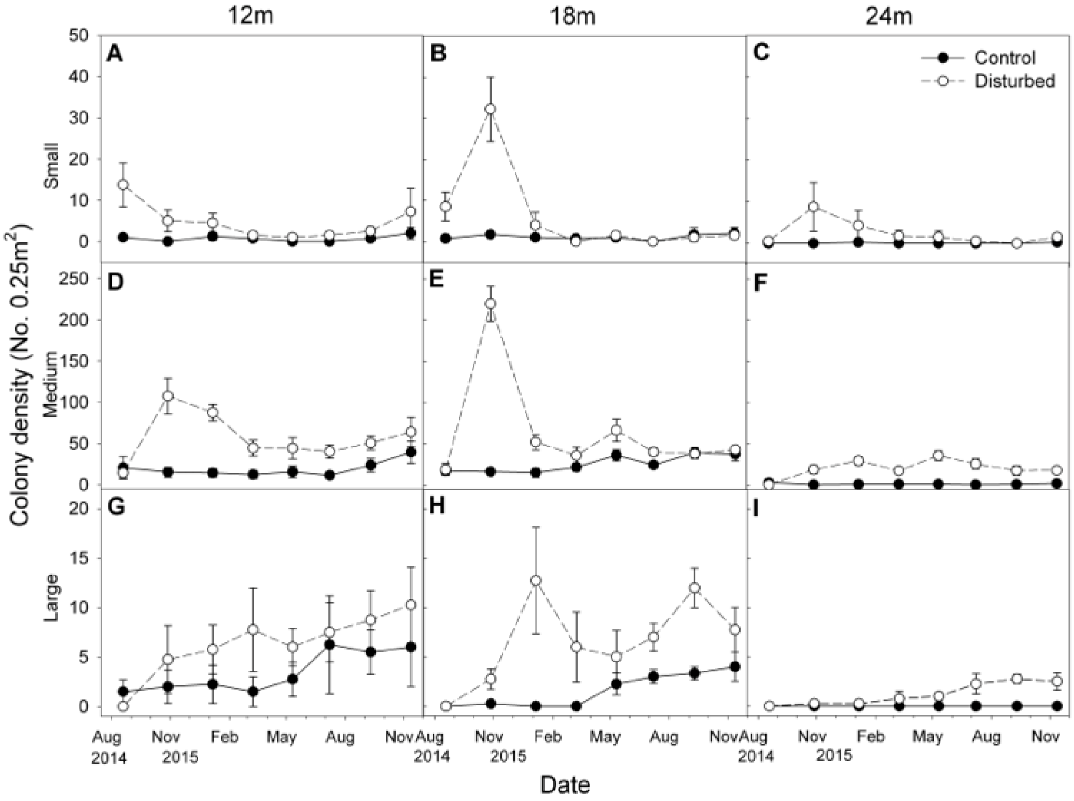

Figure 19. Density of small (A-C), medium (D-F), and large (G-I) *Watersipora* colonies in the disturbed and control plots at 12 m (A, D, G), 18 m (B, E, H), and 24 m (C, F, I) on Platform B. Mean values ±1SE, n = 4 plots/depth.

5.3.4 Maintenance cleaning and *Watersipora* abundance

Composition of the existing epifaunal community at Platform Gina did not differ significantly between locations (conductor pipes vs. legs, $p = 0.30$, $pseudo\text{-}F_{1,12} = 1.256$) or depths (6 vs. 12 m, $p = 0.38$, $pseudo\text{-}F_{1,12} = 1.011$) prior to maintenance cleaning (Two-way PERMANOVA, Fig. 21A and B). *Watersipora* cover also did not differ significantly between locations ($p = 0.39$, $pseudo\text{-}F_{1,12} = 0.853$) or depths ($p = 0.26$. $pseudo\text{-}F_{1,12} = 1.362$) prior to the maintenance cleaning (Two-way PERMANOVA). Native anemones (mainly *Corynactis californica* and *Anthopleura sp.*) dominated the community (50 – 80% cover), followed by *Watersipora* (5 – 20% cover), barnacles, sponges, tubiculous amphipods (5 – 10% cover each), and hydroids (1 – 5% cover) (Fig. 21A and B).

Watersipora cover on the conductor pipes and legs was < 20% in August 2014 (Fig. 22). However, between January and July 2015, *Watersipora* cover increased dramatically, and was significantly higher on the cleaned conductor pipes, reaching mean cover of 44 – 60 %, compared with < 10% cover on the undisturbed legs after 18 months ($p < 0.05$, Table 16, Fig. 22A and B). W*atersipora* cover did not differ significantly between depths of 9 and 12 m (depth, $p > 0.05$, Table 15, 16).

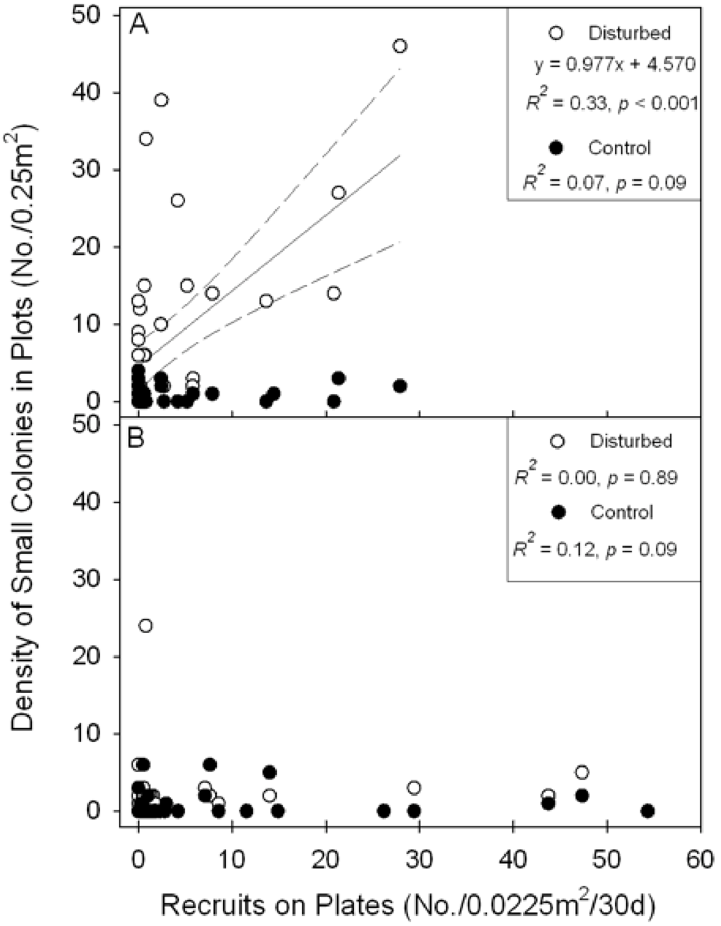

Figure 20. Relationship between the density of small colonies in the disturbed and control plots versus larval supply, estimated using settlement plates deployed monthly, during the first (August 2014 – March 2015, A) and second (May 2015 – November 2015, B) halves of the experiment on Platform B.

95% confidence intervals around the regression line also shown (dashed lines).

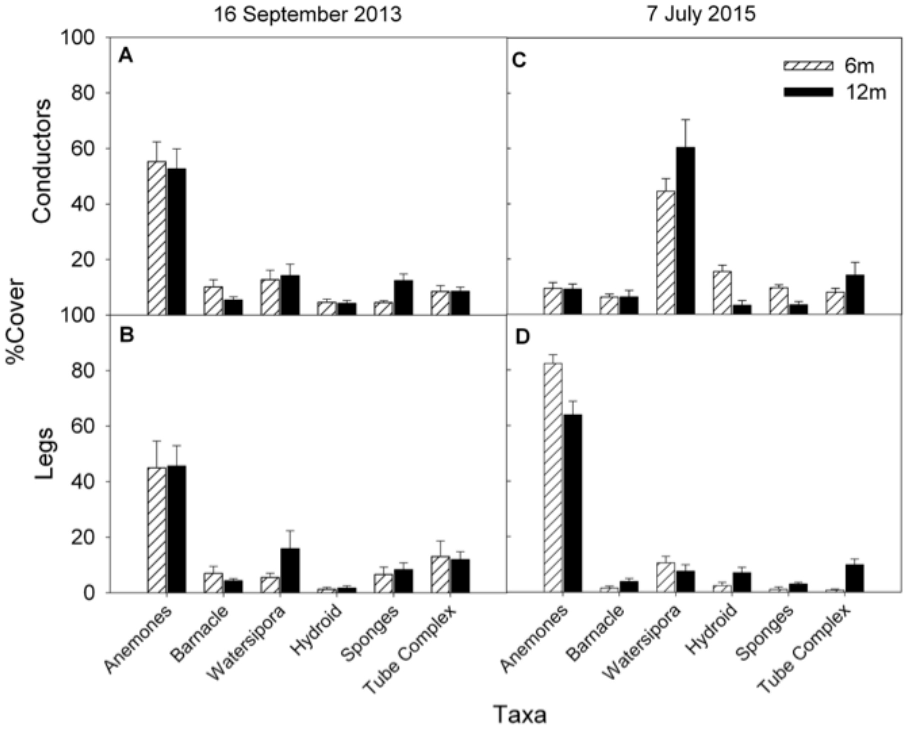

Figure 21. Invertebrate community composition on the conductor pipes (A and C) and legs (B and D) of Platform Gina before (September 2013, A and B) and after (July 2015, C and D) the maintenance "cleaning" in Spring 2014 at 6 m and 12 m.
Mean cover ±1SE, n = conductors or legs/depth.

5.4 Discussion

5.4.1 *Watersipora* establishment and patterns of abundance

This study is the first to experimentally investigate factors that facilitate the extensive colonization of offshore structures by non-native species; previous studies (Bulleri and Airoldi 2005, Clark and Johnston 2009, Bracewell et al. 2013) have been confined to nearshore habitats. Our results provide ecological information that is directly applicable to developing maintenance recommendations to manage the spread of these species among offshore structures and between these structures and natural reefs. Anthropogenic disturbance strongly facilitated colonization of offshore platforms by non-native *Watersipora,* and this positive response to disturbance persisted up to 15 months following removal of native epifauna. *Watersipora* was abundant at shallower depths (> 40% and > 60% cover at 6 m and 12 m at Platform Gina, and > 20% cover at 12 m at Platform B), although this taxon was less successful (< 4% cover) in our deepest plots at 24 m at Platform B. The broad depth distribution of *Watersipora* on offshore platforms suggests that this bryozoan has the potential to occupy a greater range of habitat on the open coast than previously expected based on studies restricted to shallower depths in harbours and coastal embayments (Sorte and Stachowicz 2011, Needles and Wendt 2013).

Watersipora's ability to opportunistically occupy and maintain space may have consequences for community composition and ecosystem function on offshore structures. Disturbance shifted the

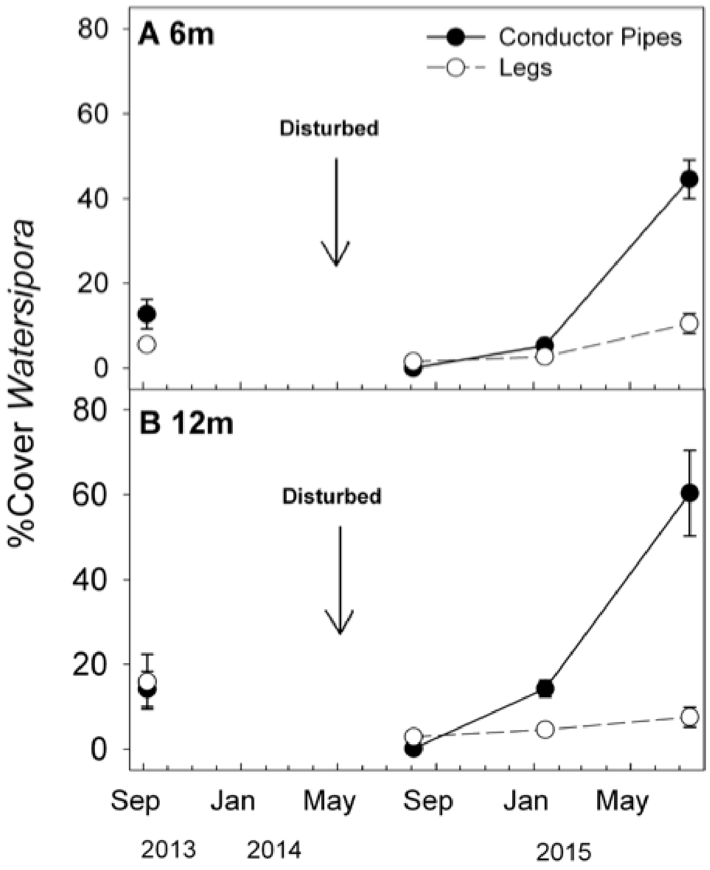

Figure 22. *Watersipora* cover on the conductor pipes and legs at Platform Gina at 6 m (A) and 12 m (B) before and after maintenance cleaning by the operators.
Only the conductor pipes were cleaned (to a depth > 12 m) in Spring 2014. Mean cover ±1SE, n = 4 conductors or legs/depth.

dominant species at the shallower depths of both Platforms B and Gina from native anemones to non-native *Watersipora*. The success and persistence of *Watersipora* is likely attributable to defence mechanisms widely documented in bryozoans (Anderson and Haygood 2007; Floerl, Pool and Inglis 2004) that inhibit overgrowth or recruitment by native taxa. In addition to displacing other sessile species, *Watersipora*'s three-dimensional structure adds complex microhabitat that differs from that created by native species, and can favour different assemblages of mobile taxa (Stachowicz and Byrnes 2006, Sellheim, Stachowicz and Coates 2010). Given the dramatic increase of *Watersipora* in our region over the past 1.5 decades (Simons et al. 2016), this non-native species is likely to have profound and lasting effects on the communities inhabiting offshore platforms.

5.4.2 Controls on *Watersipora* abundance

Settlement space is widely recognized as the limiting resource in benthic communities (Stachowicz et al. 1999, Stachowicz et al. 2002). Because the availability of limiting resources can determine a community's vulnerability to invasion (Davis et al. 2000, Olyarnik et al. 2008), disturbance that increases primary space availability should enhance invasion success. In our experiment at Platform B, both native invertebrates and *Watersipora* rapidly colonized primary substrate in the disturbed plots, and bare space was reduced by almost 90% within two months after disturbance. This developing post-disturbance community included a greater proportion of *Watersipora* compared to the established community in the control plots, confirming the importance of primary substrate availability to *Watersipora*'s establishment success.

Watersipora recruitment was greatly enhanced in the disturbed plots when bare space was available immediately following removal of the existing community. The settlement plate data revealed that *Watersipora* recruitment, and by proxy, larval availability, was highest in late summer – fall of both 2014 and 2015. However, recruitment to the plots, estimated by the density of small colonies, occurred mainly during the first recruitment season in 2014, when primary space was available. The significant relationship between larval availability and recruitment during this period was consistent with Clark and Johnston's (2009) findings of a linear dose-response curve for *Watersipora* recruiting to disturbed areas. However, during *Watersipora*'s second recruitment season in 2015, few or no small colonies were detected in the disturbed plots, which no longer had primary space available for colonization. The lack of a significant relationship between larval availability and the density of small colonies in the disturbed plots in the second year suggests that larval availability is an important driver of *Watersipora* colony density when bare space is available, but not when there is a space-occupying epifaunal assemblage.

The lack of a relationship between recruitment to the settlement plates and the density of small colonies in the undisturbed control plots in both the 2014 and 2015 recruitment periods suggests that established benthic invertebrates can reduce the recruitment success of incoming non-native propagules. Established epifauna can negatively affect incoming planktonic larvae by simply pre-empting space (Osman and Whitlatch 1995a and b, Levin et al. 2002) or consuming larvae (Mileikovsky 1974, Cowden et al. 1984, Young and Gotelli 1984). Unlike shelled organisms (e.g. barnacles and mussels), soft-bodied anemones, which accounted for a large fraction (50 – 80% cover) of the undisturbed community at both study platforms, are completely unsuitable for secondary colonization and can therefore inhibit *Watersipora* recruitment. These inhibitory effects were also evident after approximately one year of community development in the experimentally disturbed plots, when there was no longer a correlation between larval availability and recruitment. The lack of a relationship between larval availability and recruitment to both the disturbed and control plots one year after disturbance suggests that the developing community inhibited recruitment in a manner that was similar to an established community.

In addition to influencing *Watersipora*'s recruitment to primary space, the removal of potential competitors and predators through disturbance may have affected colony size. *Watersipora* colonies occupying primary space in the disturbed plots attained larger sizes than colonies occupying secondary space in the control plots. Similarly, studies in bays and harbours have found that *Watersipora* recruits settling to secondary space experience growth reductions (Clark and Johnston 2009) as high as 30% compared to recruits on primary space (Claar et al. 2011). The range of depths in our experiment revealed that this effect was strongest at shallow depths. The increased growth rate at 12 m, evidenced by the higher density of medium and large colonies, suggests that the environment is more favourable to this species at shallower depths, potentially due to warmer temperatures (Sorte and Stachowicz 2011) or greater food availability (O'Dea and Okamura 1999).

The increased growth of *Watersipora* in the disturbed plots agrees with Levine et al.'s (2004) meta-analysis showing that established native communities have a significant role in constraining the performance of non-native species. Established native species can reduce invader success through competition for food (Okamura 1984, Svensson and Marshall 2005) or other resources (D'Antonio et al. 2001). This is especially true in benthic communities, where competition for space is considered the dominant biotic interaction (Stachowicz et al. 2002). Removing competitors through disturbance interrupts these negative interactions and enables increased growth and survival of non-native species, which could lead to the dominance of an aggressive or opportunistic invader.

5.4.3 Management applications

Our results suggest that the establishment of *Watersipora* on offshore oil platforms can be managed by adjusting the timing of maintenance cleaning to occur shortly after this bryozoan's peak reproductive period in late summer – fall. This timing could remove newly settled recruits and allow sufficient time for native species to colonize available bare space prior to the bryozoan's next reproductive period. Even relatively frequent cleaning activities (every 2 – 3 years) could be scheduled to allow adequate time for native species to colonize the bare space before the recruitment period of *Watersipora*. This practice could be employed across other maritime industries, such as offshore renewable energy and mariculture, and might be extended to other non-native species with comparable life histories. In this regard, like other marine ecosystems, disturbance and propagule supply interactively influence invasion success (Britton-Simons and Abbott 2008, Clark and Johnston 2009, Airoldi and Bulleri 2011), so the timing of disturbance events relative to recruitment periods can have a profound effect on the abundance of non-native species (Stachowicz et al. 2002). However, these decisions should be made on a case-by-case basis to account for differences in site-specific characteristics, such as species assemblages or physical factors.

Our results may also inform decision-making regarding the decommissioning of offshore oil and gas platforms. Some stakeholders prefer decommissioning alternatives that maintain deeper parts (> 26 m) of the platform structure to function as an artificial reef (Schroeder and Love 2004, Smyth et al. 2015). In California, such "rigs-to-reefs" alternatives can be considered if they comply with the National Fishing Enhancement Act (1984) and the California Marine Resources Legacy Act (2010). In the case of platforms with established *Watersipora* populations, the low abundance of this species at 24 m suggests that if a reefing option is selected, removing the shallow portions of the platform may reduce the ability of this non-native species to persist locally. However, more information is needed on the dispersal potential of *Watersipora* at deeper depths to understand the consequences of this decommissioning alternative.

The global distribution of *Watersipora* and likely proliferation of marine artificial structures increases the range of potential applications of our study, and underscores the need for similar studies to inform management practices. Artificial structures can act as "reproductive hotspots" (Ling et al. 2002) that deliver non-native propagules to nearby natural reefs (Sammarco et al. 2012). Consequently, the ecosystem impacts of non-native species on artificial structures could extend beyond the immediate habitat. Artificial structures potentially enable greater dispersal of non-native larvae by providing a network of hard substrate "stepping stones" in regions of unsuitable soft-bottom habitat (Sammarco et al. 2004, Adams et al. 2014, Simons et al. 2016). This effect could be greater in high-flow offshore environments, which may further increase habitat connectivity (Simons et al. 2016). Targeted management of artificial marine structures that incorporates ecological knowledge into the siting, deployment date, and timing of maintenance practices can potentially help managers mitigate the impacts of non-native species at regional scales.

Supporting Information

Table 9. Results of the linear mixed effects model evaluating the effects of treatment (disturbed vs. control), depth (12, 18, 24 m), and time (week) on the percent cover of *Watersipora* in the disturbance experiment at Platform B.

Significant treatment, depth, and interaction effects ($p \leq 0.05$) highlighted in bold. An expanded analysis evaluating the effect of treatment and depth for each time is provided in Table 10.

Source	*df*	*F*	*p*
Intercept	1, 25.766	107.711	< 0.001
Treatment	1, 25.766	16.249	**< 0.001**
Depth	2, 26.086	9.113	**0.001**
Time	7, 102.058	7.950	**< 0.001**
Treatment * Depth	2, 26.086	0.377	0.690
Treatment * Time	7, 102.058	7.907	**< 0.001**
Depth * Time	13, 105.521	1.495	0.131
Treatment * Depth * Time	13, 105.521	1.301	0.224

Table 10. Results of linear mixed effects models evaluating the effect of treatment (disturbed vs. control) and depth (9, 12, 18 m) for each time period on the cover of *Watersipora* in the disturbance experiment at Platform B.
Significant treatment, depth, and interaction effects ($p \le 0.05$) highlighted in bold.

		0 weeks		9 weeks		19 weeks		27 weeks	
Source	*df*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Intercept	1, 18	10.931	**0.004**	36.251	**<0.001**	29.887	**<0.001**	20.014	**<0.001**
Treatment	1, 18	10.931	**0.004**	8.374	**0.01**	13.259	**0.002**	5.926	**0.026**
Depth	2, 18	0.699	0.51	4.696	**0.023**	4.787	**0.022**	2.211	0.139
Treatment x Depth	2, 18	0.699	0.51	1.481	0.254	2.554	0.106	0.488	0.621
		35 weeks		44 weeks		53 weeks		62 weeks	
Intercept	1, 18	73.367	**<0.001**	62.564	**<0.001**	73.367	**<0.001**	71.281	**<0.001**
Treatment	1, 18	17.129	**0.001**	3.982	0.061	17.129	**0.001**	13.348	**0.002**
Depth	2, 18	4.802	**0.021**	8.032	**0.003**	4.802	**0.021**	6.295	**0.008**
Treatment x Depth	2, 18	0.097	0.908	0.034	0.967	0.097	0.908	0.329	0.724

Table 11. Results of generalized linear regression model (GLM) with underlying Poisson distribution evaluating the effects of depth (12, 18, 24 m) and time (days) on the density of *Watersipora* recruits on settlement plates.

Effects evaluated on untransformed data. Significant depth, time and interaction effects ($p \leq 0.05$) highlighted in bold. An expanded analysis evaluating the effect of treatment for each time and time for each treatment is provided in Table 12ab.

Source	*df*	*Wald ChiSquare*	*p*
Intercept	1	205.011	**<0.001**
Depth	1	61.214	**<0.001**
Time (days)	1	210.173	**<0.001**
Depth * Time (days)	1	28.671	**<0.001**

Table 12a. Results of generalized linear regression models with underlying Poisson distribution evaluating the effects of time period at each depth (12, 18, 24 m) on the density of *Watersipora* recruits on settlement plates.
Significant effect of time period on the density of recruits ($p \leq 0.05$) by depth highlighted in bold.

		Recruits	
Source	*df*	*Wald ChiSquare*	*p*
12 m			
Intercept	1	15.745	**<0.001**
Time(days)	1	250.525	**<0.001**
18m			
Intercept	1	6.286	**0.012**
Time(days)	1	92.193	**<0.001**
24m			
Intercept	1	7.205	**0.007**
Time(days)	1	7.907	**0.005**

Table 12b. Results of generalized linear regression models with underlying Poisson distribution evaluating the effects of depth (12, 18, 24 m) at each time period on the density of *Watersipora* recruits on settlement plates.
Significant depth effects (*p* ≤ 0.05) highlighted in bold.

		Recruits	
Source	*df*	*Wald ChiSquare*	*p*
12 August 2014			
Intercept	1	0.011	0.915
Depth	1	1.322	0.250
11 September 2014			
Intercept	1	0.547	0.460
Depth	1	0.083	0.773
28 October 2014			
Intercept	1	1.287	0.256
Depth	1	2.971	0.085
4 December 2014			
Intercept	1	1.552	0.213
Depth	1	0.983	0.321
6 January 2015			
Intercept	1	0.008	0.928
Depth	1	0.007	0.932
12 February 2015			
Intercept	1	0.004	0.944
Depth	1	0.007	0.935

Source (con’t)	*df*	*Wald ChiSquare*	*p*
10 March 2015			
Intercept	1	.	**.**
Depth	1	0	1
16 April 2015			
Intercept	1	4.674	0.031
Depth	1	0	1
11 May 2015			
Intercept	1	.	**.**
Depth	1	0	1
11 June 2015			
Intercept	1	0.016	0.900
Depth	1	00.015	0.902
13 August 2015			
Intercept	1	811.790	**< 0.001**
Depth	1	180.673	**< 0.001**
10 September 2015			
Intercept	1	412.074	**< 0.001**
Depth	1	79.107	**< 0.001**
6 October 2015			
Intercept	1	23.106	**< 0.001**
Depth	1	0.134	0.714

Source (con’t)	*df*	*Wald ChiSquare*	*p*
12 November 2015			
Intercept	1	1.933	0.164
Depth	1	1.297	0.255

Table 13. Results of linear mixed effects models evaluating the effects of treatment (disturbed vs. control), depth (12, 18, 24 m) and time (week) on the density of *Watersipora* colonies in the disturbance experiment at Platform B.
Effects evaluated on untransformed and transformed (Box Cox transformation) data separately for small, medium, and large colonies. Lambda value used, and skew and kutrosis values before and after transformation are also provided. Significant treatment, depth, and interaction effects (*p* ≤ 0.05) highlighted in bold.

	Small colonies (untransformed, skew=4.3, kur=21.4)			Small colonies (Box Cox λ=0.25, skew=0.7, kur=-0.8)		
Source	*df*	*F*	*p*	*df*	F	*p*
Intercept	1, 42.306	52.317	**<0.001**	1, 40.851	152.283	**<0.001**
Treatment	1, 42.306	28.715	**<0.001**	1, 40.851	28.464	**<0.001**
Depth	2, 42.296	4.151	**0.023**	2, 40.844	6.587	**0.003**
Time	7, 84.379	7.651	**<0.001**	7, 88.072	4.419	**<0.001**
Treatment * Depth	2, 42.296	1.242	0.299	2, 40.844	1.845	0.171
Treatment * Time	7, 84.379	7.482	**<0.001**	7, 88.072	2.635	**0.016**
Treatment * Depth * Time	28, 84.385	4.017	**<0.001**	28, 88.153	1.439	0.102
	Medium colonies (untransformed, skew=3.2, kur=13.6)			Medium colonies (Box Cox λ=0.5, skew=0.7, kur=1.4)		
Intercept	1, 30.158	299.843	**<0.001**	1, 23.523	640.731	**<0.001**
Treatment	1, 30.158	76.102	**<0.001**	1, 23.523	66.467	**<0.001**
Depth	2, 30.157	33.353	**<0.001**	2, 23.523	37.577	**<0.001**
Time	7, 95.065	34.418	**<0.001**	7, 98.044	27.485	**<0.001**

Con’t	Medium colonies (untransformed, skew=3.2, kur=13.6)			Medium colonies (Box Cox λ=0.5, skew=0.7, kur=1.4)		
	df	*F*	*p*	*df*	F	*p*
Treatment * Depth	2, 30.157	2.988	0.065	2, 23.523	0.545	0.587
Treatment * Time	7, 95.065	36.612	**<0.001**	7, 98.044	29.375	**<0.001**
Treatment * Depth * Time	28, 95.727	13.857	**<0.001**	28, 98.492	5.815	**<0.001**
	Large colonies (untransformed, skew=2.2, kur=5.2)			Large colonies (Box Cox λ=0.5, skew=0.8, kur=-0.3)		
Intercept	1, 27.858	36.808	**<0.001**	1, 27.35	96.036	**<0.001**
Treatment	1, 27.858	9.931	**0.004**	1, 27.35	18.482	**<0.001**
Depth	2, 27.858	6.042	**0.007**	2, 27.349	10.89	**<0.001**
Time	7, 106.487	3.78	**0.001**	7, 107.357	8.2	**<0.001**
Treatment * Depth	2, 27.858	1.146	0.332	2, 27.349	0.461	0.636
Treatment * Time	7, 106.487	2.441	**0.023**	7, 107.357	4.25	**<0.001**
Treatment * Depth * Time	28, 108.302	1.727	**0.025**	28, 108.457	1.984	**0.007**

Table 14a. Results of generalized linear regression models with underlying Poisson distribution evaluating the effects of treatment (disturbed vs. control) and depth (12, 18, 24 m) at each time period on the density of *Watersipora* colonies in the disturbance experiment at Platform B.
Effects evaluated separately for small, medium, and large colonies. Colony densities were not transformed prior to analysis. Significant treatment, depth, and treatment * depth effects ($p \leq 0.05$) highlighted in bold.

		Small colonies (< 5 mm^2)		Medium colonies ($5\text{-}1000$ mm^2)		Large colonies (> 1000 mm^2)	
Source	*df*	*Wald ChiSquare*	*p*	*Wald ChiSquare*	*p*	*Wald ChiSquare*	*p*
0 weeks							
Intercept	1	137.67	**<0.001**	185.457	**<0.001**	0.001	0.982
Treatment	1	23.92	**<0.001**	2.077	0.150	0.000	0.990
Depth	1	39.39	**<0.001**	32.219	**<0.001**	0.000	0.998
Treatment * Depth	1	0.002	0.966	0.014	0.907	0.003	0.957
9 weeks							
Intercept	1	66.60	**<0.001**	3627.117	**<0.001**	27.970	**<0.001**
Treatment	1	71.82	**<0.001**	532.694	**<0.001**	5.315	**0.021**
Depth	1	1.83	0.176	132.303	**<0.001**	13.355	**<0.001**
Treatment * Depth	1	0.068	0.795	8.112	**<0.004**	1.564	0.211

		Small colonies (< 5 mm^2)		Medium colonies (5-1000 mm^2)		Large colonies (> 1000 mm^2)	
Source	*df*	*Wald ChiSquare*	*p*	*Wald ChiSquare*	*p*	*Wald ChiSquare*	*p*
19 weeks							
Intercept	1	8.384	0.004	1583.217	**<0.001**	55.828	**<0.001**
Treatment	1	20.842	**<0.001**	243.960	**<0.001**	0.027	0.870
Depth	1	0.029	0.863	113.732	**<0.001**	9.356	**0.002**
Treatment * Depth	1	1.760	0.185	1.684	0.194	0.021	0.886
27 weeks							
Intercept	1	0.062	0.802	658.636	**<0.001**	59.684	**<0.001**
Treatment	1	2.955	0.086	96.614	**<0.001**	0.025	0.875
Depth	1	0.115	0.734	43.321	**<0.001**	18.308	**<0.001**
Treatment * Depth	1	1.954	0.162	0.295	0.587	0.018	0.894
35 weeks							
Intercept	1	0.084	0.771	718.296	**<0.001**	37.918	**<0.001**
Treatment	1	6.017	**0.014**	163.291	**<0.001**	9.090	**0.003**
Depth	1	0.373	0.542	2.955	0.086	11.622	**0.001**
Treatment * Depth	1	0.076	0.783	10.834	**0.001**	0.462	0.486

		Small colonies (< 5 mm^2)		Medium colonies (5-1000 mm^2)		Large colonies (> 1000 mm^2)	
Source	*df*	*Wald ChiSquare*	*p*	*Wald ChiSquare*	*p*	*Wald ChiSquare*	*p*
44 weeks							
Intercept	1	2.020	0.155	545.300	**<0.001**	49.160	**<0.001**
Treatment	1	2.907	0.088	124.822	**<0.001**	12.100	**0.001**
Depth	1	2.685	0.101	11.789	**0.001**	9.494	**0.002**
Treatment * Depth	1	0.396	0.529	4.758	**0.029**	5.706	**0.017**
53 weeks							
Intercept	1	9.500	**0.002**	780.645	**<0.001**	66.058	**<0.001**
Treatment	1	0.009	0.925	43.966	**<0.001**	22.112	**<0.001**
Depth	1	7.328	0.007	58.944	**<0.001**	8.700	**0.003**
Treatment * Depth	1	1.682	0.195	1.410	0.235	4.158	**0.041**

		Small colonies (< 5 mm^2)		Medium colonies (5-1000 mm^2)		Large colonies (> 1000 mm^2)	
Source	*df*	*Wald ChiSquare*	*p*	*Wald ChiSquare*	*p*	*Wald ChiSquare*	*p*
62 weeks							
Intercept	1	41.261	**< 0.001**	1088.160	**<0.001**	80.411	**<0.001**
Treatment	1	4.482	0.034	41.759	**<0.001**	20.781	**<0.001**
Depth	1	16.710	**< 0.001**	96.099	**<0.001**	16.577	**<0.001**
Treatment * Depth	1	0.565	0.452	4.052	**0.044**	0.001	0.969

Table 14b. Results of generalized linear regression models with underlying Poisson distribution evaluating the effects of treatment (disturbed vs. control) only with depth (12, 18, 24 m) for each time period on the density of *Watersipora* colonies for cases with significant interactions between treatment and depth (Table 14a).
Significant treatment effects ($p \le 0.05$) highlighted in bold.

Treatment effects only	*df*	Depth (m)	*Wald ChiSquare*	*p*
Medium colonies				
19 weeks	1	12	203.235	**<0.001**
	1	18	411.537	**<0.001**
	1	24	25.786	**<0.001**
35 weeks	1	12	49.581	**<0.001**
	1	18	34.550	**<0.001**
	1	24	54.327	**<0.001**
44 weeks	1	12	56.150	**<0.001**
	1	18	16.078	**<0.001**
	1	24	30.480	**<0.001**
62 weeks	1	12	22.753	**<0.001**
	1	18	1.501	0.221
	1	24	34.760	**<0.001**
Large colonies				
44 weeks	1	12	0.453	0.501
	1	18	6.030	0.014
	1	24	*	*
53 weeks	1	12	4.760	0.029
	1	18	12.841	**<0.001**
	1	24	*	*

*density = 0 in Control

Table 15. Results of linear mixed effects model evaluating the effects of treatment (cleaned vs. uncleaned), depth (6, 9 m), and time (6, 12, 18 months) on the cover of *Watersipora* following maintenance cleaning at Platform Gina.

Significant treatment, depth, and interaction effects (p ≤ 0.05) highlighted in bold. An expanded analysis evaluating the effect of treatment for each time is provided in Table 16.

Source	*df*	*F*	*p*
Intercept	1, 11.838	213.552	<0.001
Treatment	1, 11.839	18.068	**0.001**
Depth	1, 11.840	1.913	0.192
Time	2, 22.308	103.803	**<0.001**
Treatment x Depth	1, 11.838	1.852	0.199
Treatment x Time	2, 22.308	44.063	**<0.001**
Depth x Time	2, 22.308	0.931	0.409
Treatment x Depth x Time	2, 22.308	1.628	0.219

Table 16. Results of linear mixed effects model evaluating the effect of treatment (cleaned vs. uncleaned) and depth (9, 12 m) for each time period on the cover of *Watersipora* following maintenance cleaning at Platform Gina.
Significant treatment, depth, and interaction effects ($p \leq 0.05$) highlighted in bold.

		Time					
		6 months		12 months		18 months	
Source	*df*	F	p	F	p	F	p
Intercept	1, 12	32.576	<0.001	115.422	<0.001	210.263	<0.001
Treatment	1, 12	32.576	<0.001	8.492	0.013	44.088	<0.001
Depth	1, 12	0.368	0.556	4.471	0.056	0.518	0.485
Treatment * Depth	1, 12	0.368	0.556	2.443	0.144	1.909	0.192

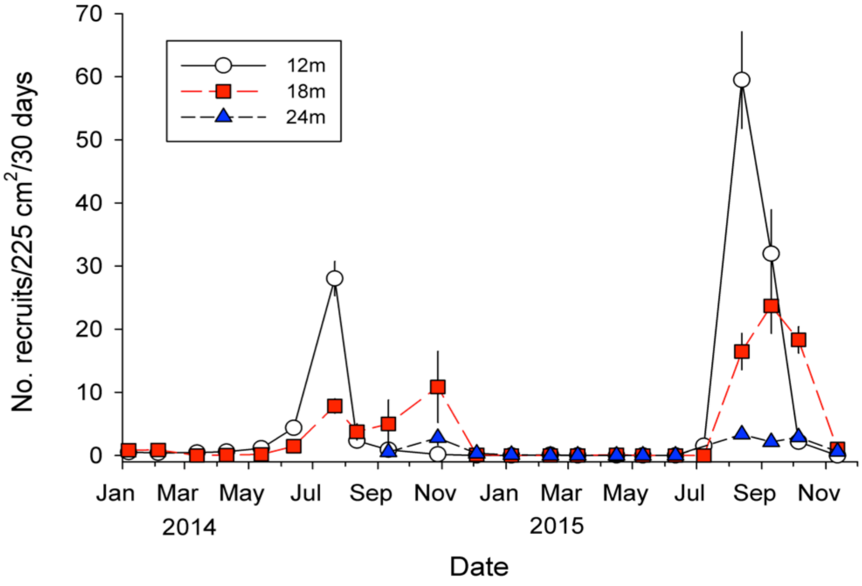

Figure 23. Expanded settlement plate time series from Platform B.
Data from 24 m depth not available prior to August 2014.

6 Distribution and Potential Larval Connectivity of the Non-native *Watersipora* (Bryozoa) Among Harbors, Offshore Oil Platforms, and Natural Reefs

6.1 Introduction

The introduction and spread of invasive non-native species is a widely recognized threat to the functioning of communities and ecosystems worldwide (Ruiz et al. 1997; Mooney and Cleland 2001; Bax et al. 2003; Ehrenfeld 2010; Simberloff et al. 2013). Managing the spread of these species requires information on their distribution and potential for dispersal into new areas (Williamson 1996; Mack 2000; Hui et al. 2011). In the marine environment, harbors and protected embayments, in particular, are well known sites of successful primary invasion by non-native marine invertebrates and algae as a result of high propagule pressure and the availability of suitable habitat (Carlton and Geller 1993; Cohen et al. 2005; de Rivera et al. 2005; Ruiz et al. 2009). The strong association of non-native taxa with coastal infrastructure, in general, has led to concerns regarding the role of this infrastructure in facilitating propagule dispersal and the spread of non-native species into natural areas (Bulleri and Airoldi 2005; Glasby et al. 2007; Ruiz et al. 2009; Simkanin et al. 2012; Dafforn et al. 2012; Adams et al. 2014; Epstein and Smale 2018).

Although non-native species are widely associated with harbors and other coastal infrastructure, there have been few studies investigating potential larval connectivity of taxa in harbors with natural coastal reef habitat, although harbors and the marinas, buoys, boats, and breakwaters within them have been inferred as potential sources of non-native propagules to the open coast (Ruiz et al. 2009; Simkanin et al. 2012; Epstein et al. 2018). One explanation for the dearth of studies could be that although non-native species are prevalent in harbors, most of these species are rarely reported either as present or abundant from fully open coastal waters (Cohen et al. 2005; de Rivera et al. 2005; Glasby et al. 2007; CDFG 2008; Ruiz et al. 2009; Daffron et al. 2012; Airoldi et al. 2015; Zabin et al. 2018). An emerging exception, however, may be the foliose encrusting bryozoan *Watersipora*. The genus *Watersipora* is cosmopolitan with a complex taxonomic history, reported from harbors and coastal embayments worldwide (Vieira et al. 2014). We follow the revision of the genus by Viera et al. (2014) that recognizes the formerly identified *W. subtorquata* as *W. subatra* in our area, but acknowledge that variation in the genetic structure of harbor populations found by Mackie et al. (2012) may signal a diversity of genotypes here.

Watersipora spp. are widely reported in the harbors of southern California (Cohen et al. 2005, Anderson and Haygood 2007; CDFG 2008; Santschi 2012) and also on offshore oil and gas platforms in the Santa Barbara Channel (SBC) (Page et al. 2006; Simons et al. 2016; Viola et al. 2018). Under favorable conditions, *Watersipora* is an aggressive competitor for space, capable of forming thick three-dimensional masses that alter local community structure by overgrowing native epifauna and by providing novel habitat for sessile and mobile invertebrates (Sellheim et al. 2010). The presence of this bryozoan on offshore platforms to depths of at least 24 m (Page et al. 2006; Viola et al. 2018) suggested that it could be more widely distributed in the open coastal environment than previously thought. However, there are few records of *Watersipora* on natural subtidal rocky reef or in the rocky intertidal zone of the open coast (but see Zabin et al. 2018).

Propagules dispersing from harbors to the open coast could seed and sustain populations of non-native taxa and facilitate their spread. For example, Epstein and Smale (2018) found a positive association between the abundance of the non-native alga, *Undaria pinnatifida*, in harbors and on nearby natural reefs, suggesting the importance of propagule pressure in sustaining this alga on natural reefs in the UK. Zabin et al. (2018) recently reported a positive association between frequency of occurrence of *Watersipora* in quadrats and distance from Monterey Harbor, California also suggesting the potential importance of harbors as a source of non-native propagules to the open coast. However, there have been few studies investigating the potential role of ocean circulation in dispersing taxa with short planktonic larval durations (PLD), such as *Watersipora*, between harbors and the open coast. *Watersipora* similar to other common epifaunal taxa in harbors, including ascideans and other bryozoans, has a short, non-feeding larval stage with a maximum PLD generally considered to be < 24 hours (Ng and Keough 2003). The longer distance dispersal of taxa with short PLDs is thus generally considered to be through anthropogenic vectors, particularly the transport of reproductive colonies on boat hulls (Floerl et al. 2004; Davidson et al. 2010; Ferreira et al. 2006; Zabin et al. 2014). Although the attachment and transport of *Watersipora* and other taxa with short PLDs on boat hulls is well documented, the potential extent to which ocean circulation could facilitate dispersal from artificial to natural habitat over shorter distances is unclear. Such information would be useful for managers planning the placement of artificial reefs and aquaculture facilities (e.g., Ventura Shellfish Enterprise, http://venturashellfishenterprise.com/), and the control of non-native populations on natural reefs.

Offshore oil and gas platforms are also possible sources of *Watersipora* larvae to natural habitat in the SBC. Since initially discovered on one offshore platform in the Santa Barbara Channel (SBC), California in 2001 (Page et al. 2006), *Watersipora* has been found on three additional platforms (Simons et al. 2016). Simons et al. (2016) used paired ocean circulation and particle tracking models to explore potential larval connectivity of *Watersipora* among seven offshore oil and gas platforms in the SBC (a subset of 16 total platforms in the SBC), and from harbors to these platforms. The modeling revealed that transport by ocean circulation provided a possible alternative explanation to hull fouling for the spread of *Watersipora* from one platform to three nearby platforms over a period of 12 years. This modeling also suggested little to no potential connectivity of harbors to these platforms, but revealed a net poleward flow of nearshore coastal waters over this period that could transport larvae originating from harbors along the coast to natural reef habitat.

A total of 16 platforms are located in the SBC between the mainland and the northern Channel Islands that could provide a source of *Watersipora* larvae to natural reefs in the region. Nine of these platforms had not been surveyed for *Watersipora* prior to the present study. Because the PLD is short, local retention of *Watersipora* larvae immediately following release is projected to be high, but dispersal distances of up to several kilometers may be possible over 24 h in open ocean conditions (Simons et al. 2016).

Although offshore infrastructure such as oil platforms have been hypothesized as providing stepping stone habitat that could facilitate the spread of non-native species (reviewed in Macreadie et al. 2011; Mineur et al. 2012), few modeling studies have explored possible larval connectivity via ocean circulation between offshore infrastructure and natural habitat. These published studies have suggested that offshore structures could increase connectivity by acting as intermediate stepping-stone habitat, thereby contributing to species range expansions, but also suggest the importance of local hydrodynamics and PLD in driving observed patterns (Adams et al. 2014; Henry et al. 2018).

Shallow subtidal rocky reef outcrops border the mainland coast along the northern boundary of the SBC providing potential destination habitat for *Watersipora* larvae. For example, rocky reefs are present within three to four kilometers of the Santa Barbara harbor mouth, although they are rare in the vicinity of harbors in the eastern SBC (Johnson et al. 2013). The SBC is bordered on the south by the northern Channel Islands, protected within the Channel Islands National Park and Channel Islands National Marine Sanctuary. Eleven Marine Protected Areas and two marine reserves are also found within the northern Channel Islands (Fig. 24). Rocky intertidal and subtidal habitat surrounding these islands provides potential destination sites for *Watersipora* larvae that might originate from harbors, platforms, or other sources. Information on the distribution and abundance, and potential vectors of dispersal of non-native species into sensitive Channel Island rocky habitat would help inform the control, including possible removal, of these populations.

In this study, we conducted an extensive survey to characterize the distribution and abundance of *Watersipora* on natural rocky reefs, coastal artificial habitat, and offshore oil and gas platforms in the SBC. We then use a three-dimensional biophysical model to assess the potential connectivity of *Watersipora* larvae directly from harbors and offshore platforms to open coast natural and artificial habitat where it was detected in the field survey, continuing the analysis in Simons et al. (2016) that examined potential connectivity among a subset of platforms and harbors. Potential connectivity is defined as the probability of larval transport from a source site to a destination site via ocean circulation (Mitarai et al. 2009; Watson et al. 2010). Using these results, we assess the potential dispersal of invertebrate larvae with short PLDs such as *Watersipora* from harbors and offshore platforms to natural habitat in the SBC, including the northern Channel Islands.

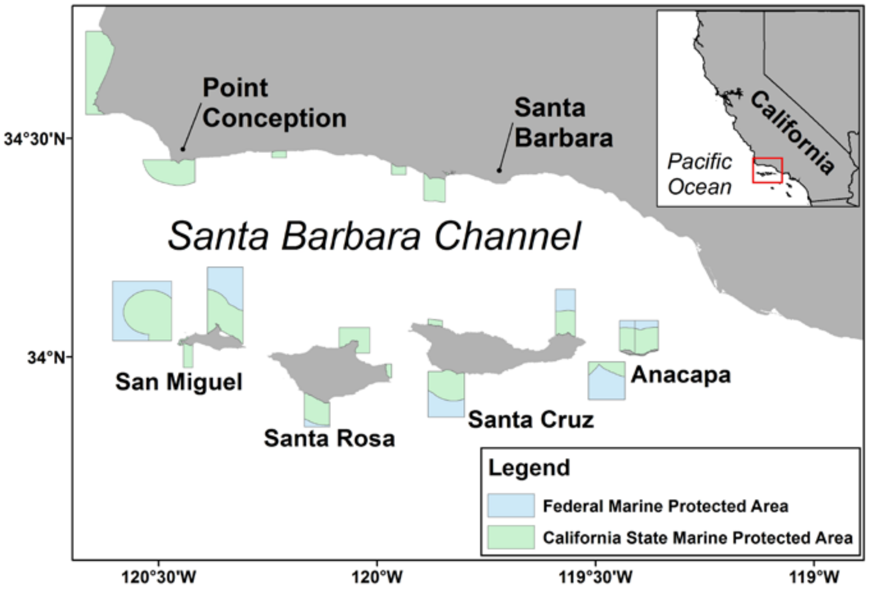

Figure 24. Santa Barbara Channel and study area.
The northern Channel Islands include San Miguel, Santa Rosa, Santa Cruz, and Anacapa island.

6.2 Methods

6.2.1 Distribution and abundance of *Watersipora*

To characterize the distribution of *Watersipora*, we surveyed a total of 61 open coastal sites in the SBC from 2014 – 2016; 22 sites on the mainland, 23 sites at the northern Channel Islands, and 16 offshore oil and gas platforms. The surveyed coastal sites included 32 subtidal rocky reefs, 8 artificial structures, and 5 rocky intertidal sites (Table 17, Fig. 25).

To survey the subtidal rocky reefs for the presence of *Watersipora*, two scuba divers swam along a 2 x 100 m belt transect run parallel to the shoreline along the reef in 6 to 12 m water depth recording any presence of the bryozoan. Transects were situated where possible to capture both horizontal and vertical topographic relief. If *Watersipora* was not found along this initial 2 x 100 m transect, two additional transects of the same length were qualitatively surveyed (up to 600 m^2). To quantify *Watersipora* abundance, paired photographs were taken every other meter on both the vertical and horizontal surfaces along a 20 m segment in the middle of the transects, yielding 20 images for each transect. If *Watersipora* was found along a 100 m transect, the remaining one or two transects were shortened to 20 m in length with photographs taken every other meter as above.

Photographs were taken with a Canon EOS 6D digital camera with a 14 mm wide-angle lens enclosed in an underwater housing. The camera and two strobes were mounted on a frame above a 41 x 62 cm (0.25 m^2) quadrat. From the photographs, we estimated the percent cover of any *Watersipora* occupying the visible layer in each photo plot using point contact on a grid of 100 uniformly spaced points superimposed onto each digital image and entered into the BisQue online image management and analysis system (http://bioimage.ucsb.edu/; Kvilekval et al. 2010). Contacts under each point were scored manually, automatically recorded in XML files, and subsequently exported for analysis. If large understory algae were present, photographs were taken before and after the algae had been removed using clippers. GPS locations for the beginning and end of each transect were recorded. A total of 1,317 photographs were scored for our surveys. To provide greater geographic coverage, we include additional qualitative diver surveys encompassing ~660 m^2 in water depths of 6 to 12 m at nine reef sites at the mainland and Santa Cruz and Santa Rosa Islands conducted in association with surveys of the Santa Barbara Channel Marine Biodiversity Observation Network (SBC MBON, Table S17).

We surveyed all 16 offshore oil and gas platforms in the SBC (Table 17, Fig. 25). The platforms are located across a range of water depths (29–363 m) and distances from shore (2.9–15.9 km) (Love et al. 2003). Qualitative presence/absence surveys of ~30 minutes duration were conducted by a team of two divers swimming among the conductor pipes at depths of 6 m, 12 m, and 18 m systematically searching for *Watersipora*. The conductor pipes (~1.6 m in diameter; Page et al. 1999) enclose the piping that conveys the oil and gas to the surface for processing. The abundance as percent cover of *Watersipora* on offshore platforms drops off dramatically at depths greater than 18 m (Page et al. 2006; Viola et al. 2018). To quantify the abundance of *Watersipora* present on each platform, we photographed 48-0.25 m^2 plots: one each located on the inside and outside of the four corner legs and four randomly selected conductor pipes at depths of 6 m, 12 m, and 18 m. A total of 655 photographs were scored from the platform surveys.

We surveyed eight other artificial structures along the shoreline that included the subtidal portions of pier pilings, a constructed island, pipelines, and a bird roost (Table 17, Fig. 25). These surveys were qualitative, recording presence or absence based on searching during a typical dive of 30 minutes. We also surveyed five rocky intertidal sites on the mainland coast (Table 17, Fig. 25). Intertidal sites were selected that were spatially heterogeneous, characterized by benches with mid to low intertidal pools, ledges, and cobbles, and abundant in shaded habitat supporting high species richness of encrusting benthic epifauna. Intertidal surveys were conducted as presence/absence by a single individual at a site and ranged from two to three hours.

Table 17. Summary of sites surveyed for *Watersipora* in the Santa Barbara Channel (SBC), including offshore oil and gas platforms, harbors, other artificial structures, subtidal rocky reefs, and rocky intertidal habitats.

Location	Total surveyed	*Watersipora* recorded
Offshore oil platforms	16	7
Harbors	4	4
Other artificial structures		
Mainland	5	3
Island	3	2
Subtidal rocky reefs		
Mainland	12	5
Island	20	2
Rocky intertidal		
Mainland	5	3
Total	*65*	*26*

6.2.2 Biophysical modeling of larval dispersal and connectivity

A three-dimensional biophysical model was used to estimate potential larval connectivity of *Watersipora* from the harbors and oil platforms to natural and artificial shoreline habitat in the SBC. Biophysical models are used to estimate larval connectivity for a wide range of applications including spatial fisheries management, design and placement of marine reserves, and evaluating possible effects of offshore infrastructure on habitat connectivity (Roberts 1997; Levin 2006; Costello et al. 2010; Adams et al. 2014). The biophysical model consisted of a coupled ocean circulation model and particle-tracking model, where the particles simulated larval transport. Following Watson et al. (2010) and Mitarai et al. (2009), potential connectivity was defined as the probability of larval dispersal from a source site to a destination site estimated by particle tracking simulations. The three-dimensional ocean circulation model was a high-resolution Regional Ocean Modeling System (ROMS) applied to the Southern California Bight (Shchepetkin and McWilliams 2005; Dong and McWilliams 2007). The model domain encompassed a 258 km by 386 km grid with 1 km horizontal resolution and 40 vertical levels that included the southern California coastline including the eight Channel Islands (Fig. 24). 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).

The biophysical model has been rigorously calibrated against field observations and shown to accurately capture mean, interannual, seasonal, and intraseasonal mesoscale dynamics of the Southern California Bight, including the SBC (Dong et al. 2009, 2011; Simons et al. 2015). Six hour averaged three-dimensional velocity fields produced by the ROMS were used to drive the three-dimensional particle tracking model following methods in Carr et al. (2008) and Mitarai et al. (2009). ROMS velocity fields were available for 12 years from 1996 – 2007. Particles were moved forward in time using a fourth-order accurate Adams-Bashforth-Moulton predictor-corrector scheme and a 900 s time step. Observational data from drifter experiments validated the particle tracking model (Ohlmann and Mitarai 2010).

Since our goal was to identify potential larval connectivity of *Watersipora* populations from harbors and offshore platforms to inshore habitat within the SBC, source and destination sites targeted in the modeling are those where *Watersipora* was found during the surveys, which are described in the following section (Table 17, Fig. 25). To estimate potential connectivity, particles were first released from the harbors and platforms source sites. In prior work, *Watersipora* was observed in four harbors in the SBC, Santa Barbara, Ventura, Channel Islands, and Port Hueneme (Cohen et al. 2005; Anderson and Haygood 2007; CDFG 2008; Santschi 2012), and are included as source sites in this study. To release particles from the harbors, the particles were placed at the first water grid cell adjacent to the harbor location near the shoreline. This procedure assumes that harbors are a source of *Watersipora* larvae, which is supported by the presence of *Watersipora* on Stearn's Wharf near the entrance to Santa Barbara harbor (personal observation). Particles were released from all platforms colonized by *Watersipora* vertically every 0.1 m from 1 to 18 m below the surface, the depth range at which *Watersipora* is most abundant (Simons et al. 2016; Viola et al. 2018).

Particles were released every three hours and tracked passively for 12 or 24 h. These PLDs were selected to represent a mid-range and maximum PLD for the taxon (Ng and Keough 2003; Cohen et al. 2005). Typical of other bryozoan taxa, newly released *Watersipora* larvae show positive phototaxis (personal observation; Ryland 1960), but are small and weak swimmers (Chia et al. 1984; Bradbury and Snelgrove 2001) and are thus unlikely to change their vertical position in the water column enough to influence their horizontal transport. Consequently, the dispersal of *Watersipora* larvae was modeled as passive particles. The particle release frequency was selected to meet the criteria for robustness in particle tracking models (Simons et al. 2013). Particles were released from June through October, the estimated reproductive season for *Watersipora* based on larval recruitment data from 2014 to 2017 (Viola et al. 2018). To achieve model robustness, a total of 985,000 particles were released from each source site over the 12-year modeling period following the methods in Simons et al. (2013).

To estimate the potential extent of larval dispersal from the harbors and platforms, the individual particle trajectories, calculated by the biophysical model, were transformed into two-dimensional particle density distributions (PDDs) for each source site for PLDs of 12 and 24 h. Using the three-dimensional distribution of all particles released from a harbor or platform source over the reproductive season (June to October) for a single year, an annual PDD was produced by summing the number of particles within a grid cell over depth (Mitarai et al. 2009; Simons et al. 2013). The annual PDDs for each source were then averaged over the 12 model years from 1996-2007 to obtain a long-term average of particle dispersal. Potential connectivity was quantified in the form of a source-destination matrix by using the values of the 12-year averaged PDDs from each source site (harbors and platforms) at the destination sites (inshore natural and artificial reefs). The values of the potential connectivity in the matrix represent the monthly mean number of particles released from a source site that arrived at a destination site.

6.3 Results

6.3.1 Distribution and abundance of *Watersipora*

Watersipora was widely distributed in the SBC (Table 1, Fig. 25), occurring at 50% of sites along the mainland coast and 43% of the offshore oil platforms. On the mainland, *Watersipora* was present at five out of 12 subtidal rocky reef sites (M2, M4, M6, M7, and M11) and on three out of five artificial structures, including a roosting platform for seabirds (M3), a pier (M5), and the rock revetment of an artificial island (M10). Although *Watersipora* was present at the two subtidal reef sites closest (4.5, 6.5 km) to SBH, it was also found at sites quite distant from the harbor, including the Naples Reef State Marine Conservation Area (SMCA) and in the rocky intertidal at Gaviota, 26.5 and 54 km west, respectively, from SBH (Table 17, Fig. 25). *Watersipora* was also found during our surveys in trace amounts at three of five rocky intertidal sites (M1, M8, and M9) on the mainland.

The distribution of *Watersipora* was more limited at the northern Channel Islands, occurring only on Santa Cruz Island at two of the 12 subtidal reef sites (SC1 and SC2), one of which (SC2) is a boat anchorage, and at the two piers (SC3 and SC4), which are used primarily by vessels providing transportation to and from the island. Where *Watersipora* was found on rocky subtidal reefs on the mainland and Santa Cruz Island, it was patchily distributed, but averaged > 10% cover on vertical surfaces along the 3-20 m transects at two subtidal rocky reefs (M2 and M11) (Table 18).

Watersipora was present on seven of 16 offshore platforms, including the cluster of four platforms reported in Simons et al. (2016), plus two platforms located 10 km offshore of SBH, and on Platform Harmony at the western end of the channel. Cover on offshore platforms varied from trace amounts on Platform Harmony to exceeding 20% on both vertical and horizontal surfaces at platform Gail (Table 18; Page et al. 2008; Viola et al. 2018). Examples of *Watersipora* on an offshore platform, subtidal rocky reefs, and rocky intertidal habitat are shown in Figure 26.

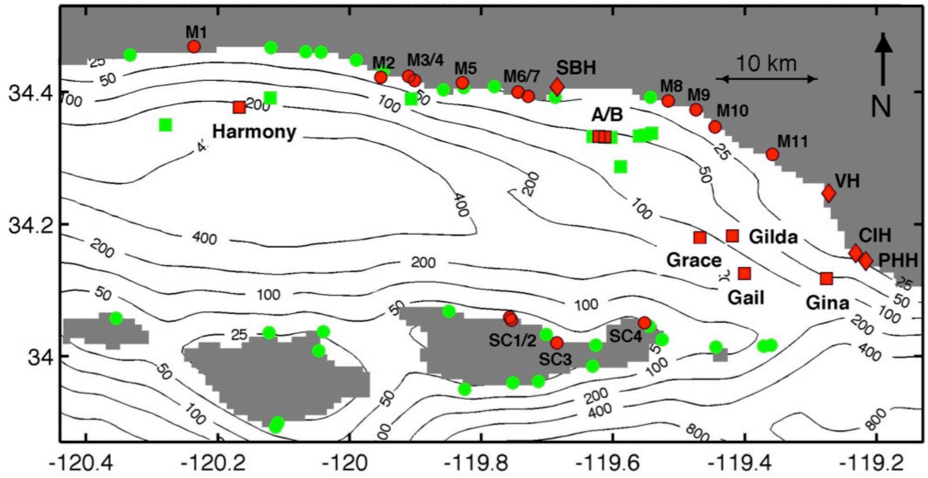

Figure 25. Survey locations at oil and gas platforms (squares), harbors (diamonds), and reefs (circles). Red symbols identify the locations where Watersipora was present.
Green symbols identify the locations where Watersipora was not present. SBH=Santa Barbara Harbor, VH=Ventura Harbor, CIH= Channel Islands Harbor, and PHH=Port Hueneme Harbor. Bathymetry contours in meters are shown by the black lines.

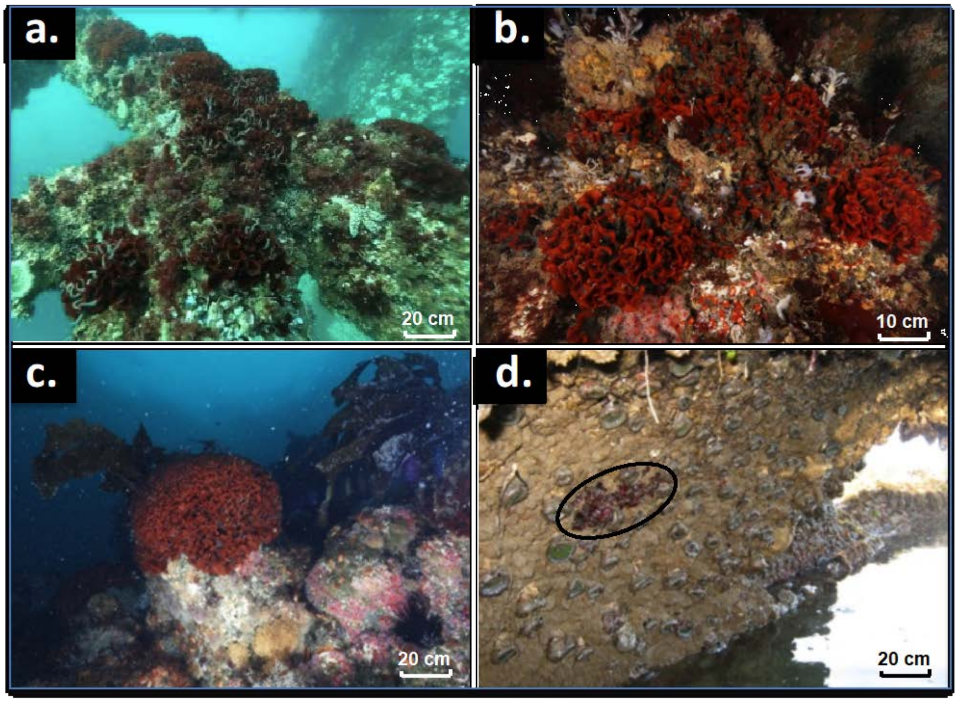

Figure 26. Examples of Watersipora subatra from (a) offshore oil and gas Platform B, (b) subtidal rocky reef at Solimar (M11), (c) subtidal rocky reef at Diablo Achorage, Santa Cruz Island (SC1), and (d) rocky intertidal ledge at Carpinteria (M8).
Scale is approximate.

6.3.2 Biophysical modeling of larval dispersal and connectivity

We explored potential connectivity of 10 source sites to 12 destination sites where *Watersipora* was found in the field surveys. The source sites include four harbors (Santa Barbara, Ventura, Channel Islands, and Port Hueneme), and six offshore oil platforms (Harmony, A/B, Grace, Gilda, Gail, and Gina) (Fig. 25). The 12 destination sites included natural rocky reefs and shoreline artificial structures along the mainland coast (M1, M2, M3/4, M5, M6/7, M8, M9, M10, and M11), and three sites on Santa Cruz Island (SC1/2, SC3, and SC4) (Fig. 2). Where sites are less than one kilometer apart and located in the same model grid cell, they are treated as a single site (e.g. platform A/B, M3/4, M6/7, and SC1/2).

Biophysical modeling reveals that proxy *Watersipora* larvae (as PDDs) released from all four harbors are largely retained close to their release sites and that larval density decreases sharply with increasing distance up and down coast from the harbors (Table 19, Fig. 27ab). There was little difference in the PDDs assuming either a 12 or 24 h PLD, except that PDDs with a 24 h PLD extend farther up and down coast over a slightly greater area.

Table 18. Mean percent cover (±1se) of *Watersipora* at natural rocky reef and offshore platform survey sites.
Cover of *Watersipora* on rocky reefs determined within a 20 x 2 m section of the initial 100 x 2 m transect. Cover of *Watersipora* on platforms determined within sampled 0.25 m^2 plots. Sample size in parentheses. See Methods for details.

	Orientation	
Location	Vertical	Horizontal
Rocky reef		
Arroyo Burro (M6)	0 (2)	0.1 ± 0.1 (40)
Diablo (SC1)	6.4 ± 2.4 (32)	1.6 ± 0.4 (32)
Ellwood (M4)	0.03 ± 0.03 (34)	0 (34)
Fry's (SC2)	<<1.0 (trace)[1]	0
Mohawk (M7)	0.2 ± 0.1 (35)	1.0 ± 0.6 (39)
Naples (M2)[2]	13.7 ± 2.3 (32)	2.3 ± 0.7 (32)
Solimar (M11)	12.7 ± 5.4 (12)	5.3 ± 1.6 (26)
Platforms		
A	<<1.0 (trace)[1]	0
B	11.9 ± 2.5 (32)	4.6 ± 1.1 (16)
Gina	11.4 ± 2.5 (32)	6.7 ± 1.7 (16)
Gail	28.5 ± 5.1 (32)	23.2 ± 6.6 (15)
Gilda	3.0 ± 1.7 (32)	0.4 ± 0.2 (16)
Grace	0.5 ± 0.3 (32)	0 (16)
Harmony	<<1.0 (trace)[1]	0

[1] Observed during qualitative swimming surveys only

[2] Marine Protected Area

Table 19. Potential connectivity statistics for source-destination pairs with greater than zero connectivity (> 0 particles km^{-2}).

Source Site	Destination Site[1]	Distance from Source Site (km)	PLD (h)	Potential Connectivity[1](No. particles km^{-2})[2]	Percent time with zero connectivity[3]
Santa Barbara Harbor (SBH)	M6/7	4.5	12	2,372 ± 1,293	0
	M2	25.1	24	1 ± 13	85
	M3/4	20.7	24	6 ± 15	73
	M5	13.4	24	132 ± 131	15
	M6/7	4.5	24	3,182 ± 1,092	0
Platform A/B	M5	21.0	24	1 ± 8	92
Platform Grace	SC4	16.4	24	4 ± 2	92

[1] Sites within 1 km of each other are combined

[2] Potential connectivity presented as monthly mean particle density (No. particles km^{-2}) ± 1 standard deviation

[3] Percent time with zero connectivity over the study period of June-October 1996-2007

There is high and continuous potential connectivity, assuming a 12 h PLD, between SBH and the closest destination reef that has *Watersipora* (M6/7), 4.5 km distant from the harbor mouth (Table 19, Fig. 28a). However, other mainland sites with *Watersipora* show no potential connectivity with harbors assuming a PLD of 12 h (Table 19). Increasing the PLD to 24 h increases potential connectivity to include three other sites (M2, M3/4, M5) in addition to M6/7: a rocky reef, pier, and a constructed island. However, connectivity is much higher (three orders of magnitude) and continuous for reef sites nearest the harbor (M6/7) compared with the other sites and decreases precipitously, both in particle density and percentage of time connected, for sites with increasing distance from the harbor (Table 19, Fig. 28b).

In the offshore environment occupied by the oil platforms, proxy larvae disperse over a much larger area and with lower particle density, as also shown in Simons et al. (2016) for a subset of platforms (Fig. 27cd). The smallest ellipses are from platforms A/B and Gina, which are the platforms closest to the shoreline and consequently subject to the slowest current flows (Winant et al. 2003). The highest particle density comes from the area around platforms Gilda, Gail and Grace, where the PDDs overlap one another. The lowest density comes from platform Harmony, where the center of the ellipse has been completely advected away from the platform. In a water depth of 392 m, platform Harmony is the

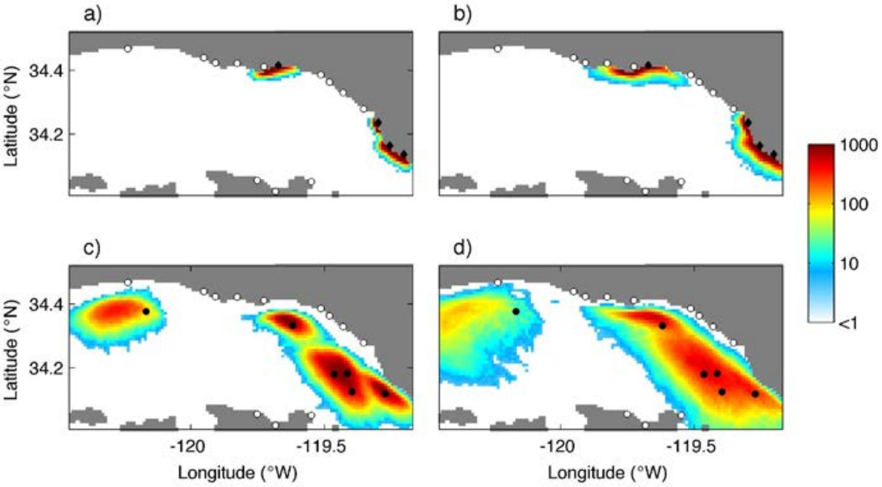

Figure 27. Particle density distributions (PDDs) averaged over 12 years for (a) harbor sources and a PLD of 12 h, (b) harbor sources and a PLD of 24 h, (c) platform sources and a PLD of 12 h, and (d) platform sources and a PLD of 24 h.
Black circles identify the platforms. The black diamonds identify the harbors. The white circles identify the destination reef sites. PDDs from individual sources have been added to together. Units are in mean monthly number of particles km-2 on a log scale.

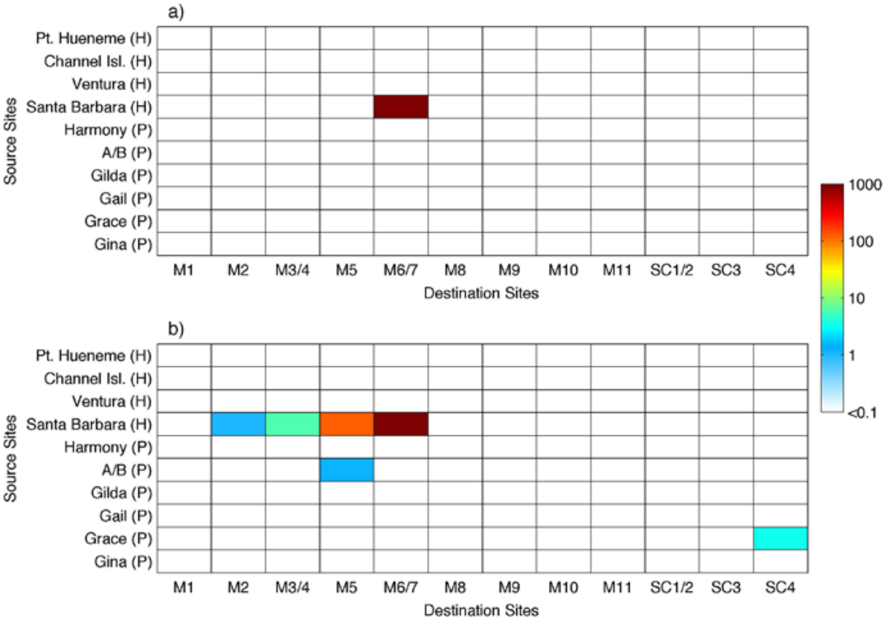

Figure 28. Potential connectivity matrix (log scale) for (a) 12 h PLD and (b) 24 h PLD. For the source sites, (H) identifies a harbor and (P) identifies a platform.
Units are in mean monthly number of particles km^{-2}.

deepest of the six source site platforms and thus exposed to the strongest offshore flows (Winant et al. 2003). For all platforms, PDDs with a 24 h PLD are much more disperse than the PDDs with a 12 h PLD, covering larger areas with lower particle densities, and dispersion predominantly towards to the western end of the SBC.

There is little evidence from the modeling to support offshore platforms acting as intermediate “stepping stones” that would facilitate the dispersal of harbor populations of *Watersipora* to the Channel Islands. Simons et al. (2016) reported previously that the potential connectivity of harbors to platforms was very low. Here, we find no or extremely weak connectivity between the platforms and any of the natural reef destination sites. The only potential connectivity detected between a platform and the northern Channel Islands assumes a 24 h PLD. In this scenario, there is very weak connectivity between platform Grace and site SC4, a pier on east end of Santa Cruz Island, but monthly mean particle density is only 4 particles km^{-2} and there is no connectivity for 92% of the time (Table 19).

6.4 Discussion

Watersipora spp. is widely recognized as an important fouling organism of marine vessels (Davidson et al. 2010; Floerl et al. 2014) and has been commonly reported in harbors and coastal embayments of California for the past two decades (Cohen et al. 2005; CDFG 2008). Despite its prevalence on coastal infrastructure in the region, however, the present study is the first, to our knowledge, to report the widespread occurrence of this non-native bryozoan on natural subtidal and intertidal rocky reef habitat in southern California. Previously, *Watersipora* has been reported in more limited surveys on subtidal rocky reef near Monterey harbor (Zabin et al. 2018), at rocky intertidal sites in southern and central California (Pister 2009; Zabin et al. 2018), and on settlement plates deployed at Catalina Island, southern California (terHorst and Dudgeon 2009). Worldwide, the genus appears to be expanding in distribution (e.g., Ryland et al. 2009; Bishop et al. 2015; Porter et al. 2017; Maric et al. 2017), but with few reports of its occurrence from natural open coast habitat (Malherbe and Samways 2014).

Although harbors are widely recognized sites of invasion by non-native species, the potential for dispersal of non-native propagules from harbors to natural habitat via ocean circulation is not clear, but poor connectivity could provide one explanation for the relative absence or low abundance of these species in natural habitat. Our modeling reveals high mean and nearly continuous potential connectivity between SBH and the reef sites (Mohawk, Arroyo Burro reefs, M6/7) located in closest proximity (4.5 km distant), leading to the conclusion that ocean currents could transport *Watersipora*, and other taxa with PLDs of 12 to 24 hours, from this harbor to natural habitat across this distance. Unlike SBH, natural rocky reef destination sites for *Watersipora* larvae are much less common in the vicinity of our harbor sites in the eastern SBC (Ventura, Channel Islands, and Port Hueneme (Johnson et al. 2013), which would limit its spread outside of harbors in that direction.

Although our biophysical modeling revealed potential connectivity between Santa Barbara Harbor and the nearest reef site, there was little to no connectivity between the harbor and reef sites separated by more than 4.5 km assuming either a 12 h or 24 h PLD. This lack of connectivity implies that the mean monthly magnitude and direction of current flow were insufficient to transport simulated *Watersipora* larvae greater distances within 24 h. Connectivity as modeled here provides a upper bound, but robust estimate of potential larval dispersal distance, based solely on passive transport by ocean currents and does not include nonphysical factors such as larval production and mortality (Mitarai et al. 2009; Watson et al. 2010) or possible changes in the larval condition over time in the water column that may affect successful settlement and metamorphosis (Marshall and Keogh 2003; Sams et al. 2015). For this reason, we believe that the modeling accurately predicts that larvae with PLDs of 24 h or less are extremely unlikely to reach destination sites with little to no connectivity to source sites solely via ocean circulation.

The number and frequency with which larvae arrive at a destination site over time, or propagule pressure, are important factors in controlling the establishment of and sustaining non-native populations (Lockwood et al. 2005; Clark and Johnston 2009). In addition to estimates of mean connectivity, our modeling provides an estimate of the proportion of time source and destination sites exhibit any connectivity (> 0 particles/km^2). For four source-destination pairs (SBH-M2, SBH-M3/4, platform A/B-M5, and platform Grace-SC4), the modeling reveals not only very low mean potential connectivity with a particle density 1-6 particles km^{-2} but also long periods of time (73-92%) during the study period with no connectivity (Table 19). Both the very low potential connectivity and high proportion of time with no connectivity suggest that *Watersipora* at these destination sites are unlikely to have originated via larval dispersal directly from harbor or platform sites.

Given the rapid decline in connectivity between SBH and natural reefs at distances of > 4 km, we hypothesize that intermediate stepping stone habitat would be required for the dispersal of *Watersipora* along the mainland coast beyond this distance. Since our reef sites were spaced on average 5.2 ± 1.4 km apart to the west of the harbor (x ±1SD, range 3.5 to 7.3 km), unsurveyed intermediate habitat with *Watersipora* would probably be required for step-wise dispersal to distant reef sites. Alternatively, hull fouling could have been responsible for initial introductions. The attachment and transport of *Watersipora* on boat hulls has been reported in California (Davidson et al. 2010; Zabin et al. 2014) and elsewhere (Floerl et al. 2014; Ashton et al. 2014), but there are no data with which to evaluate this possibility in our area. The introduction of *Watersipora* to natural reefs via boat hulls would be highly stochastic, as pointed out by Epstein and Smale (2018) for *Undaria*, and require the transport of colonies to the destination site and release of larvae during a relative narrow reproductive window or possible sloughing off of colonies. In addition, the recipient reef community would need to be susceptible to invasion, for example, by having been recently disturbed (Needles et al. 2015; Viola et al. 2018). However, this mechanism may be the only explanation for destination sites with little to no connectivity that are isolated and distant from any potential source site (such as M1-4 and M8-M11). Both stepping-stones and hull fouling mechanisms would increase larval connectivity between source and destination sites beyond that predicted by the modeling and could include source populations outside of our study area.

Sites distant from the mainland include those within the Channel Islands National Marine Sanctuary. We found *Watersipora* at two of 12 natural reefs surveyed (SC1, SC2), in addition to the two piers (SC3, SC4) within the Sanctuary. The distance across the SBC from harbor or platform to our nearest destination sites at the Channel Islands is > 30 km, far exceeding the modeled potential dispersal distance of *Watersipora* larvae. Anthropogenic transport is the most likely dispersal vector of *Watersipora* to Santa Cruz Island. Commercial boat traffic out of Santa Barbara, Ventura, and Channel Islands harbors uses the pier sites, and small boats visit the vicinity of rocky reef sites (Cabral et al. 2017). The distance between the nearest pier and reef sites, which are separated by a minimum of ~8 km, suggests separate *Watersipora* introductions to these sites, but more information is required on the possible existence of intermediate populations. The two reef sites on Santa Cruz Island with *Watersipora* are separated by < 1 km, suggesting that a single inoculation of one of the sites could have provided larvae to the other via larval dispersal. Once established, *Watersipora* on the piers and reefs of Santa Cruz Island are potential sources of larvae to other island reef habitat, including nearby Marine Protected Areas. The cover of *Watersipora*, in general, was found to be higher on vertical than horizontal surfaces (Table 18). Given that island rocky reefs generally possess steeper profiles overall than mainland reefs (Pondella II et al. 2015), the establishment of *Watersipora* at new sites may proceed at a faster rate at this island.

Offshore platforms provide the main source of hard substrate between the mainland coast and the northern Channel Islands (Fig. 2), but the use of offshore platforms as stepping stone habitat seems unlikely to account for the occurrence of *Watersipora* at Santa Cruz Island sites since there was little to no connectivity from the platforms to the island. Offshore infrastructure has been proposed to increase connectivity (Adams et al. 2014; Henry et al. 2018) and offshore oil platforms have been implicated in the stepwise spread of a non-native invasive coral (*Tubastraea coccinea*) in the Gulf of Mexico (Sammarco et al. 2004, 2012). In the case of platforms in the SBC, the short PLD of *Watersipora* combined with high sustained flows in the open channel quickly dilutes simulated larvae, which reduces connectivity via ocean circulation between the platforms and the Channel Islands.

Another possibility that would increase connectivity beyond modeled estimates is the rafting of sexually reproducing colonies into new areas on moveable substrates, such as floating kelp or other debris (Kuhlenkamp and Kind 2013; McCuller and Carlton 2018). In this rafting scenario, the floating substrate with attached *Watersipora* travels to new suitable natural or artificial habitat and establishes *Watersipora* colonies. In many hours of diving, we have not observed *Watersipora* attached to floating kelp or other debris, but this possibility cannot be ruled out.

The slow flows and complex bathymetry of the nearshore reported here and in Simons et al. (2016) appears to favor local retention, producing high densities of simulated larvae near the harbors and shoreline and the high potential connectivity between SBH and reef sites nearest the harbor (M6/7). Notable, however, is the absence of a positive association between *Watersipora* abundance (as cover) and connectivity (Table 19), a relationship that might be expected if propagule supply is driving abundance (Clark and Johnston 2009). *Watersipora* cover along transects at two reef sites (Naples reef, M2) is 50 times higher than at Arroyo Burro (M6) and Mohawk (M7) reefs, which are located in much closer proximity to Santa Barbara harbor (Tables 18, 19). This contrasts with the observations in Zabin et al. (2018), which report a positive relationship between the abundance (cover) of *Watersipora* on subtidal reefs and proximity to Monterey harbor and suggest that local physical and biological conditions could affect *Watersipora* abundance independent of harbor supplied propagules at our sites.

Our findings of potential connectivity between Santa Barbara harbor and nearby reefs could be extended to other non-native taxa with short PLDs widely reported from the harbors of southern California and worldwide. These taxa include ascidians (e.g., *Botrylloides violaceus*, *Botryllus schlosseri*, *Ciona* spp., and *Styela clava*) and other bryozoans (e.g., *Cryptosula pallasiana*) (Cohen 2011; Santschi 2012). Although our results suggest that propagules of taxa with PLDs of 12 to 24 h could disperse from harbors to reach nearby natural reefs, these taxa are rarely encountered along the open coast, including artificial structures in the SBC (Page et al., unpublished data on 22 subtidal rocky reefs; Santa Barbara Coastal Long Term Ecological Research (SBC LTER) annual monitoring 2001 to 2017, unpublished data, http://sbc.lternet.edu/data/) or elsewhere (Wasson et al. 2005; Zabin et al. 2018).

Mechanisms limiting the distribution and abundance of *Watersipora* on natural reefs as well as the establishment of other non-native taxa that might show larval connectivity with harbors require study, but probably involve forms of biotic resistance to invaders, such as predation on planktonic larvae and recent recruits by invertebrates and fish (Mileikovsky 1974; Cowden et al. 1984; Dumont et al. 2011a,b; Forrest et al. 2013; Gestoso et al. 2018) and competition for space with other epifauna and benthic macroalgae (Osman and Whitlatch 1995; Levin et al. 2002; Miller and Etter 2011). Previous studies have indicated that the existing epifaunal assemblage can inhibit the successful establishment of *Watersipora*. These studies show an increase in *Watersipora* abundance following disturbance that removes this assemblage (Clark and Johnston 2009; Needles et al. 2015; Viola et al. 2018). In addition, our findings of higher *Watersipora* cover on vertical faces suggest that general reef topography could affect the local abundance of *Watersipora*. Substrate slope has been shown to dramatically affect the composition of subtidal reef assemblages by mediating competitive interactions between benthic invertebrates and macroalgae (Knott et al. 2004; Miller and Etter 2011). Understory macroalgae are more abundant on horizontal than shaded vertical surfaces and may physically inhibit *Watersipora* recruitment and reduce the survival and growth of newly recruited individuals. It would be valuable to investigate the physical and biological mechanisms that enable the establishment of *Watersipora* on SBC coastal reefs, but limit the establishment of other non-native epifauna that are also found in harbors.

The results of biophysical modeling indicate that potential connectivity from harbors to mainland natural reefs is generally restricted to reefs closest to the harbor mouth for species with short PLDs like *Watersipora*. Potential connectivity may be enhanced for *Watersipora* if a harbor is seeding local stepping stone habitats that provide propagules to more distant sites or if hull fouling on boats from the harbor provides sufficient propagule pressure to enable colony establishment. Although resident *Watersipora* populations on offshore platforms in the SBC have little to no potential connectivity with mainland and northern Channel Island reefs, *Watersipora* on offshore platforms could be a source of propagules to the hulls of service vessels (crew boats, barges, mobile drilling rigs) that transit to nearshore habitat, enhancing connectivity beyond modeled estimates. In this regard, ancillary data, for example from genetic analysis (Hellberg et al. 2002; Brooks 2003; Sammarco et al. 2012; Baguette et al. 2013), would be extremely beneficial in exploring possible connectivity pathways between coastal infrastructure and natural habitats.

Although *Watersipora* is more widespread on natural reefs than expected, there appear to be opportunities to manage current and future invasions through the control of sources of propagules via the application of best management practices in harbors (Johnson et al. 2012; Daffron et al. 2017) and on offshore oil platforms (Viola et al. 2018) and potentially through the manual removal or reduction of existing field populations. In particular, populations at the Channel Islands, which are isolated and unlikely to receive regular inputs of larvae, would appear amenable to manual removal to reduce the potential for spread to uninvaded areas, including MPAs. The biophysical modeling reveals that careful consideration of potential connectivity to source populations in the placement of mariculture infrastructure with respect to harbors and other sources of non-native propagules could also help to reduce the potential for stepwise spread to natural habitat. This consideration would be most impactful in areas of little natural rocky reef habitat, such as the eastern SBC. Finally, longer-term data on the population dynamics of *Watersipora* on natural reefs are needed to discern whether these populations are increasing, which will help inform the urgency of management actions.

7 Significant Findings and Management Applications

7.1 Significant Findings

Regional differences in invertebrate assemblages on offshore oil and gas platforms in the Southern California Bight are attributable in part to variation in the abundance of *Watersipora*

Diver surveys of 23 offshore oil and gas platforms in the Southern California Bight in 2013-2014 revealed that shallow water (< 18 m depth) invertebrate assemblages varied among four regions defined *a priori* by differences in sea surface temperature. Variation in platform assemblages was broadly associated with SST; however, assemblages of platforms in the southeast Santa Barbara Channel were distinct due to the high cover of the non-native bryozoan *Watersipora*. Invertebrate assemblages also varied idiosyncratically among platforms within a region likely due to the vagaries of larval supply and local environmental conditions that includes disturbance from platform maintenance cleaning operations. Surveys also revealed that mussels, often reported as abundant historically, did not consistently dominate shallow water platform invertebrate assemblages. Over smaller spatial scales, the idiosyncratic differences in invertebrate assemblages among platforms within regions indicates that these assemblages would have to be considered on a platform-by-platform basis under various decommissioning scenarios.

***Watersipora* appears to be expanding in distribution and abundance in the Santa Barbara Channel**

Surveys of assemblages of seven offshore oil and gas platforms in the Santa Barbara Channel revealed the spread of *Watersipora* from one platform in 2001 to four platforms in 2013. Modeling suggested that larval dispersal via currents could account for this spread, but also that *Watersipora* is unlikely to spread from these four platforms to the three other surveyed platforms through larval dispersal. In addition, modeling results suggest that taxa with planktonic larval durations (PLDs) of 24 hours or less, such as *Watersipora*, released from offshore platforms can disperse further than larvae with similar PLDs released from nearshore habitat. The enhanced dispersal distance of larvae released from offshore platforms could be driven by higher current flows in the offshore hydrodynamic environment and larval release above the seafloor.

Disturbance that removes the invertebrate assemblage attached to the platform, for example from maintenance cleaning, can enhance the recruitment and cover of *Watersipora*

Manipulative experiments and field observations revealed that the removal of dense epifaunal invertebrate assemblages attached to offshore platforms in the Santa Barbara Channel creates a disturbance that facilitates the establishment of *Watersipora*. *Watersipora* recruitment was elevated in experimentally disturbed plots, compared to controls, following an experimental disturbance. However, one year after the experimental disturbance, sessile invertebrates occupied all available settlement space in the disturbed plots, and there was little recruitment of *Watersipora* into these plots despite the availability of larvae, indicated by larval recruitment onto settlement plates. Similarly, the removal of attached invertebrates from another platform during maintenance cleaning by the operators resulted in the colonization of cleared surfaces by *Watersipora* and the attainment of high cover over time compared to uncleaned surfaces. Both the experimental manipulation and the larger scale maintenance cleaning suggest that the attached epifauna consumed or outcompeted *Watersipora* larvae, inhibiting the establishment of this bryozoan.

***Watersipora* occurs on some natural reefs, as well as offshore oil platforms and harbors**

The presence of coastal infrastructure has led to concerns regarding the role of artificial habitat in facilitating species range expansions and the spread of non-native species to natural areas. In the Santa

Barbara Channel (SBC), California, USA, the non-native bryozoan *Watersipora* spp., which has a maximum planktonic larval duration of 24 h, was reported only in harbors and from offshore oil platforms prior to this study. To assess the distribution and potential spread of *Watersipora* between coastal infrastructure and natural habitat in the SBC, we surveyed 61 sites, including natural and artificial habitat, and evaluated the potential dispersal connectivity of *Watersipora* larvae from harbors and oil platforms to natural reefs using survey results and three-dimensional biophysical modeling. *Watersipora* was more widely distributed than expected, occurring on approximately 50% of the oil platforms and mainland reef sites, but only 17% of the island reef sites. Modeling indicated high potential connectivity of *Watersipora* populations from one harbor to a nearby reef, but little to no potential connectivity from this harbor to other more distant reefs. The modeling estimated little potential connectivity from offshore platforms to the reef sites. Our results suggest that the successful dispersal of *Watersipora* larvae from harbors and oil platforms to distant reef sites would likely require intermediate stepping stone sites or transport via vessel hull fouling.

7.2 Management Applications

Although *Watersipora* is more widespread on natural reefs than expected, there appear to be opportunities to manage current and future invasions through the control of sources of propagules via the application of best management practices in harbors and on offshore oil platforms and potentially through the manual removal or reduction of existing field populations. In particular, populations at the northern Channel Islands, which are isolated and unlikely to receive regular inputs of larvae, would appear amenable to manual removal to reduce the potential for spread to uninvaded areas, including MPAs. The biophysical modeling reveals that careful consideration of potential connectivity to source populations in the placement of mariculture infrastructure with respect to harbors and other sources of non-native propagules could also help to reduce the potential for stepwise spread to natural habitat. This consideration would be most impactful in areas of little natural rocky reef habitat, such as the eastern SBC. Finally, longer-term data on the population dynamics of *Watersipora* on natural reefs are needed to discern whether these populations are increasing, which will help inform the urgency of management actions.

Maintenance operations for offshore structures can include the manual removal of subtidal epibenthic invertebrates attached to the structure. This anthropogenic disturbance enhanced the establishment of *Watersipora*. The timing of disturbance relative to *Watersipora*'s reproductive season was an important driver of this pattern. Our results suggest that the establishment of *Watersipora* on offshore oil platforms can be managed by adjusting the timing of maintenance cleaning to occur shortly after this bryozoan's peak reproductive period in late summer – fall. This timing could remove newly settled recruits and allow sufficient time for native species to colonize available bare space prior to the bryozoan's next reproductive period. Even relatively frequent cleaning activities (every 2 – 3 years) could be scheduled to allow adequate time for native species to colonize the bare space before the recruitment period of *Watersipora*. This practice could be employed across other maritime industries, such as offshore renewable energy and mariculture, and might be extended to other non-native species with comparable life histories. In this regard, like other marine ecosystems, disturbance and propagule supply interactively influence invasion success (Britton-Simons and Abbott 2008; Clark and Johnston 2009, Airoldi and Bulleri 2011), so the timing of disturbance events relative to recruitment periods can have a profound effect on the abundance of non-native species (Stachowicz et al. 2002). However, these decisions should be made on a case-by-case basis to account for differences in site-specific characteristics, such as species assemblages or physical factors.

Our results may also inform decision-making regarding the decommissioning of offshore oil and gas platforms. Some stakeholders prefer decommissioning alternatives that maintain deeper parts (> 26 m) of the platform structure to function as an artificial reef (Schroeder and Love 2004; Smyth et al. 2015). In California, such “rigs-to-reefs” alternatives can be considered if they comply with the National Fishing Enhancement Act (1984) and the California Marine Resources Legacy Act (2010). In the case of platforms with established *Watersipora* populations, the low abundance of this species at 24 m suggests that if a reefing option is selected, removing the shallow portions of the platform may reduce the ability of this non-native species to persist locally. However, more information is needed on the dispersal potential of *Watersipora* at deeper depths to understand the consequences of this decommissioning alternative.

The global distribution of *Watersipora* and likely proliferation of marine artificial structures increases the range of potential applications of our study, and underscores the need for similar studies to inform management practices. Artificial structures can act as “reproductive hotspots” (Ling et al. 2002) that deliver non-native propagules to nearby natural reefs (Sammarco et al. 2012). Consequently, the ecosystem impacts of non-native species on artificial structures could extend beyond the immediate habitat. Artificial structures potentially enable greater dispersal of non-native larvae by providing a network of hard substrate “stepping stones” in regions of unsuitable soft-bottom habitat (Sammarco, Atchison and Boland 2004; Adams et al. 2014; Simons et al. 2016). This effect could be greater in high-flow offshore environments, which may further increase habitat connectivity (Simons et al. 2016). Targeted management of artificial marine structures that incorporates ecological knowledge into the siting, deployment date, and timing of maintenance practices can potentially help managers mitigate the impacts of non-native species at regional scales.

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9 Study Products and Publications

Manuscripts published, in press and in review:

Rahimi AM, Miller RJ, Fedorov DV, Sunderrajan S, Doheny BM, Page HM, Manjunath BS. 2014. Marine biodiversity classification during dropout regularization. Proceedings, ICPR Workshop on Computer Vision for Analysis of Underwater Imagery, pp. 80-87.

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Viola SM. 2016. Anthropogenic disturbance facilitates a non-native species on offshore oil platforms. Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara. 30 pp.

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Department of the Interior (DOI)

The Department of the Interior protects and manages the Nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors the Nation’s trust responsibilities or special commitments to American Indians, Alaska Natives, and affiliated island communities.

Bureau of Ocean Energy Management (BOEM)

The mission of the Bureau of Ocean Energy Management is to manage development of U.S. Outer Continental Shelf energy and mineral resources in an environmentally and economically responsible way.

BOEM Environmental Studies Program

The mission of the Environmental Studies Program is to provide the information needed to predict, assess, and manage impacts from offshore energy and marine mineral exploration, development, and production activities on human, marine, and coastal environments. The proposal, selection, research, review, collaboration, production, and dissemination of each of BOEM’s Environmental Studies follows the DOI Code of Scientific and Scholarly Conduct, in support of a culture of scientific and professional integrity, as set out in the DOI Departmental Manual (305 DM 3).