

Research Article

Distribution and potential larval connectivity of the non-native *Watersipora* (Bryozoa) among harbors, offshore oil platforms, and natural reefs

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Abstract

Non-native marine species thrive on artificial habitat. Expanding coastal infrastructure has led to concerns that increasing artificial habitat will facilitate the spread of non-native species overall and to natural ecosystems. In the Santa Barbara Channel (SBC), California, USA, the non-native bryozoan *Watersipora subatra* (Ortmann, 1890) has previously been reported only in harbors and on offshore oil platforms. To assess the distribution and potential for spread of *W. subatra* between coastal infrastructure and natural habitat in the SBC, we surveyed 61 open coastal sites, including natural and artificial habitat, and evaluated the potential dispersal connectivity of *W. subatra* larvae from harbors and oil platforms to natural reefs using survey results and three-dimensional biophysical modeling. We discovered that this bryozoan has invaded natural reefs in the region. *W. subatra* was present on approximately 50% of the oil platforms and mainland reef sites, but only 17% of offshore island reef sites. Modeling indicated high potential connectivity from one harbor to the closest reef with *W. subatra*, 4–5 km distant from the harbor mouth, but dispersal to the more distant sites would likely require intermediate stepping stone sites or anthropogenic transport of spawning adults. Populations on offshore platforms, in contrast, were virtually unconnected to reef sites through ocean circulation. The survey data indicated potential opportunities to manage current and future invasions through the control of larval sources. In particular, manual removal of small isolated populations on reefs at the northern Channel Islands would reduce this source of larvae to uninvaded areas. Consideration of potential connectivity in the placement of mariculture infrastructure along the coast with respect to harbors and other sources of non-native propagules could also help to reduce the potential for stepwise spread of non-natives to natural reef habitat.

Key words: marine infrastructure, rocky reefs, biophysical modeling, non-native species

Introduction

The introduction and spread of non-native species is a widely recognized threat to the functioning of biological communities and ecosystems worldwide (Ruiz et al. 1997; Mooney and Cleland 2001). 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 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, in general, with coastal infrastructure has led to concerns regarding the role of this infrastructure in facilitating propagule dispersal and the spread of non-native species into natural habitat (Bulleri and Airoidi 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 harbors are potential sources of non-native propagules (Ruiz et al. 2009; Simkanin et al. 2012; Epstein and Smale 2018), there have been few studies investigating potential larval connectivity of non-native species between harbors and coastal reef habitats. One explanation for the scarcity 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 open coastal habitats (Ruiz et al. 1997; Cohen et al. 2005; de Rivera et al. 2005; Glasby et al. 2007; CDFG 2008; Dafforn et al. 2012; Airoidi et al. 2015; Zabin et al. 2018). An emerging exception, however, is the foliose encrusting bryozoan *Watersipora*, a non-native taxon that was likely originally introduced into California coastal waters via hull fouling (Cohen 2011).

Populations of the bryozoan genus *Watersipora* Neviani, 1896 are now reported from harbors and coastal embayments worldwide (Vieira et al. 2014). *Watersipora* spp. have been widely reported in southern California waters, including in harbors (Cohen et al. 2005; Anderson and Haygood 2007; CDFG 2008; Santschi 2012) and on offshore oil and gas platforms in the Santa Barbara Channel (SBC, Figure 1) (Page et al. 2006; Simons et al. 2016; Viola et al. 2018). *Watersipora* has a complex taxonomic history, and we follow the revision of the genus by Vieira et al. (2014) that recognizes the formerly identified *W. subtorquata* (d'Orbigny, 1852) as *W. subatra* (Ortmann, 1890) in the SBC, but acknowledge that variation in the genetic structure of harbor populations found by Mackie et al. (2012) may signal a diversity of genotypes here. Under favorable conditions, *W. subatra* (hereafter, *Watersipora*) is an aggressive competitor for space capable of forming thick three-dimensional masses that alter local community structure by overgrowing native epifauna and providing novel habitat for sessile and mobile invertebrates (Sellheim et al. 2010). The presence of *Watersipora* on offshore platforms in the SBC to depths of up to 24 m (Page et al. 2006; Viola et al. 2018) suggested that this non-native bryozoan could be widely distributed in the open coastal environment. However, there are few reports of *Watersipora* on natural subtidal rocky reef or in the rocky intertidal zone of the open coast (i.e., Zabin et al. 2018).

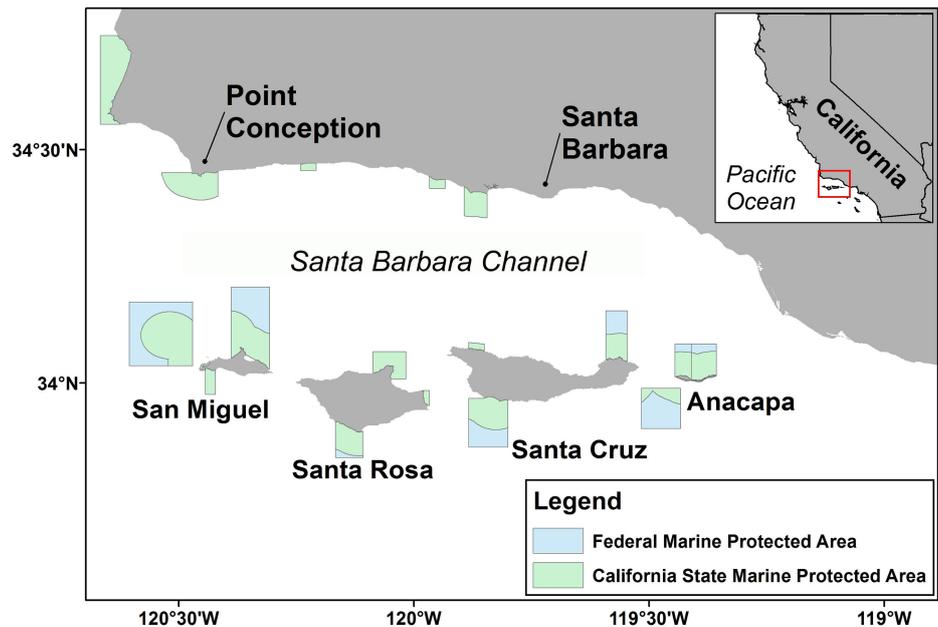


Figure 1. Santa Barbara Channel (SBC) study area with the locations of MPAs. The northern Channel Islands include San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands. The Channel Islands National Park extends 1.8 km from shore around each island. The Channel Islands National Marine Sanctuary extends 10.8 km offshore around the archipelago.

Similar to other common epifaunal taxa in harbors, including ascidians and other bryozoans, *Watersipora* has a short non-feeding larval stage with a maximum planktonic larval duration (PLD) of about 24 hours (Ng and Keough 2003). Thus, long distance dispersal of *Watersipora* and other taxa with short PLDs is generally considered to be through the transport of reproductive colonies attached to boat hulls (Davidson et al. 2010; Floerl et al. 2014; Zabin 2014). However, over short distances the extent to which ocean circulation could facilitate dispersal of these taxa from harbors to natural habitats remains unclear. Such information would be useful for managers planning the placement of artificial reefs and aquaculture facilities and the control of non-native populations on natural reefs. 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*, on natural reefs and distance from harbors in the United Kingdom, suggesting the importance of propagule pressure in sustaining this alga on natural reefs. Zabin et al. (2018) recently reported a positive association between frequency of occurrence of *Watersipora* in quadrats on reefs 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 no studies to our knowledge that have investigated the potential role of ocean circulation in dispersing taxa with short planktonic larval durations (PLD), such as *Watersipora*, between harbors and open coast reef habitats.

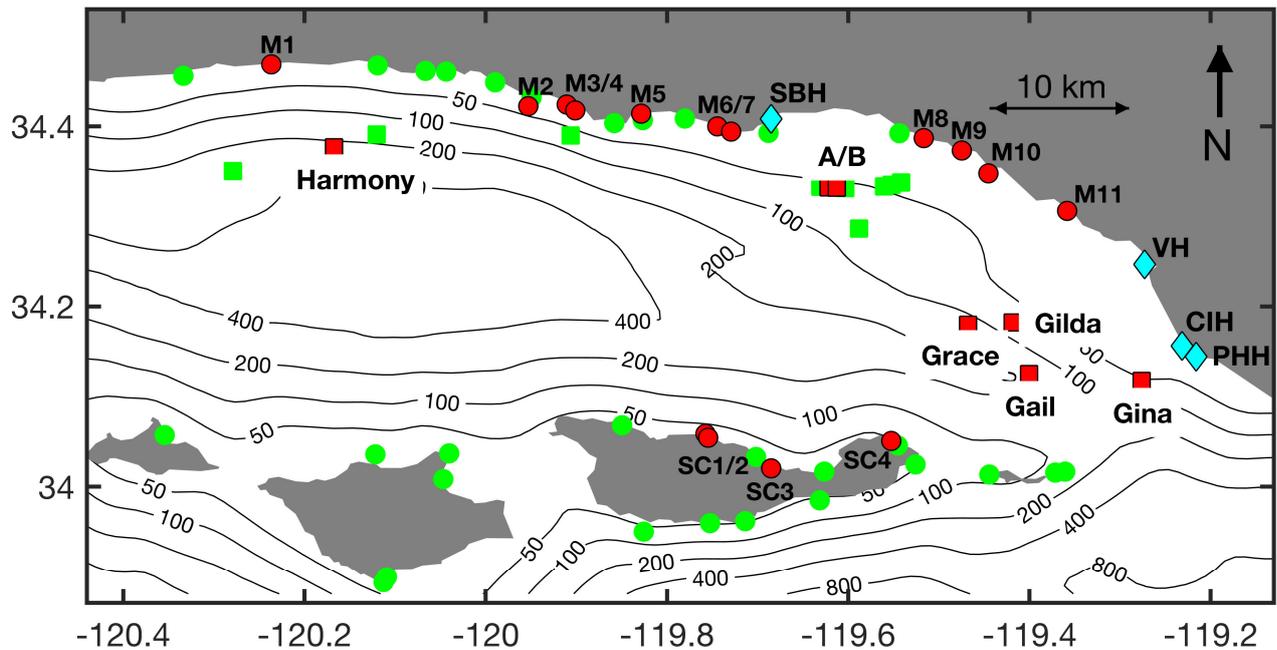


Figure 2. Survey locations at oil and gas platforms (squares), harbors (diamonds), and reefs (circles). Red symbols identify the locations where *Watersipora* was present. Green symbols identify the locations where *Watersipora* was not present. Blue diamonds identify the harbors where *Watersipora* was not present. SBH = Santa Barbara Harbor, VH = Ventura Harbor, CIH = Channel Islands Harbor, and PHH = Port Hueneme Harbor. The black lines show bathymetry contours in meters. The latitude and longitude of all survey points are included in Supplementary material Table S1.

Oil and gas platforms, the largest offshore infrastructure in the SBC are also possible sources of *Watersipora* larvae to natural reefs. A total of 16 offshore platforms are located in the SBC between the mainland coast and the northern Channel Islands (Figure 2). Since initially discovered on one platform in the SBC in 2001 (Page et al. 2006), *Watersipora* has been found on three additional platforms (Simons et al. 2016, Figure 2). Nine of the 16 SBC platforms had not been surveyed for *Watersipora* prior to this study. 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 the 16 total platforms) and from four harbors in the SBC to the seven 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. In this study we extend that analysis to an evaluation of potential dispersal from the harbors and platforms to natural reef habitats. Due to its short PLD, local retention of *Watersipora* larvae immediately following release is projected to be high, but dispersal distances of up to 10 kilometers may be possible over 24 h in open ocean conditions (Simons et al. 2016), suggesting that at least some of these platforms could provide a source of *Watersipora* larvae to natural reefs.

Although offshore infrastructure, such as oil and gas platforms, has been hypothesized to provide 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 habitats. These studies have suggested that offshore structures could increase connectivity by acting as intermediate stepping stone habitat, thereby contributing to species range expansions, but also emphasize the importance of local hydrodynamics and PLD in driving observed patterns of larval dispersal (Adams et al. 2014; Henry et al. 2018).

Rocky intertidal and subtidal habitats harboring diverse communities of sessile invertebrates, including bryozoans, are plentiful around the northern Channel Islands and the SBC mainland, providing suitable habitat for *Watersipora* larvae originating from harbors, platforms, or other sources. Shallow subtidal rocky reef outcrops border the mainland coast along the northern boundary of the SBC, including within three to four kilometers of the Santa Barbara harbor mouth (Figure 2). SBC is the location of the Channel Islands National Park and Channel Islands National Marine Sanctuary, as well as fifteen Marine Protected Areas and two marine reserves (Figure 1). Information on the distribution, abundance, and potential vectors of dispersal of non-native species into sensitive rocky habitats in this region would help inform the management and 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 used a three-dimensional biophysical model to assess potential larval connectivity of *Watersipora* populations directly from harbors and offshore platforms to open coast natural and artificial habitat where it was detected in the field survey. Using these results, we assess the role of offshore oil platforms as sources or stepping stone habitat that might facilitate the spread of *Watersipora*, from harbors to open coast natural habitat in the SBC, including the northern Channel Islands.

Materials and methods

Distribution and abundance of Watersipora

To characterize the distribution of *Watersipora*, we surveyed a total of 61 open coastal sites in the SBC from 2013 to 2017 that included 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 1 and Supplementary material Table S1, Figure 2).

Fourteen of the mainland sites (natural and artificial) were located to the west of Santa Barbara Harbor (SBH), beginning approximately 4.5 km from the harbor mouth, and spaced on average 3.6 ± 1.3 km apart (mean \pm 1SD, range 1.1 to 10.8 km). Fewer sites were surveyed to the east of the SBH, with the nearest site located approximately 13 km from the harbor

Table 1. Summary of sites surveyed for *Watersipora subatra* in the Santa Barbara Channel (SBC), including offshore oil and gas platforms, harbors, other artificial structures, subtidal rocky reefs, and rocky intertidal habitats. Details on individual sites provided in Table S1.

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

mouth. Rocky reef becomes less common to the east of the harbor, and is generally sparser along the mainland coast in the eastern than western SBC (Johnson et al. 2013). The 20 subtidal reef sites surveyed at the northern Channel Islands were located in areas visited by recreational and commercial boats. Surveys were generally conducted in water depths ranging from 6 to 12 m where *Watersipora* was previously found to be most abundant (Simons et al. 2016; Viola et al. 2018).

To qualitatively survey the subtidal rocky reefs for the presence of *Watersipora*, two scuba divers swam along a 2×100 m belt transect run parallel to the shoreline, recording presence/absence of the bryozoan. Where possible transects were situated to capture both horizontal and vertical topographic relief. If *Watersipora* was not found along this initial 2×100 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 26 cm above a $41 \text{ cm} \times 62 \text{ cm}$ (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 using 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 m² 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 by the Santa Barbara Channel Marine Biodiversity Observation Network (SBC MBON, Table S1).

We surveyed all 16 offshore oil and gas platforms present in the SBC (Tables 1 and S1, Figure 2). 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 haphazardly placed 0.25 m² plots per platform: 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. The platforms were oriented differently such that the photoplots did not conform to a specific compass heading. 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 (< 8 m depth) of pier pilings, a constructed island, pipelines, and a concrete bird roost (Tables 1 and S1, Figure 2). 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 (Tables 1 and S1, Figure 2). Intertidal sites possessed rock benches with mid to low intertidal pools, ledges, and cobbles, and abundant shaded habitat supporting high species richness of encrusting benthic epifauna. Intertidal surveys were conducted as presence/absence by one of the authors (JHR Goddard) at a site and ranged from two to three hours in duration.

Biophysical modeling of larval dispersal and connectivity

To estimate potential larval connectivity of *Watersipora* from the harbors and platforms to natural and artificial shoreline habitat, we used a three-dimensional biophysical model of the SBC. Biophysical models are used globally 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). Our biophysical model consisted of a three-dimensional coupled

ocean circulation and particle-tracking model, which simulates 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 as estimated by the particle tracking simulations.

The three-dimensional ocean circulation model was a Regional Ocean Modeling System (ROMS) applied to the Southern California Bight (Shchepetkin and McWilliams 2005; Dong and McWilliams 2007). The model domain contains the southern California coastline and the eight Channel Islands, which includes the SBC (Figure S1), and has one kilometer horizontal resolution and 40 vertical levels. Details on the lateral and surface boundary conditions are documented in Dong and McWilliams (2007) and Dong et al. (2009). The circulation model has been rigorously calibrated against field observations and shown to accurately capture mean, interannual, and seasonal mesoscale dynamics of the Southern California Bight, including the SBC (Dong et al. 2009, 2011; Simons et al. 2015). Following methods in Carr et al. (2008) and Mitarai et al. (2009), six-hour-averaged three-dimensional velocity fields produced by the circulation model were used to drive the three-dimensional particle tracking model and were available for 12 years from 1996–2007.

Since our goal was to identify whether harbors and offshore platforms could facilitate *Watersipora* spread to natural habitat via larval dispersal within the SBC, source and destination sites selected for the modeling are those where *Watersipora* was found during the surveys, as described in the following section (Tables 1 and S1, Figure 2). To estimate larval transport and potential connectivity, particles were 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. Following the methods from Simons et al. (2016), particles were vertically released from the source sites, platforms colonized by *Watersipora*, and the four harbors, from one to 18 m below the surface, the depth range at which *Watersipora* is most abundant (Simons et al. 2016; Viola et al. 2018).

The particle tracking time representing PLD was set to 12 h and 24 h. These PLDs were selected to represent a possible midrange and maximum PLD for the taxon (Ng and Keough 2003; Cohen et al. 2005). Typical of other bryozoans, newly released *Watersipora* larvae show positive phototaxis (Ryland 1960; HM Page and RJ Miller, *personal observation*), but the larvae 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, *Watersipora* larvae were considered passive particles in the model. Particles were released from June through October, the estimated reproductive season for *Watersipora*

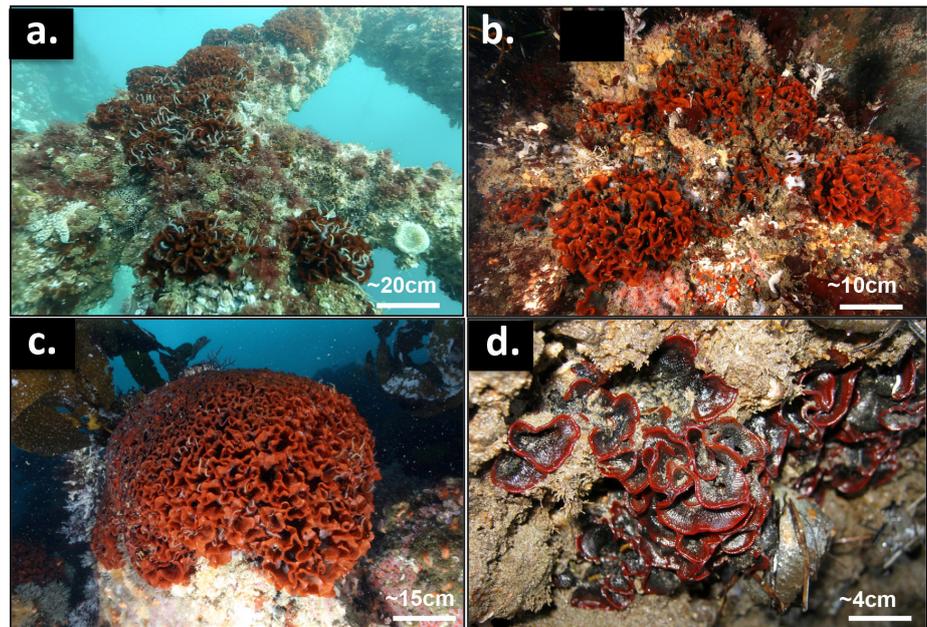


Figure 3. Examples of *Watersipora subatra* from (a) offshore oil and gas Platform B, (b) subtidal rocky reef at Solimar (M11), (c) subtidal rocky reef at Diablo Point, Santa Cruz Island (SC1), and (d) rocky intertidal ledge at Carpinteria (M8). Scale approximate. Photo by B. Doheny.

based on larval recruitment data collected in the study region from 2014 to 2017 (Viola et al. 2018). To avoid an under-sampling error that occurs when too few particles are used in biophysical modeling studies (Simons et al. 2013), a particle release frequency of 3 h was selected, and thus a total of 985,000 particles were released from each source site over the 12-year model period.

To quantify the potential extent of larval dispersal from each platform and harbor source site, particle tracking results were transformed into two-dimensional particle density distributions (PDDs) for 12 and 12 h PLDs following the methods in Simons et al. (2016). Monthly PDDs were calculated using the particles released over one month from a harbor or platform source. The monthly PDDs for each source were then averaged over the reproductive season of June–October for 12 model years (1996–2007) to obtain a long-term monthly average PDD. Potential connectivity was quantified in the form of a source-destination matrix by using the values of the monthly averaged PDDs from each source site, harbors and platforms, at the destination sites, open coastal natural and artificial habitat (Mitarai et al. 2009; Simons et al. 2016). 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.

Results

Distribution and abundance of Watersipora

Watersipora was widely distributed in the SBC (Tables 1 and S1, Figure 2), occurring at 50% of sites along the mainland coast and 43% of the offshore oil platforms. Examples of *Watersipora* on an offshore platform, subtidal rocky reefs, and rocky intertidal habitat are shown in Figure 3. On the

Table 2. Mean percent cover (± 1 se) of *Watersipora subatra* at natural rocky reef and offshore platform survey sites. Cover of *Watersipora* on rocky reefs determined within 0.25 m² plots along a 20 m x 2 m transect. Cover of *Watersipora* on platforms determined within 0.25 m² plots on legs and conductor pipes. Sample size in parentheses. See Methods for details.

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

¹Observed during qualitative swimming surveys only

²Marine Protected Area

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 (M6 and M7) closest (4.5 km) to SBH, it was also found at sites quite distant from the harbor, including the Naples Reef State Marine Conservation Area (M2, SMCA) and in the rocky intertidal at Gaviota (M1), 26.5 and 54 km west, respectively, from SBH (Tables 1 and S1, Figure 2). *Watersipora* was also found 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 greater than 10% cover on vertical surfaces along the three 20 m transects at the two subtidal rocky reefs (M2 and M11) (Table 2).

Watersipora was present on seven of 16 offshore platforms (Figure 2), including the cluster of four platforms (Gail, Gina, Grace, and Gilda) in the eastern SBC originally reported in Simons et al. (2016), three additional platforms (A and B) located 10 km offshore of SBH, and Platform Harmony at the western end of the SBC. Cover on offshore platforms varied from

Table 3. 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 ² | 95% Confidence Interval ² | Percent time with zero connectivity ³ |
|----------------------------|-------------------------------|--------------------------------|---------|-------------------------------------|--------------------------------------|--|
| Santa Barbara Harbor (SBH) | M6/7 | 4.5 | 12 | 2,372 | 2,203–6,837 | 0 |
| | M6/7 | 4.5 | 24 | 3,182 | 2,330–8,030 | 0 |
| | M5 | 13.4 | 24 | 132 | 132–546 | 15 |
| | M3/4 | 20.7 | 24 | 6 | 6–45 | 73 |
| | M2 | 25.1 | 24 | 1 | 1–10 | 85 |
| Platform A/B | M5 | 21.0 | 24 | 1 | 1–6 | 92 |
| Platform Grace | SC4 | 16.4 | 24 | 4 | 4–13 | 92 |

¹Sites within 1 km of each other are combined

²Potential connectivity and 95% confidence interval presented as monthly mean particle density (number of particles km^{-2})

³Percent time with zero connectivity over the study period of June–October 1996–2007

trace amounts on Platform Harmony to exceeding 20% on both vertical and horizontal surfaces at Platform Gail (Table 2; Page et al. 2008; Viola et al. 2018).

Biophysical modeling of larval dispersal and connectivity

We explored the 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 and gas platforms (Harmony, A/B, Grace, Gilda, Gail, and Gina) (Figure 2). 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) (Figure 2). Where sites were less than one kilometer apart and located in the same model grid cell, they were treated as a single site (e.g. platform A/B, M3/4, M6/7, and SC1/2).

Biophysical modeling quantified as PDDs, revealed that simulated *Watersipora* larvae 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 3, Figure 4a, b). There was little difference in the results from a 12 h versus 24 h PLD, except that PDDs with a 24 h PLD extend farther up and down coast over a slightly greater area (Figure 4a, b).

Assuming a 12 h PLD, highest continuous potential connectivity was calculated between SBH and the closest destination reef (M6/7) where *Watersipora* was observed, 4.5 km west of the harbor mouth (Table 3, Figure 5a). However, all other mainland and island sites where *Watersipora* was present show no potential connectivity with harbors for a PLD of 12 h (Table 3, Figure 5a). By increasing the PLD to 24 h, the potential connectivity from SBH expanded to include three other mainland sites (M2, M3/4, and M5) in addition to M6/7, that are rocky reefs, a pier, and a constructed island (Table S1, Figure 5b). However, potential connectivity was still three orders of magnitude higher and continuous for reef sites nearest the harbor (M6/7) compared to the other destination sites (M2, M3/4, and M5) and

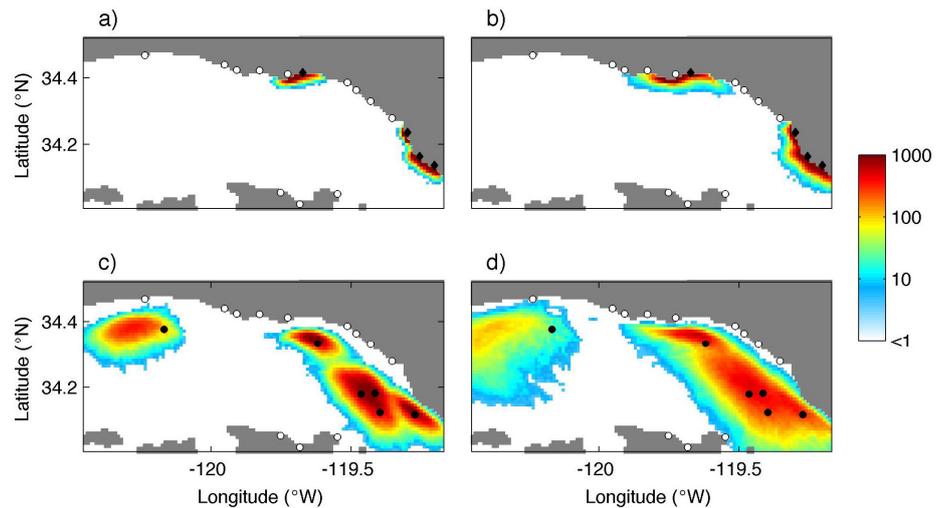


Figure 4. Particle density distributions (PDDs) averaged over 12 years for (a) harbor sources and a PLD of 12 h, (b) harbor sources and a PLD of 24 h, (c) platform sources and a PLD of 12 h, and (d) platform sources and a PLD of 24 h. Black diamonds are harbors (a, b), white circles are destination reef sites (a–d) and black circles identify the platforms (c, d). PDDs from individual sources have been added together. Units are in mean monthly number of particles km^{-2} on a log scale.

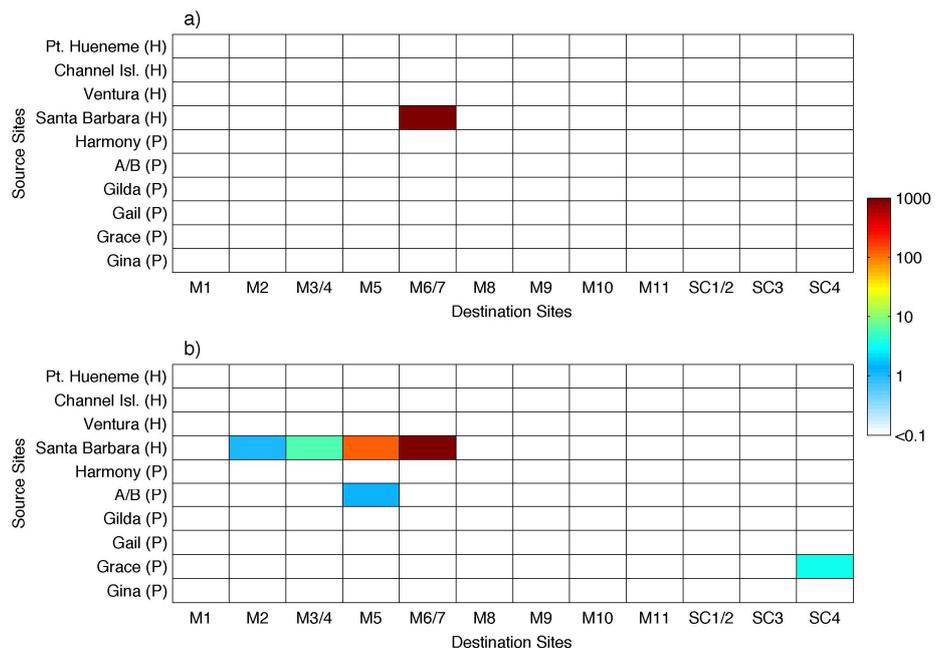


Figure 5. Potential connectivity matrix (log scale) for (a) 12 h PLD and (b) 24 h PLD for *Watersipora*. For the source sites, (H) identifies a harbor and (P) identifies a platform. Units are in mean monthly number of particles km^{-2} .

decreased precipitously, both in particle density and percentage of time connected, for sites with increasing distance from the harbor (Table 3).

In the offshore high-flow environment occupied by the oil platforms, the simulated larvae disperse over a much larger area and with lower particle density (Figure 4c, d), as also shown in Simons et al. (2016) for a subset of platforms. The smallest ellipses were 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

came from the area around platforms Gilda, Gail, and Grace, where the PDDs overlapped one another. The lowest density came from Platform Harmony, where the center of the ellipse was completely advected away from the platform. In a water depth of 392 m, Platform Harmony is the 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 were much more dispersed than the PDDs with a 12 h PLD, covering larger areas with lower particle densities and advecting predominantly towards to the western end of the SBC. This pattern of westward dispersal follows the mean characteristic flow patterns observed in the SBC, which are driven by the poleward flowing Southern California Counter Current (Harms and Winant 1998; Dong et al. 2009).

There was 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 northern Channel Islands. Simons et al. (2016) previously reported “moderate” larval connectivity, assuming a PLD of 24 h, between two harbors (Channel Islands and Port Hueneme) and Platform Gina, located approximately 6–7 km offshore. However, here we found no or extremely weak connectivity between the platforms and any of the natural reef destination sites. The only potential connectivity recorded from a platform to an island site was very weak between Platform Grace and site SC4, a pier on east end of Santa Cruz Island, with monthly mean particle density at only 4 particles km⁻² and no connectivity 92% of the time at a 24 h PLD (Table 3).

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 the prevalence of *Watersipora* on coastal infrastructure in the region, 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 habitats in southern California. Previously, *Watersipora* has been reported in more limited surveys on subtidal rocky reefs in central California near Monterey harbor (Zabin et al. 2018), and at rocky intertidal sites in southern (Pister 2009) and central California (Zabin et al. 2018). Worldwide, the genus appears to be expanding in distribution (e.g., Ryland et al. 2009; Bishop et al. 2015; Porter et al. 2017; Marić et al. 2017), but with few reports of its occurrence in natural open coast habitats (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 habitats via ocean circulation is not clear, and poor larval connectivity could provide one explanation for the relative absence or low

abundance of these species in natural reef habitats. Our modeling reveals high mean and nearly continuous potential larval connectivity between Santa Barbara Harbor and reef sites (Arroyo Burro reefs-M6, Mohawk-M7) located 4.5 km from the harbor, leading to the conclusion that ocean currents could transport *Watersipora*, and other taxa with PLDs of 12 to 24 hours, from the harbor to natural habitats across this distance. Unlike Santa Barbara Harbor, natural rocky reef destination sites for *Watersipora* larvae are much less common in the vicinity of the harbor sites in the eastern SBC (Ventura, Channel Islands, and Port Hueneme) (Johnson et al. 2013), which would limit the ability of *Watersipora* larvae to spread outside of these harbors.

Although our biophysical modeling revealed potential larval connectivity between SBH and the nearest reef site, there was little to no potential connectivity between the harbor and reef sites greater than 4.5 km distant, assuming either a 12 h or 24 h PLD. This lack of potential connectivity implies that the mean magnitude and direction of current flow was insufficient to transport simulated *Watersipora* larvae distances greater than ~ 4.5 km within 24 h. As modeled in this study, potential connectivity provides a robust upper bound estimate of potential larval dispersal distance, as it is 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 larval condition over time that may affect successful settlement and metamorphosis (Marshall and Keogh 2003; Sams et al. 2015). For these reasons, we hypothesize 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 and stability of non-native populations (Lockwood et al. 2005; Clark and Johnston 2009). In addition to estimates of mean potential larval connectivity, our modeling provides an estimate of the percentage of time over the 12-year study period that source and destination sites exhibit zero potential connectivity. For four of the seven source-destination pairs (SBH-M2, SBH-M3/4, Platform A/B-M5, and Platform Grace-SC4) that show greater than zero potential connectivity, 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 (Figure 5, Table 3). Both the very low potential connectivity and high proportion of time with no potential connectivity suggest that *Watersipora* found at these destination sites are unlikely to have originated via direct larval dispersal from harbor or platform sites.

Given the rapid decline in potential connectivity between from SBH to natural and artificial sites at distances of > 4.5 km, we hypothesize that intermediate stepping stone habitat would be required for the dispersal of

Watersipora along the mainland coast beyond this distance. Since *Watersipora* was found 54 km to the west of SBH at site M1, intermediate habitat with *Watersipora* would probably be required for stepwise dispersal to these distant 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 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, requiring visitation of the site by infested boats during the bryozoan's reproductive period and sufficient propagule pressure to enable establishment. 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). Both stepping-stone habitats 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.

We found *Watersipora* at two of 12 natural reefs surveyed (SC1, SC2) and at two piers (SC3, SC4) on Santa Cruz Island within the Channel Islands National Marine Sanctuary. The smallest distance across the SBC from a harbor or platform source site to a destination site within the Channel Islands NMS is ~ 17 km from Platform Grace to the pier at Scorpion Anchorage at Santa Cruz Island. Modeled potential connectivity between these two sites was extremely low (Table 3, Figure 5b). For this reason, we suggest that 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 on Santa Cruz Island, and small boats also regularly visit the vicinity of rocky reef sites (Cabral et al. 2017). The distance between the closest pier (SC3) and reef sites (SC1/2) on Santa Cruz Island is about 8 km, suggesting separate *Watersipora* introductions to these sites, but more information is required on the possible existence of intermediate populations that could serve as stepping stones. The two reef sites (SC1/2) 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 habitats, including nearby Marine Protected Areas. The cover of *Watersipora*, in general, at mainland and Channel Island reefs was found to be higher on vertical than horizontal surfaces (Table 2). Given that island rocky reefs generally possess steeper profiles and more vertical walls overall than mainland reefs (Pondella et al. 2015), the establishment of *Watersipora* at new sites may proceed at a faster rate along the island's coast than on the mainland.

Offshore platforms provide the main source of hard substrate between the mainland coast and the northern Channel Islands (Figure 2), but the use of offshore platforms as stepping stone habitat appears to be unlikely to account for the occurrence of *Watersipora* at Santa Cruz Island sites, since there was little to no potential connectivity from the platforms to the island (Figure 5). 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, 2012a). However, 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, reducing larval connectivity via ocean circulation between the platforms and the northern Channel Islands.

Without further study, the role of anthropogenic vectors in dispersing *Watersipora* within the SBC, though a likely transmission pathway, remains ambiguous and undocumented. The probable role of hull fouling as a vector of initial *Watersipora* introduction to one oil platform (Gilda) was discussed in Simons et al. (2016). Introduction of *Watersipora* could have occurred via service vessels, including crew boats and barges, that can approach and remain in close proximity to a platform, whereas recreational boats are not permitted to tie up or closely approach offshore platforms in the SBC. However, there is no information on whether *Watersipora* is attached to boats that visit platforms or reefs or on the past frequency and pathways of boat traffic that would permit an evaluation of this possible transmission pathway. Nevertheless, anthropogenic transport remains the most viable hypothesis for the introduction of *Watersipora* to offshore platforms and to the northern Channel Islands given the low probability of larval connectivity to possible source populations.

Another possibility that would increase connectivity beyond modeled estimates is the rafting of sexually reproducing colonies into new areas on mobile 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 ocean 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 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 potential connectivity (Table 3). A positive relationship between *Watersipora* abundance and connectivity might be expected if propagule supply from the harbor is

driving abundance (Clark and Johnston 2009). However, *Watersipora* cover along transects at Naples reef (M2) was 50 times higher than at Arroyo Burro (M6) and Mohawk (M7) reefs, which are located in much closer proximity to SBH (Tables 2 and 3), suggesting the importance of local physical and biological factors in influencing *Watersipora* abundance at these sites.

Our findings of potential larval connectivity between SBH and nearby reefs could be extended to other non-native taxa with short PLDs widely reported from the harbors of southern California and worldwide, including 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 species 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) 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 2008, 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, while other non-native epifauna that are also found in harbors are apparently unsuccessful in invading these habitats.

The results of biophysical modeling indicate that potential larval 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 larval connectivity with mainland and northern Channel Island reefs, *Watersipora* on offshore platforms could be a source of propagules to the hulls of service vessels, such as crew boats, barges, and 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. 2012b; 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 propagule sources via the application of best management practices in harbors (Culver et al. 2012; Dafforn 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 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. Biophysical modeling reveals that careful consideration of larval connectivity 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 of these species to natural habitat. 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.

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References

- Adams TP, Miller RG, Aleynik D, Burrows MT (2014) Offshore marine renewable energy devices as stepping stones across biogeographical boundaries. *Journal of Applied Ecology* 51: 330–338, <https://doi.org/10.1111/1365-2664.12207>

- Airoldi L, Turon X, Perkol-Finkel S, Rius M (2015) Corridors for aliens but not for natives: effects of marine urban sprawl at the regional scale. *Diversity and Distributions* 21: 755–768, <https://doi.org/10.1111/ddi.12301>
- Anderson CM, Haygood MG (2007) Alpha-proteobacterial symbionts of marine bryozoans in the genus *Watersipora*. *Applied Environmental Microbiology* 73: 303–311, <https://doi.org/10.1128/aem.00604-06>
- Ashton G, Davidson I, Ruiz G (2014) Transient small boats as a long-distance coastal vector for dispersal of biofouling organisms. *Estuaries and Coasts* 37: 1572–1581, <https://doi.org/10.1007/s12237-014-9782-9>
- Baguette M, Blanchet S, Legerand D, Stevens VM, Turlure C (2013) Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews* 88: 310–326, <https://doi.org/10.1111/brv.12000>
- Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy* 27: 313–323, [https://doi.org/10.1016/s0308-597x\(03\)00041-1](https://doi.org/10.1016/s0308-597x(03)00041-1)
- Bishop J, Wood C, Yunnice A, Griffiths C (2015) Unheralded arrivals: non-native sessile invertebrates in marinas on the English coast. *Aquatic Invasions* 10: 249–264, <https://doi.org/10.3391/ai.2015.10.3.01>
- Bradbury IR, Snelgrove PVR (2001) Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 811–823, <https://doi.org/10.1139/cjfas-58-4-811>
- Brooks CP (2003) A scalar analysis of landscape connectivity. *Oikos* 102: 433–439, <https://doi.org/10.1034/j.1600-0579.2003.11511.x>
- Bulleri F, Airoldi L (2005) Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology* 42: 1063–1072, <https://doi.org/10.1111/j.1365-2664.2005.01096.x>
- Cabral RB, Gaines SD, Johnson BA, Bell TW, White C (2017) Drivers of redistribution of fishing and non-fishing effort after the implementation of a marine protected area network. *Ecological Applications* 27: 416–428, <https://doi.org/10.1002/eap.1446>
- Carlton JT, Geller JB (1993) Ecological roulette - the global transport of nonindigenous marine organisms. *Science* 261: 78–82, <https://doi.org/10.1126/science.261.5117.78>
- Carr SD, Capet XJ, McWilliams JC, Pennington JT, Chavez FP (2008) The influence of diel vertical migration on zooplankton transport and recruitment in an upwelling region: estimates from a coupled behavioral-physical model. *Fisheries Oceanography* 17: 1–15, <https://doi.org/10.1111/j.1365-2419.2007.00447.x>
- CDFG (2008) California Department of Fish and Game. Introduced aquatic species in the marine and estuarine waters of California. Appendix C, Introduced and Cryptogenic Species in California by Location. <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=15404>
- Chia FS, Bucklandnicks J, Young CM (1984) Locomotion of marine invertebrate larvae - a review. *Canadian Journal of Zoology* 62: 1205–1222, <https://doi.org/10.1139/z84-176>
- Clark GF, Johnston EL (2009) Propagule pressure and disturbance interact to overcome biotic resistance of marine invertebrate communities. *Oikos* 118: 1679–1686, <https://doi.org/10.1111/j.1600-0706.2009.17564.x>
- Cohen AN (2011) The Exotics Guide: Non-native marine species of the North American Pacific Coast. Center for Research on Aquatic Bioinvasions, Richmond, CA, and San Francisco Estuary Institute, Oakland, CA. <https://www.exoticguide.org/>
- Cohen AN, Harris LH, Bingham BL, Carlton JT, Chapman JW, Lambert CC, Lambert G, Ljubenkov JC, Murray SN, Rao LC, Reardon K, Schwindt E (2005) Rapid assessment survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. *Biological Invasions* 7: 995–1002, <https://doi.org/10.1007/s10530-004-3121-1>
- Costello C, Rassweiler A, Siegel D, De Leo G, Micheli F, Rosenberg A (2010) The value of spatial information in MPA network design. *Proceedings of the National Academy of Sciences of the United States of America* 107: 18294–18299, <https://doi.org/10.1073/pnas.0908057107>
- Cowden C, Young C, Chia F (1984) Differential predation on marine invertebrate larvae by two benthic predators. *Marine Ecology Progress Series* 14: 145–149, <https://doi.org/10.3354/meps014145>
- Culver CS, Johnson LT, Lande MD (2012) IPM for Boats: Integrated Pest Management for Hull Fouling in Southern California Coastal Marinas. UCCE-SD Technical Report No. 2012-2 California Sea Grant College Program Report No. T-074, 28 pp, <http://ucanr.org/sites/coast/publications>
- Dafforn K (2017) Eco-engineering and management strategies for marine infrastructure to reduce establishment and dispersal of non-indigenous species. *Management of Biological Invasions* 8: 153–161, <https://doi.org/10.3391/mbi.2017.8.2.03>
- Dafforn KA, Glasby TM, Johnston EL (2012) Comparing the invasibility of experimental “reefs” with field observations of natural reefs and artificial structures. *PLoS ONE* 7: e38124, <https://doi.org/10.1371/journal.pone.0038124>

- Davidson IC, Zabin CJ, Chang AL, Brown CW, Sytsma MD, Ruiz GM (2010) Recreational boats as potential vectors of marine organisms at an invasion hotspot. *Aquatic Biology* 11: 179–191, <https://doi.org/10.3354/ab00302>
- deRivera CE, Ruiz GM, Crooks JA, Wasson K, Lonhart SI, Fofonoff P, Steves BP, Rumrill SS, Brancato MS, Pegau WS, Bulthuis DA, Preisler RK, Schoch GC, Bowlby E, DeVogelaere A, Crawford MK, Gittings SR, Hines, AH, Takata L, Larson K, Huber T, Leyman AM, Collinetti E, Pasco T, Shull S, Anderson M, Powell S (2005) Broad-scale non-indigenous species monitoring along the West Coast in national marine sanctuaries and national estuarine research reserves. Report to the National Fish and Wildlife Foundation, Washington DC, 125 pp
- Dong CM, McWilliams JC (2007) A numerical study of island wakes in the Southern California Bight. *Continental Shelf Research* 27: 1233–1248, <https://doi.org/10.1016/j.csr.2007.01.016>
- Dong CM, Idica EY, McWilliams JC (2009) Circulation and multiple-scale variability in the Southern California Bight. *Progress in Oceanography* 82: 168–190, <https://doi.org/10.1016/j.pocan.2009.07.005>
- Dong CM, McWilliams JC, Hall A, Hughes M (2011) Numerical simulation of a synoptic event in the Southern California Bight. *Journal of Geophysical Research-Oceans* 116: C05018, 20 pp, <https://doi.org/10.1029/2010jc006578>
- Dumont C, Harris L, Gaymer C (2011a) Anthropogenic structures as a spatial refuge from predation for the invasive bryozoan *Bugula neritina*. *Marine Ecology Progress Series* 427: 95–103, <https://doi.org/10.3354/meps09040>
- Dumont CP, Gaymer CF, Thiel M (2011b) Predation contributes to invasion resistance of benthic communities against the non-indigenous tunicate *Ciona intestinalis*. *Biological Invasions* 13: 2023–2034, <https://doi.org/10.1007/s10530-011-0018-7>
- Ehrenfeld JG (2010) Ecosystem Consequences of Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics* 41: 59–80, <https://doi.org/10.1146/annurev-ecolsys-102209-144650>
- Epstein G, Smale DA (2018) Environmental and ecological factors influencing the spillover of the non-native kelp, *Undaria pinnatifida*, from marinas into natural rocky reef communities. *Biological Invasions* 20: 1049–1072, <https://doi.org/10.1007/s10530-017-1610-2>
- Floerl O, Pool TK, Inglis GJ (2014) Positive interactions between nonindigenous species facilitate transport by human vectors. *Ecological Applications* 14: 1724–1736, <https://doi.org/10.1890/03-5399>
- Forrest BM, Fletcher LM, Atalah J, Piola RF, Hopkins GA (2013) Predation limits spread of *Didemnum vexillum* into natural habitats from refuges on anthropogenic structures. *PLoS ONE* 8: e82229, <https://doi.org/10.1371/journal.pone.0082229>
- Glasby TM, Connell SD, Holloway MG, Hewitt CL (2007) Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Marine Biology* 151: 887–895, <https://doi.org/10.1007/s00227-006-0552-5>
- Harms S, Winant CD (1998) Characteristic patterns of the circulation in the Santa Barbara Channel. *Journal of Geophysical Research-Oceans* 103: 3041–3065, <https://doi.org/10.1029/97jc02393>
- Hellberg ME, Burton RS, Neigel JE, Palumbi SR (2002) Genetic assessment of connectivity among marine populations. *Bulletin of Marine Science* 70: 273–290
- Henry L-A, Mayorga-Adame CG, Fox AD, Polton JA, Ferris JS, McLellan F, McCabe C, Kutti T, Roberts JM (2018) Ocean sprawl facilitates dispersal and connectivity of protected species. *Science Reports* 8: 11346, <https://doi.org/10.1038/s41598-018-29575-4>
- Hui C, Krug RM, Richardson DM (2011) Modeling spread in invasion ecology: a synthesis. Chapter 25. In: Richardson DM (ed), *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*, 1st edn. Wiley-Blackwell, Oxford, UK, pp 329–343, <https://doi.org/10.1002/9781444329988.ch25>
- Johnson SY, Dartnell P, Cochrane GR, Golden NE, Phillips EL, Ritchie AC, Kvitek RG, Greene HG, Krigsman LM, Endris CA, Seitz GG, Gutierrez CI, Sliter RW, Erdey MD, Wong FL, Yoklavich MM, Draut AE, Hart PH (2013) California State Waters Map Series—Offshore of Ventura, California: U.S. Geological Survey Scientific Investigations Map 3254, pamphlet 42 pp, 11 sheets, <https://doi.org/10.3133/sim3254>
- Knott NA, Underwood AJ, Chapman MG, Glasby TM (2004) Epibiota on vertical and on horizontal surfaces on natural reefs and on artificial structures. *Journal of the Marine Biological Association of the United Kingdom* 84: 1117–1130, <https://doi.org/10.1017/s0025315404010550h>
- Kuhlenkamp R, Kind B (2013) Arrival of the invasive *Watersipora subtorquata* (Bryozoa) at Helgoland (Germany, North Sea) on floating macroalgae (*Himantalia*). *Marine Biodiversity Records* 6: e73, <https://doi.org/10.1017/s1755267213000481>
- Kvilekval K, Fedorov D, Obara B, Singh A, Manjunath BS (2010) Bisque: a platform for bioimage analysis and management. *Bioinformatics* 26: 544–552, <https://doi.org/10.1093/bioinformatics/btp699>

- Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integrative and Comparative Biology* 46: 282–297, <https://doi.org/10.1093/icb/icj024>
- Levin PS, Coyer JA, Petrik R, Good TP (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. *Ecology* 83: 3182–3193, [https://doi.org/10.1890/0012-9658\(2002\)083\[3182:cweons\]2.0.co;2](https://doi.org/10.1890/0012-9658(2002)083[3182:cweons]2.0.co;2)
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20: 223–228, <https://doi.org/10.1016/j.tree.2005.02.004>
- Love MS, Schroeder DM, Nishimoto MM (2003) The ecological role of oil and gas production platforms and natural outcrops on fishes in southern and central California: a synthesis of information. United States Department of the Interior, United States Geological Survey, Biological Resources Division, Seattle, Washington, 98104, Outer Continental Shelf Study (OCS) Mineral Management Service (MMS) 2003-032, <https://doi.org/10.5962/bhl.title.149923>
- Mack R (2000) Assessing the extent, status, and dynamism of plant invasions: current and emerging approaches. Chapter 7. In: Mooney HA, Hobbs RJ (eds), *Invasive species in a changing world*. Island Press, Washington, D.C., pp 141–168
- Mackie JA, Darling JA, Geller JB (2012) Ecology of cryptic invasions: latitudinal segregation among *Watersipora* (Bryozoa) species. *Science Reports* 2: 871, <https://doi.org/10.1038/srep00871>
- Macreadie PI, Fowler AM, Booth DJ (2011) Rigs-to-reefs: Will the deep sea benefit from artificial habitat? *Frontiers in Ecology and the Environment* 9: 455–461, <https://doi.org/10.1890/100112>
- Malherbe H, Samways M (2014) Rocky shores of a major southern African Marine Protected Area are almost free from intertidal invertebrate alien species. *Koedoe* 56: 1206, <https://doi.org/10.4102/koedoe.v56i1.1206>
- Marić M, Ferrario J, Marchini A, Marchini A, Occhipinti-Ambrogi, Minchin D (2017) Rapid assessment of marine non-indigenous species on mooring lines of leisure craft: new records in Croatia (eastern Adriatic Sea). *Marine Biodiversity* 47: 949–956, <https://doi.org/10.1007/s12526-016-0541-y>
- Marshall DJ, Keough MJ (2003) Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. *Marine Ecology Progress Series* 255: 145–153, <https://doi.org/10.3354/meps255145>
- McCuller M, Carlton J (2018) Transoceanic rafting of Bryozoa (Cyclostomata, Cheilostomata, and Ctenostomata) across the North Pacific Ocean on Japanese tsunami marine debris. *Aquatic Invasions* 13: 137–162, <https://doi.org/10.3391/ai.2018.13.1.11>
- Mileikovsky SA (1974) On predation of pelagic larvae and early juveniles of marine bottom invertebrates by adult benthic invertebrates and their passing alive through their predators. *Marine Biology* 26: 303–311, <https://doi.org/10.1007/bf00391514>
- Miller R, Etter R (2008) Shading facilitates sessile invertebrate dominance in the rocky subtidal Gulf of Maine. *Ecology* 89: 452–462, <https://doi.org/10.1890/06-1099.1>
- Miller R, Etter R (2011) Rock walls: small-scale diversity hotspots in the subtidal Gulf of Maine. *Marine Ecology Progress Series* 425: 153–165, <https://doi.org/10.3354/meps09025>
- Mineur F, Cook EJ, Minchin D, Bohn K, MacLeod A, Maggs CA (2012) Changing Coasts: Marine aliens and artificial structures. *Oceanography and Marine Biology: An Annual Review* 50: 189–234, <https://doi.org/10.1201/b12157-5>
- Mitarai S, Siegel DA, Watson JR, Dong C, McWilliams JC (2009) Quantifying connectivity in the coastal ocean with application to the Southern California Bight. *Journal of Geophysical Research-Oceans* 114: C10026, <https://doi.org/10.1029/2008jc005166>
- Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States* 98: 5446–5451, <https://doi.org/10.1073/pnas.091093398>
- Needles LA, Gosnell JS, Waltz GT, Wendt DE, Gaines SD (2015) Trophic cascades in an invaded ecosystem: native keystone predators facilitate a dominant invader in an estuarine community. *Oikos* 124: 1282–1292, <https://doi.org/10.1111/oik.01865>
- Ng TYT, Keough MJ (2003) Delayed effects of larval exposure to Cu in the bryozoan *Watersipora subtorquata*. *Marine Ecology Progress Series* 257: 77–85, <https://doi.org/10.3354/meps257077>
- Osman RW, Whitlatch RB (1995) The influence of resident adults on recruitment: a comparison to settlement. *Journal of Experimental Marine Biology and Ecology* 190: 169–198, [https://doi.org/10.1016/0022-0981\(95\)00035-p](https://doi.org/10.1016/0022-0981(95)00035-p)
- Page HM, Dugan JE, Dugan DS, Richards JB, Hubbard DM (1999) Effects of an offshore oil platform on the distribution and abundance of commercially important crab species. *Marine Ecology Progress Series* 185: 47–57, <https://doi.org/10.3354/meps185047>
- Page HM, Dugan JE, Culver CS, Hoesterey JC (2006) Exotic invertebrate species on offshore oil platforms. *Marine Ecology Progress Series* 325: 101–107, <https://doi.org/10.3354/meps325101>

- Page HM, Culver CS, Dugan JE, Mardian B (2008) Oceanographic gradients and patterns in invertebrate assemblages on offshore oil platforms. *Journal of Marine Science* 65: 851–861, <https://doi.org/10.1093/icesjms/fsn060>
- Pister B (2009) Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. *Marine Biology* 156: 861–873, <https://doi.org/10.1007/s00227-009-1130-4>
- Pondella II D, Williams JP, Claisse J, Schaffner R, Ritter K, Schiff K (2015) The physical characteristics of nearshore rocky reefs in the Southern California Bight. *Bulletin of the Southern California Academy of Sciences* 114: 105–122, <https://doi.org/10.3160/0038-3872-112.3.217>
- Porter J, Nunn JD, Ryland JS, Minchin D, Spencer Jones ME (2017) The status of non-native bryozoans on the north coast of Ireland. *BioInvasions Records* 6: 321–330, <https://doi.org/10.3391/bir.2017.6.4.04>
- Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278: 1454–1457, <https://doi.org/10.1126/science.278.5342.1454>
- Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. *American Zoologist* 37: 621–632, <https://doi.org/10.1093/icb/37.6.621>
- Ruiz GM, Freestone AL, Folonoff PW, Simkanin C (2009) Habitat distribution and heterogeneity in marine invasion dynamics: the importance of hard substrate and artificial structure. In: Wahl M (ed), *Marine hard bottom communities: patterns, dynamics, diversity, and change*. Ecological Studies, Springer-Verlag, Berlin Heidelberg, pp 321–332, https://doi.org/10.1007/b76710_23
- Ryland JS (1960) Experiments on the influence of light on the behaviour of polyzoan larvae. *Journal of Experimental Biology* 37: 783–800
- Ryland JS, De Blauwe H, Lord R, Mackie JA (2009) Recent discoveries of alien *Watersipora* (Bryozoa) in Western Europe, with redescription of species. *Zootaxa* 2093: 43–59
- Sammarco PW, Atchison AD, Boland GS (2004) Expansion of coral communities within the Northern Gulf of Mexico via offshore oil and gas platforms. *Marine Ecology Progress Series* 280: 129–143, <https://doi.org/10.3354/meps280129>
- Sammarco PW, Atchison AD, Boland GS, Sinclair J, Lirette A (2012a) Geographic expansion of hermatypic and ahermatypic corals in the Gulf of Mexico, and implications for dispersal and recruitment. *Journal of Experimental Marine Biology and Ecology* 436–437: 36–49, <https://doi.org/10.1016/j.jembe.2012.08.009>
- Sammarco PW, Brazeau DA, Sinclair J (2012b) Genetic connectivity in scleractinian corals across the northern Gulf of Mexico: Oil/gas platforms, and relationship to the Flower Garden Banks. *PLoS ONE* 7: 25–29, <https://doi.org/10.1371/journal.pone.0030144>
- Sams MA, Warren-Myers F, Keough MJ (2015) Increased larval planktonic duration and post-recruitment competition influence survival and growth of the bryozoan *Watersipora subtorquata*. *Marine Ecology Progress Series* 531: 179–191, <https://doi.org/10.3354/meps11339>
- Santschi CAT (2012) Spatial patterns in recruitment and development of the assemblage of sessile epibenthic invertebrates in Santa Barbara harbor. Master of Arts in Ecology, Evolution and Marine Biology Thesis. University of California, Santa Barbara, 62 pp
- Sellheim K, Stachowicz JJ, Coates RC (2010) Effects of a nonnative habitat-forming species on mobile and sessile epifaunal communities. *Marine Ecology Progress Series* 398: 69–80, <https://doi.org/10.3354/meps08341>
- Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modeling* 9: 347–404, <https://doi.org/10.1016/j.ocemod.2004.08.002>
- Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what’s what and the way forward. *Trends in Ecology and Evolution* 28: 58–66, <https://doi.org/10.1016/j.tree.2012.07.013>
- Simkanin C, Davidson IC, Dower JF, Jamieson G, Therriault TW (2012) Anthropogenic structures and the infiltration of natural benthos by invasive ascidians. *Marine Ecology* 33: 499–511, <https://doi.org/10.1111/j.1439-0485.2012.00516.x>
- Simons RD, Siegel DA, Brown KS (2013) Model sensitivity and robustness in the estimation of larval transport: A study of particle tracking parameters. *Journal of Marine Systems* 119: 19–29, <https://doi.org/10.1016/j.jmarsys.2013.03.004>
- Simons RD, Nishimoto MM, Washburn L, Brown KS, Siegel DA (2015) Linking kinematic characteristics and high concentrations of small pelagic fish in a coastal mesoscale eddy. *Deep-Sea Research Part 1: Oceanographic Research Papers* 100: 34–47, <https://doi.org/10.1016/j.dsr.2015.02.002>
- Simons RD, Page HM, Zaleski S, Miller R, Dugan JE, Schroeder DM, Doheny B (2016) The effects of anthropogenic structures on habitat connectivity and the potential spread of non-native invertebrate species in the offshore environment. *PLoS ONE* 11: e0152261, <https://doi.org/10.1371/journal.pone.0152261>

- Vieira LM, Jones MS, Taylor PD (2014) The identity of the invasive fouling bryozoan *Watersipora subtorquata* (d'Orbigny) and some other congeneric species. *Zootaxa* 3857: 151–182, <https://doi.org/10.11646/zootaxa.3857.2.1>
- Viola SM, Page HM, Zaleski SF, Miller RJ, Doheny B, Dugan JE, Schroeder DM, Schroeter SC (2018) Anthropogenic disturbance facilitates a non-native species on offshore oil platforms. *Journal of Applied Ecology* 55: 1583–1593, <https://doi.org/10.1111/1365-2664.13104>
- Wasson K, Fenn K, Pearse JS (2005) Habitat differences in marine invasions of Central California. *Biological Invasions* 7: 935–948, <https://doi.org/10.1007/s10530-004-2995-2>
- Watson JR, Mitarai S, Siegel DA, Caselle JE, Dong C, McWilliams JC (2010) Realized and potential larval connectivity in the southern California bight. *Marine Ecology Progress Series* 401: 31–48, <https://doi.org/10.3354/meps08376>
- Williamson MH (1996) *Biological Invasions*. 1st ed. Chapman & Hall, London, New York, 244 pp
- Winant CD, Dever EP, Hendershott MC (2003) Characteristic patterns of shelf circulation at the boundary between central and southern California. *Journal of Geophysical Research - Oceans* 108: C2, 3021, <https://doi.org/10.1029/2001jc001302>
- Zabin C (2014) Small boats provide connectivity for nonindigenous marine species between a highly invaded international port and nearby coastal harbors. *Management of Biological Invasions* 5: 97–112, <https://doi.org/10.3391/mbi.2014.5.2.03>
- Zabin CJ, Marraffini M, Lonhart SI, McCann L, Ceballos L, King C, Watanabe J, Pearse JS, Ruiz GM (2018) Non-native species colonization of highly diverse, wave swept outer coast habitats in Central California. *Marine Biology* 165: 31, <https://doi.org/10.1007/s00227-018-3284-4>

Supplementary material

The following supplementary material is available for this article:

Table S1. Sites surveyed for *Watersipora subatra*.

Figure S1. Model domain of Southern California Bight. The Santa Barbara Channel and study area are identified by the red box.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2019/Supplements/AI_2019_Page_et_al_SupplementaryTable.xlsx

http://www.reabic.net/aquaticinvasions/2019/Supplements/AI_2019_Page_et_al_SupplementaryFigure.pdf