


Anthropogenic disturbance facilitates a non-native species on offshore oil platforms

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Abstract

1. Anthropogenic practices that facilitate species introductions must be identified and modified to improve management and control the spread of non-native taxa in many environments. Maintenance practices that remove dense epifaunal invertebrates attached to offshore structures create a disturbance that may facilitate the establishment of non-native species.
2. We evaluated the effect of disturbance on the abundance (percent cover) of a non-native bryozoan, *Watersipora subatra*, on an offshore oil platform in the Santa Barbara Channel, USA by removing the existing epifaunal community in experimental plots and comparing *Watersipora* cover in these plots to that in undisturbed control plots over a 15-month period. We explored the importance of larval supply and the epifaunal community in driving observed patterns, using measurements of *Watersipora* larval availability and colony recruitment and growth in the disturbed and control plots. We also examined the effect of disturbance on *Watersipora* establishment at the larger, platform-scale over c. 18 months with comparative surveys of cleaned and uncleaned portions of another oil platform.
3. Both the experimental disturbance and the larger platform cleaning facilitated *Watersipora* establishment, with cover increasing from c. 5% to 20–60% at shallower (≤ 12 m) depths within 15 to 18 months following disturbance.
4. Initial *Watersipora* recruitment to the disturbed plots occurred during a period of elevated larval availability, as indicated by recruitment onto settlement plates. However, 1 year after the experimental disturbance, sessile invertebrates occupied all available settlement space, and there was little recruitment of *Watersipora* into disturbed plots despite the availability of larvae.
5. *Synthesis and applications.* Maintenance operations for offshore structures can include the manual removal of subtidal epibenthic invertebrates attached to the structure. Our study at offshore oil platforms found that this anthropogenic disturbance enhanced the establishment of the non-native invertebrate *Watersipora subatra*. The timing of disturbance relative to *Watersipora*'s reproductive season was an important driver of this pattern. Scheduling maintenance practices to occur soon after the reproductive period of *Watersipora* could allow adequate time for

native species to recruit and occupy the available bare space, thereby reducing the potential for establishment of this non-native species.

KEYWORDS

artificial habitat, disturbance, epibenthic invertebrates, non-native species, offshore structures, oil platforms, recruitment, *Watersipora subatra*

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 (De Mesel, Kerckhof, Norro, Rumes, & Degraer, 2015; Page, Dugan, Culver, & Hoesterey, 2006; Sammarco, Porter, Sinclair, & Genazzio, 2014). These artificial islands may serve as “stepping stones” of habitat that increase regional connectivity via planktonic larval dispersal, thereby facilitating species range expansions (Adams, Miller, Aleynik, & Burrows, 2014; Sheehy & Vik, 2009; 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 (Adams et al., 2014; Sheehy & Vik, 2009; Simons et al., 2016), because non-native species can negatively impact community composition and ecosystem function (Levin, Coyer, Petrik, & Good, 2002; Needles & Wendt, 2013; Sellheim, Stachowicz, & Coates, 2010). Because thousands of offshore energy structures exist worldwide and thousands more are planned (EWEA, 2016; Parente, Ferreira, Moutinho dos Santos, & Estanislau, 2006), 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, Dugan, & Piltz, 2010; Van der Stap, Coolen, & Lindebloom, 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 (Cowden, Young, & Chia, 1984; Mileikovskiy, 1974; Young & Gotelli, 1984), pre-empting space (Levin et al., 2002; Osman & Whitlatch, 1995a, 1995b), or reducing the growth, reproduction, and survival of recruits (Claar, Edwards, & Stachowicz, 2011; Clark & Johnston, 2009). Because some epifaunal invertebrates recruit in seasonal pulses (Stachowicz & 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 & 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, Jones, & Taylor, 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 (CDFG, 2008; Cohen et al., 2005). *Watersipora*'s global distribution includes Australia, Brazil, Japan and New Zealand, and it was recently reported in Europe (Bishop, Wood, Yunnice, & Griffiths, 2015; Vieira et al., 2014). Like other bryozoans, *Watersipora* has a short (<24 hr) non-feeding larval stage (Ng & Keough, 2003; Wisley, 1958) 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, Pool, & Inglis, 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 & Byrnes, 2006). Once established, this bryozoan can persist and spread to other artificial and natural habitats (Needles & Wendt, 2013; Simons et al., 2016; Sorte & Stachowicz, 2011).

We investigated the influence of disturbance in facilitating *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.

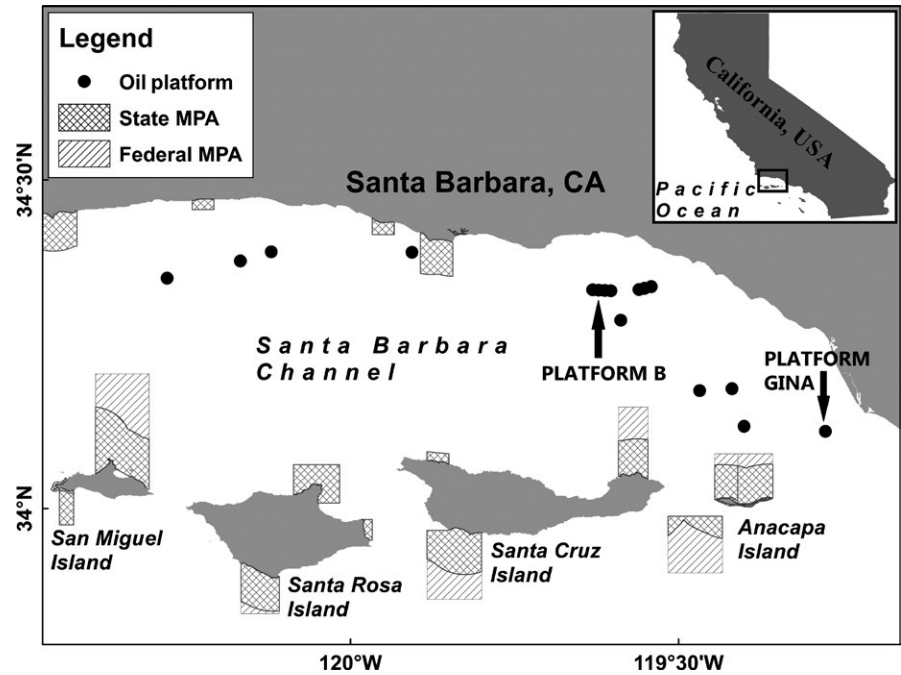


FIGURE 1 Map showing location of the study platforms in the Santa Barbara Channel

2 | MATERIALS AND METHODS

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 (Figure 1). Platform B (34°19'N, 119°37'W), installed in 1968, is located c. 9 km offshore in a water depth c. 58 m and platform Gina (34°07'N, 119°16'W), installed in 1981, is c. 6 km offshore in a depth of c. 30 m. The two platforms differ in size (platform footprint at the seafloor: B: 48 × 40 m, Gina: 28 × 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.

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 × 0.62 m (0.25 m²) 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 × 0.62 m quadrat frame (Page, Culver, Dugan, & Mardian, 2008). The plots were re-photographed approximately every 2 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/bisque>, 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 ($p < .001$, Table S1), the effects of treatment and depth at each time were evaluated (Table S2). Percent cover data were arcsine-transformed ($x' = \arcsine(\sqrt{x})$) prior to analysis.

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 cm² unglazed ceramic tile attached to a 16 × 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 & Kotze, 2010), with depth and time as fixed factors. On finding a significant interaction between depth and time ($p < .001$, Table S3), the effects of depth at each time, and time for each depth, were evaluated (Table S4).

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 mm², medium: 5–1,000 mm², large: >1,000 mm²) 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 ($p < .05$, Table S5), the effects of treatment and depth for each time were evaluated, using generalized linear models assuming a Poisson distribution (Table S6). 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.

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 & 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 c. 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 m² 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, & 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 & July 2015). On finding a significant interaction between treatment and time ($p < .001$, Table S7), the effects of time for each treatment and treatment at each time were evaluated (Table S8). All analyses were conducted using SPSS 24 (IBM), and PERMANOVA+ for PRIMER (PRIMER-E Ltd).

3 | RESULTS

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 tubicolous amphipods (10%–20%), hydroids (10%–20%), barnacles (5%–10%) and sponges (c. 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 (Figure 2).

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 (Figure 3a–c). In the control plots, epifaunal invertebrates occupied 100% of the primary space for the duration of the experiment (Figure 3a–c). *Watersipora* cover increased significantly over time in the disturbed (time, $F_{7,67.538} = 10.378$, $p < .001$), but not control (time, $F_{7,69.332} = 1.724$, $p = .118$) plots, and was significantly higher in the disturbed compared to the control plots in all weeks except week

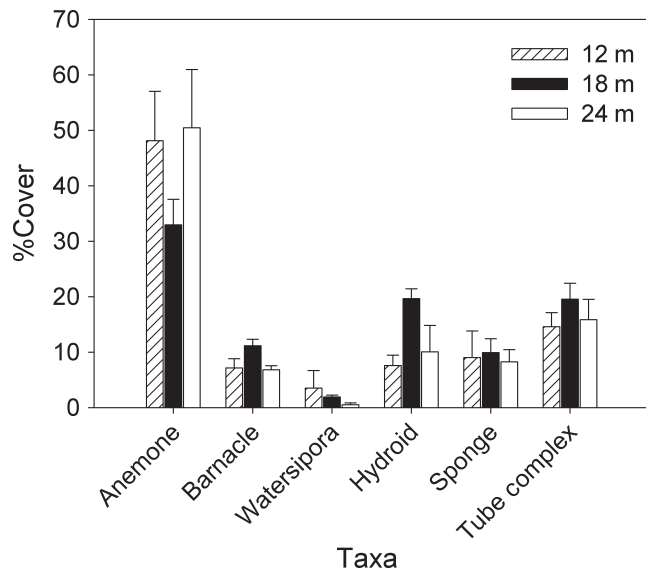


FIGURE 2 Initial invertebrate community composition on the conductor pipes of Platform B in August 2014 at depths of 12, 18 and 24 m. Mean cover $\pm 1SE$, $n = 4$ plots/depth

44 ($p < .05$, Table S2). *Watersipora* cover also varied consistently with depth beginning at week 35, with no interaction between treatment and depth for any time period ($p > .09$, Table S2). At 12 and 18 m, mean cover of *Watersipora* in the disturbed plots ranged from 6%–20% to 7%–16%, respectively, compared with 2%–9% and <1%–6% in the control plots (Figure 3d–f). At 24 m, mean cover of *Watersipora* remained low during the experiment in both the disturbed (<5%) and control plots (<1%, Figure 3d–f).

3.2 | Spatial and temporal patterns in abundance of *Watersipora* larvae

Watersipora recruitment onto ceramic tiles varied with time at each depth ($p \leq .005$, Table S4a). In both 2014 and 2015, recruitment occurred primarily in late summer–fall, with negligible recruitment during the rest of the year (Figure 3g–i, Figure S1). 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 ($p < .05$, Wilcoxon pairwise test, Figure 3g–i).

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 mm²) colonies, was higher in disturbed compared to control plots up to 19 weeks ($p < .001$, Table S6, Figure 4a–c). In addition to higher densities of recruits, the disturbed plots had a consistently higher density of medium colonies (5–1,000 mm²) from 9 weeks to the end of the experiment ($p < .001$, Table S6a,b, Figure 5d–i). Finally, the densities of large *Watersipora* colonies (>1,000 mm²) were generally higher in the disturbed compared with the control plots from 27 weeks to the end of the

experiment ($p \leq .03$, Table S6a,b, Figure 4d–i), with a significant depth effect from 9 weeks on ($p < .05$, Table S6a, Figure 5d–i).

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, ($p < .001$, $R^2 = .31$; Figure 5a). 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) ($p = .8$, Figure 5b). 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 ($p > .05$; Figure 5a,b).

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, $p = .30$, $pseudo-F_{1,12} = 1.256$) or depths (6 vs. 12 m, $p = .38$, $pseudo-F_{1,12} = 1.011$) prior to maintenance cleaning (Two-way PERMANOVA, Figure 6a,b). *Watersipora* cover also did not differ significantly between locations ($p = .39$, $pseudo-F_{1,12} = 0.853$) or depths ($p = .26$, $pseudo-F_{1,12} = 1.362$) 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) (Figure 6a,b).

Watersipora cover on the conductor pipes and legs was <20% in August 2014 (Figure 7). 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 ($p < .05$, Table S8, Figure 7a,b). *Watersipora* cover did not differ significantly between depths of 9 and 12 m (depth, $p > .05$, Tables S7 and S8).

4 | DISCUSSION

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 (Bracewell, Robinson, Firth, & Knights, 2013; Bulleri & Airoidi, 2005; Clark & Johnston, 2009) 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.

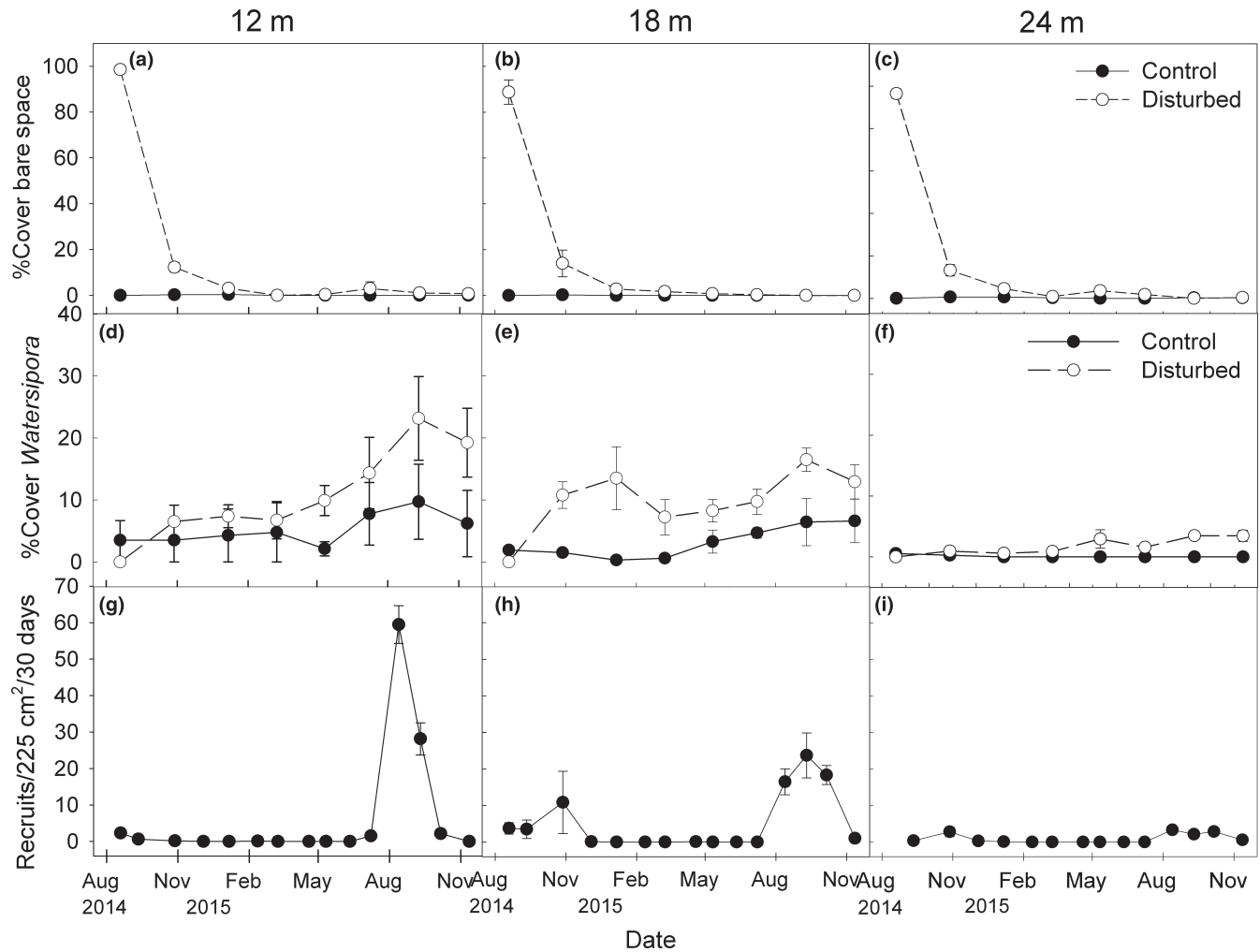


FIGURE 3 (a–c): Availability of bare space over time at depths of 12 m (a), 18 m (b), and 24 m (c) in the disturbed and control plots on Platform B. Mean cover $\pm 1SE$, $n = 4$ plots/depth. (d–f): *Watersipora* cover over time in the disturbed and control plots at 12 m (d) 18 m (e), and 24 m (f) on Platform B. Mean cover $\pm 1SE$, $n = 4$ 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 $\pm 1SE$, $n = 4$ plates/depth

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 (Needles & Wendt, 2013; Sorte & Stachowicz, 2011).

Watersipora's ability to opportunistically occupy and maintain space may have consequences for community composition and ecosystem function on offshore structures. Disturbance shifted the 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 & Haygood, 2007; Floerl et al., 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 (Sellheim et al., 2010; Stachowicz & Byrnes, 2006). 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.

4.2 | Controls on *Watersipora* abundance

Settlement space is widely recognized as the limiting resource in benthic communities (Stachowicz, Fried, Osman, & Whitlatch, 2002; Stachowicz, Whitlatch, & Osman, 1999). Because the availability of limiting resources can determine a community's vulnerability to invasion (Davis, Grime, & Thompson, 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

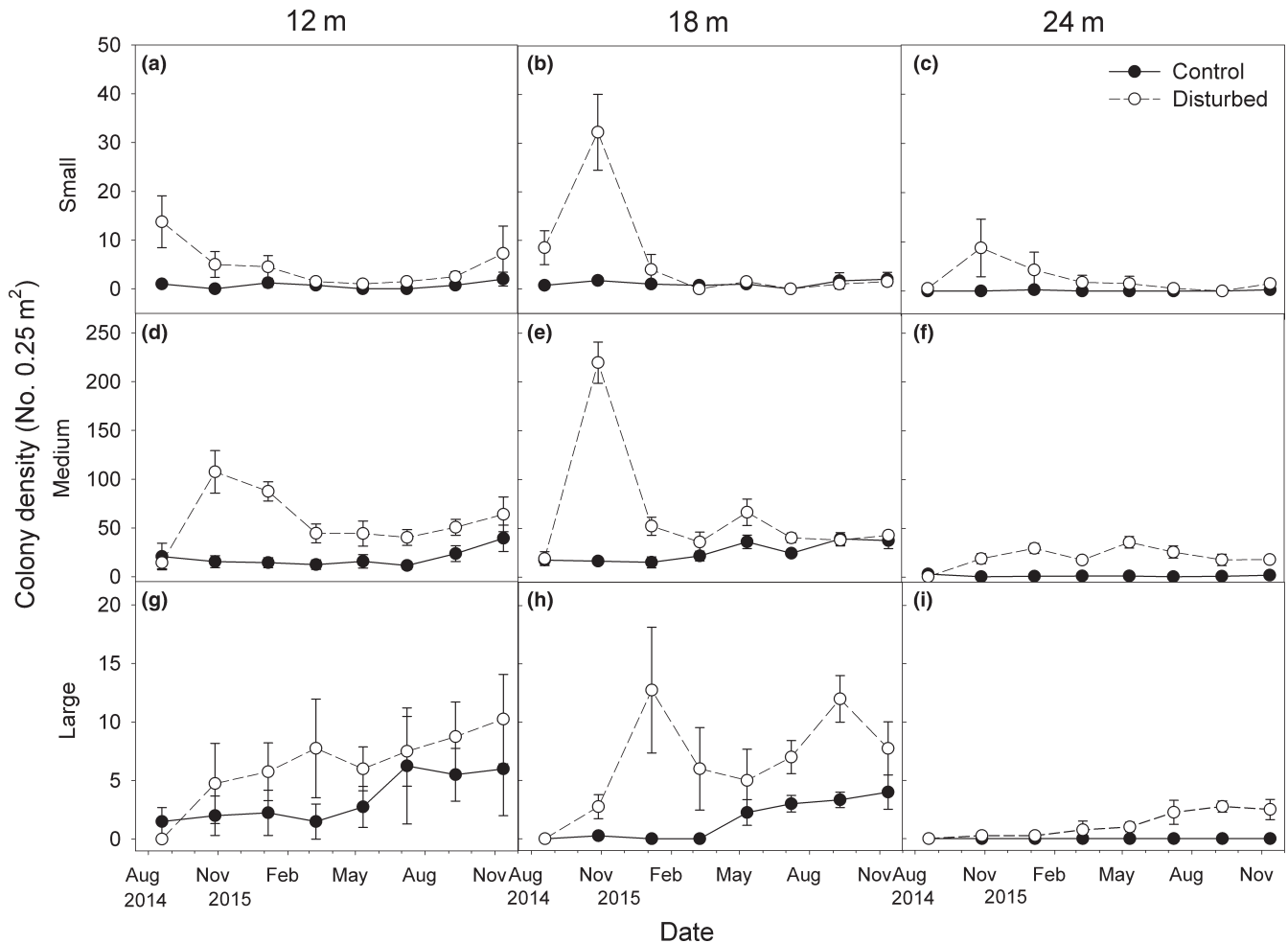


FIGURE 4 Density of small (a–c), medium (d–f), and large (g–i) *Watersipora* colonies in the disturbed and control plots at 12 m (a, d, g), 18 m (b, e, h), and 24 m (c, f, i) on Platform B. Mean values $\pm 1SE$, $n = 4$ plots/depth

disturbed plots, and bare space was reduced by almost 90% within 2 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 (Levin et al., 2002; Osman & Whitlatch, 1995a, 1995b) or consuming larvae (Cowden et al., 1984; Mileikovsky, 1974; Young & 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 c. 1 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

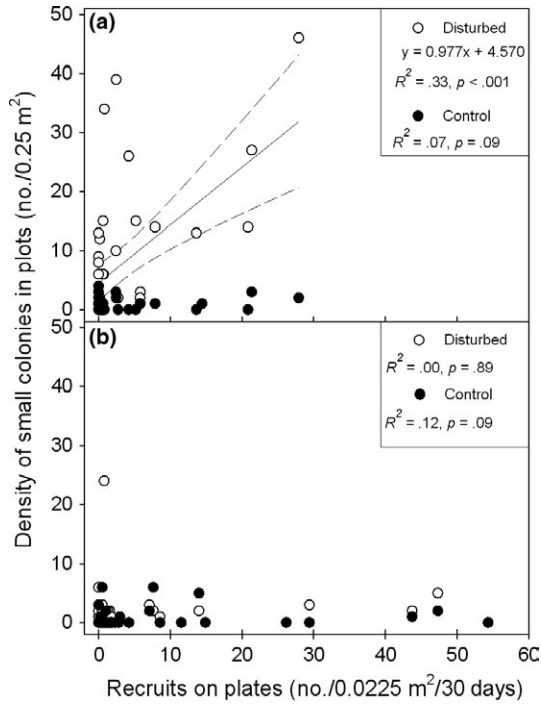


FIGURE 5 Relationship between the density of small colonies in the disturbed and control plots versus larval supply, estimated using settlement plates deployed monthly, during the first (August 2014–March 2015), (a) and second (May 2015–November 2015), (b) halves of the experiment on Platform B. 95% confidence intervals around the regression line also shown (dashed lines)

1 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 & 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 & Stachowicz, 2011) or greater food availability (O'Dea & Okamura, 1999).

The increased growth of *Watersipora* in the disturbed plots agrees with Levine, Adler, and Yelenik'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 & Marshall, 2015) or other resources (D'Antonio, Levine, & Thomsen, 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.

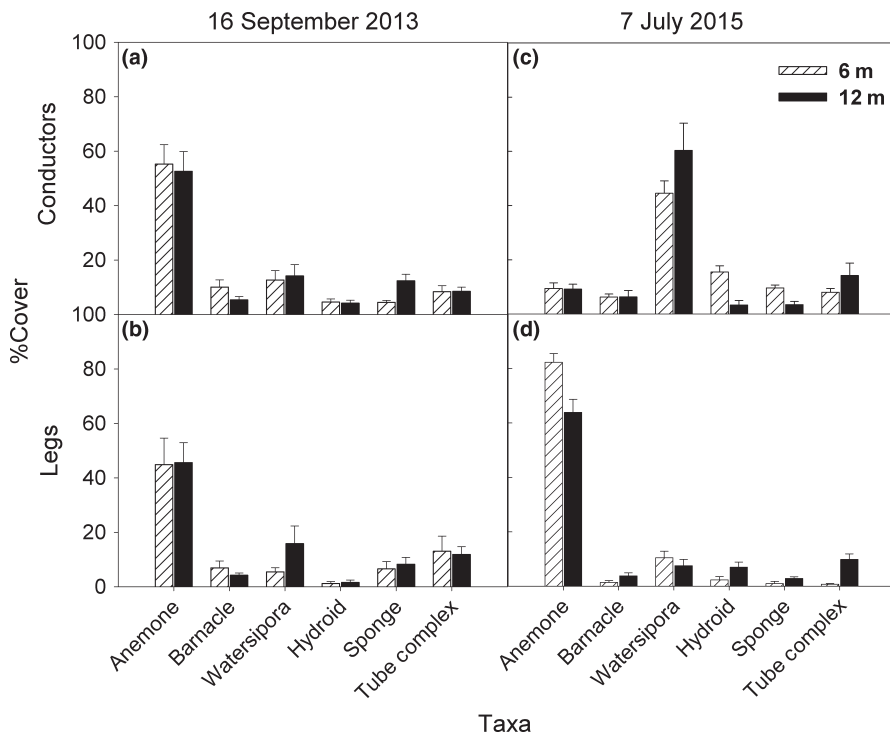


FIGURE 6 Invertebrate community composition on the conductor pipes (a & c) and legs (b & d) of Platform Gina before (September 2013), (a & b) and after (July 2015), (c & d) the maintenance "cleaning" in Spring 2014 at 6 and 12 m. Mean cover $\pm 1SE$, $n = 4$ conductors or legs/depth

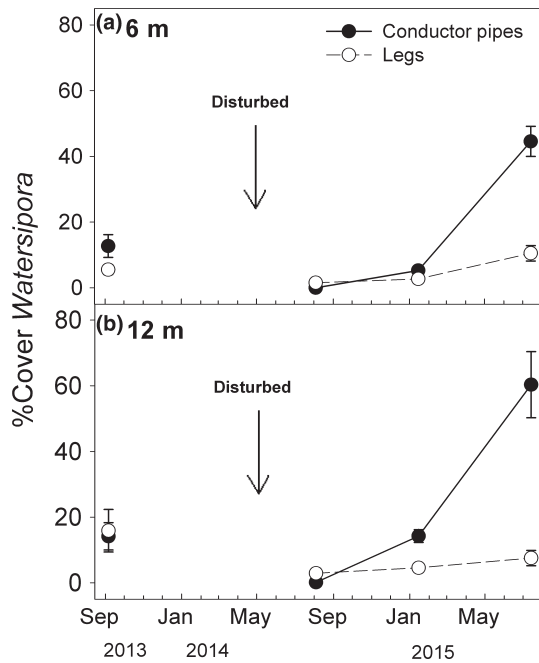


FIGURE 7 *Watersipora* cover on the conductor pipes and legs at Platform Gina at 6 m (a) and 12 m (b) before and after maintenance cleaning by the operators. Only the conductor pipes were cleaned (to a depth >12 m) in Spring 2014. Mean cover \pm 1SE, $n = 4$ conductors or legs/depth

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 (Airoldi & Bulleri, 2011; Britton-Simmons & Abbott 2008; Clark & Johnston, 2009), 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 & 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, Johnson, Mundy, Morris, & Ross, 2002) that deliver non-native propagules to nearby natural reefs (Sammarco, Atchison, Boland, Sinclair, & Lirette, 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 (Adams et al., 2014; Sammarco, Atchison, & Boland, 2004; 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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AUTHORS' CONTRIBUTIONS

H.P., S.V., J.D., R.M., D.S., S.Z., and B.D. all contributed to the design of this study. S.V., B.D., H.P., D.S., S.Z., and R.M. participated in data collection; S.V., H.P. and S.S. analysed the data; and S.V. and H.P. led the writing of the manuscript. All authors gave critical contributions to the manuscript draft and gave final approval for publication.

DATA ACCESSIBILITY

All data are publicly available through the Long Term Ecological Research Network Data Portal. <https://doi.org/10.6073/pasta/f0867874601471476a966022dfc5bb2c> (Viola & Page, 2018).

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