

Spatial and temporal dynamics of the overwater structure fouling community in southern California

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Abstract. Overwater structures within coastal estuaries are novel habitats that may facilitate the introduction and spread of non-native fouling organisms, although permitting agencies lack quantitative data to develop mitigation measures. To explore this habitat impact, abundance (percentage cover) and community composition of fouling communities were examined over space and time, using photoquadrats on floating docks. Floating dock pontoons within 12 bays and harbours were sampled throughout southern California to document spatial patterns in non-native species. To evaluate community development on newly available substrate, dock floats within Alamitos Bay were sampled quarterly for 1 year following removal of fouling organisms. Percentage coverage of non-native species was greater than coverage of native or cryptogenic species both underneath and along the sides of structures in outer and inner bay areas of embayments and community composition varied significantly among sampling locations. The percentage cover of non-native species and community composition in cleared floats rapidly converged on those of uncleared control floats, suggesting that seasonal dynamics are a strong driver of non-native species colonisation. Quantification of these dynamics could serve as a starting point in the development of mitigation measures and highlights the importance of evaluating all possible impacts from coastal development projects during the permitting process.

Additional keywords: biological invasion, estuary, fouling, marina.

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Introduction

As population densities in coastal regions have increased, stressors on bay and estuarine habitats have intensified (Castilla 1999; Thom *et al.* 2005; Lotze *et al.* 2006). Among these stressors is the expansion of overwater structures such as docks, piers and wharfs. The environmental concern most frequently associated with these structures is a reduction in primary productivity through shading of intertidal and subtidal habitats (Nightingale and Simenstad 2001; Thom *et al.* 2008). However, other impacts from overwater structures are less commonly explored, including altered hydrology, aggregation of piscivorous fishes and the facilitation of non-native fouling species (but see Lambert and Lambert 2003; Glasby *et al.* 2007; Ruiz *et al.* 2009). The lack of focus on non-native species facilitation is particularly troubling, given the high ecological and economic cost associated with invasive species (Wilcove *et al.* 1998; Stachowicz *et al.* 1999; Pimental *et al.* 2005; Keller *et al.* 2007), which can rapidly disassemble marine communities (Wilcove *et al.* 1998), particularly in estuarine ecotones (Carlton 1989; Carlton and Geller 1993). Given that hull fouling has long been known to be a pathway for invasion (Carlton 1989; Clarke

Murray *et al.* 2012), and overwater structures provide a suitable semi-permanent habitat for settlement of species introduced by vessel traffic, it is logical that research and management for invasive species targets these habitats.

Like other artificial substrates, such as metals and plastic (Tyrrell and Byers 2007), overwater structures are believed to facilitate non-native species because they introduce novel substrate in habitats that have little native hard structure (Wasson *et al.* 2005; Airoidi *et al.* 2015). Because few native fouling species found in estuarine environments have evolved to exploit these habitats, novel habitat more suitable to exploitation by non-native organisms is created by these structures. A non-native fouling species may initially become established on an overwater structure through any number of pathways (e.g. aquaculture, aquarium dumping, hull fouling on long-distance vessels). Once on the structure, the species may be further spread by local vessel traffic to other locations in the region (Clarke Murray *et al.* 2011). Many fouling species have short dispersal distances (Marshall and Keough 2003; Darbyson *et al.* 2009; Canary *et al.* 2011) and the higher density of novel substrate and recreational vessels found in many bays and harbours may

further facilitate spread. Furthermore, as fouling species may exhibit seasonal reproduction (Bates 2005), the timing of structure placement may expose it to greater propagule rain from non-native species. These introduced species may also expand into sensitive native habitats such as eelgrass (Worcester 1994; Carman and Grunden 2010), kelp forest (Miller *et al.* 2007) and rocky reef (Bullard *et al.* 2007). Therefore, impacts are not limited to the immediate vicinity of overwater structures and may cause wide-ranging ecosystem damage.

Overwater structure development is regulated in the United States under Section 10 of the *Rivers and Harbors Act* and may be influenced during consultation by the essential fish habitat provisions in the *Magnuson–Stevens Fishery Conservation and Management Act* and the *Endangered Species Act*, among other statutes. At present, little consideration is given during the planning process to the potential for increased abundance of non-native species. Many factors are likely to be responsible for the current situation, including a lack of awareness, perceived inability to effect change and need for additional data on fouling species dynamics on overwater structures. Because it is likely that fouling communities vary on the basis of seasonality, prevalence of invasion pathways such as vessel traffic and various other abiotic and biotic factors, capturing variability provides a more complete representation of non-native species footprint throughout a region. Additional information on non-native fouling-species colonisation across space and time will help resource managers define the potential problem and identify a starting point from which to incorporate this issue into the regulatory process (Gordon 1998; Manchester and Bullock 2000; Hejda and Pysek 2006) and potentially identify locations and times of the year (i.e. the importance of initial conditions to structuring the fouling community) that may be at greater risk of non-native species colonisation.

Although it has previously been documented that overwater structures facilitate non-native species (Airolidi *et al.* 2015), the goal of the present study is to identify spatial and temporal patterns in the fouling communities on overwater structures throughout a highly developed coastal region, the Southern California Bight. Southern California contains many bays and harbours interconnected by boat traffic, with a high density of overwater structures (NMFS 2013). For example, Newport Bay contains ~16.99 ha, San Diego Bay 213.67 ha and Mission Bay 7.28 ha of overwater coverage (NMFS 2013). Newport Bay has gained ~0.4 ha in the past 10 years (National Marine Fisheries Service, unpubl. data). Although these acreages may not be substantial when compared with the total bay area, they may be sufficient for continued facilitation of non-native species. The present study aims to quantify the density of non-native species on overwater structures, specifically floating docks, throughout southern California, and their variation with respect to basic habitat variables. In addition, the study shows how non-native fouling species colonise a novel overwater structure under varying conditions. We expect density of non-native species to be high throughout the region and vary across sampling sites on the basis of site-specific dynamics. Furthermore, we expect non-native species density to increase rapidly on simulated novel overwater structure. Results may form the basis for potential offsetting measures in response to continued development of overwater structures in bays and harbours.

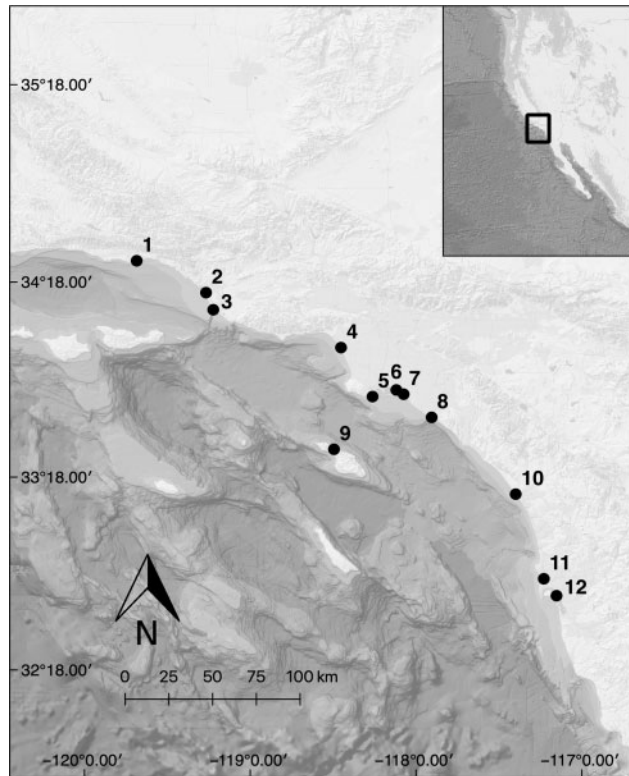


Fig. 1. Map of surveyed harbours in the spatial study: Santa Barbara Harbor (1), Ventura Harbor (2), Channel Islands Harbor (3), Marina del Rey (4), Port of Los Angeles (5), Alamos Bay (6), Huntington Harbor (7), Newport Bay (8), Big Fisherman's Cove (9), Oceanside Harbor (10), Mission Bay (11) and San Diego Bay (12).

Materials and methods

Spatial survey

The fouling invertebrate (i.e. sessile organisms) and algal fouling communities on overwater structures were sampled at 12 locations throughout southern California (Fig. 1). Although structure design and material differed among sites, all were pontoon-supported floating docks. Where system characteristics allowed, two docks were sampled in 'inner bay' and 'outer bay' locations to capture communities both close and distant in proximity to the entrance channel. This survey effort was possible in all but Oceanside Harbor and Big Fisherman's Cove where no inner bay site was present. It was expected that inner and outer bay locations would experience varying abiotic conditions, such as flow. Although no data were collected on circulation at inner and outer bay sites, maximum ebb velocity was recorded as 0.29 m s^{-1} at the outer bay site in Port of Los Angeles and 0.13 m s^{-1} at inner bay site (Seabergh and Outlaw 1984). Largier *et al.* (1997) found that water-residence time in the vicinity of the San Diego inner bay site was ~20 days longer than it was in the outer bay location. Fouling community data were collected using photoquadrats by divers on SCUBA ($20 \times 20 \text{ cm}$) placed haphazardly and taken with an Olympus Tough 8010 (Olympus China Inc., Beijing, P.R. China) on its 'Underwater Wide 1' setting with flash on. All photoquadrats were taken on permanently subtidal pontoons no more than 1 m

below the water line. The tidal range in southern California is ~ 2.13 m and all docks were located in areas at least 2.44 m deep. At least three images were taken along the side of the structure and at least two were taken underneath by divers swimming under the dock and placing the photoquadrat against the structure and shooting the camera upwards. Data were collected once at each site from March through October, which is generally considered the high growth season for aquatic vegetation (the authors know of no similar season for invertebrates) in southern California, to limit seasonal variability (NMFS 2014). On several occasions, tissue samples were collected to share with taxonomic experts for identification assistance.

Data were analysed using the Coral Point Count program (CPC; Kohler and Gill 2006). Using CPC, 50 random points were displayed across each image and the organism underneath each point was identified to the lowest taxonomic level possible and assigned as native, non-native or cryptogenic (i.e. it is unknown whether the species is native or introduced). In cases where no identifying characteristics were visible, the species was recorded as unknown. Percentage cover for each species was calculated by multiplying the number of points that intersected with an individual of that species by two. Images and tissue samples were sent to taxonomic experts to assist in identification. However, this was not possible for every picture and, given the large volume of images in the study, some tradeoffs were necessary. For example, differentiating between the native *Halichondria panicea* (Pallas, 1766) and non-native *H. bowerbanki* (Burton, 1930) was not possible from an image, and colonies were sufficiently common to preclude that level of tissue analysis. In these cases, individuals were listed as cryptogenic.

Temporal study

So as to evaluate non-native fouling-species colonisation of overwater structures over time, the fouling community was cleared from a subset of floats in Alamitos Bay to simulate a novel structure. Within Alamitos Bay marina, the following two bay locations were established: (1) an 'outer bay' location close to the channel entrance and (2) an 'inner bay' location positioned in the back portion of the marina. Collecting data at outer and inner bay locations was intended to capture the effect of abiotic differences on colonisation of non-native species. At each location, four experimental floats were cleared ('removal'), and four similarly sized floats were labelled as controls ('control'). Floats were ~ 1 m wide by 1.5 m deep and 0.2 m high. The side and bottom of removal floats were cleared of fouling organisms to ensure that recolonisation would not occur through vegetative growth. Removals were performed in January 2013 ('winter'), whereas a second, independent set was cleared of growth in July 2013 ('summer') to incorporate seasonality into the study design. Floats cleared in winter and summer were located in adjacent slips at each bay location, each with an equal number of unaltered control floats. Floats were sampled with photoquadrats (20×20 cm) quarterly for the following year. That is, each float was sampled at 3 months ('Q1'), 6 months ('Q2'), 9 months ('Q3') and 12 months ('Q4') following the start of each seasonal experiment. During sampling, a random-number table was used to determine the location (i.e. distance from the edge) where each picture would be taken.

Random quadrat placement enabled capture of community variability within the float and made for a more comprehensive comparison. Images of the side and underside of each float were taken and analysed in CPC, using the same approach as in the spatial study.

Data analysis

The mean percentage covers of native and non-native fouling species in the spatial study were compared across all sampling locations with a matched paired Student's *t*-test. The effects of bay location and substrate orientation (side or underneath) were compared using a nested ANOVA where docks were nested within the sampling location. The effects of bay location and sampling system on fouling-community composition were assessed using permutational multivariate ANOVA (PERMANOVA) where only species present on at least 10% of docks were included to minimise bias from rare species. All data were analysed in R (ver. 3.0.1, R Foundation for Statistical Computing, Vienna, Austria, see <http://www.R-project.org>, accessed 1 July 2014).

To account for differences in photoquadrat orientation, percentage cover of all species was averaged using an equal ratio of side to underside photoquadrats for each float. Cover of non-native species was compared between removal and control floats for each quarterly sampling period by using Welch's two-sample *t*-tests at all combinations of winter–summer starting seasons and inner bay–outer bay locations. Using this approach, it was possible to determine the sampling period at which non-native coverage was indistinguishable between control and cleared floats. Data were not relativised for proportion of non-natives as a percentage of total fouling coverage for this analysis because we sought to evaluate gross coverage of non-native species as a function of time. Two-dimensional, non-metric multidimensional scaling (nMDS) was used to examine communities for each float, using the 'metaMDS' function in the 'vegan' package (J. Oksanen, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner, see <https://cran.r-project.org/web/packages/vegan/index.html>, accessed 1 July 2014) in R (R Foundation for Statistical Computing, see <http://www.R-project.org>). Community structure for each float was assessed using arcsine square root-transformed percentage-cover values. Differences in fouling-community composition (PERMANOVA) and similarity percentages (SIMPER) of control and removal floats by quarterly sampling period among all combinations of winter–summer experiments and inner bay–outer bay locations were respectively determined using the 'adonis' and 'simper' functions in the 'vegan' package in R (see <https://cran.r-project.org/web/packages/vegan/index.html>).

Results

Spatial

In total, 266 photoquadrats were taken at 44 docks in 12 locations throughout southern California during the spatial study. Percentage cover of non-native species was significantly higher than that of native or cryptogenic species on sampled docks throughout the region (Fig. 2; $t = 7.56$, d.f. = 43, $P < 0.001$). Eleven of the locations sampled had a higher percentage cover

of non-native species than native species. Channel Islands Harbor was the lone exception. The most dominant species included the non-native *Mytilus galloprovincialis* (Lamarck, 1819), *Watersipora subtorquata* (Soule and Soule, 1968) and cryptogenic *Halichondria* spp. (Table 1). A full table of all species encountered during sampling by location is found in Appendix 1. The coverage of non-native species was frequently, but not universally, higher underneath docks than along the side ($F_{12,64} = 5.534, P < 0.001$). Docks in outer bay locations typically had a higher coverage of non-native species than did those in inner bays ($F_{10,20} = 3.206, P = 0.013$); however, Mission Bay was the only site with a greater non-native coverage in an inner bay location. This was a result of a high coverage of the non-native tunicate, *Polyandrocarpa zorritensis* (Van Name, 1931), on docks in the inner bay location of Mission Bay.

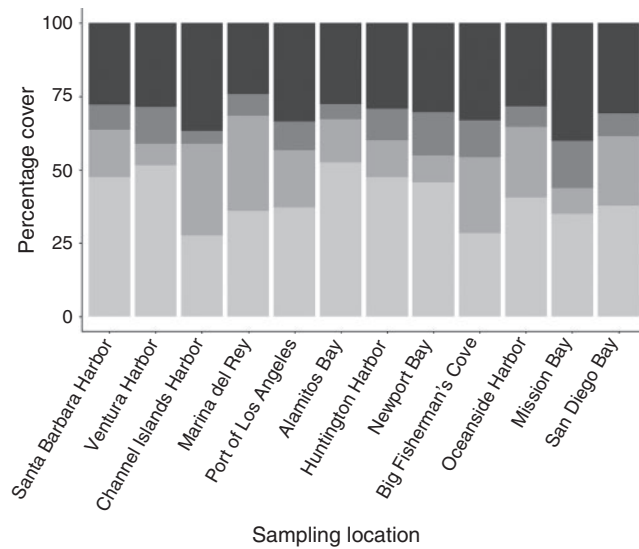


Fig. 2. Abundance of four major fouling groups, namely bare or unidentified (black), cryptogenic (80% grey), native (60% grey) and non-native (40% grey), averaged across sampled docks in each system.

Table 1. The most dominant fouling species, on the basis of mean percentage cover across all systems, are summarised over all 12 sampling sites All species were found both on the side of and underneath the structure, with the exception of the two macroalgae species that were found only on the side

Species	Mean percentage cover	Taxonomic group	Species status	Locations present
<i>Mytilus galloprovincialis</i>	12.1	Bivalvia	Non-native	12
<i>Watersipora subtorquata</i>	7.5	Bryozoa	Non-native	12
<i>Halichondria</i> spp.	3.9	Porifera	Cryptogenic	12
<i>Diplosoma listerianum</i> (Milne-Edwards, 1841)	3.9	Tunicata	Non-native	10
<i>Ciona</i> spp.	3.4	Tunicata	Non-native	10
<i>Dictyota flabellate</i> (Collins, 1901)	3.2	Phaeophyceae	Native	5
<i>Zoobotryon verticillatum</i> (Delle Chiaje, 1822)	2.9	Bryozoa	Non-native	11
<i>Grateloupia</i> spp.	2.3	Rhodophyta	Non-native	7
<i>Polyandrocarpa zorritensis</i>	2	Tunicata	Non-native	2
Spirorbidae	2	Annelida	Cryptogenic	11
<i>Botrylloides diegensis</i> (Ritter and Forsythe, 1917)	1.8	Tunicata	Non-native	11
<i>Bugula neritina</i> (Linnaeus, 1758)	1.6	Bryozoa	Non-native	9
<i>Haliclona</i> spp.	1.3	Porifera	Native	6
<i>Botrylloides violaceus</i> (Oka, 1927)	1.2	Tunicata	Non-native	9

PERMANOVA indicated that the fouling community differed significantly by system, bay location and their interaction (Fig. 3; $F_{11,22} = 6.77, P = 0.001$; $F_{1,22} = 9.14, P = 0.001$; $F_{9,22} = 4.35, P = 0.001$). Additional findings of interest from the spatial study included apparent southern range expansions of the non-native serpulid tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923) located in Newport Bay, Huntington Harbor and San Diego Bay (previously known primarily north of Point Conception but also Port of Los Angeles; Pernet *et al.* 2016).

Temporal

Over the course of the temporal study, 326 photoquadrats were taken at 32 floats during six sampling events. Non-native species

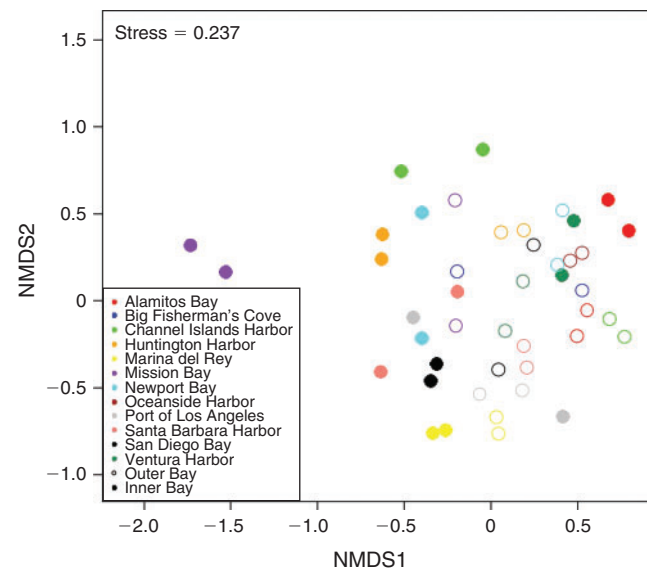


Fig. 3. Non-metric multidimensional scaling (NMDS) plot of community composition at docks within each sampling site. Solid circles represent inner bay areas and open circles represent outer bay. The two Mission Bay docks standing out from the rest were dominated by the non-native colonial tunicate, *Polyandrocarpa zorritensis*.

quickly (i.e. by the first sampling event) recolonised removal floats in both inner and outer bay locations, regardless of which season the experiment began. Removal floats did not have a significantly different cover of non-native species than did control floats during any post-removal sampling period with the exception of the inner bay floats from the winter experiment during Q1 (Table 2, Fig. 4). Fouling communities on the removal floats showed quick and permanent recovery (e.g. non-significant differences in community structure from the control) in the inner bay for both seasonal experiments (Table 3, Fig. 5). However, in the outer bay, the communities never exhibited non-significant differences in consecutive quarterly sampling periods for either seasonal experiment and showed no apparent recovery by the end of the study. SIMPER analyses consistently identified the main drivers of significant community differences between control and removal floats in the outer bay as a higher cover of *Mytilus galloprovincialis* (mean contribution to dissimilarity: 19%) at control sites and a higher cover of *Water-sipora subtorquata* (9%), bare substrate (7%), *Halichondria* spp. (6%), *Bugula neritina* (5%) and *Amathia verticillata* (5%) at removal sites.

Discussion

The dominance of non-native species in the fouling community of overwater structures in southern California found in the present study is consistent with the results of similar studies in the literature that have shown greater abundances of non-native fouling organisms on artificial structures in bays and harbours (Lambert and Lambert 1998; Glasby *et al.* 2007; Tyrrell and Byers 2007). Only the following two locations did not follow this trend: Channel Islands Harbor had more coverage of native

Table 2. Welch's two-sample *t*-test table comparing percentage of non-native cover between control and removal floats during each sampling period by bay location and starting season in Alamitos Bay
The control floats had a significantly higher cover of non-native species than the removal floats only for the winter removal experiment at the inner bay site in Q1. Significant differences ($P < 0.05$) between treatments (at $\alpha = 0.05$) are denoted by an asterisk

Bay location	Starting season	Sampling period	d.f.	<i>t</i>	<i>P</i> -value
Inner bay	Summer	Q1	6	2	0.092
Inner bay	Summer	Q2	6	1.84	0.116
Inner bay	Summer	Q3	4.33	0.11	0.919
Inner bay	Summer	Q4	5.96	-0.11	0.919
Inner bay	Winter	Q1	2.99	4.76	0.018*
Inner bay	Winter	Q2	5.99	-0.26	0.803
Inner bay	Winter	Q3	4.03	-1.13	0.321
Inner bay	Winter	Q4	4.13	1.05	0.352
Outer bay	Summer	Q1	3.07	1.66	0.194
Outer bay	Summer	Q2	6	2.43	0.051
Outer bay	Summer	Q3	5.07	0.81	0.457
Outer bay	Summer	Q4	2.58	-0.96	0.418
Outer bay	Winter	Q1	4.75	0.18	0.866
Outer bay	Winter	Q2	5.64	-1.69	0.145
Outer bay	Winter	Q3	6	2.08	0.083
Outer bay	Winter	Q4	5.91	1.59	0.164

fouling organisms than non-native and the difference at Big Fisherman's Cove was close to zero. The structures in both these locations were immediately adjacent to rocky substrate, which was unique among other survey locations. Many overwater structures are built on soft-bottom habitats and are, therefore, isolated from generalist predators that inhabit rocky substrates and may consume non-native species (Dumont *et al.* 2011). In addition, Big Fisherman's Cove is located on Catalina Island and is more similar to an open coastline than any other location in the present study and is likely to receive lower volumes of vessel traffic than are harbours that house hundreds of vessels, which has been known to affect non-native species coverage (Page *et al.* 2006). With the exception of those few areas that may harbour natural isolation or provide access to predators, overwater structures consistently increase the coverage of non-native species in a given system.

The variation in fouling-community composition across space is surprising, given the high degree of connectedness by recreational vessels among most of these locations and the presence of dominant species at the majority of sites sampled. However, it is possible fouling organisms may inhibit or attract certain species on a seasonal basis (Sutherland 1978) and unmeasured abiotic or biotic factors within locations may have altered community composition (Glasby 1998; Cifuentes *et al.* 2010). We attempted to control for seasonality by collecting data only from March through October, but the level of sampling required to tease apart seasonality and other potential contributing factors was not feasible for the spatial study. However, seasonality was apparent in Alamitos Bay during the temporal sampling. Therefore, although many of the species may be shared throughout a region, local dynamics such as boat traffic (Davenport and Davenport 2006), hydrodynamics (Floerl and Inglis 2003) and water quality (Lenz *et al.* 2011) further shape community structure and additional research into those factors may provide opportunities for minimising the opportunity for certain species to spread.

The higher abundance of non-native species in the outer bay areas in both the spatial and temporal studies may be the result of elevated vessel traffic, influence of marine conditions on larval recruitment, differences in water quality and availability of food. In the spatial study, non-native species were more abundant in the outer bay than inner bay structures, with the exception of Mission Bay, where the inner bay structures were almost uniformly covered by the non-native tunicate *Polyandrocarpa zorritensis*. If these results are interpreted through outer bay locations experiencing a higher flow than do inner bay locations, there are conflicting conclusions on the settlement and growth of non-native species by higher flow regimes in the literature, although there is consensus that flow will affect fouling-species recruitment (Judge and Craig 1997). Ritter *et al.* (2008) found that locations with artificially reduced tidal flow are less likely to be invaded, whereas Wasson *et al.* (2005) found fewer non-native species in high-flow areas of Elkhorn Slough, California. Several of the non-native species included in these studies (e.g. *W. subtorquata*, *B. neritina*) overlapped with the present work, although, more frequently, species were not found in each study, possibly explaining the differing results. Elkhorn Slough is also far less developed than were many of the sampling locations in our study and, therefore, may be less

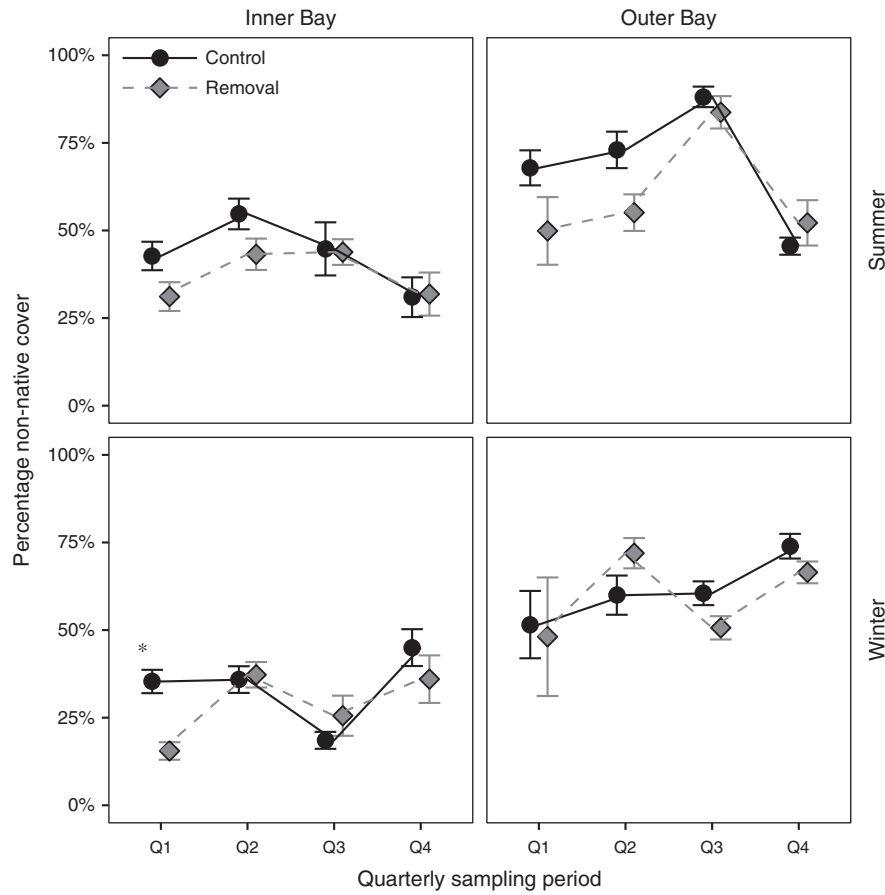


Fig. 4. Non-native coverage at control and removal floats by sampling season for each starting season and bay location. Error bars are standard errors and asterisk indicates significant differences in non-native coverage among treatments.

Table 3. PERMANOVA comparisons of removal and control community structures during each sampling period by bay location and starting season in Alamitos Bay

Significant ($P < 0.05$) differences between treatments (at $\alpha = 0.05$) are denoted by as asterisk

Bay location	Starting season	Sampling period	Dissimilarity percentage	F	R ²	P-value
Inner bay	Summer	Q1	37.9	1.21	0.17	0.376
Inner bay	Summer	Q2	34.8	1.11	0.16	0.399
Inner bay	Summer	Q3	39.3	0.86	0.12	0.529
Inner bay	Summer	Q4	34.5	1.11	0.16	0.412
Inner bay	Winter	Q1	54.1	4.75	0.61	0.100
Inner bay	Winter	Q2	33.9	1.37	0.19	0.159
Inner bay	Winter	Q3	34.1	0.69	0.1	0.656
Inner bay	Winter	Q4	38.1	0.72	0.13	0.687
Outer bay	Summer	Q1	52.1	4.4	0.47	0.029*
Outer bay	Summer	Q2	39.9	4.28	0.42	0.029*
Outer bay	Summer	Q3	34.5	2.36	0.28	0.111
Outer bay	Summer	Q4	40.1	3.62	0.42	0.025*
Outer bay	Winter	Q1	48.5	1.74	0.23	0.130
Outer bay	Winter	Q2	41.9	2.81	0.32	0.026*
Outer bay	Winter	Q3	41.2	1.79	0.23	0.112
Outer bay	Winter	Q4	31.4	3	0.33	0.037*

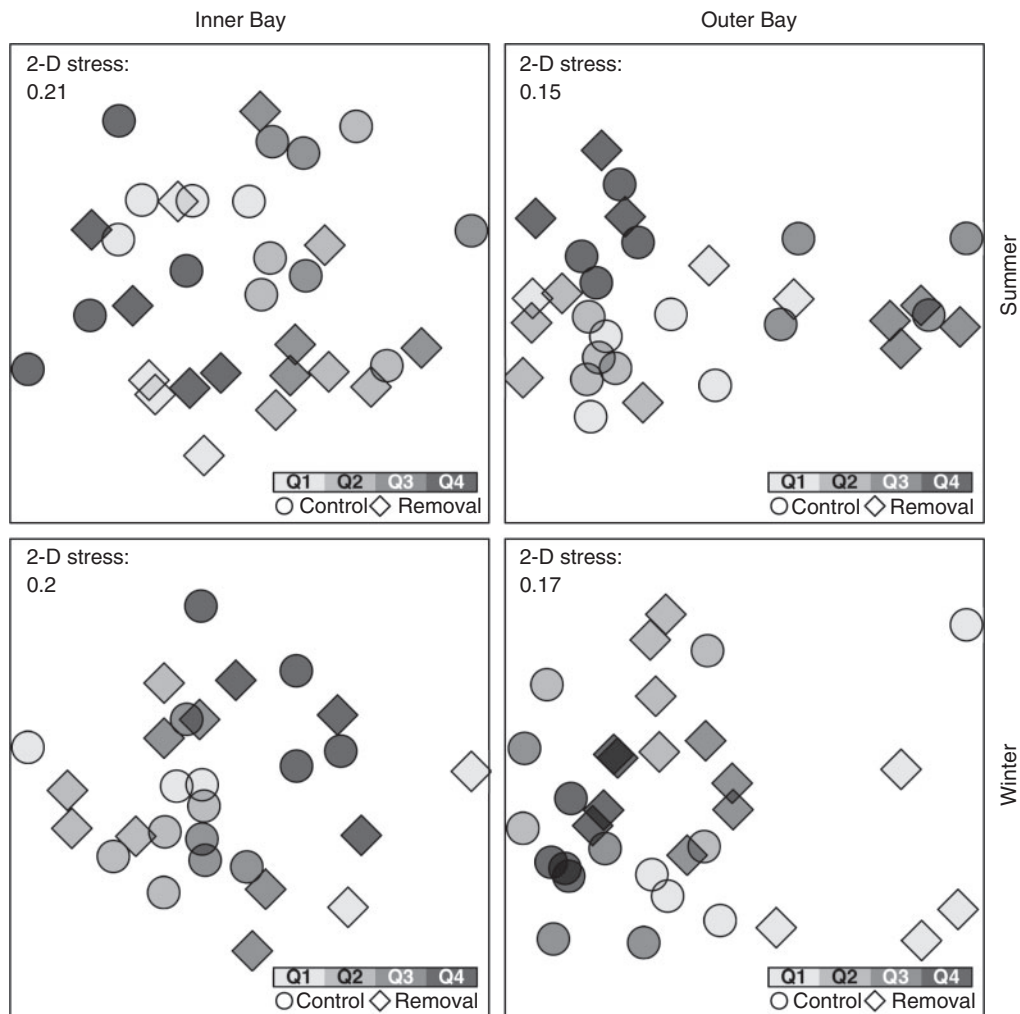


Fig. 5. Non-metric multidimensional scaling (NMDS) plots of community structure by sampling period for Control and Removal floats by starting season and bay location.

comparable. This finding has implications for coastal development in that expansion of overwater coverage in outer bay areas of coastal embayments should be viewed with additional caution.

Non-native species quickly colonised removal floats at a coverage similar to that of control floats, suggesting a very short lag in facilitation of non-native species on simulated novel overwater structure habitat. Altman and Whitlatch (2007) found that fouling plates cleared on a regular basis were colonised by non-native species much more rapidly than were plates that allowed succession to proceed without disturbance and Floerl *et al.* (2005) found that manual removal on boat hulls promoted fouling. Results of our study did not show a short-term increase in non-native species on removal floats, compared with control floats, but that may have been a result of the first sampling occurring multiple months after introducing cleared substrate rather than several weeks. Fouling species also exhibit high turnover rates (residence times of <1 year) that may reduce coverage differences between removal and control floats

(Sutherland and Karlson 1977). These results suggest that addition of a new structure will very quickly (within 3–6 months) support a coverage of non-native species similar to a structure that has existed for several years. Because non-native coverage did not reduce over time, the structures also create long-term habitat. Therefore, the positive relationship between overwater coverage and non-native species abundance exhibits only a small time-lag and is likely to be long term.

Larger changes occurred in community composition over time rather than across treatment groups in the temporal study. These communities change quickly and a climax community may not be achieved. Communities in the outer bay area differed more across treatments and over time, always remaining statistically dissimilar, regardless of when the removal floats were cleared of their fouling community. This result may be a consequence of higher propagule pressure from open water or less extreme conditions resulting from the likely higher water quality in areas more frequently flushed with ocean water that allowed continued development of the fouling community.

Inner bay areas are more likely to experience extreme shifts in water quality (e.g. hypoxia) and turn over species more rapidly. Pati *et al.* (2015) found that temporal shifts in fouling community were driven by water quality and salinity. Because salinity does not shift dramatically in the Mediterranean climate embayments found in southern California, the results from Pati *et al.* (2015) support our explanation of water quality driving more rapid community changes at inner bay sites. Because these communities do not progress into a later successional state, the removal and control compositions rapidly converged. Indeed, the main drivers for dissimilarity between floats in the outer bay are the high coverage of a climax community species (*Mytilus galloprovincialis*) on the control floats versus bare substrate and rapidly colonising non-native bryozoans (*Watersipora subtorquata*, *Bugula neritina*, and *Amathia verticillata*) on the removal floats. Moreover, consistent differences in control floats in inner bay areas over time suggest that short-term abiotic drivers that may include seasonality and rapid changes in water quality are more dominant in structuring the community than is succession to a static climax community. An experimental transplant of developing fouling communities 12 km apart showed that community structure converged on that of the destination site over time (Vieira *et al.* 2018), supporting the importance of location in community structure. These results showed that both bay location and seasonality are stronger drivers of community structure than is extended development on a novel habitat.

Space is often considered the primary limiting resource in fouling communities (Stachowicz *et al.* 2002) and non-native fouling species represented in the present study are known to be excellent competitors for this resource (Howes *et al.* 2007; Lutz-Collins *et al.* 2009). However, there are other mechanisms through which non-native fouling species in southern California may have a competitive advantage over native species, because many of the study sites from this work are located in highly urbanised watersheds that often exhibit poor water quality (Kamer *et al.* 2001; Ackerman and Schiff 2003). Non-native fouling organisms are better able to survive in polluted environments, particularly in those with high copper concentrations, as is the case in areas with vessels that use copper-based antifouling paint (Crooks *et al.* 2011) and low dissolved oxygen (Jewett *et al.* 2005). Svensson and Marshall (2015) showed that food is also an important driver of fouling-community structure. Non-native fouling species are more adept at filtering picoplankton (Comeau *et al.* 2015), a subset of the plankton community that is 0.2–2 μm and more abundant in eutrophic locations, such as those studied in the present work (McLaughlin *et al.* 2014). The interpretation of our results along with the environmental factors that facilitate proliferation of non-native species suggest multiple approaches that could mitigate for placement of additional or larger overwater structures in southern California, including exploration of alternate hull-fouling paints as non-native fouling organisms, such as the common *Watersipora subtorquata*, may be resistant to them (Piola and Johnston 2006) along with other alterations to the watershed that improve water quality and impede spread of non-native species.

The present study differed from many similar efforts on colonisation of artificial structures by non-native species in that percentage cover was collected as opposed to presence–absence

of species in rapid assessment surveys (Lambert and Lambert 1998; Cohen *et al.* 2005). There is a tradeoff in the two approaches in that the former provides greater information on habitat utilisation, whereas the latter allows increased taxonomic resolution and increased sampling intensity. However, even by using a sampling approach that leads to a lower sampling intensity, range expansion of *Ficopomatus enigmaticus* was still detected in the present study. This result suggests that monitoring overwater structures, even on a limited scale, would still be useful for detecting novel invasions. Density data on non-native fouling species also provide the means to evaluate community dynamics and the reproductive potential for further spread. Previous studies detected facilitation of non-native species by overwater structures, whereas the present work went further to identify trends in various non-native species in novel locations, and their potential for spread into adjacent sensitive habitats such as seagrass and rocky reefs. That is, future non-native species may first be detected on overwater structures and regular monitoring may give resource managers time to prepare a response.

Measurements of density are also valuable when considered alongside recent work on the effect of diversity on filtration rates (Byrnes and Stachowicz 2009; Whalen and Stachowicz 2017). Increased diversity of fouling species leads to higher water filtration, which could have myriad ecosystem and economic effects (Ruesink *et al.* 2006; Daigle and Herbinger 2009). Density would provide finer-scale information on the fouling-community composition, with particular attention being paid to species morphology (Whalen and Stachowicz 2017) that could create a more accurate estimation of filtration than species richness. This information would be important when characterising the biotic drivers that affect ecosystem function. An analysis of filtration based on the structure of fouling communities found during the present study was beyond the intended project scope, but did represent a useful application for *in situ* density data.

Because coastal development and introductions of exotic species both continue to increase with time and this region experiences a higher invasion rate than do other regions in the United States (Simkanin *et al.* 2016), future reductions in overwater coverage and non-native species are unlikely. However, quantifying the relationship between the expansion of overwater coverage and facilitation of non-native species, as was completed in the present study, is a necessary early step to a path forward in management of non-native species. For example, regular monitoring of overwater structures would allow for early response actions in the event a known, aggressive invader is detected. Alternatively, regulators may suggest offsetting measures, as mentioned above, such as mitigation for the non-native species impacts from expansion of the existing overwater coverage. The authors are not aware of any existing compensatory mitigation programs for activities that may facilitate non-native species, although possibilities include removal of structures or debris that are more frequently inhabited by non-native fouling organisms or financial contributions to larger control efforts. Regardless of the proposed approach, out of kind mitigation efforts often require quantitative data on expected impacts, which the present study has helped provide. Further research should explore changes in the structure design that may

reduce non-native species coverage and quantify impacts to adjacent sensitive habitats to inform appropriate offsetting measures. Incorporating additional research along with improved awareness among resource managers would account for an underappreciated impact from an expansion of overwater coverage and are necessary to meet regulatory goals of maintaining ecosystem function in developed areas.

Conflicts of interest

The authors declare that they have no conflicts of interest in the course of this study.

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