

Habitat formation prevails over predation in influencing fouling communities

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Abstract

Coastal human-made structures, such as marinas and harbors, are expanding worldwide. Species assemblages described from these artificial habitats are novel relative to natural reefs, particularly in terms of the abundance of nonindigenous species (NIS). Although these fouling assemblages are clearly distinctive, the ecosystem functioning and species interactions taking place there are little understood. For instance, large predators may influence the fouling community development either directly (feeding on sessile fauna) or indirectly (feeding on small predators associated with these assemblages). In addition, by providing refuges, habitat complexity may modify the outcome of species interactions and the extent of biotic resistance (e.g., by increasing the abundance of niche-specific competitors and predators of NIS). Using experimental settlement panels deployed in the field for 2.5 months, we tested the influence of predation (i.e., caging experiment), artificial structural complexity (i.e., mimics of turf-forming species), and their interactions (i.e., refuge effects) on the development of sessile and mobile fauna in two marinas. In addition, we tested the role of biotic complexity—arising from the habitat-forming species that grew on the panels during the trial—on the richness and abundance of mobile fauna. The effect of predation and artificial habitat complexity was negligible, regardless of assemblage status (i.e., native, cryptogenic, and nonindigenous). Conversely, habitat-forming species and associated epibionts, responsible for biotic complexity, had a significant effect on mobile invertebrates (richness, abundance, and community structure). In particular, the richness and abundance of mobile NIS were positively affected by biotic complexity, with site-dependent relationships. Altogether, our results indicate that biotic complexity prevails over artificial habitat complexity in determining the distribution of mobile species under low predation pressure. Facilitation of native and non-native species thus seems to act upon diversity and community development: This process deserves further consideration in models of biotic resistance to invasion in urban marine habitats.

KEYWORDS

biotic resistance, facilitation, marinas, marine invertebrates, nonindigenous species, predation, urban ecology

1 | INTRODUCTION

Worldwide, coastal hardening is increasing as protection against environmental perturbations (erosion, rising sea level, extreme storms, and flooding; Bulleri & Chapman, 2010; Firth et al., 2016) and to support the development of a diverse set of human activities (shipping, urban development, aquaculture, energy extraction, recreation). Coastal urbanization dramatically influences species diversity and ecosystem functioning across multiple spatial scales, but has nevertheless received less attention than its terrestrial counterpart (Bulleri, 2006; Bulleri & Chapman, 2010).

Adding artificial structures along natural shores is directly associated with habitat degradation, fragmentation, and loss, as well as alteration of connectivity and the local species pool (Bishop et al., 2017; Dafforn et al., 2015). These structures provide novel habitats for colonization by various species, but are not “surrogates” of the neighboring natural rocky reefs (e.g., Connell, 2001b; Fauvelot, Bertozzi, Costantini, Airoidi, & Abbiati, 2009). One specificity of their species assemblages is the high prevalence of nonindigenous species (NIS) compared with natural reefs (Airoidi, Turon, Perkol-Finkel, & Rius, 2015; Mineur et al., 2012). Although these original urban assemblages probably involve novel ecological interactions, the ecological processes maintaining and acting upon these assemblages are still to be elucidated (Chapman & Underwood, 2011). A growing body of evidence suggests that both the direction and intensity of interspecific interactions such as competition, predation (including grazing), and facilitation (e.g., via habitat formation) can be altered on urban structures compared with observations on and/or expectations for natural habitats (Ferrario, Iveša, Jaklin, Perkol-Finkel, & Airoidi, 2016; Klein, Underwood, & Chapman, 2011; Rogers, Byrnes, & Stachowicz, 2016; but see Iveša, Chapman, Underwood, & Murphy, 2010).

On intertidal seawalls, which have received much attention, a diverse set of habitat characteristics, such as substrate type, roughness, microhabitats, or slope, can influence community and functional composition (e.g., Chapman & Blockley, 2009; Firth et al., 2016; Moschella et al., 2005). Empirical and experimental studies conducted on these particular artificial structures support ecological predictions linking habitat complexity with species diversity and distribution (Loke & Todd, 2016; MacArthur & MacArthur, 1961; Tews et al., 2004). Increasing habitat complexity of marine artificial structures, for instance by adding pits or grooves in seawalls, has thus been used in ecological engineering projects (see reviews by Dafforn et al., 2015; Firth et al., 2016 and references therein). Taking into account ecological processes (such as habitat–diversity relationships) in the design of artificial marine structures is recommended as a contribution to restoration and reconciliation efforts: Marine artificial structures may provide not only coastal protection but also ecological services (Chapman & Underwood, 2011; Dyson & Yocom, 2015; Evans et al., 2017; Loke, Ladle, Bouma, & Todd, 2015). However, habitat–diversity relationships vary strongly with environmental conditions and local species pools (Loke & Todd, 2016; Matias, 2013). Expectations for a given artificial marine habitat are, to date, uncertain and further comprehensive research is needed to predict which biodiversity and ecosystem

functions should be targeted by ecological engineering approaches (Dafforn et al., 2015; Strain et al., in press). Undesirable effects such as the facilitation of NIS are of particular concern (Dafforn, 2017).

Harbors and marinas are perhaps the most invaded habitats of the marine realm (Bax, Williamson, Agüero, Gonzalez, & Geeves, 2003). Rapid spread of NIS occurs in these introduction hotspots and “invasion hubs” (Airoidi et al., 2015; Bishop, Wood, Yunnice, & Griffiths, 2015). They experience strong propagule pressure *s.l.* due to ballast water and hull fouling of cargo ships and leisure craft (Clarke Murray, Pakhomov, & Therriault, 2011; Sylvester et al., 2011). Although environmental conditions are substantially modified in marinas compared with their neighboring habitats (Floerl & Inglis, 2003; Rivero, Dafforn, Coleman, & Johnston, 2013), these “artificial” environments tend to be similar across distant locations, therefore participating in the biotic homogenization of the environment through the establishment of similar NIS communities within and among oceans (Seebens, Gastner, & Blasius, 2013; Streftaris, Zenetos, & Papanastasiou, 2005). The environmental factors that are the most strongly modified in marinas include temperature, salinity, hydrodynamics, sediment resuspension, contaminants, and light (Dafforn et al., 2015). For instance, the network of pilings, pontoons, and poorly sloped seawalls modifies the light environment and contributes to the reduction in cover of habitat-forming macrophytes (Blockley & Chapman, 2006; Bulleri & Chapman, 2010), either directly, by affecting their recruitment and performance, or indirectly, by favoring the recruitment of epibionts (Marzinelli, Underwood, & Coleman, 2011). Although the reduction or loss of natural seaweed habitats (canopy and understory) may affect associated faunal assemblages, the spatial arrangement of artificial structures creates myriad microhabitats with various structures, properties, and ultimately complexities (Dafforn et al., 2015) that may favor alternative (mostly faunal) habitat-forming species (Connell, 2001b; Sellheim, Stachowicz, & Coates, 2010), including NIS (Dafforn, 2017).

To date, the role of habitat complexity in artificial coastal habitats has mainly been investigated on fixed intertidal structures, such as seawalls and riprap (e.g., Firth, Browne, Knights, Hawkins, & Nash, 2016; Firth et al., 2016; Martins, Thompson, Neto, Hawkins, & Jenkins, 2010; Moschella et al., 2005). Less attention has been paid to floating subtidal structures such as floating pontoons which differ however in many ways (Holloway & Connell, 2002; but see Lavender, Dafforn, Bishop, & Johnston, 2017). Fouled by unique assemblages, they generally support more abundant and diverse NIS than do fixed structures (Dafforn, 2017; Dafforn, Johnston, & Glasby, 2009; Glasby, Connell, Holloway, & Hewitt, 2007). Owing to their direct proximity and similarity to vessel hulls, floating pontoons are likely to act as important stepping stones involved in the spread of NIS at local scales. These habitats undergo high disturbance due to maintenance work and multiple stressors, such as variation in salinity due to rainfall and exposure to pollutants from adjacent ships, which can give a competitive advantage to tolerant and fast-growing NIS (Piola & Johnston, 2008; Saloni & Crowe, 2015). Free space being the main limiting resource on simple hard substrata, competition is considered to be one of the most important interactions occurring among sessile species across multiple life cycles (Rius, Potter, Aguirre, & Stachowicz, 2014;