Journal of Experimental Marine Biology and Ecology 494 (2017) 10–19

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Large scale variability in the structure of sessile invertebrate assemblages in artificial habitats reveals the importance of local-scale processes

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ARTICLE INFO

Keywords:
Biofouling
Non-indigenous species
Temperature
Coastal infrastructure

ABSTRACT

Natural communities are structured by a complex suite of interacting physical and biological processes that operate across multiple spatial and temporal scales. Documenting spatiotemporal variability in ecological patterns can yield insights into the key processes influencing the distributions of species and structure of communities. Many previous studies conducted in natural habitats have recorded systematic shifts in assemblage structure along broad-scale latitudinal gradients, largely because of individual species' thermal affinities. However, it remains unclear as to whether similar patterns occur in artificial habitats, where patterns could be decoupled from natural processes. In this study, we examined patterns of spatial variability in the structure of sessile invertebrate assemblages in coastal infrastructure at multiple scales, including along a large-scale latitudinal gradient in Western Australia (WA). We deployed settlement panel arrays to sample invertebrate assemblages at 5 regions (in 2 seasons) along a latitudinal gradient spanning about 16° and > 2000 km along the coast of WA. As sea temperature co-varies predictably with latitude in this system, the study also encompassed a temperature gradient of about 10 °C. We examined spatiotemporal variability in several assemblage-level metrics, including total biomass, total cover, taxonomic richness and multivariate structure, as well as variability patterns for individual taxa. Unlike assemblages associated with natural habitats along the WA coastline, sessile invertebrate assemblages on coastal infrastructure did not vary systematically with latitude/temperature. Assemblage structure demonstrated little predictability at the regional scale, driven by processes including variability in temperature and adjacent species pools. Rather local-scale variability (and presumably processes and conditions acting at this scale) was far more important. This is an important consideration for coastal managers as local factors (e.g. the design of coastal infrastructure, human activities, hydrodynamic processes and propagule pressure) are likely to be important determinants of ecological pattern, with implications for the spread and establishment of non-indigenous species, biofouling and general ecological structure and functioning.

1. Introduction

In marine ecosystems, the distributions of species, structure of populations and composition of assemblages are influenced by a range of abiotic and biotic processes that operate across multiple spatial and temporal scales (Osman, 1977; Richmond and Seed, 1991; Perkol-Finkel and Benayahu, 2009; Bulleri and Chapman, 2010; Airoldi and Bulleri, 2011). Of the suite of interacting processes, large-scale gradients in ocean temperature may be of critical importance, as temperature is one of the most fundamental factors in determining the eco-physiological performance, demography and geographical distribution of marine organisms (Hutchins, 1947; Sunday et al., 2012; Wernberg et al., 2013). It has long been known, however, that temperature is not the sole determinant of ecological pattern, and species tolerances to other environmental parameters as well as their resource requirements, life history characteristics and dispersal capabilities are also important in determining patterns of distribution (Osman, 1977; Brown et al., 1996; Underwood et al., 2000; Lockwood et al., 2005; Clark and Johnston, 2009; Kordas et al., 2011). Unravelling the relative importance of regional and local scale processes in driving patterns of diversity and the structure of communities is a fundamental goal of ecology (Cornell and Lawton, 1992), yet current understanding is limited by a lack of studies conducted across sufficiently large spatial scales (Harrison and Cornell, 2008), particularly in the marine realm

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http://dx.doi.org/10.1016/j.jembe.2017.05.003
Received 1 July 2016; Received in revised form 30 April 2017; Accepted 6 May 2017

(but see Witman et al., 2004).

The vast majority of work examining the influence of latitudinal gradients in ocean temperature on patterns of diversity and community structure has stemmed from natural habitats, such as rocky reefs (Rivadeneira et al., 2002; Wernberg et al., 2013) and soft sediments (Ellingsen and Gray, 2002). However, artificial habitats such as breakwaters, jetties, ports and marinas now represent some of the most common coastal habitat types in many regions (Bacchiocchi and Airoldi, 2003; Bulleri and Chapman, 2004). Understanding the ecology of artificial habitats, which continue to replace natural habitats in many regions of the world, is increasingly important for managing anthropogenic impacts on marine biodiversity (Connell, 2000; Holloway and Connell, 2002). The artificial hardening of coastlines through building of infrastructure modifies hydrodynamics and transport processes (Martin et al., 2005), which has consequences for the structure and functioning of ecosystems at local and regional scales (Glasby and Connell, 1999; Airoldi et al., 2005; Martin et al., 2005). Where regions are poorly connected by of a lack of suitable natural habitat, artificial structures can act as stepping stones, diminishing geographical barriers and facilitating the dispersal of species (Airoldi et al., 2005, 2015), including sessile invertebrates which would naturally only disperse larvae over short distances (Svane and Young, 1989; Osman and Whitlatch, 1998). On a larger scale, human mediated vectors, such as ballast water, can transfer propagules well beyond their natural range. Artificially enhanced connectivity can increase both the flow of genes within species (Palumbi, 2003) and the flow of species between habitats and regions, including non-indigenous and pest species (Bulleri and Airoldi, 2005; Glasby et al., 2007; Rius et al., 2014). The complexity of interacting factors from the physical design of artificial habitats (Floerl and Inglis, 2003), natural variability of recruitment processes (Connell and Slatyer, 1977) and propagule pressure from various vectors (Drake et al., 2005) makes the understanding the ecology of coastal infrastructure challenging, particularly as the driving mechanism could be decoupled from natural processes.

There is strong evidence to suggest that assemblages of benthic organisms associated with artificial structures can be very different to those associated with natural habitats (Glasby and Connell, 1999; Connell, 2000; Holloway and Connell, 2002; Bulleri, 2005; Lam et al., 2009). Differences between assemblages on artificial and natural substrata occur very early on in succession and persist through time (Bulleri, 2005). There are many important factors driving this distinction, including habitat orientation and complexity (Chapman and Bulleri, 2003; Glasby and Connell, 1999), water motion (Floerl and Inglis, 2003), loading of nutrients, sediments and pollutants (Piola and Johnston, 2008; Dafforn et al., 2009) and the physical and chemical structure of the substrate itself (Dafforn et al., 2009). These factors influence the development of assemblages in artificial habitats, which generally differ in their composition and diversity from those in adjacent natural habitats (Glasby, 1999; Bulleri and Chapman, 2004; Vaselli et al., 2008). Moreover, artificial habitats are often linked with the transfer and establishment of marine non-indigenous species (NIS) (Carlton, 1996; Bulleri and Airoldi, 2005; Glasby et al., 2007). NIS are often more common than native species on artificial substrata (Airoldi et al., 2015), and they occur more frequently on coastal infrastructure than would be expected by chance given the available species pool (Glasby et al., 2007). Marine invasions are particularly common in or near ports because of the influence of international shipping traffic (Ruiz et al., 1997). Due to their increasing prevalence in coastal marine ecosystems and their importance within the context of managing the spread of NIS, examining multiscale spatial variability patterns in assemblage structure within artificial habitats is a critical step towards understanding processes underpinning ecological patterns.

Due to its spatial extent, spanning the tropics to temperate regions, the coastline of Western Australia (WA) provides a useful latitudinal gradient for studying changes in the structure of populations and communities in response to temperature. The Leeuwin Current is an eastern boundary current which flows poleward along the Western Australian coast transporting warm water and bringing with it the dispersal stages of a variety of warm-water marine fauna and flora (Pearce, 1991). Along this coastline, temperature has been described as a principal driver of ecological patterns (Wernberg et al., 2011, 2013) while other key environmental factors including wave exposure, nutrient availability and light are relatively consistent along the latitudinal gradient (Smale and Wernberg, 2009). This makes the WA coastline a ‘model system’ for examining the relationship between temperature and the structure of populations, communities and ecosystems (Smale and Wernberg, 2009; Foster et al., 2014).

Previous studies along the WA coastline have focused on how assemblages of macroalgae (Wernberg et al., 2010, 2011, 2013), benthic algae and invertebrates (Smale et al., 2010), demersal fish (Tuya et al., 2011; Langlois et al., 2012) and highly mobile invertebrates (Foster et al., 2014) vary with latitude. These studies have been conducted in natural habitats along the open coastline of WA, which are characterised by high species turnover and rich assemblages of macroalgae, sessile invertebrates and demersal fish. Reef-associated assemblages exhibit predictable regional scale shifts in diversity and structure associated with the oceanic temperature gradient (Smale, 2012; Wernberg et al., 2013) but, as yet, no studies have examined variability in assemblages associated with artificial habitats over similarly broad spatial scales. To date, the only regional-scale studies on sessile invertebrate assemblages developing on artificial substrata have been conducted 3–5 km offshore on rocky reef and sandy habitats and have not demonstrated a clear influence of temperature (Smale, 2012, 2013). Expanding the spatial scale and thermal breadth of observation will allow a better understanding of the importance of regional-scale variability (and processes acting at similar spatial scales) in assemblage structure within artificial habitats.

Here we examined spatial and temporal variability in the structure of sessile invertebrate assemblages inhabiting artificial habitats along a large-scale latitudinal/temperature gradient in WA. The aims of this study were: (1) to determine whether the structure of these assemblages shifts predictably along a broad-scale latitude/temperature gradient; (2) to determine the relative importance of local and regional-scale variability in assemblage structure; and (3) to examine whether spatial variability patterns are consistent in time (between summer and winter sampling periods).

2. Methods

2.1. Study area and sampling design

This study was conducted in collaboration with the WA Department of Fisheries Marine Biosecurity Research team. As part of ongoing pest species monitoring, settlement panel arrays are regularly deployed into regional ports throughout the State. For this study, sampling was conducted at 5 regions, with 2 sites nested within each. Regions included Cygnet Bay, Carnarvon, Geraldton, Albany and Esperance, spanning a geographical range of ~16° latitude (Fig. 1). Cygnet Bay is the most northern and remote site. The sampling site was located on the eastern side of the Dampier Peninsula on a pearl farm with minimal hard structure and limited vessel traffic. This region had the largest tidal variation, ranging from 1 to 10 m. Only one array was used in this region, as the other was lost during the first sampling period. Carnarvon Boat Harbour contained 2 arrays, one on each side of the service jetty, separated by only a few meters. The harbour was located on south of the Gascoyne River on a stretch of reclaimed land. The two arrays in Geraldton were located approximately 2 km from each other, one at the commercial Fishing Boat Harbour and the other at the recreational Batavia Coast Boat Harbour. In Albany, both arrays were located at the Albany Port, about 700 m from each other. The Port is located south of the city of Albany, within King George Sound. Esperance sites were located within the Esperance Port, on an exposed point in Esperance