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Benthic assemblage composition on subtidal reefs along a latitudinal gradient in Western Australia

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At regional scales, the distribution of species and the structure of assemblages vary with latitude within many marine and terrestrial systems. The oligotrophic coastal waters of Western Australia (WA) support highly speciose and endemic assemblages, yet spatial patterns in benthic structure are currently poorly known. We examined benthic assemblage composition along a latitudinal gradient of 28.5–33.5°S and a depth gradient of 14–62 m, on subtidal reefs in warm-temperate WA. We surveyed benthos using a remotely triggered digital stills camera. In total, we sampled macroalgae and sessile invertebrates at 201 sites spread across four locations. Percent cover of coarse taxonomic groups and dominant species was estimated from over 2000 photoquadrat samples. We recorded significant differences in benthic assemblage composition between locations, and along depth gradients within each location. However, the magnitude of change with depth was not consistent between locations, and shifts in assemblage composition along the depth gradients were not as pronounced as expected. The percent cover of all dominant benthic groupings differed between locations, and several key taxa, such as the kelp *Scytothalia dorycarpa*, brown foliose macroalgae, hard corals and sponges, changed predictably along the latitudinal gradient. Our study adopted a coarse taxonomic, but assemblage-wide, approach to describing macrobenthic assemblages, and clear differences between locations and depths were detected. The surveys have provided baseline data on broad scale ecosystem structure against which to detect future ecological change.

1. Introduction

Anthropogenic climate change has, and will continue to, drive changes in the distributions of species in both the terrestrial (Walther et al., 2002; Parmesan and Yohe, 2003) and marine realm (Harley et al., 2006; Hawkins et al., 2008). In marine systems species may undergo range shifts along latitudinal (Perry et al., 2005) or depth gradients (Dulvy et al., 2008), which in turn can influence competitive interactions, food and habitat availability, and reproductive success. To be able to detect and predict such responses to widespread environmental change, ecological patterns and processes must be studied at large spatial scales, which has given rise to the field of macroecology and renewed the importance of biogeography. As natural communities are notoriously patchy at small spatial scales, such as within study sites, clear ecological pattern may only be evident at large spatial scales, such as across locations or regions (Levin, 1992; Fowler-Walker and Connell, 2002; Connell, 2007). Here we present the first assessment of marine benthic assemblage composition along a regional-scale latitudinal cline in Western Australia (WA).

The coastline of WA extends from 13 to 35°S and encompasses a wide range of habitats, including mangroves, seagrass beds, embayments and exposed reefs, that support highly diverse assemblages of marine plants and animals. The West Coast bioregion, ranging from Kalbarri (~28°S) to Cape Leeuwin (~34°S) is a tropical–temperate transition zone, and supports high local species richness and endemism, particularly for macroalgae and seagrasses (Huisman et al., 1998; Phillips, 2001). The ecology of the bioregion is strongly influenced by the Leeuwin Current (LC), which originates in the nutrient-poor warm waters of the Indo-Pacific and flows polewards along the Western Australian coastline before deviating eastwards into South Australian waters (Cresswell and Golding, 1980; Pattiaratchi and Buchan, 1991; Pearce, 1991). The effects of the LC on the temperate marine ecosystem of WA include: elevated water temperatures (Pearce, 1991; Pearce et al., 2006a); poleward transport of tropical species (Ayvazian and Hyndes, 1995;

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Greenstein and Pandolfi, 2008); high interannual variability in recruitment of certain taxa (Pearce and Phillips, 1988; Caputi et al., 1996; Griffin et al., 2001); and suppression of the nutrient rich upwellings characteristic of eastern boundaries of other major ocean basins (Lourey et al., 2006; Pearce et al., 2006b). In summary the temperate marine system of WA is a uniquely oligotrophic system, characterised by a tropical–temperate transition zone consisting of many warm water species at the southern limit of their range and many cool water species at the northern limit of their range.

Within the next 50–70 yrs, sea surface temperature around Australia is predicted to increase by 1–2 °C due to anthropogenic forcing of global atmospheric CO_2. This warming will not only affect surface waters, but is likely to penetrate the water column to depths of about 500 m (Poloczanska et al., 2007). However, WA is unique in that temperatures are largely driven by the LC, which has influenced the tropical–temperate species cline along the coastline for millions of years (Pattiaratchi and Buchan, 1991). Therefore, it may be climate driven changes to current flow, rather than temperature *per se*, that have greatest influence on the structure of benthic communities. The most recent projections of the LC would suggest that, unlike the East Australian Current, it will not strengthen (Poloczanska et al., 2007). To what extent the LC will buffer benthic communities from ocean warming remains unclear, and better understanding of regional hydrology and spatial and temporal variability in the strength of the LC and its eddies are needed to improve projections from climate models. Even so, the temperate marine system of WA is characterised by a series of well connected subtidal reefs arranged along a latitudinal and ocean temperature gradient, and it is likely that species range shifts (and consequent alterations in community structure) will occur in the region.

In the last decade or so, quantitative information on the distributions and ecologies of macroalgae (Wernberg et al., 2003), echinoderms (Vanderklift and Kendrick, 2004), molluscs (Vanderklift and Kendrick, 2004; Wernberg et al., 2008), historical and extant reef corals (Greenstein and Pandolfi, 2008) and fish (Ayvazian and Hyndes, 1995; Tuya et al., 2008) have been collected from various locations along the temperate latitudinal gradient (~35–28°S). While these studies have substantially contributed to our knowledge of the benthic system, they are spatially limited as they were all conducted by SCUBA divers in shallow water (i.e. <20 m depth). However, only ~5% of the total area of WA's continental shelf lies at depths of <20 m, whereas ~70% of the entire shelf lies in depths of 20–100 m (Kendrick, unpublished data). Thus, the majority of the shelf habitat has been greatly under-sampled.

We tested the hypothesis that benthic assemblage composition changes along a latitudinal cline between 28.5 and 33.5°S in coastal waters of temperate WA. This hypothesis was developed because the region is characterised by an inshore temperature gradient of ~2 °C (Smale and Wernberg, 2009), and because the LC transports dispersive warm water invertebrate and algal species polewards. As a result, we predicted that more warm water species would recruit and persist at lower latitudes, and patterns of change would be detectable at the assemblage level. Our study also had two secondary aims. Firstly, it was envisaged that our study would aid the identification of taxa that may serve as ecological indicators to detect the effects of oceanic warming on subtidal reef communities. As water temperature varies with latitude, and many other key environmental variables (e.g. substrate availability, wave disturbance, nutrients) do not co-vary along the latitudinal gradient (Smale and Wernberg, 2009), latitude may be conservatively used as a proxy for water temperature in this system. Thus, taxa that demonstrate clear latitudinal patterns may prove to be useful ecological indicators of future warming. Secondly, we aimed to examine changes in assemblage composition along a depth gradient at each location. To achieve these goals and collect valuable ecological baseline data, comprehensive surveys of the benthos were conducted at four locations along the latitudinal gradient, at depths between 14 and 62 m.

2. Methods

2.1. Sampling locations

Sampling was conducted at four locations along the west coast of WA: the Houtman Abrolhos Islands (hereafter 'Abrolhos'), Jurien Bay ('Jurien'), Rottnest Island ('Rottnest') and Cape Naturaliste ('Naturaliste') (Table 1, Fig. 1). Mean SST ranged from 21.5 °C at Abrolhos to 19.1 °C at Naturaliste. All locations were characterised by a subtidal seascape of reef structures interspersed with (occasionally extensive) sand patches. Reefs ranged from high-profile structures that protruded several metres from the surrounding seabed to low-profile reef platforms. Bathymetric gradients at all locations were gently sloping, so that depth gradients covered similar distances. Reefs were exclusively limestone at Abrolhos, Jurien and Rottnest, and a combination of granite and limestone at Naturaliste. Previous research has suggested that levels of nutrients, light, herbivory and wave action are broadly comparable along this stretch of coastline. Jurien and Naturaliste were coastal locations, while Abrolhos and Rottnest were offshore islands, rising 80 and 18 km from the coastline of WA, respectively. Sampling was undertaken between January and October 2008. The locations were chosen to cover latitudinal range of ~5°, which corresponds to a nearshore temperature gradient of ~2 °C (Smale and Wernberg, 2009).

2.2. Sampling method and design

At each location, sampling was conducted by remotely triggered still photography at 60 or more sites (Table 1). Hydroacoustic surveys and towed video sampling of the locations were initially conducted such that the subsequently generated maps allowed our sampling to target reef habitats (rather than sand) and to allow sampling to be stratified along a depth gradient. Sites were selected to be spatially independent of one another (i.e. separated by at least 100 m) and to provide reasonable spatial coverage of each location. A total of 413 sites were sampled during the field program with a minimum of 10 photos captured at each site. Ideally, the depth gradients (and the distribution of sampling effort along them) would have been consistent across the four locations, to facilitate a two-way comparison of depth, location and interaction effects. However, due to logistics and bathymetry, this was not possible and the magnitude of the depth gradients differed between locations (Table 1 and see below).

Images were collected with a high resolution camera system mounted on a steel frame. The system consists of two cameras. The first camera is situated at an angle and provides a direct video feed to the winch operator aboard the boat, allowing the camera frame

Table 1
Locations, depths (m), and sampling details of drop camera survey. Total number of sites includes soft-sediment habitats, whereas only reef habitats were used for analysis. The number of sites sampled at 30–39 m depth (depth group 3) is indicated as these samples were used for the 'depth-standardised analyses' (see Methods for details).

Location (and latitude)	Total no sites	No. sites analysed (n)	No. sites 30–39 m	Depth range	Mean depth	Sampling dates
Abrolhos (28.5°S)	188	65	12	15–41	29	Oct. 08
Jurien (30.3°S)	78	54	14	32–60	42	Mar. 08
Rottnest (32.7°S)	87	54	23	14–62	37	Jan./June 08
Naturaliste (33.5°S)	60	28	17	19–45	35	Sept. 08