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

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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; Ayvazian et al., 1994; Roff et al., 2001).
of years (Pattiaratchi and Buchan, 1991). Therefore, it may be climate that temperatures are largely driven by the LC, which has influenced the gradient at each location. To achieve these goals and collect examine changes in assemblage composition along a depth ecological indicators of future warming. Secondly, we aimed to detect the effects of oceanic warming on subtidal reef communities. Thus, taxa that bance, nutrients) do not co-vary along the latitudinal gradient as a proxy for water temperature in this system. Therefore, taxa that many cool water species at the southern limit of their range and many warm 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 CO2. 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 speciescline 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 (Vand erklift and Kendrick, 2004), molluscs (Vand erklift and Kendrick, 2004; Wernberg et al., 2008), historical and extant reef corals (Greenstein and Pandolfi, 2008) and fish (Ava zian 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°S, 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>
<thead>
<tr>
<th>Location (and latitude)</th>
<th>Total no sites (n)</th>
<th>No. sites analysed (n)</th>
<th>No. sites 30–39 m depth range</th>
<th>Mean depth (m)</th>
<th>Sampling dates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abrolhos (28.5°S)</td>
<td>188</td>
<td>65</td>
<td>12</td>
<td>15–41</td>
<td>29 Oct 08</td>
</tr>
<tr>
<td>Jurien (30.3°S)</td>
<td>78</td>
<td>54</td>
<td>14</td>
<td>32–60</td>
<td>42 Mar 08</td>
</tr>
<tr>
<td>Rottnest (32.7°S)</td>
<td>87</td>
<td>54</td>
<td>23</td>
<td>14–62</td>
<td>37 Jan–June 08</td>
</tr>
<tr>
<td>Naturaliste (33.5°S)</td>
<td>60</td>
<td>28</td>
<td>17</td>
<td>19–45</td>
<td>35 Sept 08</td>
</tr>
</tbody>
</table>
to be positioned upright on the substrate. The second camera is positioned over a 0.96 m × 0.64 m quadrat and captures a high resolution image of the seabed (camera set-up adapted from Stokesbury et al., 2004). Images were captured using a down-facing “Canon EOS 30D digital SLR camera” (8.2 MP) fitted with a 24 mm wide angle lens and set to a fixed focal distance. Lighting was achieved with a continuous underwater lamp fitted with a diffuser. When sampling, the boat was positioned over a site and the still photography system lowered. The camera remained above, rather than within, the kelp canopy (where present) at all sites. As the boat drifted over the site, the system was raised then lowered in a haphazard fashion, upon which the next image is captured. This method generated a drift transect of at least 10 benthic images for each site. The software package “StarFix Real Time Suite” (developed by Fugro Inc.) was used with ultra-short baseline (USBL) hydroacoustic positioning and differential GPS system to provide a precise geographic position (including depth) for each image.

2.3. Sample processing

In total, over 4000 photoquadrats of the benthos were collected. When analysing images 50 random points were digitally overlaid onto each sample, and the number of points covering each benthic grouping was counted. This value was then doubled to give a proxy of percent cover. Benthic groupings included dominant flora, fauna and substratum characteristics and were largely determined a priori based on previous observations and research (Table 2). Care was taken to include conspicuous species of considerable ecological importance, such as the canopy-forming brown alga Ecklonia radiata and Sctyothalia dorycarpa, while maintaining a general, holistic approach to describing the benthos. The benthic groupings were designed so that minimal training and experience would be required to analyse the images, while aiming to retain ecological pattern by including the complete range of biota likely to be sampled. Encrusting organisms were assumed to be living unless obvious discolouration or structural damage was observed. It was evident from the images that the methods were inappropriate for sampling mobile fauna (i.e. echinoids, gastropod molluscs), which generally have low abundances, highly variable distributions and utilise cryptic habitats in Western Australia (Vanderklift and Kendrick, 2004; Wernberg et al., 2008). Therefore, mobile invertebrates were excluded from analysis and assemblage composition was derived from dominant macroalgae and sessile invertebrates.

Following image analysis, 10 images (subsamples) were randomly selected from each drift transect and averaged to give one independent sample per site. Samples were then assigned a location and depth grouping for categorical statistical analysis. For depth, the continuous depth readings for each sample were converted to discrete depth groupings by dividing each value by 10 and rounding down to the nearest whole integer (e.g. 37 m depth equals depth group 3 and 50 m depth equals depth group 5). The study aimed to describe benthic assemblages on hard substrata, but due to the complex reef/sand habitat many of the drops landed on sand or reef covered by a thin layer of sand. As such, prior to analysis all sites with >50% percent cover of ‘sand’ and/or ‘reef covered by sand’ were discarded. Even with this stratified loss of samples, 201 sites were sampled over reef with ~2000 individual photoquadrats (Table 1). However, as some images captured the transition from rocky reef to adjacent sand patches, some ‘soft sediment’ flora (i.e. seagrasses) were sampled and included in the analysis. As such, while the dominant habitat sampled here was hard substrata, sand-inundated rock platforms at the edge of reef structures (and the flora and fauna that they support) were also considered in the analysis.

2.4. Data analysis

The unbalanced nature of the surveys prevented a two-way analysis of the entire dataset, as depth groupings were not consistently sampled between locations. Instead, we took the pragmatic approach of examining the effects of location and depth in isolation, meaning that ecologically important interaction effects and the wider generality of patterns were not considered. Differences in benthic structure between locations along the latitudinal gradient were assessed in two ways. First, we used the entire dataset to test for location differences, acknowledging that location was confounded to some extent by the distribution of sampling effort along a depth gradient. Second, we selected all samples from ‘depth group 3’ (i.e. 30–39 m depth), as this depth range was sampled at all locations and included a large proportion of samples. We then tested for location differences with a smaller, but unconfounded ‘depth-standardised’ dataset, with n per location ranging from 12 to 23 (Table 1). Differences between depth groupings were examined within each location separately. Permutational analysis
of variance (PERMANOVA), based on Bray–Curtis dissimilarities of square-root transformed percent cover data, was used to test for differences in multivariate assemblage structure along the assumed environmental gradients. All data were square-root transformed prior to analysis to moderately down-weight the importance of large space occupiers, such as the kelp Ecklonia radiata. The routine was applied using the PERMANOVA+ add-on to the PRIMER 6 statistical software (Clarke and Warwick, 2001; Anderson et al., 2007). This approach allowed us to satisfactorily deal with the unbalanced designs and analyse the dataset without rigorous assumptions of normality. Main tests were conducted across one (fixed) factor and used 4999 unrestricted permutations. Significant terms were then investigated using a posteriori pairwise comparisons with the PERMANOVA t statistic and 999 permutations. In addition, PERMDISP (Anderson et al., 2007) was used to examine differences in multivariate variability in assemblage structure between locations. Finally, one-way ANOSIM tests were performed to determine the magnitude of difference between locations and depths (within locations).

Differences in assemblage composition between locations and differences along a depth gradient within locations were visualized with non-metric multidimensional scaling (nMDS) on the basis of Bray–Curtis dissimilarities of the square-root transformed percent cover data. RELATE tests were conducted to assess the strength of correlation between the Bray–Curtis similarity matrices and model matrices derived from distances between locations and distances between depth groupings (again using PRIMER 6). Finally, the percentage contributions of each benthic grouping to observed differences between locations were assessed with the SIMPER routine.

Univariate analysis (permutational ANOVA) was used to determine differences in the percent cover of dominant benthic groupings between locations. Again, tests were conducted on the entire dataset and a constrained dataset standardised by depth. Univariate analyses were conducted using a distance-based approach (as described above for the multivariate analysis) but using Euclidean distances for single response variables. Significant terms were investigated further, as required, using a posteriori pairwise comparisons. All univariate tests were based on 999 permutations.

3. Results

3.1. Multivariate assemblage-level results

We observed highly significant differences in benthic assemblage composition between the locations, both when considering the entire dataset and when standardising for depth (Table 3). The magnitude of differences between locations, as determined by ANOSIM, was moderate for both datasets. Visualisation of the samples through MDS also indicated some partitioning between all locations, and suggested that assemblages at Abrolhos were largely distinct from those at the other locations (Fig. 2). This pattern was particularly evident for the samples selected from depth group 3 only. Crucially, the MDS plots also indicated that the direction of change was not entirely along a latitudinal trajectory, principally due to relatively high similarities between Jurien and Naturaliste. This lack of latitudinal pattern was supported by the RELATE analyses, as the model matrices generated from distances between locations were poorly correlated with the biotic similarity matrices (Table 3). With regards to multivariate variability, we recorded inconsistencies between the two datasets, as dispersion within locations was significantly different when the depth-standardised dataset, but not for the entire dataset (Table 3). An examination of the MDS plot and the results of the PERMDISP test for the depth-standardised dataset indicated that significant differences in multivariate variability were due to greater dispersion at Abrolhos compared with other locations.

Pairwise comparisons with PERMANOVA showed that all the locations were significantly different from each other (P < 0.01 in all cases for both the entire dataset and the depth-standardised dataset). Again, the magnitude of dissimilarity between locations was not directly correlated with geographic distance, as Abrolhos samples and Rottnest samples were the least similar, while the samples from Jurien and Naturaliste were the most similar.

A SIMPER analysis determined which benthic groupings contributed most to the observed dissimilarity between locations (Table 4). Percent cover of the kelp Ecklonia radiata was consistently a major contributor to the observed variation between all locations.

![Fig. 2](image-url)
Differences between locations were principally due to a higher coverage of hard corals at Abrolhos. A relatively high percent cover of red foliose algae tended to discriminate the assemblages at Jurien from those at other locations, while higher cover of the canopy-forming algae *Scytothalia dorycarpa* was an important discriminator for Naturaliste assemblages. Brown foliose algae and encrusting coralline algae were also consistently high contributors to observed differences between locations.

Within each location, benthic assemblages were significantly different between depth groupings, although ANOSIM tests indicated that differences were low to moderate in magnitude (Table 3). MDS plots of samples within each location indicated a subtle but general shift in structure along a depth gradient, which was most pronounced at Naturaliste and least defined at Abrolhos (Fig. 3). Interestingly, the strength of correlation between the model matrices based on depth groupings and the biotic matrices increased with latitude from Abrolhos to Naturaliste (Table 3). This suggested that patterns along the depth gradient were not particularly pronounced at some locations, and were not spatially consistent.

### 3.2. Univariate analysis of dominant taxa

Differences between locations for ten univariate measures were analysed with PERMANOVA, using both the entire and the depth-standardised datasets (Table 5). We recorded strongly significant differences between locations for all dominant biotic groupings with both datasets. The directions of differences, as determined by pairwise comparisons, were very similar between the two datasets (Table 5). This suggested that inconsistencies in the depth gradient sampled at each location did not severely confound between-location comparisons, and further discussion relates only to patterns derived from the entire dataset.

For the kelp *Ecklonia radiata*, the differences between locations were largely driven by higher percent cover at Rottnest than the other locations (Table 5, Fig. 4). *Scytothalia dorycarpa* was not recorded at Abrolhos or Jurien but significantly increased in cover between Rottnest and Naturaliste and, as such, the percent cover of *S. dorycarpa* increased with increasing latitude along part of the gradient studied (Fig. 4). Conversely, mean percent cover of the brown foliose algae showed a general decrease with increased latitude, while the percent cover of red foliose algae differed significantly between the two southernmost locations and the two northernmost locations (Table 5, Fig. 4). Differences between locations were significant (*P* < 0.05 for all pairwise comparisons except Abrolhos and Jurien). Finally for the dominant algal groups, the percent cover of encrusting coralline algae showed no clear pattern with latitude and no consistent pattern between datasets (Table 5, Fig. 4), suggesting that its coverage may be confounded by depth inconsistences between locations.

With regards to the faunal benthic groupings, the mean percent cover of the sponges generally increased with increased latitude and, with the exception of Abrolhos and Jurien where percent cover was low, all between-location differences were significant (Table 5, Fig. 4). Finally, bryozoans had significantly lower coverage at Abrolhos than at other locations, while the percent cover of hard corals was greater at Abrolhos compared with elsewhere (Table 5, Fig. 4).

Plots of mean coverage of benthic groupings against depth for each location suggested that depth related patterns were not consistent between locations (Fig. 5). For example *Scytothalia dorycarpa* showed a different pattern along the depth gradient at Rottnest compared with Naturaliste. At Rottnest, percent cover remained consistent across depth groups 1–3, before decreasing slightly in depth group 4. In contrast, at Naturaliste the percent cover of *S. dorycarpa* was considerably greater in depth groups 1 and 2, then decreased in group 3 and was absent in group 4 (Fig. 5). Similarly, the mean percent cover of brown foliose algae generally decreased with depth at all locations except for Naturaliste, where we recorded a slight increase in percent cover between depth groups 1 and 3 (i.e. between 19 and 39 m depth). Location-specific differences in patterns of percent cover along a depth gradient for red foliose algae, sponges and bryozoans were also evident (Fig. 5). These differences may have been exacerbated by the unbalanced design, as the magnitude of the depth gradient examined was not consistent between all locations.

As could be predicted, the percent cover of the algal groups tended to peak in the shallows (i.e. 14–29 m) before decreasing with depth thereafter (Fig. 5). In contrast, sponges and bryozoans generally increased in percent cover with depth (Fig. 5). Interestingly, the depth distributions of *Ecklonia radiata* and *Scytothalia dorycarpa* differed between Naturaliste and the lower latitude samples taken at Rottnest and Jurien. To expand, at Naturaliste, both *E. radiata* and *S. dorycarpa* had greatest percent cover in depth groups 1 and 2 and were entirely absent in depth group 4. In contrast, at Rottnest although the percent cover of both species declined with depth they were both present in depth group 4 (i.e. between 40 and 49 m depth). At Jurien, where *S. dorycarpa* was not recorded but
**E. radiata** was common, the percent cover of the kelp peaked in depth group 4 and it was present in depth group 5 (i.e. 50–59 m depth).

### 4. Discussion

#### 4.1. Multivariate patterns

Overall, benthic assemblages on subtidal reefs in nearshore temperate waters of WA were characterised by a dominance of the kelp *Ecklonia radiata*, a high cover of foliose algae, and a low cover but wide occurrence of sessile invertebrates (except for high cover of hard corals at Abrolhos).

We detected significant differences in coarse-level assemblage composition between the four study locations. However, whilst there were some indications that assemblage structure changed along the latitudinal cline, the gradient was not represented well. For example, although we observed significant correlations between model matrices derived from distances between locations and biotic resemblance matrices, the strength of correlations was only low to moderate. Furthermore, the assemblages at Abrolhos were clearly distinct from those at other locations, principally because of an increased percent cover of hard corals and a decreased percent cover of the canopy forming kelps, and several dominant taxonomic groups showed clear latitudinal patterns in percent cover. Even so, overall changes between locations did not follow the latitudinal gradient, leading us to reject our principal hypothesis. This was best illustrated by the fact that assemblages at Naturaliste and Jurien were the most similar, despite being ~350 km apart. We suggest three explanations for this lack of pattern: (1) benthic composition does not significantly change along a latitudinal gradient in the study region; (2) our coarse taxonomic approach did not capture genus/species level changes in assemblage composition along the cline; and (3) the offshore islands of Abrolhos and Rottnest were not representative of nearshore habitats and these locations confounded the general latitudinal pattern. In reality, our ‘lack’ of pattern may be driven by a combination of these factors and merits further work at a finer-resolution.

Many other studies conducted at the regional scale (100–1000 km), have documented significant shifts in benthic communities along a latitudinal cline. These shifts are generally attributed to ‘bottom up’ effects, such as the proximity of upwellings, gradients in sea temperature, and the effects of disturbance and light (Bustamante and Branch, 1996; Barnes and Arnold, 1999; Connolly et al., 2001; Cummings et al., 2006; Scoh et al., 2006). Intuitively, where gradients in physical conditions are steep and environmental changes occur across smaller distances, shifts in assemblage composition are likely to be more pronounced and easier to distinguish from background (small scale) variability. In temperate

#### Table 5

Results of permutational ANOVAs to test for differences between locations in the percent cover of dominant benthic groupings. Tests were conducted on the entire dataset, which was confounded to some extent by depth (see text) and on a smaller dataset comprising only of samples collected at 30–39 m depth (depth group 3). Tests used 193 DF in total: Res = 190 and location = 3. Significance is indicated by asterisks: *P < 0.05, **P < 0.01 and ***P < 0.001. All tests used 999 permutations. The directional outcomes of pairwise tests are also shown.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Location (all depths)</th>
<th>Location (depth gr. 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td><em>Ecklonia radiata</em></td>
<td>42.9</td>
<td>11.5***</td>
</tr>
<tr>
<td><em>Scytothalia dorycarpa</em></td>
<td>14.7</td>
<td>20.79***</td>
</tr>
<tr>
<td>Brown foliose algae</td>
<td>6.7</td>
<td>7.4***</td>
</tr>
<tr>
<td>Red foliose algae</td>
<td>16.6</td>
<td>14.3***</td>
</tr>
<tr>
<td>Encrusting coralline algae</td>
<td>20.2</td>
<td>33.1***</td>
</tr>
<tr>
<td>Sponges</td>
<td>15.1</td>
<td>5.0***</td>
</tr>
<tr>
<td>Bryozoans</td>
<td>2.3</td>
<td>8.8***</td>
</tr>
<tr>
<td>Hard corals</td>
<td>108.3</td>
<td>59.5***</td>
</tr>
</tbody>
</table>
WA, the LC effectively suppresses the latitudinal temperature gradient by maintaining relatively high winter temperatures and reducing seasonal variability at the southernmost locations. For example, Smale and Wernberg (2009) reported a mean winter sea temperature of $\sim 18 ^\circ C$ at a nearshore location at 34$^\circ$S. This value is 6–9 $^\circ$C warmer than those recorded at the Cape of Good Hope (also 34$^\circ$S), on the west coast of South Africa (McQuaid and Branch, 1984), and at least 4 $^\circ$C warmer than 34$^\circ$N off the coast of California (Scoch et al., 2006). Strong latitudinal shifts in the structure of marine communities have been reported in both regions (Bustamante and Branch, 1996; Scoch et al., 2006). The lack of suppression of seawater temperature in WA, driven by the LC and the absence of significant cool water upwellings, effectively reduces the slope of the latitudinal temperature gradient so that mean seawater temperature varies by only $\sim 2 ^\circ$C over 1000 km of north–south coastline. It is likely, therefore, that temperature-driven latitudinal shifts in benthic community structure occur over larger spatial scales than considered here (i.e. the entire west coast of WA), and local patterns may have greater influence in this system compared with systems characterised by steeper gradients.

Within each location, benthic assemblage structure changed to some extent along a depth gradient. Depth is a key factor structuring nearshore benthic assemblages the world over (e.g. Dayton, 1985; Barnes, 1999), and it was not surprising that the influence of primary producers generally decreased with depth (e.g. Goldberg and Kendrick, 2004), and the percent cover of some invertebrate taxa increased along the depth gradient. Even so, differences along the depth gradient of 14–62 m were only moderate, and perhaps not as pronounced as in other subtidal systems elsewhere. This was largely because benthic algae and corals were recorded across the entire depth range (even photosynthesising plants were present across the majority of the gradient), suggesting light was not limiting across the depths sampled for primary producers in Western Australian coastal waters. The percent cover of red foliose algae, for example, showed no overall reduction along the depth cline at any location and was the most dominant benthic grouping at Jurien at depths of 30–39 m. Thus, ubiquitous primary producers effectively suppressed shifts in assemblage composition along a depth gradient in the study region.

Interestingly, the strength of the correlations between model matrices derived from depth groupings and biotic resemblance...
matrices increased with increasing latitude. Whether this is an artefact of inconsistencies in the depth gradients sampled at each location, or genuine ecological pattern, merits further study.

It is worth noting the distinct nature of the assemblages we sampled at Abrolhos. Not only were the assemblages dissimilar in their composition, but variability in assemblage structure was also pronounced relative to the other locations. The Houtman Abrolhos Islands support the southernmost coral reef systems found in the Indian Ocean, and represent an important transition zone from kelp dominated to coral dominated benthic communities (Babcock et al., 1994). Our Abrolhos samples were collected from a complex mosaic of habitat types, with kelp dominated patches interspersed with coral dominated patches. This interspersion of dominant habitat formers within a single location promoted considerable multivariable variability, especially at depths of 30–39 m. This benthic crossover zone is of great ecological interest, and could potentially offer novel insights into the influence of environmental change on habitat forming species.

4.2. Univariate patterns

The kelp *Ecklonia radiata* is a key habitat forming species in the region and was the dominant canopy-forming algae at all our study locations. It has been described as a warm temperate kelp; its ‘warm’ northern limit is thought to be just 100 km north of Abrolhos (Hatcher et al., 1987). However, *E. radiata* had relatively high percent cover at Abrolhos compared with Jurien and Naturaliste, and consequently we did not record a clear latitudinal pattern for this species. Conversely, the canopy-forming brown alga *Scytothalia dorycarpa* and the ‘brown foliose algae’ taxa did exhibit clear trends with latitude. Furthermore, the percent cover of the ‘brown foliose algae’ group, which primarily comprised of tropical or warm temperate species such as *Padina* spp. and *Dictyota* spp., was inversely related to latitude. Increasing water temperatures may result in a decreased cover and competitive ability of cool-water canopy-forming algae, and allow brown (and red) foliose algae to dominate subtidal reefs. Our results suggest that these taxa may have potential as ecological indicators of ocean warming in the region, but further work on casual relationships between temperature and the percent cover of such groups is clearly needed.

The percent cover of sponges, which were recorded at all locations, increased with latitude. While percent cover of sponges was generally low, the ubiquitous distribution of sponges and clear distributional trends related to latitude may make them good contenders for ecological indicators in the region. Finally, the percent cover of hard
corals was, as expected, markedly higher at Abrolhos compared with the other locations. It is unclear whether reef-building corals will extend their ranges polewards or increase in abundance at lower latitudes as water temperatures increase. While coral taxa present in WA today have clearly expanded and contracted their geographic ranges in response to historical climate change (Greenstein and Pandolfi, 2008), the rate of current climatic change, substrate availability and (crucially) aragonite saturation levels may prevent widespread range expansions (Kleypas et al., 1999; Lough, 2007). It is likely that species will respond differently to warming and that some species will undergo range expansions into ‘temperature refugia’ as waters warm. For this reason, and for the fact that reef-building corals are of great importance, the presence and abundance of hard corals will be important ecological indicators of environmental change in WA.

The surveys presented here have enhanced our knowledge of benthic assemblages in temperate WA. However, there are limitations concerning the sampling methodology that should be considered when interpreting our results. First, as samples were collected with a remotely triggered mounted camera system, only (roughly) horizontal substrata were surveyed. Vertical surfaces, caves, overhangs and crevices are prominent features of subtidal habitats in the region; these microhabitats support a wealth of invertebrate species and represent a significant component of the biota (Hatcher, 1989; Irving and Connell, 2002). As a result, the patterns described above relate to a subset of the entire benthic assemblage and ‘absolute’ patterns of assemblage composition along the latitudinal gradient may differ. Second, logistical constraints resulted in an unbalanced design and between-location differences in the magnitude of the depth gradient. For example, at Naturaliste 28 sites were sampled along a depth gradient of 19–45 m, whereas 54 sites were sampled at depths of 32–60 m at Jurien. While modern permutational statistical approaches can deal with unbalanced designs (Clarke and Warwick, 2001), holistic comparisons between depths and locations, and formal examinations of interaction effects were not feasible. Consequently, our observations, such as between-location differences in the depth distributions of dominant algal groups and the identification of indicator taxa, should be treated as preliminary results that can direct future research. Furthermore, effective monitoring of these assemblages would require comparable depth gradients at each location, and more sampling locations along the latitude/temperature gradient.

5. Conclusions

Sea surface temperatures on the continental shelf off WA have increased by 0.8 °C in the last fifty years (Pearce and Feng, 2007), while there are some indications that the flow of the LC, which is lower in El Nino years, has weakened during this time (Feng et al., 2003; Caputi, 2008). The species-rich nearshore assemblages at Ningaloo in the northwest and on the subtidal limestone reefs in the southwest may be partially protected from such warming by wind-driven counter currents, which carry colder water northwards during the summer months (Pearce and Pattiaratchi, 1999; Woo et al., 2006). While it is clear that the LC is a key driver of ecosystem structure in the region, current climate models are unable to predict future changes in the strength of the LC with any certainty. Similarly, the intensity and latitude of storm tracks has changed in the region, but it remains unclear how this will relate to effective hydrodynamic stress on subtidal reefs, which is also a key driver of community structure. Despite this uncertainty, it is highly likely that changes in ecosystem structure will occur in response to climate change, and our surveys have provided baseline data on benthic assemblage composition against which to detect such changes. Our study has also highlighted dominant taxa that may undergo shifts in distribution and serve as ecological indicators. The next stage of research is to use these correlations and observations to generate hypotheses to test causal links, which remains a crucial undertaking in the development of ecological indicators (Goodsell et al., 2009).

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