Biogenic habitat structure provided by temperate macroalgae change along a latitudinal gradient in ocean climate

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Abstract

Global warming is affecting all major ecosystems, including temperate reefs where canopy-forming seaweeds provide biogenic habitat. In contrast to the rapidly growing recognition of how climate affects the performance and distribution of individuals and populations, relatively little is known about possible links between climate and biogenic habitat structure. We examined the relationship between several ocean temperature characteristics, expressed on time-scales of days, months and years, on habitat patch characteristics on 24 subtidal temperate reefs along a latitudinal gradient (Western Australia; ca 34 to 27º S). Significant climate related variation in habitat structure was observed, even though the landscape cover of kelp and fucalean canopies did not change across the climate gradient: monospecific patches of kelp became increasingly dominant in warmer climates, at the expense of mixed kelp-fucalean canopies. The decline in mixed canopies was associated with an increase in the abundance of *Sargassum* spp., replacing a more diverse canopy assemblage of *Scytothalia doryocarpa* and several other large fucoids. There were no observed differences in the proportion of open gaps or gap characteristics. These habitat changes were closely related to patterns in minimum temperatures and temperature thresholds (days > 20 °C), presumably because temperate algae require cool periods for successful reproduction and recruitment (even if the adults can survive warmer temperatures). Although the observed habitat variation may appear subtle, similar structural differences have been linked to a range of effects on canopy-associated organisms through the provision of habitat and ecosystem engineering. Consequently, our study suggests that the magnitude of projected temperature increase is likely to cause changes in habitat structure and thereby indirectly affect numerous habitat-dependent plants and animals.

1. Introduction

Global warming has already affected all major ecosystems on earth (Rosenzweig et al. 2008) including temperate nearshore habitats where temperature increases of >0.5-1 ^{o}C have been measured over the past decades (Hawkins et al. 2003, Pearce & Feng 2007, Ridgway 2007). While the current understanding and documentation of the physical changes that are taking place is fairly good, the understanding of how this physical forcing translates into effects in the biological world is comparatively poor, particularly in the sea (Harley et al. 2006, Poloczanska et al. 2007). Yet, this information is critical to understanding the range of consequences of global warming, and how they might be mitigated.

Foundation species are critical to determining overall community structure in the habitats where they are found (Dayton 1972). The mechanisms behind their influence on community structure are multifaceted, but key ecological functions include modifying local environmental conditions (e.g., Wernberg et al. 2005, Irving & Connell 2006b), and the provision of habitat, i.e. a 3-dimensional physical structure that can be inhabited by various organisms (e.g., Wernberg et al. 2004, Tuya et al. 2008, Thomsen et al. 2010).

Canopy-forming macroalgae are the main foundation species on most temperate rocky reefs, where two groups, kelps (order Laminariales) and fucoids (order Fucales), are particularly abundant (Schiel & Foster 1986). Elevated temperature negatively affect most aspects of the biology of kelps and fucoids from temperate coasts (e.g., reproduction, recruitment and growth, resilience to disturbances, Kirkman 1984, Novaczek 1984, Wernberg et al. 2010, respectively) and the projected global warming has caused serious concern for permanent changes in habitat structure and loss of algal habitats (Kendall et al. 2004, Poloczanska et al. 2007) with indirect effects on other community components (Schiel et al. 2004) and ensuing loss of associated biodiversity (Graham 2004, Ling 2008) and cascading effects to higher trophic levels (Kendall et al. 2004, Ling et al. 2010). Indeed, habitat loss compounded by climate change, is probably the biggest threat to biodiversity and ecosystem function, in general (Pimm 2008).

Despite concerns for the future persistence of algal habitats and their ecological functions, there have been few direct assessments of how algal habitats (as opposed to species or individuals) might respond to increasing water temperatures. Broad-scale oceanographic events causing elevated ocean temperatures (i.e., ENSO’s on the west coast of the America’s) have consistently been associated with loss of kelp canopies and substantial changes to biogenic habitat structure (Dayton et al. 1999, Martínez et al.

2003, Edwards & Estes 2006). The influence of temperature is, however, often ambiguous because of a strong negative relationship with water-column nutrient concentrations in many kelp-dominated systems (particularly in areas of upwelling, e.g., Edwards & Estes 2006). In a unique case study of the bay-wide effects of 10 years of induced heating by a thermal effluent from a power plant, Schiel *et al.* (2004) found substantial structural changes associated with a temperature increase of a few degrees Celsius; they reported large shifts in habitat formers where kelps, for example, decreased markedly in abundance. With the exception of such unique ‘opportunistic experiments’, it is impossible to manipulate temperature in subtidal habitats across spatial scales relevant to questions of landscape structure (> 1-10’s meters, Connell & Irving 2008). Questions about the influence of water temperature on habitat structure must, therefore, follow alternative lines of enquiry. One option is to study latitudinal gradients in ocean temperature at places where confounding by other co-varying factors is minimal (e.g., Wernberg et al. 2010). Understanding how latitudinal gradients in climate influence the distribution of key organisms may be particularly relevant in relation to predicting effects of climate change, because shifts in distribution patterns along these gradients have been one of the main detectable responses of both aquatic and terrestrial organisms (Walther et al. 2002, Parmesan & Yohe 2003, Poloczanska et al. 2007).

Here, we took advantage of a latitudinal gradient in ocean temperature to explore the influence of ocean climate on biogenic habitat structure, defined as the relative abundance of key algal habitats and their patch size characteristics. In doing so, we tested the hypothesis that habitat structure would change gradually from latitude to latitude, and that the dominant kelp habitats would become increasingly fragmented at lower latitudes where ocean temperatures are higher, and presumably more stressful to temperate algae.

2. Methods

2.1. Study area and experimental design.

This study took place along a ~1,000 km stretch of the southwest coast of Western Australia, covering the latitudes 34 ºS to 27 ºS (Fig. 1A). This coastline runs north-south and its near-shore environment is characterised by limestone and sandstone reefs. The ocean climate is dictated by the Leeuwin Current, a warm surface current which, in contrast to other eastern boundary currents in the southern hemisphere, runs southward and therefore suppresses up-welling (Pearce 1991). The result is a latitudinal temperature gradient of 2-3 ºC where nutrient concentrations remain consistently low (Pearce 1991, Lourey et al. 2006, Smale & Wernberg 2009). This temperature gradient captures the range of current scenarios for global warming of Australia's temperate waters (25-year projection of 1-2 ºC increase and 50-year projection of 2-4 ºC, Poloczanska et al. 2007). Grazing pressure from fish and invertebrates is also low throughout this region (Wernberg et al. 2008, Vanderklift et al. 2009).

The reefs along the coastline host a diverse algal flora dominated by a canopy of the only kelp in Western Australia, *Ecklonia radiata* (a species similar to northern kelps such as *Eisenia arborea* and *Laminaria digitata*) and a rich assemblage of fucalean algae mainly from the genera *Cystophora*, *Sargassum* and *Scytothalia* (Wernberg et al. 2003, Smale et al. 2010). Similar reef habitats and canopies characterise rocky reefs throughout temperate Australasia (Wernberg et al. 2003, Connell & Irving 2008).

All sampling was completed within one month (November 2005) and followed a hierarchical design with four regions (each representing a different temperature regime) evenly separated by ~2º latitude (Fig. 1A). Six independent reefs, 8-12 m deep and separated by a minimum of 1 km, were nested within each region. The depth (transect start and end) and structural complexity (count of intersecting topographic features of 1-2 m and >2 m vertical relief) was measured at 25 transects (see below) for each reef. There were no differences in depth or vertical relief among regions ($MS_{depth} = 5.61$, $F_{(3,20)} = 1.0$, $P = 0.428$; $MS_{LN(1\text{-}2m+1)} = 0.56$, $F_{(3,20)} = 0.96$, $P = 0.430$; $MS_{LN(>2m+1)} = 0.24$, $F_{(3,20)} = 0.58$, $P = 0.634$). Also, differences in light among regions due to latitude (5-10%) were masked by differences among reefs within regions due to differences in depths among them (~25%) (see calculations in Stæhr & Wernberg 2009).

Here, each reef was considered a biologically independent replicate of the ocean climate represented by each region. This is justified because subtidal temperatures vary little

(<5%) between reefs at similar depth ranges (Smale & Wernberg 2009), and because most propagules from canopy-forming macroalgae have short dispersal distances (metres or less, e.g. *Sargassum spinuligerum*: Kendrick & Walker 1991) resulting in low genetic connectivity between reefs (e.g. *Ecklonia radiata*: Coleman et al. 2009).

2.2. Ocean climate.

The unique ocean climate, and the broad latitudinal patterns of temperature change along the southwest coast, has long been established (Pearce 1991, Fig. 1A). Recently, Smale & Wernberg (2009) showed strong correlations between temperatures at 8-10 m depth and satellite-derived sea surface temperatures (SST) in this area. Consequently, historic satellite derived SST's obtained by the Advanced Very High Resolution Radiometer (AVHRR) aboard the National Oceanic and Atmospheric Administration (NOAA) series of satellites could here be used to describe the ocean climate of each region prior to measurement of habitat structure.

SST's have been archived by the Australian Bureau of Meteorology. Daily SST maps of Australian waters were used to generate temperature profiles for each of the four study regions (Australian Bureau of Meteorology, www.bom.gov.au) (see Smale & Wernberg 2009 for details). Two data sets were generated; one covering seven years (1999-2005, assessed every 15th of January, April, July and October) and one covering 1 year (November 2004 – October 2005, assessed every 1st, 10th and 20th of each month). Ambient water temperature was also measured at the time of sampling (Onset Tidbit pendant loggers, logging every 5 minutes ~5 cm above the bottom at all six reefs within each region). The combination of these measures integrates long-term temperature exposure across >1 full generation of *Ecklonia radiata* (life span 1-4 years, Wernberg 2005), and more acute effects due to the particular year, season and time of sampling. The mean temperature, maximum and minimum temperatures, and number of 'hot' days > 20 ^{o}C, were used as proxies for chronic thermal exposure, extreme thermal exposure, and 'adverse' thermal exposure, respectively; 20 ^{o}C corresponds to the approximate threshold where temperature starts to negatively affect the productivity and growth of *E. radiata* (Kirkman 1984, Hatcher et al. 1987).

2.3. Habitat structure.

The overall biogenic habitat structure of each reef was quantified by running ten 25 m transects along haphazard compass bearings and recording the distances (to nearest 10 cm) of habitat change. This technique has previously been successfully applied to describe habitat structure in algal dominated assemblages in other subtidal habitats (Kennelly 1987, Wernberg 2006, Connell & Irving 2008). We distinguished between four major habitat types: (1) mono-specific kelp canopy (>90% *Ecklonia radiata*), (2) fucalean canopy (>50% fucalean algae), (3) mixed kelp and fucalean canopy (50-90% kelp and 10-50% fucalean algae) and (4) canopy-free areas (gaps of < 10% canopy algae), typically dominated by small foliose red algae (<25 cm) (e.g., *Hennedya crispa*) or articulated coralline algae (e.g., *Amphiroa anceps*). The distinction between these habitat types were based on previous studies documenting how they affect their immediate surroundings differently, and support different associated benthic, phytal and fish communities (Harman et al. 2003, Irving et al. 2004, Wernberg et al. 2005, Irving & Connell 2006a, Tuya et al. 2008). Habitat structure was sampled in November 2005 (early Austral summer), a time where the kelp canopy has recovered from the thinning and pruning of winter storms (Wernberg & Goldberg 2008).

Overall, 24 descriptors of habitat structure were considered, six for each habitat type: habitat cover was calculated as the proportion of each transect occupied by each habitat type. Median, mean and maximum habitat patch sizes (1-dimensional linear distance) as well as the number of habitat patches for each habitat type were determined for each reef after pooling all transects. Patch mode was not considered because there were virtually no differences (~1 m for all habitat types).

2.4. Statistical analyses.

Differences in mean ocean temperature characteristics between adjacent regions were tested by either ordinary or paired *t*-tests (Zar 1996). Overall patterns in ocean climate were assessed by principal components analysis (PCA, Clarke & Gorley 2006) based on all nine temperature characteristics (cf. Table 1), and the presence of sequential change from region to region tested by non-parametric serial correlation (RELATE, Clarke & Gorley 2006).

Differences in biogenic habitat structure among regions, taking all 24 habitat characteristics into consideration, were tested by multivariate analysis of variance by permutation (PERMANOVA, Anderson et al. 2008). Constrained ordination by canonical analysis of principal coordinates (CAP, Anderson et al. 2008) was used to characterise, and visualise, these differences, and to evaluate their correspondence with individual climate variables in the environmental matrix by canonical correlation (CCorA, Anderson et al. 2008). These analyses were based on normalised data for habitat characteristics, using euclidian distances and 999 permutations.

Subsequently, the influence of ocean climate on biogenic habitat was tested by linear regression (Zar 1996) of each habitat characteristic against PC1, the first principal components axis from the PCA of patterns in ocean climate (a univariate proxy for multivariate variation in ocean temperature characteristics). Regression analyses were done for habitat cover, habitat patch density and habitat patch size for all four habitat types, and for total cover of four dominant canopy taxa.

3. Results

3.1. Ocean climate.

There were clear differences in ocean climate along the coastline, and the overall pattern for almost all temperature characteristics was an increase from Hamelin Bay in the south towards Kalbarri in the north (Fig. 1, Table 1). Ocean temperatures showed a clear seasonal pattern of ~6-8 ºC variation between summer and winter in all four regions. Inter-annual differences were generally small, particularly after 2000 (Fig. 1B). The four regions spanned a temperature gradient of ~2-3 ºC; Hamelin Bay was substantially cooler in summer (Dec-Feb) whereas Kalbarri remained substantially warmer in winter (Jun-Oct) (Fig. 1C). Conditions at Marmion and Jurien Bay were intermediate (Table 1).

Considering all temperature characteristics simultaneously, PCA revealed a strong serial correlation in multivariate thermal climate from region to region (RELATE, $\rho = 0.926$, $P = 0.081$, n = 4), emphasising a gradual environmental change along the southwest

Australian coastline. The first principal component (PC1) accounted for 85.2% of the multivariate differences in thermal climate, and thus provided a strong univariate proxy for overall variation in thermal climate among regions, where larger values were associated with warmer (more stressful) ocean climates.

3.2. Habitat structure.

Based on all 24 descriptors, there were significant differences in biogenic habitat structure between regions (PERMANOVA, pseudo-$F = 2.36$, $P = 0.020$). The constrained ordination grouped all four regions into distinct groups (CAP, *trace statistic* = 0.410, $P = 0.030$, Fig. 2) where Kalbarri, Marmion and Jurien Bay were separated along CAP1 and Hamelin Bay from these three groups along CAP2. Canonical correlation (CCorA) against the temperature matrix revealed a significant relationship between ocean climate and biogenic habitat structure (CAP, *trace statistic* = 1.062, $P = 0.003$), where minimum temperature and the number of hot days in the year preceding sampling (2004-2005) were the best correlates of CAP1 and temperature at the time of sampling, maximum temperature in the preceding year, and the number of hot days during the preceding 7 years (1999-2005), were the best correlates of CAP2 (Table 2). These temperature characteristics have, therefore, likely influenced the formation of the observed patterns of biogenic habitat structure.

All four habitat types were present at all four regions, although only monospecific kelp canopies and open gaps were present at all 24 reefs (Fig. 3). Mono-specific kelp canopies covered 20-90% of the reefs at all sites, and was by far the dominant habitat type. In contrast, fucalean canopies covered <30% of the reefs and was generally the least common habitat type. With a median size of 2-5 m, kelp patches were also the largest, followed by mixed canopy patches (~2-3 m), fucoid canopies (~1-3 m) and open gaps (~1-1.5m).

There was substantial variation in most biogenic habitat characteristics both among and within climates (as represented by regions) (Fig. 3). For example, the cover of mono-specific kelp canopies ranged from ~10-70% on reefs within Hamelin Bay and mixed kelp and fucoid canopies from 0-30% in Kalbarri. Despite this variation, there was a significant positive relationship between PC1 for ocean climate and monospecific kelp canopy cover and median size of kelp patches, where ocean climate explained 21% and 34% of variation, respectively (Fig. 3). There was a near-significant trend for a negative relationship between ocean climate and cover and patch density of mixed canopies, with climate accounting for 13% and 15% of variation respectively ($P < 0.081$). Ocean climate explained <6% of variation in habitat characteristics related to fucoid canopies and open gaps.

Despite a positive relationship between ocean climate and cover of monospecific kelp canopies, the total cover of *Ecklonia radiata* (i.e. including kelp found within mixed canopies) did not correlate with ocean climate (Fig. 4, ocean climate explained <5% of variation in kelp cover). However, where climate explained little of the variation in the combined fucoid abundance (Fig. 3), the different fucoid taxa still showed significant, but opposing, relationships with climate, explaining 21-37% of the variation of these taxa (Fig. 4). In particular, where the relationship was positive for *Sargassum* spp., it was negative for *Scytothalia doryocarpa* canopies and other fucoids.

4. Discussion

This study has shown a significant relationship between the biogenic habitat structure of temperate subtidal algal canopies and ocean climate along a latitudinal gradient. The total cover of kelp and fucoids did not change along the gradient, but changes to canopy structure and individual fucalean taxa were evident. In contrast to expectation, kelp canopies did not become increasingly fragmented in warmer, more stressful, climates. Rather, mono-specific kelp canopies became increasingly dominant as a result of a decline in mixed kelp-fucalean canopies, and an opposing relationship to climate of individual fucalean taxa. Attributing these changes solely to variation in ocean climate is, of course, impossible because of the correlative nature of this study and the potential for covariation with other important drivers along the latitudinal gradient. However, in our study area, there is a particularly low degree of confounding between the temperature gradient and other environmental factors known to drive ecological patterns across latitudinal gradients (discussed in Smale & Wernberg 2009), and we therefore believe ocean climate has a pivotal role as a driver of the observed patterns.

4.1. Ocean climate.

The unique oceanography of the southwest coast of Western Australia has long been recognised (Pearce 1991). By clearly documenting that gradual changes to the thermal climate along the coast are evident at time-scales of days, months and years, this study corroborates and expands the findings of previous studies (Pearce & Feng 2007, Smale & Wernberg 2009). Even if complexity is evident, the range of climatic variation between evenly spaced regions supports the contention that the south-western coastline is a suitable natural laboratory, where observations and experiments may be particularly relevant in relation to understanding what ecological changes are likely under projected global warming scenarios (Smale & Wernberg 2009, Wernberg et al. 2010).

4.2. Habitat structure.

The total cover of kelp did not change, but the size of monospecific kelp patches increased. Similarly, total cover of fucoids did not change, but the abundance of mixed fucoid-kelp canopies decreased, and so did the cover of *Scytothalia doryocarpa* and other fucoids, while *Sargassum* spp. increased in cover. This indicates a shift in patch structure *per se,* with a homogenisation of kelp patches towards lower latitudes and a switch in species composition of fucoids, which occupy the canopy differently; where *S. doryocarpa* is usually found as single or a few individuals interspersed between the kelps, *Sargassum* spp. often occupy distinct patches, punctuated within the kelp canopy (*personal observation*). Several mechanisms may combine to produce this pattern.

The ecological processes that underpin kelp canopy maintenance change along the latitudinal climate gradient, even if the abundance of *E. radiata* patches remains the same (Wernberg et al. 2010). At the cooler regions (Hamelin Bay and Marmion), adult kelps suppress the establishment of kelp recruits, leaving more opportunity for hardy fucoids such as *S. doryocarpa* to establish and form mixed canopies. In contrast, at the warmer regions (Jurien Bay and Kalbarri), adult kelps reinforce existing kelp patches by facilitating kelp recruitment and recruit growth (Wernberg et al. 2010). This shift from competitive to facilitative adult-recruit interactions could thus promote mixed canopies in cooler water and monospecific kelp canopies in warmer water.

The genus *Scytothalia* is endemic to the south and southwest coast of Australia, and exclusively has one species (Huisman 2000). It likely evolved from the temperate Tethyan marine flora on the south coast (Phillips 2001), and its declining abundance into warmer climates (this study, Smale et al. 2010) is presumably due to a low thermo-tolerance. However, little physiological and ecological work has been done on *S. doryocarpa*, and this hypothesis remains untested. *Sargassum*, on the other hand, is a very broadly distributed genus with many species of warm-temperate to tropical affinity in Australia (Huisman 2000). *Sargassum* spp. are competitively inferior to kelps, and in cooler water *Sargassum* spp. patches often revert to kelp within 1-2 years (Toohey et al. 2007). Potentially, the increased predominance of *Sargassum* spp. to the north is promoted by climate-related delayed post-disturbance recovery of kelp canopies (Wernberg et al. 2010).

The proportion of canopy-free gaps did not vary systematically along the climate gradient. This supports our initial assumption that there was little difference in the overall disturbance regime among regions across the latitudinal gradient. A previous study found a significant positive relationship between wave exposure and the prevalence of gaps in the canopy cover (Wernberg & Connell 2008).

In summary, climate-mediated shifts in ecological interactions within kelp canopies and the identity of dominant fucoids, promotes monospecific kelp patches at the expense of mixed canopies. It is important to stress that the increase in monospecific kelp canopies should not be taken as a sign that kelp canopies are impervious to climate effects, as recent experiments have shown that the underlying concurrent physiological changes (e.g., Stæhr & Wernberg 2009), makes the canopy less resilient to additional perturbation (Wernberg et al. 2010). Also, mixed canopies are currently a defining feature across vast expanses of the Australian south coast (Connell & Irving 2008, Wernberg & Connell 2008, Smale et al. 2010). Because of the east-west facing coast line, even a slight southward shift in isotherms could, therefore, result in habitat changes across thousands of kilometres of coastline.

4.3. Important climate factors.

Climate variables representing both acute, seasonal and inter-annual temperature regimes were found among the five best correlates of habitat structure, and all (except temperature at the time of sampling) concerned extreme or adverse conditions. This suggests a complex influence of ocean temperature, driven by differences in the outer temperature envelope rather than mean conditions.

Temperature thresholds can be a major determinant of broad-scale species distributions (Schils & Wilson 2006). The two climate variables best correlated to habitat structure were minimum temperature and hot days >20 °C in the preceding year. Presumably the importance of these variables relate to the recruitment and growth of the habitat formers present at the time of sampling. For temperate algae, reproduction and recruitment is often restricted to substantially lower temperatures than the upper limit for adult survival (Novaczek 1984, Matson & Edwards 2007), and growth and productivity has been shown to be adversely affected at high temperatures (Kirkman 1984, Hatcher et al. 1987). The high correlation of these variables could then be due to a required window where temperatures are low enough to successfully complete reproduction and recruitment, and subsequently enough cool days to attain biomass and canopy cover.

4.4. Non-climate sources of variation.

A prominent feature for all habitat characteristics was the great amount of variation from reef to reef within each region, which in many cases was of equal magnitude to variation across the entire climate gradient. This point to a strong influence of non-climatic drivers of habitat structure. A range of physical and biological processes could be contributing to this variation.

A study from South Australia, where the same canopy types dominate subtidal reefs, found substantial differences in habitat cover and patch sizes between the seaward and shoreward sides of small islands (Wernberg & Connell 2008). These patterns were attributed to differences in wave exposure, where high wave exposure was associated with larger patches of all habitat types and kelp dominance, whereas low wave exposure was associated with smaller patches and fucoid dominance. Mixed canopies differed little with wave exposure. With the exception of studies on wave exposure and gap properties, there have been very few direct assessments of the potential drivers of habitat structure on algal dominated reefs. There is abundant evidence to document how other environmental (e.g., reef geology and geomorphology, Harman et al. 2003, Toohey et al. 2007) and ecological (e.g., herbivores and recruitment, Connell & Irving 2008, Ling 2008, Wernberg & Connell 2008) properties can affect the distribution and abundance of habitat-forming organisms. While habitat structure is not necessarily related to the relative abundance of habitat forming organisms (this study), it seems likely that similar environmental and ecological properties have influenced reef to reef differences in habitat structure in this study.

Notwithstanding variability among reefs within each region it is important to recognise that the selection of reef sites within regions was constrained to minimise the influence of non-climatic drivers between regions (e.g., approximately the same range of depths and wave exposures were targeted). Consequently, to the extent possible, non-climatic drivers of canopy structure did not confound the analysis of the climatic signal.

4.5. Ecological implications.

The ecological function of different algal canopies can vary considerably. Due to variation in phenology and thallus structure, kelps and fucoids often present different habitat qualities (e.g., temporal stability, interstitial space, protection from predation, nutritional value: Wernberg et al. 2004, Tuya et al. 2008). Monospecific *Ecklonia* canopies, mixed *Ecklonia*-fucalean canopies and fucalean canopies have also been shown to modify their immediate environments differently (e.g., light, abrasion, sedimentation: Wernberg et al. 2005, Irving & Connell 2006b). As both provision of habitat and ecosystem engineering are key mechanisms by which algal canopies affect associated biota, a number of studies have documented how patches of kelp, fucalean or mixed canopies support different phytal (Wernberg et al. 2004, Tuya et al. 2008), benthic (Goodsell et al. 2004, Irving et al. 2004) and fish (Harman et al. 2003, Tuya et al. 2009) communities.

Metre-scale variation in biogenic habitat structure underpins the uniquely high biodiversity of the Australian west and south coast (Wernberg et al. 2003, Smale et al. 2010). Specifically, macroalgal assemblages under monospecific kelp canopies are species poor (Kendrick et al. 1999, Wernberg et al. 2005, Wernberg & Goldberg 2008) and a loss of macroalgal diversity may follow a reduction in canopy heterogeneity (e.g., Toohey et al. 2007). It is therefore possible, even if overall landscape composition may change little in terms of the dominant habitat-forming species, that an increasing dominance of monospecific kelp canopies, at the expense of mixed canopies, following a shift in dominant fucoids from *Scytothalia* to *Sargassum*, could have significant ecological implications.

4.6. Conclusion.

Significant changes in biogenic habitat structure (increase in monospecific kelp patches, decrease in mixed canopies, and change in fucoid species) were found along a latitudinal gradient in ocean temperature, equivalent to projected temperature increases for the upcoming 25-50 years. Consequently, the results of this study suggests that, if algal canopies respond to global warming in a way similar to the way they respond to increasingly warm climate along the studied latitudinal gradient, then the magnitude of projected climate change is great enough to cause a significant reduction in diversity of biogenic habitats on temperate reefs. This is likely to be ecologically significant even if habitat shifts are not catastrophic.

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Table 1. Ocean temperature characteristics of the regions studied. Temperature data for time of sampling were measured *in situ* where habitat characteristics were sampled. Temperature data for 2004-2005 and 1999-2005 were obtained by remote sensing (see methods).

Temperature characteristics	**Hamelin Bay**	**Marmion**	**Jurien Bay**	**Kalbarri**	**Pattern**
Time of sampling (Tidbit data logger)					
Mean (^{o}C, ± SE)	17.95 ± 0.03	19.34 ± 0.11	19.97 ± 0.13	21.21 ± 0.11	H < M < J < K ($P < 0.001$)[a]
2004-05 (SST, AVHRR)					
Mean (^{o}C, ± SE)	19.82 ± 0.27	20.93 ± 0.43	21.08 ± 0.48	22.94 ± 0.34	H < M = J < K ($P < 0.001$)[b]
Minimum (^{o}C)	17.28	17.28	16.35	19.14	H = M = J < K
Maximum (^{o}C)	23.79	24.72	25.65	25.65	H < M < J = K
Hot days >20 ^{o}C (%)	55.6	61.1	61.1	94.4	H < M = J < K
1999-2005 (SST, AVHRR)					
Mean (^{o}C, ± SE)	19.48 ± 0.50	20.13 ± 0.51	21.42 ± 0.52	22.10 ± 0.53	H < M < J < K ($P < 0.010$)[b]
Minimum (^{o}C)	15.18	15.18	16.28	17.22	H = M < J < K
Maximum (^{o}C)	27.16	27.16	28.24	29.32	H = M < J < K
Days >20 ^{o}C (%)	46.4	60.7	71.4	78.6	H < M < J < K

[a] Ordinary *t*-tests

[b] Paired *t*-tests, paired by sampling dates

Table 2. Canonical eigenvectors (correlation coefficients) for individual ocean temperature characteristics in relation to the constrained ordination of biogenic habitat structure on reefs within regions. The five best correlated variables are highlighted in bold.

Temperature Variable	**CAP1 ($\delta_1^2 = 0.54$)**	**CAP2 ($\delta_2^2 = 0.45$)**
Temperature, time of sampling	-0.152	**-0.486**
Mean temperature 2004-2005	-0.305	-0.399
Minimum temperature 2004-2005	**-0.636**	0.060
Maximum temperature 2004-2005	0.083	**-0.474**
Percent hot days >20 ºC, 2004-2005	**-0.489**	-0.038
Mean temperature 1999-2005	-0.139	-0.107
Minimum temperature 1999-2005	-0.314	0.273
Maximum temperature 1999-2005	-0.336	0.268
Percent hot days >20 ºC, 1999-2005	-0.052	**-0.465**

Fig. 1. A: Position of the four regions included in this study on the southwest coast of Western Australia. Summer (short dash) and winter (long dash) isotherms after Pearce (1991). B: Sea Surface Temperature (SST) measured by remote sensing (AVHRR). The dotted line indicate 20 ^{o}C, a threshold for when the growth and productivity of *Ecklonia radiata* starts to decline (Kirkman 1984, Hatcher et al. 1987).

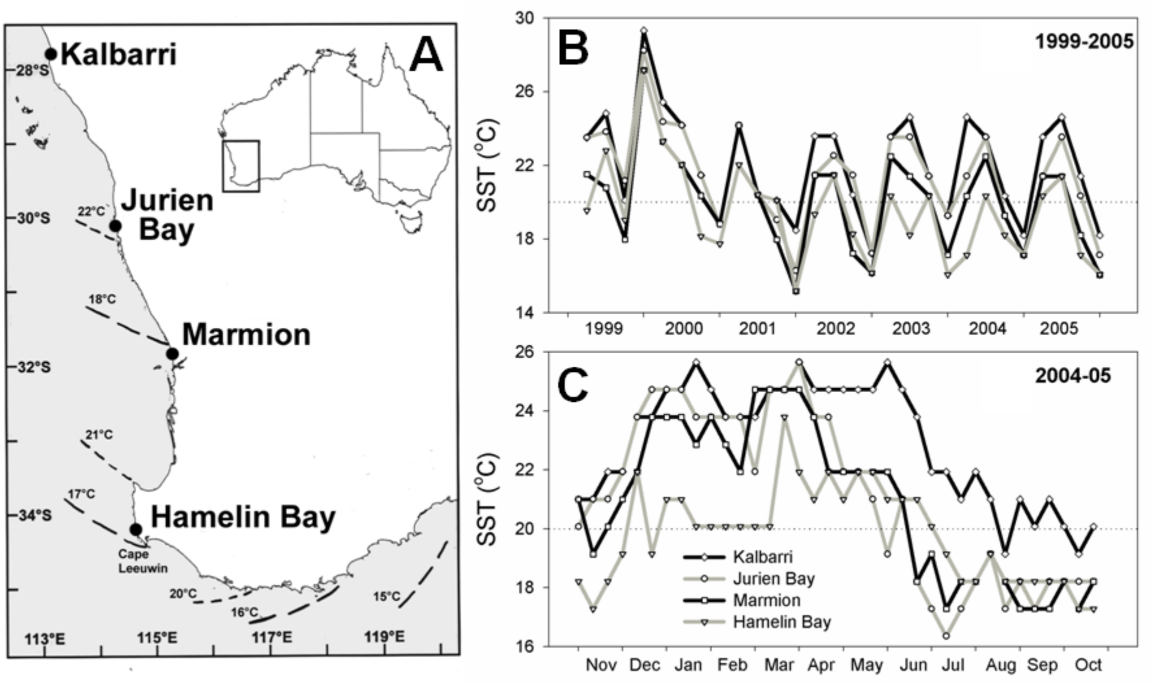

Fig. 2. Constrained ordination of principal coordinates for habitat structure at six reefs within Hamelin Bay (HAM), Marmion (MAR), Jurien Bay (JUR) and Kalbarri (KAL).

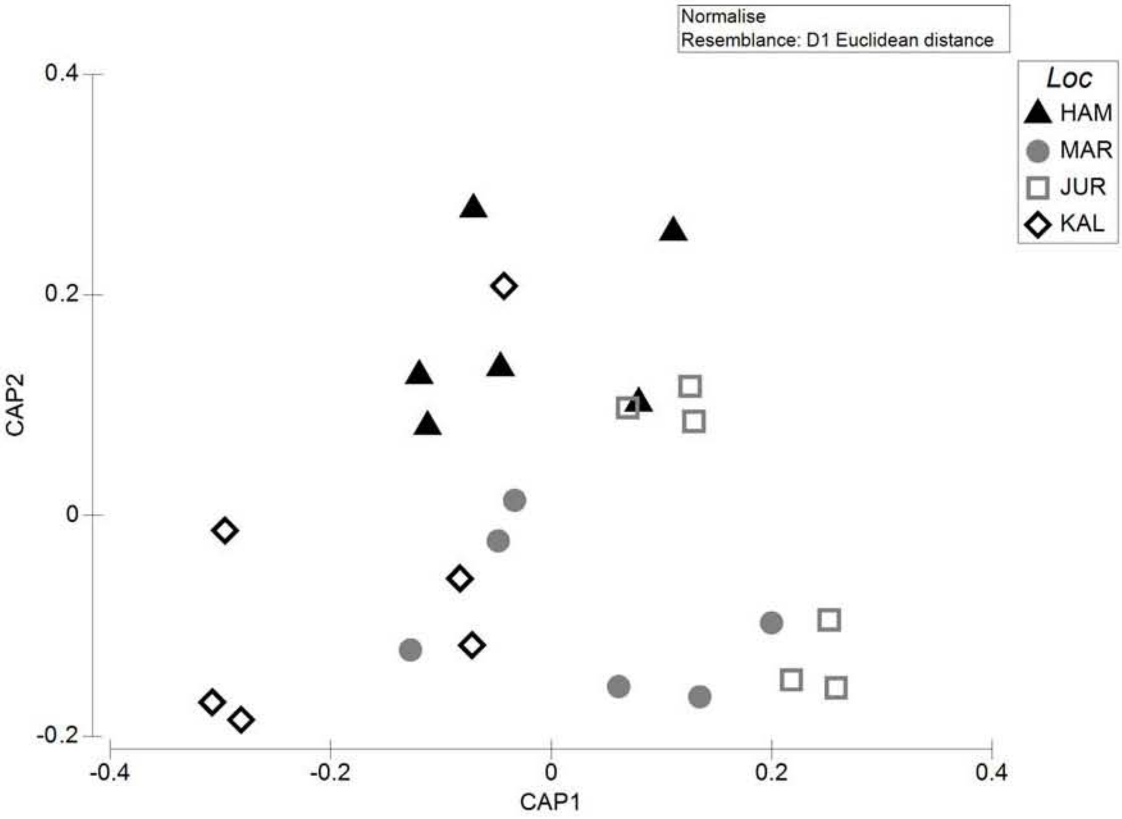

Fig. 3. Relationship between ocean climate at four regions (from left to right: Hamelin Bay, Marmion, Jurien Bay and Kalbarri) and characteristics of the biogenic habitat at 6 independent sites within each region. Kelp canopy refer to mono-specific patches of *E. radiata*. The ocean climate incorporates temperature variation at multiple temporal scales (cf. Table 1). Solid lines indicate significant relationships ($P < 0.05$) and dashed lines near-significant relationships ($0.05 < P < 0.10$).

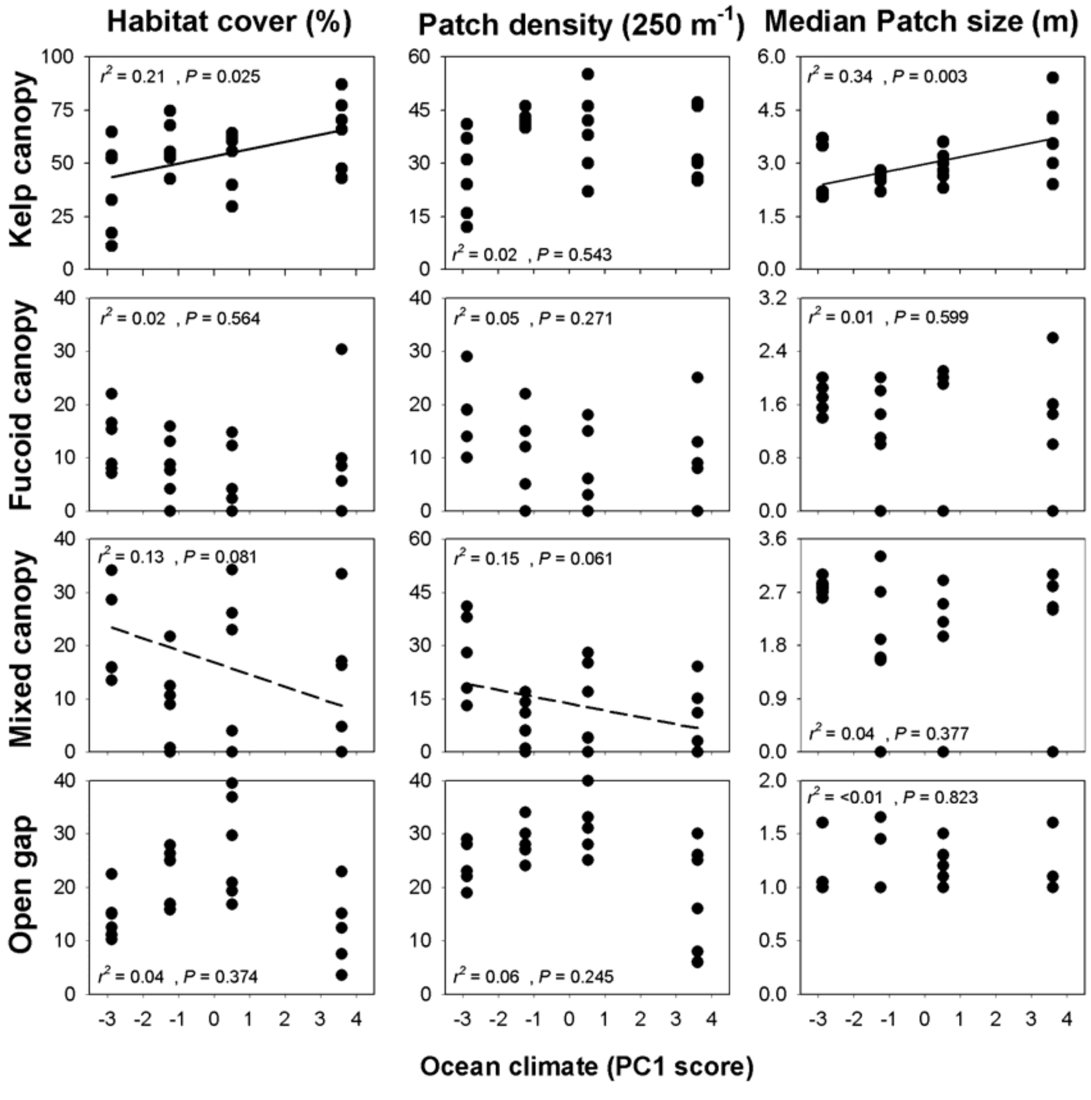

Fig. 4. Relationship between ocean climate and abundance of dominant canopy-forming taxa. Note, *E. radiata* also includes kelps found in mixed canopies. Increments in ocean climate corresponds to (from left to right) the studied regions (Hamelin Bay, Marmion, Jurien Bay and Kalbarri). Solid lines indicate significant relationships ($P < 0.05$).