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Short-term temporal dynamics of algal species in a subtidal kelp bed in relation to changes in environmental conditions and canopy biomass

Thomas Wernberg [a,b,*], Nisse Goldberg [b]

[a] *Centre for Ecosystem Management, Edith Cowan University, Joondalup, WA 6027, Australia*
[b] *School of Plant Biology, Botany Building MO90, University of Western Australia, Crawley, WA 6009, Australia*

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Abstract

Understanding temporal variation at the scale of weeks to months is critical to understanding broad temporal patterns in diversity in the same way as understanding diversity across landscapes relies on understanding variation at the scale of meters. However, whereas small-scale spatial variation in temperate reef algal assemblages has been extensively studied, fine-scale temporal changes have not been well addressed. By sampling the macroalgae of a subtidal reef near Perth (Australia), dominated by the small kelp *Ecklonia radiata*, every ∼40 days over a 2-year period, we were able to test whether temporal changes in species richness, assemblage structure and species turn-over were related to seasonal changes in surface temperature, solar radiation and wave height. A total of 93 macroalgal taxa were identified, and species richness per sampling time ranged from 25 to 64 taxa 1.25 m^{-2}. Biomass of *E. radiata* was positively correlated with changes in sea surface temperature and light, and negatively correlated with wave height. Species richness, assemblage structure and turn-over of other macroalgae were more associated with seasonal changes in kelp biomass than environmental variables *per se*. We conclude that seasonal changes in environmental conditions drive changes in the kelp canopy, which in turn drive changes in species richness and assemblage structure. This suggests that habitat-formers such as kelps can exert a strong temporal influence on associated communities, analogous to well-described spatial influences. Thus, as kelp canopy biomass expands and retracts over time-scales of weeks to months, so does available space for colonization and growth, resulting in a high species turn-over. Species richness is therefore increased and maintained through time, in the same way as canopy-gap mosaics increase and maintain species richness across spatial landscapes.

Keywords: kelps; short-term changes; species diversity; species turn-over; subtidal; Western Australia

1. Introduction

Maintenance of high diversity of macroalgae in many temperate rocky reef communities relies on biotic and abiotic factors and processes that vary spatially and temporally. In multi-layered assemblages dominated by canopy algae, spatial variation in diversity varies on the order of meters to tens of meters, and these patterns are commonly attributed to interactions between canopy layers and wave disturbance (Kendrick et al., 1999; Benedetti-Cecchi, 2001; Foster and Vanblaricom, 2001; Wernberg et al., 2003b; Goldberg and Kendrick, 2004). By direct interference or by indirect modification of the local environment, canopy layers influence the recruitment, survival and physiological performance of other algal species (Toohey et al., 2004; Wernberg et al., 2005; Irving and Connell, 2006a). Wave disturbance causes localised removal of canopy biomass, and thus creates and maintains a mosaic of canopy-dominated patches and open gaps (Menge et al., 2005; Wernberg, 2006). Differences in environmental conditions (e.g., frond abrasion, sedimentation, light availability: Toohey et al., 2004; Wernberg et al., 2005; Irving and Connell, 2006a) between canopy patches and gaps influence species composition such that the species richness and diversity of algae in canopy-dominated patches are relatively low compared to gaps (Kendrick et al., 1999;

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* Corresponding author.
E-mail address: wernberg@graduate.uwa.edu.au (T. Wernberg).

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Wernberg et al., 2005). Consequently, the canopy-gap mosaic maintains beta diversity across the reef landscape.

Temporal dynamics in species turnover also promote species diversity at local scales (Magurran, 2007). Temporal changes in subtidal algal assemblages have been associated with seasonal patterns in light, temperature, water motion, and nutrient enrichment via upwelling and ocean circulation patterns (Breda and Foster, 1985; Núnez-López and Casas Valdez, 1998; Diaz-Pullido and Garzon-Ferreira, 2002). In southern and western Australia, temporal changes in algal assemblages have shown ambiguous patterns. Shepherd and Womersley (1970) found that algal assemblages in South Australia remained relatively similar irrespective of season whereas Goldberg (2005) found algal assemblages in south-western Australia significantly different between seasons and between years for the same season. Goldberg (2005) suggested that year-round exposure to Southern Ocean swells might have a greater influence on species diversity via continual species turnover than seasonal changes of environmental variables. Multiple factors can account for variation in species dynamics and these are likely to vary from place to place as well as across different spatial and temporal scales. Nevertheless, it is apparent that the nature of temporal variability in algal assemblage structure remains poorly resolved. Studies on temporal variation in macroalgal assemblages have generally focussed on inter-annual or seasonal differences, typically sampling only once per season (e.g., Núnez-López and Casas Valdez, 1998; Goldberg, 2005). Compared to studies of small-scale spatial variation in algal diversity, changes in algal diversity, on the order of weeks to months, have not been well addressed. Exactly as knowledge of small-scale spatial variation is critical to the understanding of biodiversity across broader spatial scales, so is understanding the magnitude and causes of fine-scale temporal variation for understanding differences at broader temporal scales (i.e., between seasons and years) (Magurran, 2007). Actual species richness and diversity may be severely under-estimated by ‘snap-shot’ assessments, particularly where the underlying temporal dynamics of an assemblage is characterised by high-frequency species turn-over. Recently, Magurran (2007) reviewed some of the similarities between species–area and species–time relationships, and asserted a need for greater consideration of temporal aspects in the assessment of species–abundance patterns.

This study is a quantitative assessment of the temporal dynamics of a speciose kelp-associated macroalgal assemblage. In contrast to most other studies of temporal variation in algal assemblages that sample once per season, we sampled every ∼40 days over a period of 2 years. This allowed us to assess whether fine-scale temporal changes in species richness were associated with seasonal changes in temperature, wave height, and irradiance. Relationships between species turnover and kelp abundance were also investigated to determine whether seasonal declines in kelp created a ‘temporal gap’, analogous to a gap in the spatial sense. Such ‘temporal gaps’ may provide a mechanism by which high local species diversity is maintained through time.

2. Materials and methods

2.1. Study site

The study was conducted at Marmion (S31 ° 51.09′ E115 ° 42.39′) approximately 20 km north of Perth, Western Australia. The reefs at Marmion, and along more than 1000 km of Western Australian coastline, are a series of limestone ridges running parallel to the coast 1–8 km off-shore (Searle and Semeniuk, 1985). This reef habitat is dominated by a low canopy of the small kelp *Ecklonia radiata* (C. Ag.) J. Agardh (Wernberg et al., 2003a,b). Samples were collected from a ∼30 x 30 m relatively flat, off-shore reef outcrop exposed to ocean swells (close to ‘High 3’; see map and wave exposures in Phillips et al., 1997). The depth of the reef was 7–8 m. Overall canopy cover ranged between 60% and 70% of the reef, consisting predominantly of *E. radiata* with an occasional *Sargassum* spp. and *Scytothalia doryocarpa* (Turner) Greville. The geomorphology, flora and other aspects of the reef, were similar to other reefs in the region (Kendrick et al., 1999; Wernberg et al., 2003b).

2.2. Sampling and processing

The time required for sample processing constrained us from sampling more than one reef. However, the spatial variation in kelp-associated algal assemblages in the area has been described in detail by Kendrick et al. (1999) and Wernberg et al. (2003b).

Samples were collected 17 times between May 1999 and April 2001, i.e., approximately every 40 days for 2 years. This sampling frequency was a compromise between the need for multiple samples within a season and the constraints of sample processing time. Each time, five 0.25 m^2 quadrats were tossed haphazardly on the reef, and all algae larger than approximately 1 cm were harvested by hand and with a paint scraper. This sampling technique and sampling effort was similar to what was previously used to study spatial patterns among reefs (Kendrick et al., 1999; Wernberg et al., 2003b), and post hoc species–sample analyses indicated that, on average, 70% ± 1.0 SE ($n = 17$) of the species pool was sampled at each time. Algal assemblages included both epiphytic and epilithic species because it was impossible to separate these groups during sample collection and processing. Encrusting algae were not included. The canopy was weighed immediately, whereas the understorey was stored frozen (−18 °C) until processing. Dry weights were measured after drying the samples at 60 °C until their weights remained constant. Algae were identified using Womersley (1984, 1987, 1994, 1996, 1998), Huisman and Walker (1990) and Huisman (2000).

2.3. Environmental data

Satellite-derived data on sunlight (incident energy per unit area) were obtained from the Western Australian Climate and Consultancy Section of the Bureau of Meteorology, Perth airport. Water temperatures were obtained from the Marine Research Laboratories of the Department of Fisheries, North Beach, Western Australia. Water temperature measurements were taken in the mornings and afternoons from a seawater intake approximately 10 km away from the study site. Monthly averages of solar radiation and water temperature are presented. Wave data were obtained from the Geographic Information Services Branch of the Department for Planning and Infrastructure, Perth, Western Australia. Significant wave height (largest 1/3 of waves) was measured hourly by a wave buoy located approximately 40 km southwest and off shore of Marmion. Monthly maximum values are reported.

2.4. Data analyses

Given the influence of kelp biomass on patterns in species richness, the kelp canopy was not included as part of the overall algal assemblage, and was analysed separately. The relationship between each of the environmental variables, kelp canopy biomass and species richness of the algal assemblage was assessed by product moment correlation. Similarly, multivariate relationships were assessed by correlating the similarity matrices (RELATE, Clarke and Warwick, 2001) of environmental (Euclidian distance) and algal (Bray–Curtis similarity between sample date centroids) data to each other and to model matrices for cyclicity and seriation, testing for seasonality and gradients following individual environmental variables and kelp canopy biomass, respectively. Prior to analyses, environmental data were normalised and algal data (dry weight biomass) were 4th-root transformed. This relatively severe transformation was chosen to reduce the different weighting of large and small species which, from a biodiversity point of view, are equally important. Frequency of occurrence was calculated by counting how many sampling times each species was recorded. Species turn-over was calculated by counting how many species were lost or gained from all five quadrats between successive sampling times. This measure of turn-over is representative of the assemblage given the sampling effort, rather than absolute.

3. Results

The physical environment showed a clear seasonal pattern consistent with what would be expected from a temperate system in the southern hemisphere: incident solar radiation (Fig. 1A) and surface temperature (Fig. 1B) peaked in summer (December to February), while wave height peaked in winter (June to August) (Fig. 1C). These seasonal changes in the environment were very similar over the two consecutive years of our study (Fig. 2A, $\rho_{\text{cyclicity}} = 0.546$) and were closely matched by variation in kelp biomass (Fig. 1D, Table 1). In contrast, mean algal species richness was only weakly correlated with temporal changes in environmental variables (Fig. 1E; Table 1) and there was only weak evidence of seasonality in algal assemblage structure (Fig. 2B; $\rho_{\text{cyclicity}} = 0.195$). In addition, changes in algal assemblages over time were not associated with the overall seasonality of environmental change ($\rho_{\text{environment } vs. \text{ algae}} = -0.001$) or changes in any of the individual environmental variables (Table 1; $\rho < -0.010$). The seasonality of the algal assemblage was however associated with changes in kelp biomass, which, in turn, was correlated with observed environmental changes (Table 1). In particular, kelp biomass was inversely related to algal species richness (Fig. 3; Table 1). In spring, kelp biomass was low (~75 g dw 0.25 m^{-2}) and species richness was relatively high (~25 species per 0.25 m^{-2}). Conversely, in summer, kelp biomass was high (~400 g dw 0.25 m^{-2}) and species richness was low (~10 species per 0.25 m^{-2}).

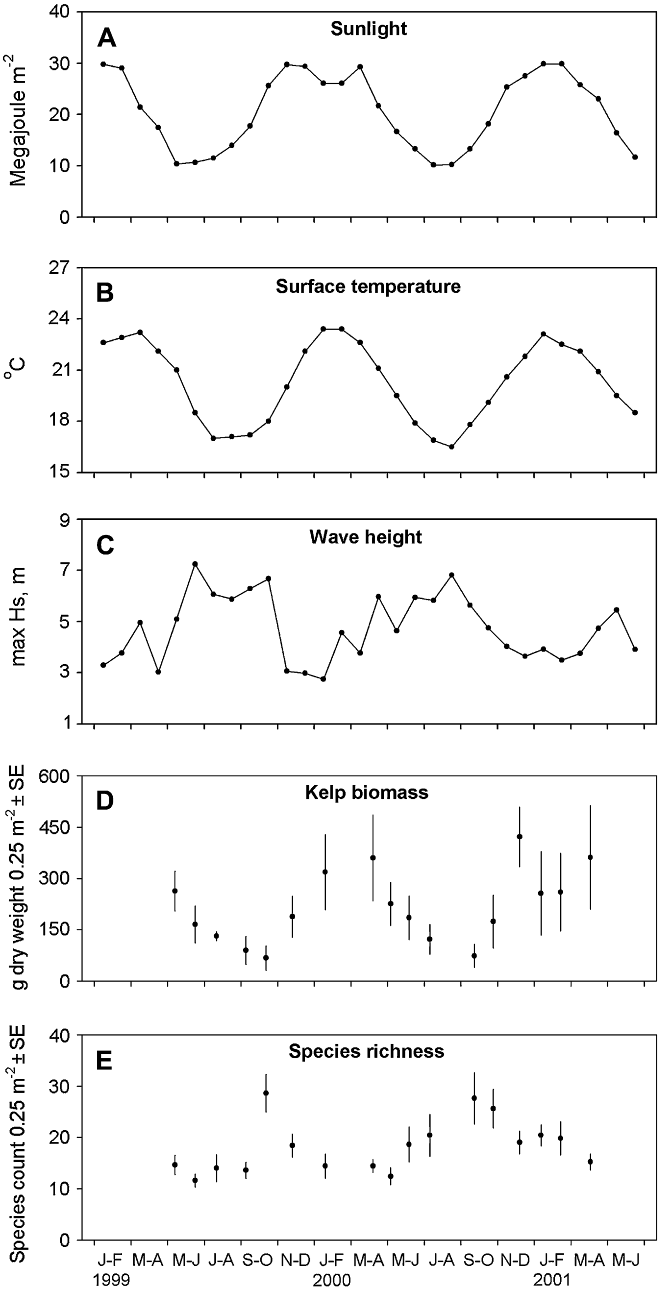

Fig. 1. Temporal variation in environmental factors, kelp (*E. radiata*) canopy biomass and species richness ($n = 5$) of the macroalgal assemblage.

A total of 93 macroalgal taxa were identified from the 85 samples. Total species richness per sampling time, combining all five 0.25 m^2 quadrats, ranged from 25 to 64 taxa per

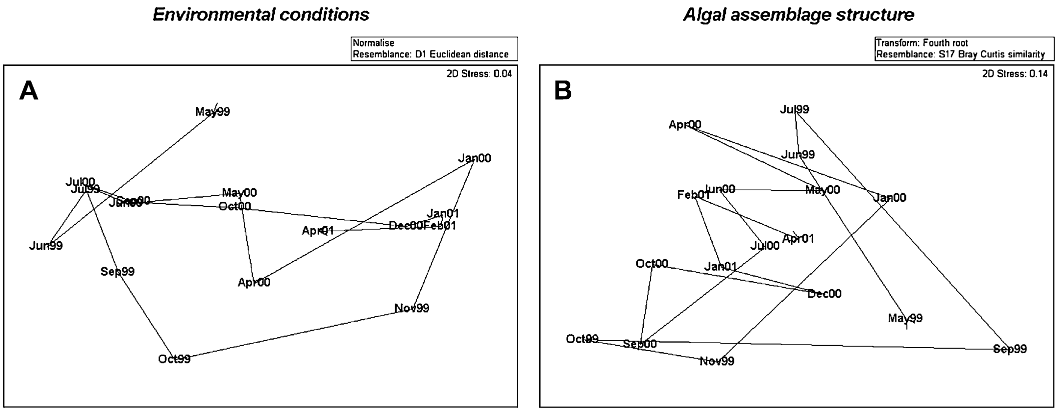

Fig. 2. Ordinations (nMDS) of (A) environmental conditions and (B) centroids of algal assemblage structure at each sampling time. Kelp (*E. radiata*) canopy biomass was not included with the macroalgae.

1.25 m^2 (Fig. 4A). The curve of cumulative species richness showed that 70 of 93 (75%) species were found within the first year (Fig. 4A). Turn-over of species between successive sample times was generally high, ranging between 45 and 103% of total species richness (turn-over can be higher than richness because it includes both species gained and lost) (Fig. 4B). The magnitude and proportion of species loss *versus* gain followed seasonal dynamics in kelp biomass: the number of species lost was greater during periods of kelp recovery (i.e., October and November, 2000, and September and October, 2001) and species gain was greater during periods of kelp senescence and removal by wave energy (i.e., August, 1999, and May to July, 2000). Overall, there was a large spread in the frequency of occurrence of individual taxa: 42% of all taxa were rare or very infrequent, only occurring 4 times or less; 33% of the taxa were frequent, occurring 5–11 times; and 25% of the taxa were very frequent, occurring 12–17 times. Representatives from each group in terms of biomass are listed in Table 2.

4. Discussion

Temporal dynamics in algal species richness, assemblage structure and species turnover at Marmion was a function of a complex interplay between environmental change and the influence of the dominant kelp, *Ecklonia radiata*. Kelp biomass was directly correlated with environmental variation, whereas species richness of algae was associated with temporal changes in kelp biomass.

Table 1
Product–moment correlation coefficients and Spearmans ρ for matching patterns of environmental conditions, kelp canopy biomass, species richness and assemblage structure of algae (assemblage structure was measured as the fourth-root transformed dry weight biomass of species present)

	Kelp canopy biomass[a]	Species richness[a]	Algal assemblage structure[b]
Sunlight	0.453	0.203	−0.001
Surface temperature	0.803	−0.003	−0.010
Wave height	−0.563	−0.160	−0.023
Kelp canopy biomass	–	−0.388	0.125

[a] Product–moment correlation coefficients.

[b] Spearmans ρ. Note that, unlike ordinary correlation coefficicents, no meaning can be attached to negative values of ρ (Clarke and Warwick, 2001).

Seasonal change in the biomass of the dominant habitat-forming alga, *E. radiata,* was correlated with all of the considered environmental variables, and in particular with seawater temperature. Given the co-varying nature of temperature, light and wave height, it is difficult to separate the contribution of their individual effects. Nevertheless, collectively, these results provide a strong indication that environmental variation directly influences seasonal change in *E. radiata* biomass. The influence of temperature on species growth has sometimes been associated with nutrient enrichment through up-welling (Guimaraens and Coutino, 1996; Diaz-Pullido and Garzon-Ferreira, 2002). Nutrients are unlikely to explain the patterns of seasonal change observed at Marmion because nutrient levels do not fluctuate much between seasons at Marmion. For example, throughout the years of 2004 and 2005, mean phosphate levels (<0.3 μM) were constant and nitrate levels (<2.0 μM) remained relatively low (Keesing et al., 2006). Instead, *E. radiata* may be responding to seasonal changes in

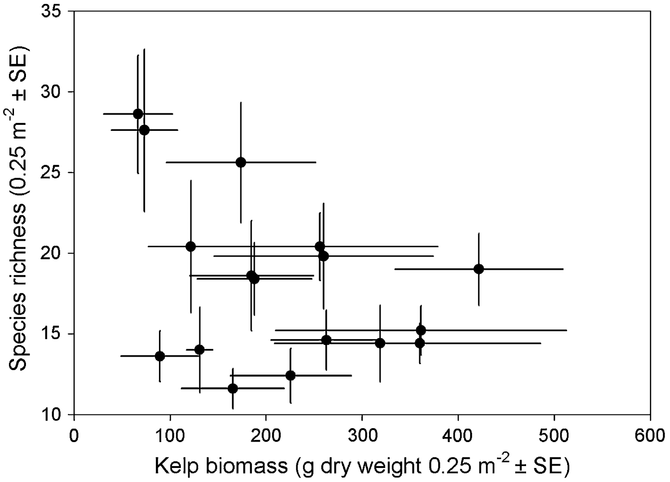

Fig. 3. Species richness *versus* kelp biomass for each of the 17 sampling times ($n = 5$).

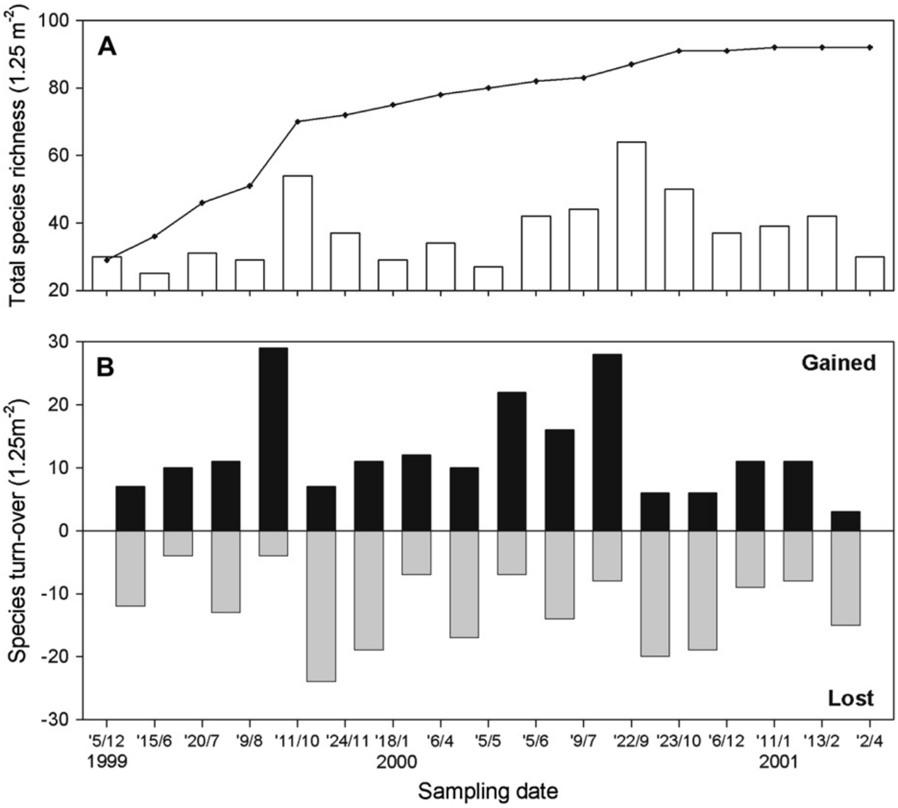

Fig. 4. Total number of species found in all five 0.25 m^2 quadrats per sample time combined (white bars), cumulative total species richness (line) (A), and the number of taxa gained or lost between successive sample times (B).

quantum dose (absolute amount of light) and photoperiod (day length). In northern New Zealand, Novaczek (1984a,b) found that growth and reproduction of *E. radiata* depended on quantum dose of light, whereas photoperiod has been identified as a primary factor controlling growth of kelps in polar waters (Lüning and Dieck, 1989; Makarov et al., 1999). It seems plausible that the seasonal increase in kelp canopy biomass is triggered and sustained by a combination of longer days and increased light levels. At the other end of the seasonal cycle, the negative correlation with wave height clearly implies the influence of wave disturbance in thinning the canopy, both as the loss of entire individuals and as pruning of attached individuals (Thomsen et al., 2004). On an annual basis, pruning may account for up to 50% of biomass loss in *E. radiata* in New Zealand (Novaczek, 1984a). Pruning may also be an important mechanism of canopy thinning at Marmion, where the biomass of individual mature sporophytes is ~50% smaller in winter compared to the summer maximum (Kirkman, 1984).

In contrast to temporal patterns in kelp biomass, species richness or assemblage structure was not well correlated with any of the environmental factors. The particularly poor correlation between species richness and sea surface temperature support Kain's (1989) suggestion that temperature *per se* is not the main driver of seasonality in algal populations (but see Heine, 1983; Núnez-López and Casas Valdez, 1998). The strongest patterns for species richness and assemblage structure were negative correlations with kelp canopy biomass. Likewise, species losses and gains through time matched the recovery and decline of *E. radiata*, respectively. This study did not consider possible lag-effects but the negative effects of kelp canopies on species richness have been well documented at Marmion (Toohey et al., 2004; Wernberg et al., 2005). It is thus evident that the temporal dynamics in the biomass and cover of the dominant species can influence local species richness and turnover of associated algae. Kim et al. (1998) also observed greatest species richness in winter when canopy genera (e.g., *Ecklonia* and *Sargassum*) had lowest cover in Korean waters. These temporal patterns probably reflect that reproduction, recruitment and growth of many species, particularly ones with ephemeral life-histories (cf. Shepherd, 1981), match the seasonality in the habit of the dominant habitat-formers. For example, in California, the recruitment of understory species is greater in winter when the cover of the giant kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh is at a minimum (Breda and Foster, 1985). Whether or not these coincidental patterns reflect the co-evolution of oppositely phased life-histories, as it has been suggested for epiphytal animals (Wernberg et al., 2004), or simply a mechanistic response to the seasonal release of space and favourable conditions, as implied by Shepherd's (1981) 'ephemeral strategy', cannot be inferred from this study. Kennelly's (1987) report of similar understory recruitment in treatments of complete and partial *E. radiata* canopy removal on the east coast of Australia, suggests that there is no straight forward relationship between the amount of resources released (space, light) and the response of the assemblage. Perhaps this also

Table 2
Most important (in terms of biomass) rare or infrequent species, frequent species and very frequent species (*Ecklonia radiata* not included; C, Chlorophyta; P, Phaeophyta; R, Rhodophyta. Occurrence is presence at any sampling time. Biomass is grams dry weight 0.25 m^{-2} ± standard error; '–' single occurrence, no error)

	Frequency of occurrence	Biomass per occurrence
Rare or infrequent species (recorded 1–4 times)	39 species (42% of the assemblage)	0.19 ± 0.08
Kuetzingia canaliculata Greville (Sonder) (R)	3	2.67 ± 1.51
Metagoniolithon radiatum (Lamarck) Ducker (R)	1	1.63 –
Dasya extensa Sonder *ex* Kützing (R)	1	0.62 –
Codium laminarioides Harvey (C)	1	0.34 –
Diapse ptilota (Hook.f. & Harv.) Kylin (R)	3	0.21 ± 0.15
Frequent species (recorded 5–11 times)	31 species (33% of the assemblage)	0.53 ± 0.27
Scytothalia doryocarpa (Turner) Greville (P)	8	8.17 ± 2.69
Nizymenia furcata (Harvey) Chiovitti, Saunders & Kraft (R)	5	2.94 ± 2.33
Sarcomenia delesserioides Sonder (R)	5	0.98 ± 0.73
Laurencia elata (C. Agardh) Hooker & Harvey (R)	8	0.62 ± 0.26
Lobophora variegate (Lamouroux) Womersley (P)	8	0.46 ± 0.28
Very frequent species (recorded 12–17 times)	23 species (25% of the assemblage)	1.43 ± 0.43
Sargassum spp. (P)	17	7.20 ± 1.78
Dictyomenia sonderi Harvey (R)	17	6.22 ± 1.59
Chauviniella coriifolia (Harvey) Papenfuss (R)	17	3.58 ± 0.68
Rhodopeltis australis (Harvey) Harvey (R)	16	3.46 ± 0.75
Pollexfenia pedicillata Harvey (R)	17	1.74 ± 0.28
Rhodymenia sonderi P. Silva (R)	17	1.59 ± 0.27
Amphiroa anceps (Lamarck) Decaisne (R)	13	1.54 ± 0.73
Pterocladia lucida (Turner) J. Agardh (R)	17	1.51 ± 0.51
Peyssonnelia capensis Montagne (R)	15	0.89 ± 0.23
Plocamium spp. (R)[a]	16	1.48 ± 0.42

[a] Not identified to species. Likely to represent equal parts of *P. mertensii* and *P. preissianum* as these are often found together (Wernberg, personal observation).

points to the importance of timing in addition to canopy thinning *per se*.

The broad range in individual responses of understory algae to seasonal environmental changes and the presence of a canopy layer make it very difficult to identify specific factors or threshold values that control temporal patterns in species richness (Wernberg et al., 2005). For instance, in San Ignacio Lagoon, Baja California Sur, Mexico, seasonal patterns in algal abundances varied among locations as a function of species composition and inter-specific interactions rather than as a response to environmental changes (Núnez-López and Casas Valdez, 1998). Algae may be obligate understory species that survive best in low light conditions (e.g., Shepherd, 1981); obligate gap species that survive best outside a kelp canopy (Toohey et al., 2004; Wernberg et al., 2005); or tolerant species, able to cope with variable light conditions. For example, *Rhodymenia sonderi* and *Pterocladia lucida* were two of the most frequently occurring species found in this study, and both species have been described as tolerant to the presence and absence of kelp cover (Kendrick et al., 1999; Toohey et al., 2004; Wernberg et al., 2005). Although light can stimulate algal growth, any species' response may be a function of timing and duration of incident light. For example, Levitt and Bolton (1990) identified two temperate understory rhodophytes that responded more to seasonal changes in irradiance and photoperiod than to changes in instantaneous light availability. In contrast, Heine (1983) observed that understory algae can respond to high light levels with rapid growth, irrespective of seasonal patterns of irradiance. At Marmion, many algae may not need a seasonal cue (e.g., temperature or photoperiod) to initiate growth and development, as indicated by the ~25% of the species that were observed on most sample dates.

Removal of canopy biomass by waves has been widely recognized as a primary driver of algal diversity across space in southwestern Australia and in other temperate waters (Kendrick et al., 2004; Wernberg, 2006). Interestingly, in contrast to the clear seasonality in species richness, there was only weak evidence of seasonality in assemblage structure, i.e., the temporal development of the algal assemblage was not strongly characterised by re-occurring subsets of algal species. So, while canopy-patches and gaps in the spatial sense are characterised by relatively consistent and predictable assemblages (Irving and Connell, 2006b), this appears to be less so for canopy patches and gaps in the temporal sense.

5. Conclusion

We conclude that, over the course of a year, there was large variation in kelp biomass as well as species richness and assemblage structure of reef macroalgae. Seasonal changes in environmental conditions drove changes in the kelp canopy, which in turn influenced changes in species richness and assemblage structure. Habitat-forming species such as kelps can exert a strong temporal influence on associated communities, which in many ways resembles well-described spatial influences. Thus, as kelp canopy biomass expands and retracts over time-scales of weeks to months, so does available space for colonization and growth, resulting in a high species turn-over.

High species richness is therefore maintained over time, in the same way as canopy-gap mosaics increase and maintain species richness across spatial landscapes.

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