Manuscript Draft

Manuscript Number: ECSS-D-07-00220R1

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

Article Type: Research Paper

Keywords: Kelps; Short-term changes; Species diversity; Species turn-over; Subtidal; Western 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.

Perth 5 July 2007

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D. S. McLusky,
Editor, Estuarine, Coastal and Shelf Science

Response to reviewers comments, ms no. ECSS-D-07-00220: Wernberg & Goldberg – Short-term turn-over of algal species....

Dear Prof. D. S. McLusky

Thank you for facilitating the review of our manuscript. We were very happy to receive the assessments so soon and even more so because they were supportive.

We have addressed all issues raised by the two reviewers, and we have made an effort to incorporate their suggested changes. Both reviewers found that the research addressed important and timely questions, and that the manuscript was well written. The majority of their comments concerned small issues. Only reviewer 2 expressed some concern over the sufficiency of the sampling effort at each sampling time. While we understand the concern, we do not believe this is an issue. Details on this and other points raised are provided in the following pages. We hope you will find our responses satisfactory, and that you can now accept this manuscript for publication in ECSS.

Yours Sincerely,

A handwritten signature in blue ink, appearing to read 'Thomas Wernberg'.

Thomas Wernberg, corresponding author

Response to reviewers comments

Questions and concerns by the reviewers are given in italics immediately followed by our reply in bold. Line numbers in our responses refer to the revised manuscript.

Reviewer 1 (Scoresby Shepherd)

Reviewer 1 was very supportive of the manuscript. He used the amusing, but thought-provoking, scoring system recently proposed by Sand-Jensen to assess the overall qualities of the paper, and found it to very interesting. Our only poor scores were for lack of illustrations and lack of humour. Consequently, we have added a joke at the beginning of each new section (just kidding, of course). We have added an extra plot to Fig. 4A as requested (see later). However, on request we can also supply relevant photographs of high quality, if further illustration is desirable either directly in the paper or elsewhere in the journal (e.g., cover page or similar).

Introduction

I note some emphasis on temporal species richness. Here the very recent paper of Magurran (Ecol. Letters 2007, 10, 347-54) is relevant.

We thank Shepherd for pointing us to this interesting and highly relevant paper. We have cited it where appropriate and incorporated some of its main points (e.g., L85-87).

Methods

I puzzled about just how exposed the site was. Was it on the outermost reefs shown in Phillips et al. 1997? Or subject to some protection ?.....

Yes, as stated in line 105, the reef was located on the outer-most reefs shown in Phillips et al 1997. It was, in fact, very close to the reef they called 'high 3'. This information has been added (line 106).

2.2 How was algal assemblage structure measured? (see Table 1)

Assemblage structure was measured as the 4th root transformed dry weight biomass of species present. Definition added to table 1.

2.4 I. 143 seriation (tho it's in OED) is a rare word. Is its OED meaning of 'Serial succession' appropriate here?

We believe the word 'seriation' is used appropriately because it is used as a qualifier to describe the model matrix (not the actual sequence of environmental change) which was designed to test serial succession in biological communities. Moreover, Clarke & Warwick (2001), who designed the PRIMER routine RELATE, uses this word to describe all tests of sequential correlation. No change.

Results

I. 181. "ubiquitous" is a term describing spatial pattern, whereas it is used here for a temporal pattern. You might have to coin a phrase !

Here, and elsewhere in the manuscript, we have avoided the use of 'ubiquitous' by rephrasing to 'very frequent'.

I wd liked to have seen another figure, perhaps added to Fig. 5, showing cumulative species richness over time....

We have added the requested graph as a plot to Fig. 4A, and added commentary (L.182-183).

Discussion

I. 187 correlated with ! Done

I. 200 Nutrients may be more important than acknowledged. What abt Kirkman's study (I cant recall the date) showing high nutrient release (spikes) during storms ?

We are not aware of this particular work by Kirkman and we have not been able to locate it; could it perhaps be from some of his seagrass work? We have no evidence that severe weather can cause such spikes – it seems very plausible for soft sediment systems such as seagrass beds, but less so for hard reefs. We have specified (L. 210) that the time-scale for our statement seasonal variation in nutrient levels. Although storms are more frequent at certain times of the year (ie winter), they do occur in all seasons (e.g. Lemm et al 1999). Therefore, if nutrient spikes released during storms were a driver of species richness, 'random' peaks in richness would be expected.

I. 225 reflect. L. 229 reflect ! Done

I. 242 et seq. Algal strategies listed and discussed by Shepherd (1979) *Ecological strategies of algae etc Bot. Marina* 24, 457 etc. A strategy there discussed is one related to disturbance, i.e. ephemerality as a strategy by which an alga grows rapidly if a canopy gap is created.

Shepherd's paper was relevant in outlining several life-strategies (ephemerality, low-light tolerance, dominance), providing an excellent background for the discussion. We have cited the paper where relevant (L. 240, 246, 259).

I. 245 *Rhodymenia sonderi*. This is not in Womersley's vol 3B. Is it a new species?

***Rhodymenia sonderi* was previously *R. australis*. The new name is used by Huisman (2000), whereas *R. australis* is what is used in Womersley's book. No change.**

I. 246. "most ubiquitous" Ubiquitous means distributed everywhere, so I doubt linguistically whether it can have a superlative. Just as the word 'unique' cannot have 'more unique', so we cannot have 'more ubiquitous'.

Changed to most frequently occurring

References

Adequate. Two refs have spp written in roman eg I. 359, 361.

References checked and inconsistencies rectified.

Table 1 Define assemblage structure in caption, if not in text. **Done.**

Table 2. *Plocamium* spp. When several spp are aggregated, obviously frequency will be high. Is it possible to separate them ?

Unfortunately not as these were not identified to species at the time of sample processing. Experience tells us, however, that it is likely to represent equal parts *P. mertensii* and *P. preissianum* as both of these species are common and frequently found together. A note explaining this has been added to the table.

Reviewer 2

Reviewer 2 found the ms well written, the question pertinent and the format appropriate. Essentially, the reviewer only expressed concerns over whether the

sampling effort was sufficient to make statements about species-turn-over. The point is valid, but it does not, in our opinion, compromise the study. In this study we have employed the same sampling techniques and sampling effort as in previous studies of spatial variation (turn-over) in assemblage structure. Given the similarities between species-area and species-time distributions (Magurran 2007), there is no conceptual difference between comparing multiple reefs at one time or one reef at multiple times. This is further elaborated below.

Introduction

Lines 72-74 - comment: more than one causal factor in temporal variation is likely and complex interactions between factors at varying temporal scales is expected. In almost all instances the driving forces of temporal variation will be locally or regionally specific, and would explain the difficulties in resolving temporal variability and problems in making generalisations both among and between locations.

Good point. We have added the essence of the comment to the introduction (L. 72-73).

Line 86 - why was ~40 days chosen as the sampling interval? Is this interval related to the life-cycles of the understorey assemblage?

The exact value is coincidental. We aimed at ~1 month because this is short enough to allow multiple samples within each natural season, yet long enough to be logistically feasible and allow some change to take place. We have added this reasoning to the methods section (L. 117-118)

Methods

Lines 110-112 - although the authors state a reason for sampling only one reef, I believe that this has significantly compromised the ability to draw conclusions and generalisations from their results. How typical is the kelp bed and its associated assemblage compared to other reefs in the area? Is there any evidence to support / refute this? Would results differ for a reef that differed in some factor such as wave exposure, depth, surface topography of the reef, or even kelp density itself?

Based on our extensive knowledge and experience with macroalgal assemblages throughout Western Australia, we believe the reef we studied was typical in all aspects. We therefore consider the loss of inference space minimal. We have emphasised this by reference to our previous work (L. 109-110).

It is correct that our results may not be directly applicable to situations where key physical variables are different (exposure, depth, kelp density etc). However, sampling more reefs would probably not have changed this because any sensible experimental design would have attempted to standardise (limit the range of) these conditions across the reefs sampled to avoid confounding the spatial patterns.

Lines 113-115 - I have serious concerns that the sampling effort described here was inappropriate for adequately capturing the temporal variability of the understory assemblage. By their very nature, most understory species are both small stature and randomly dispersed in space, and I am unconvinced that five 0.25 m² quadrats (which equates to <1.5% of the reef area) would allow adequate description of the fine-scale temporal variability of these species. This scale and effort is probably sufficient for the larger, ubiquitous kelp, but a more sensitive method should have been applied to the smaller macroalgal species. For example, to properly capture species 'turn-over', a larger number of samples using a point-intercept method to record presence-absence may have been more appropriate. The destructive quadrat sampling used was probably, at best, adequate for estimates of biomass and species richness, but I strongly contend that it enables species 'turn-over' to be described.

Optimal sampling design (quadrat size, number of quadrats etc) depends on the size and distribution pattern of the species under investigation. Obviously, when dealing with an assemblage where the size of individuals range several orders of magnitude (~1cm to ~200cm), and both spatial and temporal patterns of occurrence is highly variable among species, there will be no one quadrat size or no one level of replication that will be appropriate for ALL species. As detailed above, the sampling technique and sampling effort applied is standard practice. This level of sampling effort has been repeatedly been shown to be efficient for quantitative surveys of algal assemblages on reefs in Western Australia and elsewhere (Wernberg et al. 2003 and references herein). As previously stated (and asserted by Magurran 2007) there is no conceptual difference between

comparing multiple reefs at one time and comparing one reef at multiple times. Nowhere do we make the claim that our measure of turnover is absolute – it is representative of the assemblage given the sampling effort. We have specified this in under the methods (line 159-160). Moreover, using species-sample curves, we have estimated how large a fraction of the assemblage was sampled at each sampling time; the value of ~70% is not far off what is achieved in most spatial surveys (Wernberg et al. 2003). The information has been added (L.122-124) and will allow readers a more informed background to evaluate the results.

The small stature of the understorey algae is irrelevant as turn-over only considers presence/absence without regard to biomass. Moreover, turnover as defined here, is not confused by quadrat to quadrat variation because turnover was determined from presence/absence within all 5 quadrats at each time period.

Sampling more quadrats with a non-destructive in situ method (e.g., point intercept as suggested) would not be possible because many (!) species are difficult to identify even to genus without microscopy. Such a survey would only (!) be able to identify a very small subset of large, distinct and common species and would be highly inappropriate for looking at rare or taxonomically tricky species. In our opinion, there is no real alternative to what we have done.

To alleviate this reviewers concern about our use of the term ‘turn-over’, we have made a small change to the title of the manuscript, replacing ‘turn-over’ with ‘temporal dynamics’. The new title is slightly broader and reduces the emphasis on this part of the study.

Line 123 on - environmental data. Given the small stature of most understorey species, and the moderating influence of the overlying kelp canopy, it strikes me that the scale at which environmental data were measured is too coarse to be compatible with the scale at which the understorey assemblage was measured, and may explain why correlations between them could not be found. Understorey species are quite likely adapted to be able to respond rapidly to changes in certain environmental conditions at scales of days to weeks, and the presence of an overlying kelp canopy (in varying density over the annual cycle) has a moderating effect on the environmental conditions experienced by the understorey assemblage.

The size and stature of the understory is irrelevant. Coarse patterns of light and temperature affects the physiology of small and large algae alike. The drag from wave exposure directly affects large algae more than small algae (e.g. Thomsen et al 2004), but small algae are affected by whiplash from large algae (e.g. Toohey et al 2004). It is correct that, superimposed on these coarse seasonal changes in environmental variables, are effects of habitat-modification by the kelps. However, that is exactly the point! – seasonal change affects only the kelp, but it's modification of local conditions affects the understory. No change.

Were prevailing winds and currents accounted for when calculating wave exposure?

No because we did not calculate wave exposure. We provide reference to Phillips et al 1997 (L. 106) where a map and wave exposures are presented.

Line 149 - again, I am uncomfortable with the concept of species turn-over as presented here. Surely the number of species gained or lost is a direct function of the sampling effort which, as I have stated, I consider inadequate.

Not correct. If this was so, then why does species richness increase and decline when sampling effort is constant? Turnover is representative of the assemblage; the assemblage is richer at some times of the year compared to other times. See also responses to lines 113-115 above. No change.

Results

Lines 159-162 - it seems that the lack of evidence of seasonality in the understory assemblage could be related to the scale at which environmental factors were measure, or a lack of power to detect such seasonality, or both. Perhaps somewhat conversely, I find that the argument presented that kelp is influenced by environmental variation, and that the understory assemblage is in turn influenced by kelp variation, is circular. Surely this suggests that there actually was some degree of seasonality in the understory assemblage, but that there was insufficient power to detect it. Certainly the data in Figure 1 suggests that there is in fact seasonality in the understory assemblage, but that a lag phase is present.

Not correct. The reviewer is confusing species richness and assemblage structure. There is seasonality in species richness, but not in assemblage

structure. Species richness does not take the identity of species into consideration; it is a univariate, 1-dimensional measure. Assemblage structure takes both identity and abundance (fourth-root transformed dry weight) into consideration; it is a n-dimensional, multivariate measure. The distinction is clearly pointed out in lines 274-279. See also response to lines 123 on, above. No change.

Lines 170 on - again, I believe that the loss or gain of species is directly related to the sampling regime and not to real changes in the assemblage. From my own observations, very few macroalgal species that are associated with kelp beds will disappear completely over an annual cycle - most are persistent year-round but with variations in biomass.

We disagree. The change in species richness over time is real. It is not an artefact of the sampling regime. See also response to lines 149 on, above. No change.

Is it possible to determine what proportion of the variation in kelp biomass was due loss of whole plants, and what proportion was due to partial erosion of plants? ie., was kelp density monitored over the study period? The provision of new primary space for colonisation could influence variation in the understorey assemblage.

It is not possible from our data as we only sampled biomass. However, a previous study by Kirkman (1984) found large seasonal variation in the biomass of individual kelp thalli, suggesting that pruning is an important process. This is now discussed (L. 223-225). See also the existing discussion (L. 247-251) on recruitment in complete vs. thinned experimental plots.

Discussion

Line 220-221 - apart from perhaps two maxima, I did not find the pattern in Fig 4 as provided overwhelming evidence for the authors claim.

We believe the match is striking and clear from comparing Fig's 1D and 4B; periods of species gain (black bars) are periods where kelp biomass is declining or low, whereas periods of species loss (grey bars) are when kelp biomass is increasing or high. No change.

Conclusion

Are the authors able to make any comment on the generality of their results to other reefs in the region? The final sentence implies a steady increase in species richness - is this intended?

In order to keep the conclusion as short as possible, we have chosen not to do that here. How this reef relates to other reefs is clear from the methods section. Minor change to wording to avoid implied increase (L.95-96, 286).

Figures & Tables

*Table 2 – are natural differences in the abundance and life histories of the various species accounted for in any way? For instance, *Codium laminarioides* is an infrequently occurring species and its release from an overlying kelp canopy would not necessarily result in an increase (or decrease) in its abundance due to its intrinsically slow growth, low dispersal rates, etc. Similarly, *Sargassum* has a natural cycle of growth and senescence which is unrelated to variations in kelp biomass. What did the seasonal variation in other large, canopy-forming species (eg *Scytothalia*) show? *Jeannerettia pedicillata* is a redundant name.*

How could life histories be accounted for? We are only describing patterns of change and they are a part of that change. The influence of life histories and strategies have been discussed, cf. Shepherd (1981) and Shepherd's comments in that regard. Turn-over counts only presence/absence regardless of seasonal variation in the biomass of species like *Sargassum* and *Scytothalia* (see table 2). For assemblage structure, biomass was considered but weighed down (cf. L.153-156).

***J. pedicillata* has been changed to *Pollexfenia pedicillata*, the appropriate name according to algaebase.com**

Figure 3 - species richness follows the trends in wave height and SST, albeit with a lag phase. Could it be that the lack of correlation between environmental factors and the understorey assemblage was due to a lack of power, or an inability to allow for the lag phase in analyses?

We did not consider lag-effects. This seems redundant given the relative strong suggestion of direct effects through wave exposure and kelp biomass. This is discussed in L.233-237.

Editor's comments:

*Huisman 2000 add total number of pages. Something is missing after Vol? **Done.***

Keesing et al. 2006 appears to be an unpublished report.... supply fuller details....

Keeping this reference is important to document consistently low levels of inorganic nutrients. The report is available via the internet. We have provided the extra information requested.

*Womersley - 5 refs - add total page numbers for each. Again something missing after Vol? **Done.***

*Figure 4 - Redraw Graph A as a bar chart not an x-y graph. **Done.***

1

2

3 Running head: Species turn-over of algae

4

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

7

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18

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.

Key words: Kelps; Short-term changes; Species diversity; Species turn-over; Subtidal; Western Australia

45 Maintenance of high diversity of macroalgae in many temperate rocky reef communities
46 relies on biotic and abiotic factors and processes that vary spatially and temporally. In multi-
47 layered assemblages dominated by canopy algae, spatial variation in diversity varies on the
48 order of meters to tens of meters, and these patterns are commonly attributed to interactions
49 between canopy layers and wave disturbance (Kendrick et al. 1999, Benedetti-Cecchi 2001,
50 Foster & Vanblaricom 2001, Wernberg et al. 2003b, Goldberg & Kendrick 2004). By direct
51 interference or by indirect modification of the local environment, canopy layers influence the
52 recruitment, survival and physiological performance of other algal species (Toohey et al.
53 2004, Wernberg et al. 2005, Irving & Connell 2006a). Wave disturbance causes localised
54 removal of canopy biomass, and thus creates and maintains a mosaic of canopy-dominated
55 patches and open gaps (Menge et al. 2005, Wernberg 2006). Differences in environmental
56 conditions (e.g., frond abrasion, sedimentation, light availability: Toohey et al. 2004,
57 Wernberg et al. 2005, Irving & Connell 2006a) between canopy patches and gaps influence
58 species composition such that the species richness and diversity of algae in canopy-dominated
59 patches are relatively low compared to gaps (Kendrick et al. 1999, Wernberg et al. 2005).
60 Consequently, the canopy-gap mosaic maintains beta diversity across the reef landscape.

61 Temporal dynamics in species turnover also promote species diversity at local scales
62 (Magurran 2007). Temporal changes in subtidal algal assemblages have been associated with
63 seasonal patterns in light, temperature, water motion, and nutrient enrichment via upwelling
64 and ocean circulation patterns (Breda & Foster 1985, Núñez-López & Casas Valdez 1998,
65 Diaz-Pullido & Garzon-Ferreira 2002). In southern and western Australia, temporal changes
66 in algal assemblages have shown ambiguous patterns. Shepherd & Womersley (1970) found
67 that algal assemblages in South Australia remained relatively similar irrespective of season
68 whereas Goldberg (2005) found algal assemblages in southwestern Australia significantly
69 different between seasons and between years for the same season. Goldberg (2005) suggested

70 that year-round exposure to Southern Ocean swells might have a greater influence on species
71 diversity via continual species turnover than seasonal changes of environmental variables.
72 Multiple factors can account for variation in species dynamics and these are likely to vary
73 from place to place as well as across different spatial and temporal scales. Nevertheless, it is
74 apparent that the nature of temporal variability in algal assemblage structure remains poorly
75 resolved. Studies on temporal variation in macroalgal assemblages have generally focussed on
76 inter-annual or seasonal differences, typically sampling only once per season (e.g., Núñez-
77 López & Casas Valdez 1998, Goldberg 2005). Compared to studies of small-scale spatial
78 variation in algal diversity, changes in algal diversity on the order of weeks to months have
79 not been well addressed. Exactly as knowledge of small-scale spatial variation is critical to the
80 understanding of biodiversity across broader spatial scales, so is understanding the magnitude
81 and causes of fine-scale temporal variation for understanding differences at broader temporal
82 scales (i.e., between seasons and years) (Magurran 2007). Actual species richness and
83 diversity may be severely under-estimated by ‘snap-shot’ assessments, particularly where the
84 underlying temporal dynamics of an assemblage is characterised by high-frequency species
85 turn-over. Recently, Magurran (2007) reviewed some of the similarities between species-area
86 and specie-time relationships, and asserted a need for greater consideration of temporal
87 aspects in the assessment of species-abundance patterns.

88 This study is a quantitative assessment of the temporal dynamics of a speciose kelp-
89 associated macroalgal assemblage. In contrast to most other studies of temporal variation in
90 algal assemblages that sample once per season, we sampled every ~40 days over a period of
91 two years. This allowed us to assess whether fine-scale temporal changes in species richness
92 were associated with seasonal changes in temperature, wave height, and irradiance.
93 Relationships between species turnover and kelp abundance were also investigated to
94 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 1,000 km of Western Australian coastline, are a series of limestone ridges running parallel to the coast 1-8 km off-shore (Searle & 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, 2003b). 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. 2003).

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 m² 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

121 technique and sampling effort was similar to what was previously used to study spatial
122 patterns among reefs (Kendrick et al. 1999, Wernberg et al. 2003), and *post hoc* species-
123 sample analyses indicated that, on average, $70\% \pm 1.0$ SE ($n = 17$) of the species pool was
124 sampled at each time. Algal assemblages included both epiphytic and epilithic species
125 because it was impossible to separate these groups during sample collection and processing.
126 Encrusting algae were not included. The canopy was weighed immediately, whereas the
127 understory was stored frozen (-18°C) until processing. Dry weights were measured after
128 drying the samples at 60°C until their weights remained constant. Algae were identified
129 using Womersley (1984, 1987, 1994, 1996, 1998), Huisman & Walker (1990) and Huisman
130 (2000).

131

132 *2.3 Environmental data*

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

143

144 *2.4 Data analyses*

145 Given the influence of kelp biomass on patterns in species richness, the kelp canopy was not
146 included as part of the overall algal assemblage, and was analysed separately. The relationship

147 between each of the environmental variables, kelp canopy biomass and species richness of the
148 algal assemblage was assessed by product moment correlation. Similarly, multivariate
149 relationships were assessed by correlating the similarity matrices (RELATE, Clarke &
150 Warwick 2001) of environmental (Euclidian distance) and algal (Bray-Curtis similarity
151 between sample date centroids) data to each other and to model matrices for cyclicity and
152 seriation, testing for seasonality and gradients following individual environmental variables
153 and kelp canopy biomass, respectively. Prior to analyses, environmental data were normalised
154 and algal data (dry weight biomass) were 4th-root transformed. This relatively severe
155 transformation was chosen to reduce the different weighting of large and small species which,
156 from a biodiversity point of view, are equally important. Frequency of occurrence was
157 calculated by counting how many sampling times each species was recorded. Species turn-
158 over was calculated by counting how many species were lost or gained from all five quadrats
159 between successive sampling times. This measure of turn-over is representative of the
160 assemblage given the sampling effort, rather than absolute.

161

162 3 RESULTS

163 The physical environment showed a clear seasonal pattern consistent with what would be
164 expected from a temperate system in the southern hemisphere: incident solar radiation (Fig.
165 1A) and surface temperature (Fig. 1B) peaked in summer (December to February) while wave
166 height peaked in winter (June to August) (Fig. 1C). These seasonal changes in the
167 environment were very similar over the two consecutive years of our study (Fig. 2A, $\rho_{\text{cyclicity}} =$
168 0.546) and were closely matched by variation in kelp biomass (Fig. 1D, Table 1). In contrast,
169 mean algal species richness was only weakly correlated with temporal changes in
170 environmental variables (Fig. 1E, Table 1) and there was only weak evidence of seasonality in
171 algal assemblage structure (Fig. 2B, $\rho_{\text{cyclicity}} = 0.195$). In addition, changes in algal
172 assemblages over time were not associated with the overall seasonality of environmental

173 change ($\rho_{\text{environment vs. algae}} = -0.001$) or changes in any of the individual environmental
174 variables (Table 1, $\rho < -0.010$). The seasonality of the algal assemblage was however
175 associated with changes in kelp biomass, which, in turn, was correlated with observed
176 environmental changes (Table 1). In particular, kelp biomass was inversely related to algal
177 species richness (Fig. 3, Table 1). In spring, kelp biomass was low ($\sim 75 \text{ g dw } 0.25 \text{ m}^{-2}$) and
178 species richness was relatively high ($\sim 25 \text{ species } 0.25 \text{ m}^{-2}$). Conversely, in summer, kelp
179 biomass was high ($\sim 400 \text{ g dw } 0.25 \text{ m}^{-2}$) and species richness was low ($\sim 10 \text{ species } 0.25 \text{ m}^{-2}$).

180 A total of 93 macroalgal taxa were identified from the 85 samples. Total species
181 richness per sampling time, combining all five 0.25 m^2 quadrats, ranged from 25 to 64 taxa
182 per 1.25 m^2 (Fig. 4A). The curve of cumulative species richness showed that 70 of 93 (75%)
183 species were found within the first year (Fig. 4A). Turn-over of species between successive
184 sample times was generally high, ranging between 45 to 103 % of total species richness (turn-
185 over can be higher than richness because it includes both species gained and lost) (Fig. 4B).
186 The magnitude and proportion of species loss *versus* gain followed seasonal dynamics in kelp
187 biomass: the number of species lost was greater during periods of kelp recovery (i.e. October
188 and November, 2000, and September and October, 2001) and species gain was greater during
189 periods of kelp senescence and removal by wave energy (i.e. August, 1999, and May through
190 July, 2000). Overall, there was a large spread in the frequency of occurrence of individual
191 taxa: 42% of all taxa were rare or very infrequent, only occurring 4 times or less; 33% of the
192 taxa were frequent, occurring 5 to 11 times; and 25% of the taxa were very frequent,
193 occurring 12 to 17 times. Representatives from each group in terms of biomass are listed in
194 Table 2.

195

196 4 DISCUSSION

197 Temporal dynamics in algal species richness, assemblage structure and species turnover at
198 Marmion was a function of a complex interplay between environmental change and the

199 influence of the dominant kelp, *Ecklonia radiata*. Kelp biomass was directly correlated with
200 environmental variation, whereas species richness of algae was associated with temporal
201 changes in kelp biomass.

202 Seasonal change in the biomass of the dominant habitat-forming alga, *E. radiata*, was
203 correlated with all of the considered environmental variables, and in particular with seawater
204 temperature. Given the co-varying nature of temperature, light and wave height, it is difficult
205 to separate the contribution of their individual effects. Nevertheless, collectively, these results
206 provide a strong indication that environmental variation directly influences seasonal change in
207 *E. radiata* biomass. The influence of temperature on species growth has sometimes been
208 associated with nutrient enrichment through up-welling (Guimaraens & Coutino 1996, Diaz-
209 Pullido & Garzon-Ferreira 2002). Nutrients are unlikely to explain the patterns of seasonal
210 change observed at Marmion because nutrient levels do not fluctuate much between seasons
211 at Marmion. For example, throughout the years 2004 and 2005, mean phosphate levels (<0.3
212 μM) were constant and nitrate levels ($<2.0 \mu\text{M}$) remained relatively low (Keesing et al. 2006).
213 Instead, *E. radiata* may be responding to seasonal changes in quantum dose (absolute amount
214 of light) and photoperiod (day length). In northern New Zealand, Novaczek (1984a, 1984b)
215 found that growth and reproduction of *E. radiata* depended on quantum dose of light, whereas
216 photoperiod has been identified as a primary factor controlling growth of kelps in polar waters
217 (Lüning & Dieck 1989, Makarov et al. 1999). It seems plausible that the seasonal increase in
218 kelp canopy biomass is triggered and sustained by a combination of longer days and increased
219 light levels. At the other end of the seasonal cycle, the negative correlation with wave height
220 clearly implies the influence of wave disturbance in thinning the canopy, both as the loss of
221 entire individuals and as pruning of attached individuals (Thomsen et al. 2004). On an annual
222 basis, pruning may account for up to 50% of biomass loss in *E. radiata* in New Zealand
223 (Novaczek 1984a). Pruning may also be an important mechanism of canopy thinning at

224 Marmion, where the biomass of individual mature sporophytes is ~50% smaller in winter
225 compared to the summer maximum (Kirkman 1984).

226 In contrast to temporal patterns in kelp biomass, species richness or assemblage
227 structure was not well correlated with any of the environmental factors. The particularly poor
228 correlation between species richness and sea surface temperature support Kain's (1989)
229 suggestion that temperature *per se* is not the main driver of seasonality in algal populations
230 (but see Heine 1983, Núñez-López & Casas Valdez 1998). The strongest patterns for species
231 richness and assemblage structure were negative correlations with kelp canopy biomass.
232 Likewise, species losses and gains through time matched the recovery and decline of *E.*
233 *radiata*, respectively. This study did not consider possible lag-effects but the negative effects
234 of kelp canopies on species richness have been well documented at Marmion (Toohey et al.
235 2004, Wernberg et al. 2005). It is thus evident that the temporal dynamics in the biomass and
236 cover of the dominant species can influence local species richness and turnover of associated
237 algae. Kim et al. (1998) also observed greatest species richness in winter when canopy genera
238 (e.g., *Ecklonia* and *Sargassum*) had lowest cover in Korean waters. These temporal patterns
239 probably reflect that reproduction, recruitment and growth of many species, particularly ones
240 with ephemeral life-histories (cf. Shepherd 1981), match the seasonality in the habit of the
241 dominant habitat-formers. For example, in California, the recruitment of understory species is
242 greater in winter when the cover of the giant kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh
243 is at a minimum (Breda & Foster 1985). Whether or not these coincidental patterns reflect the
244 co-evolution of oppositely phased life-histories, as it has been suggested for epiphytal animals
245 (Wernberg et al. 2004), or simply a mechanistic response to the seasonal release of space and
246 favourable conditions, as implied by Shepherd's (1981) 'ephemeral strategy', cannot be
247 inferred from this study. Kennelly's (1987) report of similar understory recruitment in
248 treatments of complete and partial *E. radiata* canopy removal on the east coast of Australia,
249 suggests that there is no straight forward relationship between the amount of resources

250 released (space, light) and the response of the assemblage. Perhaps this also points to the
251 importance of timing in addition to canopy thinning *per se*.

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

272 Removal of canopy biomass by waves has been widely recognized as a primary driver
273 of algal diversity across space in south western Australia and in other temperate waters
274 (Kendrick et al. 2004, Wernberg 2006). Interestingly, in contrast to the clear seasonality in
275 species richness, there was only weak evidence of seasonality in assemblage structure, i.e. the

276 temporal development of the algal assemblage was not strongly characterised by re-occurring
277 subsets of algal species. So, while canopy-patches and gaps in the spatial sense are
278 characterised by relatively consistent and predictable assemblages (Irving & Connell 2006b),
279 this appears to be less so for canopy patches and gaps in the temporal sense.

280

281 5 CONCLUSION

282 We conclude that, over the course of a year, there was large variation in kelp biomass as well
283 as species richness and assemblage structure of reef macroalgae. Seasonal changes in
284 environmental conditions drove changes in kelp canopy, which in turn influenced changes in
285 species richness and assemblage structure. Habitat-forming species such as kelps can exert a
286 strong temporal influence on associated communities, which in many ways resembles well-
287 described spatial influences. Thus, as kelp canopy biomass expands and retracts over time-
288 scales of weeks to months, so does available space for colonization and growth, resulting in a
289 high species turn-over. High species richness is therefore maintained through time, in the
290 same way as canopy-gap mosaics increase and maintain species richness across spatial
291 landscapes.

292

293 ACKNOWLEDGEMENTS

294 This study was funded by grants to TW from The Danish Natural Science Research Council
295 and The Danish Research Academy. The Department for Conservation and Land
296 Management, marine conservation branch, Perth, issued the permits to work within Marmion
297 Marine Park. M. Polifrone, B. Toohey, M. Vanderklift and A. J. Smit assisted in the field. G.
298 Kendrick helped with the identification of difficult specimens. M. Vanderklift and G.
299 Kendrick provided useful comments on various stages of this study and manuscript.

300

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CAPTIONS FOR FIGURES

409

410

411 **Fig. 1:** Temporal variation in environmental factors, kelp (*E. radiata*) canopy biomass and
412 species richness of the macroalgal assemblage.

413

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

417

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

419

420 **Fig. 4:** Total number of species found in all five 0.25 m² quadrats per sample time combined
421 (white bars), cumulative total species richness (line) (A), and the number of taxa gained or
422 lost between successive sample times (B).

423

424

425 **Table 1.** Product-moment correlation coefficients (*) and spearmans ρ (#) for matching
 426 patterns of environmental conditions, kelp canopy biomass, species richness and assemblage
 427 structure of algae. Assemblage structure was measured as the fourth-root transformed dry
 428 weight biomass of species present. Note that, unlike ordinary correlation coefficients (*), no
 429 meaning can be attached to negative values of ρ (#) (Clarke & Warwick 2001).

	Kelp canopy biomass*	Species Richness	Algal assemblage structure#
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

430

431

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

* Not identified to species. Likely to represent equal parts of *P. mertensii* and *P. preissianum*

as these are often found together (Wernberg, personal observation).

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