

Temporal variation in subtidal macroalgal assemblages at Black Island, Recherche Archipelago

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Abstract

Temporal patterns in subtidal macroalgal diversity have not been described for much of temperate, southern Australia. To characterize temporal variation in species diversity, subtidal macroalgal assemblages were compared between austral spring and autumn collections from Black Island, Western Australia. Macroalgae (> 1 cm in length) from 0.25 m² quadrats were harvested from the south-eastern and southern sides of the island in depths < 10 m and 10–20 m in October 2002 and 2003 and April 2003 and 2004. Macroalgae were sorted, wet-weighed, and identified. A three-way analysis of variance tested for differences in total biomass, and density of thalli in the canopy with time, site, and depth. Analysis of similarity was used to test for differences in macroalgal assemblages among sampling times. Key environmental variables for the area were compiled from previous reports. A total of 254 species of macroalgae were recorded, consisting of canopy, understory, and epiphytic species. Average total biomass was not significantly different among sampling times. Density of thalli per 0.25 m² was greater and more variable in depths < 10 m than in depths 10–20 m. Macroalgal assemblages differed significantly among sampling times (Clarke's R values > 0.5, P = 0.001), and between samples collected from the same season but in different years. Each species was present, on average, in only 15% of the sampled quadrats. Chlorophyll *a*, seawater temperature, and salinity estimates did not vary much throughout the year with a range of 0.6 mg m⁻³ for chlorophyll *a*, 2.3 °C for seawater temperature, and 0.2 ppt for salinity. Year-round exposure to wind and wave energy from Southern Ocean gales and storms may drive the high species turnover and variability in density of thalli in depths < 10 m.

Keywords: Australia, exposure, macroalgae, seasonality, subtidal.

Introduction

Changes in composition and relative abundance of subtidal macroalgae have been correlated to seasonal patterns in temperate, sub-tropical and tropical habitats. For example in central California, temperate *Macrocystis* kelp forests have a predictable seasonal pattern: a minimum surface kelp canopy during stormy winter months and a maximum in summer and autumn months; recruitment of understory annual species greatest in spring and summer; and perennial species present throughout the year, though during winter only holdfasts may be present (Reed & Foster 1984, Breda & Foster 1985). In temperate southern Korean reefs, species richness is greatest in winter and cover is greatest in spring (Kim *et al.* 1998). In sub-tropical Baja California Sur, Mexico, algal biomass is lowest in spring with a maximum in summer when seawater temperatures are highest (Nunez-Lopez & Valdez 1998). In tropical coral reef habitats in Colombia, increases in the biomass of algal turfs were correlated to seasonal rains in April-June and October-December, and increases in the abundance of *Dictyota* spp. were linked to periods of upwelling in August and February (Diaz-Pullido & Garzon-Ferreira 2002).

By comparison, seasonal variations in subtidal macroalgal assemblages have not been described along

much of the southern coast of Western Australia due, in part, to the remoteness of field sites and rough subtidal conditions. In Tasmania, growth in subtidal macroalgae was reported in spring-summer and winter-spring with similar densities of canopy taxa throughout the year (Edgar 1983). In South Australia, Shepherd and Womersley (1970) observed that more common species were present throughout the year with growth evident from winter to early summer and algal thalli were denuded by midsummer. Inadequate data of smaller species precluded any conclusions regarding seasonal abundances (Shepherd & Womersley 1970). Building upon the findings of Shepherd and Womersley (1970) and Edgar (1983), the present study describes temporal variation in subtidal macroalgal assemblages at Black Island in the Recherche Archipelago and relates findings to local oceanographic variables. Standing crop (biomass), density of thalli in the canopy, and macroalgal diversity (species richness and relative abundance) were compared among four sampling times in the austral spring (October 2002 and 2003) and autumn (April 2003 and 2004) at two sites and depth strata. Fertile specimens were also reported.

Methods

Study site

Black Island (33° 55 S, 122° 00 E) is located in Esperance Bay, Western Australia, and is part of the

Recherche Archipelago, a collection of over 100 islands that spans 250 km. Typical of the islands in the archipelago, Black Island is granitic with subtidal reefs consisting of gently-sloping platforms and boulder fields that extend to depths of 30 m. The southern side of the island is relatively exposed to south-westerly swell rolling in from the Southern Ocean. The south-eastern side of the island is relatively sheltered from ocean swell. Subtidal macroalgal assemblages consist of a multi-specific, fucalean canopy that overlays an understory (species < 30 cm in length) with a few dominant taxa (< 5 genera) and a greater number (> 150 species) of relatively rare species (Goldberg & Kendrick 2004). The macroalgal assemblage at Black Island is typical of islands in the Recherche Archipelago with a canopy dominated by Fucalean species on the wave-sheltered side of the island, *Ecklonia radiata* and *Scytothalia dorycarpa* on the wave-exposed side of the island, and species-rich understory assemblage (Goldberg & Kendrick 2004). In addition, environmental variables collected in Esperance Bay would be relevant to any temporal variability observed in algal species diversity at Black Island. Urchins are uncommon and herbivorous fish have not been observed to diminish algal biomass in the Recherche Archipelago (Fowler-Walker & Connell 2002, personal observation in 2002 and 2003).

Description of seasonal variation in oceanographic parameters

Seasonal estimates of oceanographic parameters (seasonal chlorophyll *a*, sea surface temperature, wind speed, salinity, and wave height estimates) were compiled from previous and ongoing studies. Chlorophyll *a* estimates in Esperance Bay were taken from van Hazel *et al.* (2001). Sea surface temperatures (° Celsius) were provided by A. Pearce, CSIRO (unpubl. data, 26 October 2004). Data were collected by a StowAway Tidbit Temperature Logger that was deployed at a depth of 1.5 m and attached to a jetty piling at Woody Island, 3 km south of Black Island. Mean monthly sea surface temperatures were averaged over each season, 2001–2004: summer (Dec-Feb), autumn (Mar-May), winter (Jun-Aug), and spring (Sept-Nov). Additional temperature data were included from measurements recorded in Esperance (33° 51 S, 121° 54 E) in 1998 and provided by the Australian Oceanographic Data Centre (AODC 2004). Seasonal wind speeds (km hr⁻¹) from Esperance were supplied by the

Western Australia Office of the Bureau of Meteorology (Climate and Consultancy Section 2004). Salinity data and wave height data were compiled from archived information. Salinity data (ppt) for Esperance waters were provided by the AODC. Mean salinity per month was averaged per season. Significant wave height data (m) were collected from Magistrates Rocks, located within Esperance Bay from March 1982 to February 1983 (van Hazel *et al.* 2001).

Oceanographic estimates were similar throughout the year. In 2000, chlorophyll *a* concentrations were slightly greater (1.0 mg m⁻³) in autumn than in spring (0.4 mg m⁻³) (van Hazel *et al.* 2001). Between 2001 and 2004, mean seasonal sea surface temperatures differed by 2.3 °C with coldest temperatures occurring in spring (16.3 °C) and warmest temperatures in summer and autumn (19.0 °C; Table 1). Salinity was 0.2 ppt greater in summer and autumn compared to winter and spring (Table 1). Wave heights of 1 m were common, and waves > 2 m occurred 20–30% of the time throughout the years 1982 and 1983 (Table 1). Regardless of season, wind direction was variable throughout the year and wind speeds > 10 km hr⁻¹ occurred > 57% of the time (Table 1).

Sampling methods

At Black Island, subtidal macroalgal assemblages were sampled in austral spring and autumn. Austral spring samples were collected in October 2002 and 2003, and autumn samples were collected in April 2003 and 2004. Macroalgae were collected in spring to sample species diversity following winter storms, and in autumn to sample species diversity following summer growth periods (Womersley & Shepherd 1970).

To test if temporal variation in macroalgal assemblages differed spatially along Black Island, two sites were sampled. These sites differed with exposure to wave energy. The southern site (33° 55.417 S, 121° 59.562 E) was located off a point and faced south-westerly swells. The south-eastern site (33° 55.188 S, 122° 00.003 E) was located within a narrow embayment protected from south-westerly swells.

Two depth strata were sampled because subtidal macroalgal assemblages differed between depths < 10 m and depths 10–20 m in a previous study. Goldberg and Kendrick (2004) documented an assemblage dominated by canopy taxa in depths < 10 m, and a mixed

Table 1

Oceanographic parameters measured in the Recherche Archipelago.

Parameter	Summer	Autumn	Winter	Spring
Sea surface temperature (mean °C ± se)				
a. May 2001 to Jan 2004, excluding Mar-May 2003 (A. Pearce, CSIRO)	a. 18.7 ± 0.18	a. 19.0	a. 17.2 ± 0.26	a. 16.3 ± 0.17
b. 1998 (AODC 2004)	b. 19.3	b. 19.3	b. 17.3	b. 16.5
Salinity (mean ppt ± se), Jan to Dec 1998 (AODC 2004)	35.9 ± 0.09	35.9 ± 0.03	35.7 ± 0.03	35.7 ± 0.03
Percent occurrence of significant wave height > 2 m March 1982–February 1983 (van Hazel <i>et al.</i> 2001)	20%	25%	30%	20%
a. Predominant wind direction Years 1995 and 2000 (van Hazel <i>et al.</i> 2001)	a. East/Southeast	a. East/Southeast, North/Northwest	a. Northwest	a. No dominant wind direction
b. Approximate percent occurrence of wind speed > 20 km hr ⁻¹ , January 2002–May 2004 (Climate and Consultancy Section 2004)	b. > 73%	b. > 57%	b. > 67%	b. > 74%

assemblage of canopy and understory taxa in depths 10–20 m at Black Island and other islands in the Recherche Archipelago. At each site, 0.25 m²-quadrats were placed randomly in depths < 10 m and 10–20 m (n = 6 per depth stratum). In each quadrat, macroscopic algae (> 1 cm long) were collected by hand and with a paint scraper. Macroalgae were sorted, wet-weighed, and fertile material was noted. Species identifications were made using Womersley (1984, 1987, 1994, 1996, 1998, 2003) and Huisman (2000). *Sargassum* species that were vegetative were identified to subgenus.

Data analysis

A three-way ANOVA was used to test for differences in average biomass and density of thalli in the canopy (fixed factors: time: n = 4, site: n = 2, and depth: n = 2). Data were square-root (X + 0.5) transformed to satisfy assumptions of equal variances and normality (Zar 1984).

To test for differences among the macroalgal assemblages with time, multivariate analyses were performed with biomass data. Data were fourth-root transformed to minimize ranges of biomass estimates (Clarke & Gorley 2001). From a Bray-Curtis similarity matrix (Bray & Curtis 1957), a one-way analysis of similarity (ANOSIM; PRIMER ver. 6 software, Plymouth) was used to test for the significance of assemblage differences among sampling times. ANOSIM calculates a Clarke's R test statistic that typically ranges between zero and one. Assemblages are considered to be relatively similar the closer the value is to zero (Clarke 1993). Differences in assemblages among sampling times were tested with a one-way ANOSIM within each depth-site combination. Separate tests were conducted because assemblages were significantly different between depths

and sites (Clarke's $R_{\text{depth}} = 0.66$, $P = 0.001$; and Clarke's $R_{\text{site}} = 0.52$, $P = 0.001$).

Results

A total of 254 species of macroalgae were recorded. Total species richness per sampling event showed no consistent difference between autumn and spring samples (Table 2). Species richness was greatest in spring 2003, irrespective of depth or site. At the southern site, average species richness per sampling time (\pm se) was similar between depths < 10 m and 10–20 (42 \pm 5 species per sampling time and 43 \pm 5 species per sampling time, respectively). At the south-eastern site, average species richness (\pm se) was lower in depths < 10 m than in depths 10–20 m (36 \pm 5 species per sampling time and 55 \pm 6 species per sampling time, respectively; Table 2). Average species richness per 0.25 m² ranged between 10 and 27 species.

Average total biomass per 0.25 m² was not significantly different among sampling times but the interaction term "depth x site" was significant (Table 3, Fig 1). Average total biomass was two-fold greater at the southern site than south-eastern site in depths 10–20 m (Fig 1). Per sampling time, 67% of the species contributed < 5 g per 0.25 m², regardless of depth or site. These species were primarily from the understory assemblage.

Table 2

Total species richness per sampling event. n = 6 per sampling event, site, and depth stratum.

Sampling Event	Southern site		South-eastern site	
	< 10 m	10–20 m	< 10 m	10–20 m
Spring 2002	36	38	25	38
Autumn 2003	45	32	34	61
Spring 2003	54	53	49	62
Autumn 2004	33	49	37	58

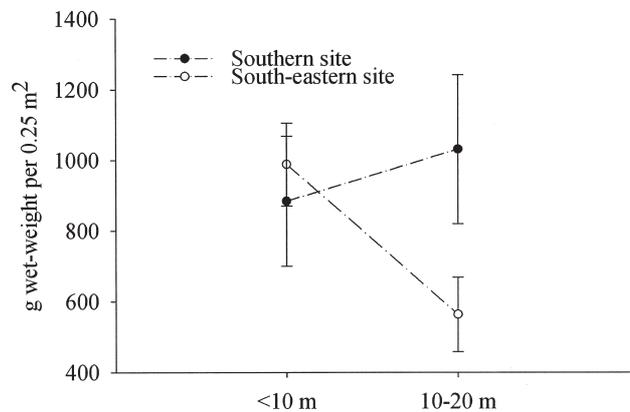


Figure 1. Illustration of "depth x site" interaction term for total macroalgal biomass per 0.25 m² (mean \pm se) at Black Island. n = 6 per site and depth stratum combination.

Table 3

A three-way analysis of variance testing for differences in total macroalgal biomass and density of thalli in the canopy. Data were square-root (X + 0.5) transformed. Fixed factors: time, depth, and site. n = 6 per sampling event and depth stratum.

Source	d.f.	Total macroalgal biomass g wet-weight 0.25 m ⁻²		Density of thalli 0.25 m ⁻² for canopy species	
		MS	F	MS	F
Time	3	85.12	2.00	6.27	5.81**
Depth	1	159.72	3.74	93.79	86.93**
Site	1	210.41	4.93*	18.80	17.43**
T x D	3	102.63	2.41	8.67	8.03**
T x S	3	69.47	1.63	4.07	3.78*
D x S	1	613.09	14.37**	29.89	27.71**
T x D x S	3	26.00	0.61	10.88	10.08**
Error	80	42.65		1.08	

*P < 0.05; ** P < 0.01

Table 4

Biomass (mean g wet-weight \pm se) of species that contributed > 50 g 0.25 m $^{-2}$ in at least one sampling event and depth combination **A**: southern site, **B**: south-eastern site. n = 6 per sampling event and depth stratum.

(A) Southern site					
Species	Depth (m)	Spring 2002	Autumn 2003	Spring 2003	Autumn 2004
^c <i>Acrocarpia robusta</i> (J. Agardh) Womersley	< 10	39 \pm 31	73 \pm 46	459 \pm 377	70 \pm 68
	10–20	118 \pm 68		45 \pm 29	28 \pm 27
<i>Caulerpa sedoides</i> C. Agardh f. <i>geminata</i> (Harvey) Weber-van Bosse	< 10		43 \pm 20	96 \pm 38	13 \pm 7
<i>Codium mamillosum</i> Harvey	< 10	7 \pm 7	*	28 \pm 12	*
	10–20	97 \pm 35	11 \pm 11	72 \pm 24	343 \pm 63
^c <i>Cystophora brownii</i> (Turner) J. Agardh	< 10	297 \pm 90	91 \pm 67	39 \pm 24	164 \pm 64
	10–20	66 \pm 66			
^c <i>Cystophora gracilis</i> Womersley	< 10	160 \pm 71	28 \pm 13		*
^c <i>Cystophora monilifera</i> J. Agardh	10–20	73 \pm 36	8 \pm 8	14 \pm 14	10 \pm 7
^c <i>Cystophora racemosa</i> (Harvey ex Kützing) J. Agardh	10–20		*	222 \pm 158	16 \pm 16
^c <i>Cystophora subfarcinata</i> (Mertens) J. Agardh	< 10	115 \pm 43	11 \pm 11		82 \pm 10
<i>Distromium flabellatum</i> Womersley	< 10	31 \pm 10	*	55 \pm 12	*
	10–20	24 \pm 3	*	*	*
^c <i>Ecklonia radiata</i> (C. Agardh) J. Agardh	10–20		73 \pm 50	492 \pm 268	224 \pm 192
<i>Osmundaria prolifera</i> Lamouroux	10–20	200 \pm 114			
^c <i>Sargassum</i> subgenus <i>Arthrophyucus</i>	< 10	15 \pm 9	39 \pm 11		30 \pm 21
	10–20	102 \pm 56	28 \pm 14		30 \pm 12
^c <i>Sargassum decipiens</i> (R. Brown ex Turner) J. Agardh	< 10				413 \pm 88
^c <i>Sargassum spinuligerum</i> Sonder	< 10			119 \pm 35	104 \pm 19
	10–20			22 \pm 17	*
^c <i>Scytothalia dorycarpa</i> (Turner) Greville	< 10		41 \pm 41		
	10–20		902 \pm 231	57 \pm 39	

* < 5 g. ^c = canopy species.

(B) South-eastern site

^c <i>Acrocarpia robusta</i> (J. Agardh) Womersley	< 10	17 \pm 11	49 \pm 21	158 \pm 43	6 \pm 3
<i>Amansia pinnatifida</i> Harvey	< 10	64 \pm 11			
<i>Botryocladia sonderi</i> Silva	10–20	91 \pm 12	91 \pm 28	12 \pm 8	18 \pm 7
^c <i>Caulocystis uvifera</i> (C. Agardh) Areschoug	10–20	68 \pm 47		7 \pm 7	
<i>Cladurus elatus</i> (Sonder) Falkenberg	< 10			264 \pm 72	
	10–20	36 \pm 24	43 \pm 21	*	74 \pm 56
<i>Codium mamillosum</i> Harvey	< 10	7 \pm 5		116 \pm 59	
	10–20	28 \pm 24	6 \pm 6	32 \pm 25	22 \pm 12
^c <i>Cystophora brownii</i> (Turner) J. Agardh	< 10	681 \pm 172	318 \pm 126	126 \pm 57	28 \pm 19
^c <i>Cystophora gracilis</i> Womersley	< 10	*	61 \pm 33	21 \pm 14	*
^c <i>Cystophora monilifera</i> J. Agardh	< 10	*	18 \pm 14	*	205 \pm 64
	10–20		30 \pm 30	276 \pm 180	234 \pm 122
^c <i>Cystophora subfarcinata</i> (Mertens) J. Agardh	< 10			12 \pm 12	111 \pm 96
<i>Laurencia</i> spp.	< 10		61 \pm 23	10 \pm 5	13 \pm 5
<i>Osmundaria prolifera</i> Lamouroux	10–20	49 \pm 5	69 \pm 12	36 \pm 17	52 \pm 15
^c <i>Sargassum spinuligerum</i> Sonder	< 10	50 \pm 23			
	10–20	71 \pm 44			
^c <i>Scaberia agardhii</i> Greville	< 10	382 \pm 90	66 \pm 42		530 \pm 185
	10–20	40 \pm 32	71 \pm 67	47 \pm 39	63 \pm 63
<i>Zonaria spiralis</i> (J. Agardh) Papenfuss	< 10	106 \pm 26	*	*	34 \pm 14

* < 5 g. ^c = canopy species.

Species that contributed ≥ 5 g per 0.25 m 2 included canopy taxa such as species of *Acrocarpia*, *Caulocystis*, *Cystophora*, *Sargassum*, *Ecklonia*, and *Scytothalia* (Table 4).

Density of thalli in the canopy showed no consistent difference between spring and autumn samples (Fig 2), as demonstrated by the significant interactions term "time \times depth \times site" (Table 3). Density of thalli in the canopy was more variable among sampling times in depths < 10 m than in depths 10 to 20 m (Fig 2). Excluding spring 2002 samples, density of thalli was greatest at the southern site in depths < 10 m (Fig 2).

In depths < 10 m, assemblages showed no unique spring or autumn patterns. Instead, assemblages differed significantly among sampling times (Clarke's $R_{\text{time}} = 0.89$ for southern site, 0.93 for south-eastern site, $P = 0.001$ for both sites) and between samples collected in the same season (Table 5). Of the 120 species recorded in depths < 10 m, each species was present on average in 7 of the 48 quadrats sampled. Only *Acrocarpia robusta* Womersley and *Cystophora brownii* Turner (J. Agardh) were recorded in every sampling event (season and exposure combination; Table 4).

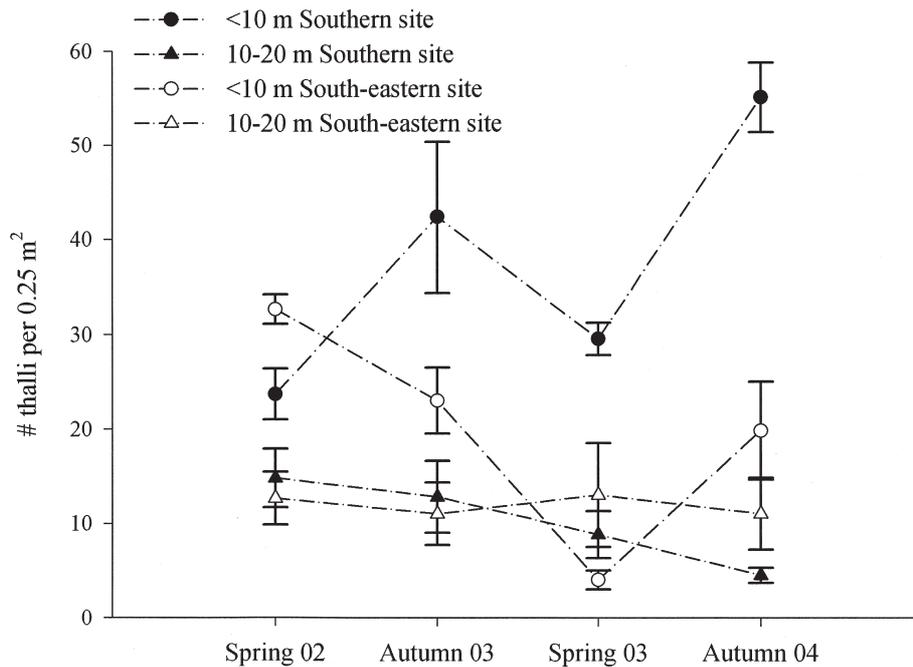


Figure 2. Density of thalli in the canopy per 0.25 m² (mean ± se) per sampling time at Black Island. n = 6 per site and depth stratum combination for each sampling time.

As in depths < 10 m, macroalgal assemblages differed among sampling times in depths 10–20 m (Clarke's $R_{\text{time}} = 0.72$ for southern site, 0.58 for south-eastern site, $P = 0.001$ for both sites), and between samples collected in the same season (Table 5). Of the 148 species recorded in depths of 10–20 m, each species was present on average in 6 of the 48 quadrats sampled. *Dilophus fastigiatus* (Sonder) J. Agardh and *Laurencia* spp. were present in every sampling event.

A number of species had greater abundances within spring or autumn samples. Because populations were

patchy, these patterns remain qualitative. *Cystophora* species generally had greater biomass in spring, particularly in spring 2002 (Table 4). Biomass of *Codium mamillosum* Harvey (except in autumn 2004, southern site) and *Distromium flabellatum* Womersley was also greater in spring samples (Table 4).

Of the species that were fertile at the time of collection, 77% were fertile in both seasons (Table 6). All canopy species were reproductive in autumn and spring (Table 6). Fucal species in the canopy had partially-depleted conceptacles in autumn.

Table 5

Clarke's R values from pairwise comparisons between sampling times at **A:** southern site and **B:** south-eastern site in depths < 10 m and 10–20 m. Comparisons were calculated using analysis of similarity. Biomass data were fourth root transformed. n = 6 per site and depth stratum combination.

(A) Southern site

	Spring 2002	< 10 m		Spring 2002	10–20 m	
		Autumn 2003	Spring 2003		Autumn 2003	Spring 2003
Autumn 2003	0.88*			1.00*		
Spring 2003	1.00*	0.73*		0.75*	0.50**	
Autumn 2004	0.95*	0.82*	1.00*	0.67*	0.91*	0.48***

* $P = 0.002$, ** $P = 0.006$, *** $P = 0.009$

(B) South-eastern site

	Spring 2002	< 10 m		Spring 2002	10–20 m	
		Autumn 2003	Spring 2003		Autumn 2003	Spring 2003
Autumn 2003	0.89*			0.96*		
Spring 2003	1.00*	1.00*		0.58*	0.58*	
Autumn 2004	0.90*	0.85*	0.98*	0.64*	0.60*	0.19**

* $P = 0.002$, ** $P = 0.067$

Table 6

Fertile specimens collected in autumn and spring from Black Island.

Species	Autumn	Spring
<i>Acrocarpia robusta</i> (J. Agardh) Womersley	*	*
<i>Amphiroa anceps</i> (Lamarck) Decaisne	*	
<i>Amphiroa gracilis</i> Harvey	*	*
<i>Caulocystis uvifera</i> (C. Agardh) Areschoug	*	*
<i>Cystophora brownii</i> (Turner) J. Agardh	*	*
<i>Cystophora expansa</i> (Areschoug) Womersley	*	*
<i>Cystophora gracilis</i> Womersley	*	*
<i>Cystophora monilifera</i> J. Agardh	*	*
<i>Cystophora pectinata</i> (Greville and C. Agardh ex. Sonder) J. Agardh	*	*
<i>Cystophora racemosa</i> (Harvey ex Kützing) J. Agardh	*	*
<i>Cystophora subfarinata</i> (Mertens) J. Agardh	*	*
<i>Distromium</i> spp.	*	*
<i>Glossophora nigricans</i> (J. Agardh) Womersley	*	*
<i>Laurencia elata</i> (C. Agardh) J. Hooker and Harvey	*	*
<i>Metagoniolithon radiatum</i> (Lamarck) Ducker	*	*
<i>Metamastophora flabellata</i> (Sonder) Setchell	*	*
<i>Myriodesma harveyanum</i> Nizamuddin and Womersley	*	*
<i>Osmundaria prolifera</i> Lamouroux	*	*
<i>Plocamium mertensii</i> (Greville) Harvey	*	*
<i>Polysiphonia decipiens</i> Montagne	*	*
<i>Ptilocladia pulchra</i> Sonder	*	*
<i>Sargassum fallax</i> Sonder	*	*
<i>Sargassum heteromorphum</i> J. Agardh	*	*
<i>Sargassum lacerifolium</i> (Turner) C. Agardh	*	*
<i>Sargassum linearifolium</i> (Turner) C. Agardh	*	*
<i>Sargassum spinuligerum</i> Sonder	*	*
<i>Sargassum tristichum</i> Greville and C. Agardh ex Sonder	*	*
<i>Scytothalia dorycarpa</i> (Turner) Greville	*	*
<i>Spyridia dasyoides</i> Sonder		*
<i>Wrangelia plumosa</i> Harvey	*	

Discussion

Subtidal macroalgae collected from a temperate southern Australian island showed no clear differences between autumn and spring samples. Instead, differences in assemblages were as great between autumn and spring as interannual differences within each sampled season. The absence of a consistent temporal pattern may be a reflection of little seasonal variability in biological and physical oceanographic parameters. Instead, exposure to wave energy may have a greater influence on species diversity, contributing to the observed species turnover at the metres-scale in autumn and spring. Diversity may be maintained with the removal of macroalgae by year-round exposure to swells > 2 m, and the successful recruitment of macroalgal species whose parent populations release propagules throughout the year or via vegetative recolonization.

Many of the oceanographic parameters measured in the archipelago were appreciably similar throughout the year, which may explain the lack of a distinctive spring or autumn assemblage. Seasonal patterns in subtidal macroalgal diversity have been correlated to periods of high or low seawater temperatures (Nunez-Lopez & Valdez 1998), upwelling periods (Diaz-Pullido and Garzon-Ferreira 2002), and storm activity (Reed & Foster

1984, Breda & Foster 1985). In the Recherche Archipelago, sea-surface temperatures, nutrients (as nominally indicated by chlorophyll *a* concentrations), salinity, and wave heights were similar throughout the year, albeit in different years than those sampled in this study. Furthermore, the narrow ranges of these environmental factors may contribute to subtidal assemblages in the Recherche Archipelago consisting of perennial canopy (*i.e.*, *Cystophora* spp. and *Sargassum* spp.) and understory (*i.e.*, *Osmundaria prolifera*, *Botryocladia sonderi*, *Codium* spp., *Caulerpa* spp., and *Distromium* spp.) species. The presence of various species throughout the year had also been observed at West Island, South Australia, though algal growth did vary seasonally (Shepherd & Womersley 1970).

Greater variability in the number of canopy individuals in depths < 10 m than in 10–20 m may be a function of wave energy attenuating with depth (Denny & Wethey 2001). Physical disturbance by swells would be greater in depths < 10 m. Removal of macroalgae by wave energy would open up space for recruitment, resulting in a mosaic of individuals that recruited at different times (Dayton *et al.* 1984). Increased opportunity for physical disturbance in conjunction with patchy recruitment may result in the observed greater range of thalli in depths < 10 m than in depths 10–20 m.

Differences between assemblages at the southern and south-eastern sites suggest that exposure to wave energy has a greater influence on diversity than factors associated with temporal variation. Site-specific differences in exposure to wave energy may explain the greater abundance of canopy species *Ecklonia radiata* and *Scytothalia dorycarpa* and indirectly, lower species richness at the southern site in depths 10–20 m. The southern site was more exposed to ocean swell than the south-eastern site which was located within an embayment. The prevalence of *E. radiata* and *S. dorycarpa* at wave-exposed sites has been observed throughout the Recherche Archipelago (Goldberg & Kendrick 2004). Total species richness was lower by as much as 50% where these species were abundant (autumn 2003, 2004, and spring 2003 samples). In contrast, where *E. radiata* and *S. dorycarpa* were not present, species richness was comparable between southern and south-eastern sites in depths 10–20 m (38 species). Lower species richness has been correlated to *E. radiata* abundance elsewhere along the south-western coast of Western Australia (Wernberg *et al.* 2003).

Similar to the findings of Shepherd and Womersley (1970), subtidal macroalgal assemblages at an island located along the southern coast of Australia did not necessarily have a unique spring or autumn assemblage. Because oceanographic parameters did not vary much throughout the year, patterns in macroalgal diversity were most likely driven by factors associated with depth and location along the Black Island. Furthermore, species richness remained high in the face of continual exposure to wave energy, indicating resilience via successful recruitment and growth.

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References

- Australian Oceanographic Data Centre 2004. Coastal sea surface temperature and salinity. Available from: <<http://www.aodc.gov.au/products/data.html>>.
- Bray J R & Curtis J T 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 7: 325–349.
- Breda V A & Foster M S 1985. Composition, abundance, and phenology of foliose red algae associated with two central California kelp forests. *Journal of Experimental Marine Biology and Ecology* 94: 115–130.
- Clarke K R 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Clarke K R & Gorley R N 2001. *Primer ver. 5: user manual/tutorial*. PRIMER-E, Plymouth.
- Climate and Consultancy Section in the Western Australia Office of the Bureau of Meteorology 2004 Commonwealth of Australia, available from: <http://www.bom.gov.au/climate/how/>.
- Dayton P K, Currie V, Gerrodette T, Keller, B D, Rosenthal R & Ven Tresca D 1984. Patch dynamics and stability of some California kelp communities. *Ecological Monographs* 54: 253–289.
- Denny M & Wethey D 2001. Physical processes that generate patterns in marine communities. In: *Marine Community* (Eds M D Bertness, S D Gaines & M E Hay). Sinauer Assoc., Inc., Sunderland. pp. 3–37.
- Diaz-Pullido G & Garzon-Ferreira J 2002. Seasonality in algal assemblages on upwelling-influenced coral reefs in the Columbian Caribbean. *Botanica Marina* 45: 284–292.
- Edgar, G J 1983. The ecology of south-east Tasmanian phytal animal communities. II. Seasonal change in plant and animal populations. *Journal of Experimental Marine Biology* 70: 159–179.
- Goldberg N A & Kendrick G A 2004. Effects of island groups, depth, and exposure to ocean waves on subtidal macroalgal assemblages in the Recherche Archipelago, Western Australia. *Journal of Phycology* 40: 631–641.
- Huisman J M 2000 *Marine Plants of Australia*. University of Western Australia Press, Nedlands.
- Kim K Y, Choi T S, Huh S H & Garbary D J 1998. Seasonality and community structure of subtidal benthic algae from Daedo Island, Southern Korea. *Botanica Marina* 41: 357–365.
- Nunez-Lopez R A & Valdez M C 1998. Seasonal variation of seaweed biomass in San Ignacio Lagoon, Baja California Sur, Mexico. *Botanica Marina* 41: 421–426.
- Reed D C & Foster M S 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65: 937–948.
- Shepherd S A & Womersley H B S 1970. The sublittoral ecology of West Island, South Australia. I. Environmental features and the algal ecology. *Transactions of the Royal Society of South Australia* 94: 105–138.
- van Hazel J, Pattiaratchi C & D'Adamo N 2001. Review of the climate and physical oceanography of the Recherche Archipelago and adjacent waters. University of Western Australia, Crawley.
- Wernberg T, Kendrick G A & Phillips J C 2003. Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. *Diversity and Distributions* 9: 427–441.
- Womersley H B S 1984. The marine benthic flora of southern Australia. Part I. South Australian Government Printing Division, Adelaide.
- Womersley H B S 1987. The marine benthic flora of southern Australia. Part II. South Australian Government Printing Division, Adelaide.
- Womersley H B S 1994. The marine benthic flora of southern Australia. Part IIIA. Australian Biological Resources Study, Canberra.
- Womersley H B S 1996. The marine benthic flora of southern Australia. Part IIIB. Australian Biological Resources Study, Canberra.
- Womersley H B S 1998. The marine benthic flora of southern Australia. Part IIIC. State Herbarium of South Australia, Adelaide.
- Womersley H B S 2003. The marine benthic flora of southern Australia. Part IIID. Australian Biological Resources Study, Canberra.
- Zar J H 1984. *Biostatistical Analysis*. 2nd ed. Prentice Hall, Englewood Cliffs, New Jersey.