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Seasonal changes in water quality and *Sargassum* biomass in southwest Australia

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ABSTRACT: *Sargassum* C. Agardh is one of the most diverse genera of marine macroalgae, and commonly inhabits shallow tropical and sub-tropical waters. This study aimed at investigating the effect of seasonality and the associated water-quality changes on the distribution, canopy cover, mean thallus length and biomass of *Sargassum* beds around Point Peron, Shoalwater Islands Marine Park, southwest Australia. Samples of *Sargassum* and seawater were collected every 3 mo from the summer of 2012 to the summer of 2014, from 4 different reef zones. A combination of *in situ* observations and WorldView-2 satellite remote-sensing images were used to map the spatial distribution of *Sargassum* beds and other associated benthic habitats. The results demonstrated strong seasonal variation in the physicochemical water parameters, canopy cover, mean thallus length, and biomass of *Sargassum*, which were significantly ($p < 0.05$) influenced by nutrient concentrations (PO_4^{3-}, NO_3^-, NH_4^+) and rainfall. However, no significant variation in any studied parameter was observed among the 4 reef zones. The highest *Sargassum* biomass peaks occurred between late spring and early summer (from September to January). The results provide essential information to guide effective conservation and management, as well as sustainable utilisation of this renewable coastal marine resource.

KEY WORDS: Physicochemical parameters · *Sargassum* beds · Seasonality · Canopy cover · Mean thallus length

INTRODUCTION

Sargassum species are brown macroalgae with a global distribution, and are especially dominant in shallow tropical and sub-tropical waters (Hanisak & Samuel 1987, Mattio et al. 2008, Mattio & Payri 2011). *Sargassum* species are commonly attached to rocks, but are also found as floating life forms. In coastal areas and around offshore islands, they form dominant communities that play vital ecological roles in marine ecosystems by providing feeding grounds for sea birds and sea lions, and essential nursery habitats for the invertebrates and larval and juvenile fish living just off these islands (Wells & Rooker 2004, Tyler 2010). *Sargassum* also represents a living, renewable resource that can be used in medicine and for the production of fertilisers, alginate and bio-fuels (Chengkui et al. 1984, Arenas & Fernández 2000, Rivera & Scrosati 2006, Hong et al. 2007).

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Approximately 46 *Sargassum* species are found along the southwest Australian (SWA) coast (DPaW 2013); the majority of these have been studied to determine their taxonomic affiliation, including the molecular basis for identification (e.g. Kendrick 1993, Kendrick & Walker 1994, Goldberg & Huisman 2004, Dixon & Huisman 2010, Dixon et al. 2012, Rothman et al. 2015), and physiology (De Clerck et al. 2008, Huisman et al. 2009, Staehr & Wernberg 2009, Kumar et al. 2011, Muñoz & Fotedar 2011). However, few studies have been carried out concerning the impact of seasonality on *Sargassum* along the subtropical/temperate coastal zone of SWA (Kendrick 1993, Kendrick & Walker 1994). Previous studies have shown that the growth, development and distribution of *Sargassum* beds are strongly influenced by physicochemical water parameters (Payri 1987, Ragaza & Hurtado 1999, Mattio et al. 2008), which play an important role in nutrient uptake via photosynthesis (Nishihara & Terada 2010). Seasonal variations in the physicochemical parameters of seawater strongly influence changes in *Sargassum* canopy structure, which, in turn, affects the density of local populations (Ang & De Wreede 1992, Arenas & Fernández 2000, Rivera & Scrosati 2006, Ateweberhan et al. 2009).

In recent years, satellite remote-sensing studies have successfully been applied to benthic marine habitat mapping and, more specifically, have been used to estimate macroalgal biomass in coastal waters (Andréfouët & Robinson 2003, Kutser et al. 2006, Benfield et al. 2007, Vahtmäe & Kutser 2007, Casal et al. 2011a, Fearns et al. 2011, Maheswari 2013). However, the clearest and most direct method of marine habitat mapping is through visual observation, also termed ground-truthing, using either SCUBA or snorkel survey methods; such work provides essential input for remote-sensing observations (Komatsu et al. 2002). A methodology for mapping *Laminariales* (kelp) in the turbid waters of Seno de Corcubión (Northwest Spain) was developed using SPOT-4 satellite images, which showed that the mapping of *Sargassum* beds could be improved through the application of higher spectral resolution images, increasing the spatial and radiometric resolution and performing new field calibrations simultaneously with the acquisition of images (Casal et al. 2011b). For example, lower resolution Landsat (30 m) and higher resolution Quickbird (2.4 m) satellite images have been used to estimate the spatial distribution of *Sargassum* beds in South West Lagoon, New Caledonia (Mattio et al. 2008). Nevertheless, only a few studies have been carried out to assess the spatial distribution of *Sargassum* species and their temporal biomass variations in marine coastal areas using high-resolution satellite remote-sensing data (Noiraksar et al. 2014, Hoang et al. 2015).

The WorldView-2 (WV-2) satellite images provide one of the highest available spatial and spectral resolutions (8 spectral sensors ranging from 400 to 1040 nm) (Lee et al. 2011, DigitalGlobe 2013). However, few detailed mapping studies of *Sargassum* have been performed using high-resolution satellite images, such as WV-2 (Hoang et al. 2015). We suggest that direct visual observations combined with high spatial resolution remote-sensing observations could represent a robust approach for minimizing costs and increasing the accuracy of detection and the determination of *Sargassum* distribution patterns in shallow coastal waters. The aim of this study was to investigate the effects of seasonal changes in water quality on canopy cover, mean thallus length and *Sargassum* biomass at a fringing limestone reef in Point Peron, SWA. We used *in situ* observations and remote-sensing methods to study the seasonal variation in physicochemical water parameters with changes in mean thallus length, canopy cover and the biomass of the *Sargassum* community and to determine how these changes impact the broader spatial distribution of *Sargassum.*

MATERIALS AND METHODS

Study sites

We selected our demonstration site at Point Peron, SWA, which is a small peninsula located within the Shoalwater Islands Marine Park, an area of approximately 67 km^2, west of the city of Rockingham, 50 km south of Perth (Fig. 1). The point is approximately 930 m long and 1450 m wide and is surrounded by a chain of limestone reefs and islands, including Garden Island to the north. As part of the Shoalwater Islands Marine Park, Point Peron has a high diversity of marine fauna and flora (DEC 2011).

The chain of limestone reefs is approximately 450 m offshore (32° 14′–32° 17′ S and 115° 39′–115° 42′ E). The coastal area of Point Peron was divided into 4 zones: the lagoon zone (LZ), back reef (BR), reef crest (RC) and fore reef (FR) zone, with a distance of approximately 100 m between each zone (Rützler & Macintyre 1982) (Fig. 2). The field studies were carried out from September 2012 to December 2014 during 4 well-defined seasons; summer (December–February), autumn (March–May), winter (July–August) and spring (September–November) (BoM 2013).

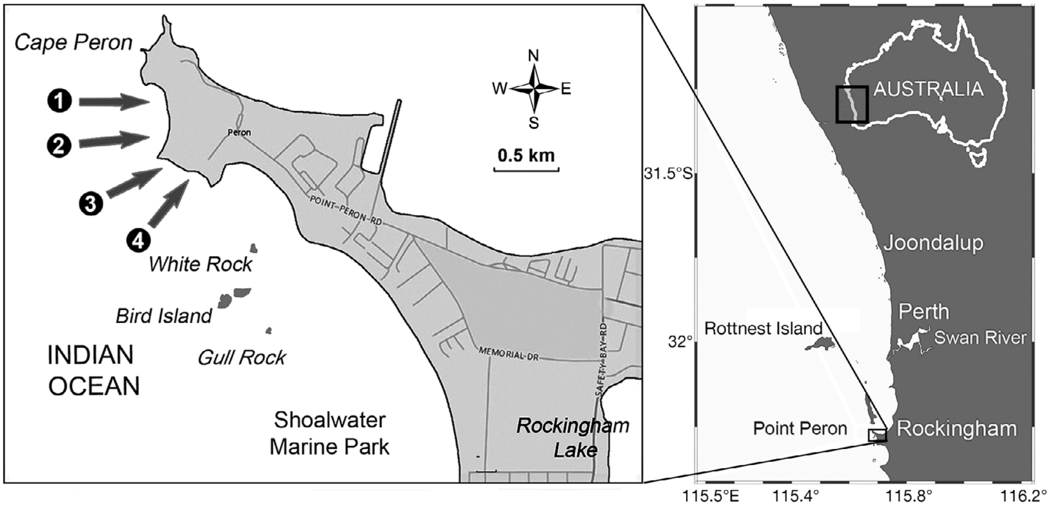

Fig. 1. Study area, with sampling sites shown by arrows. Point Peron is located approximately 50 km south of Perth, Western Australia

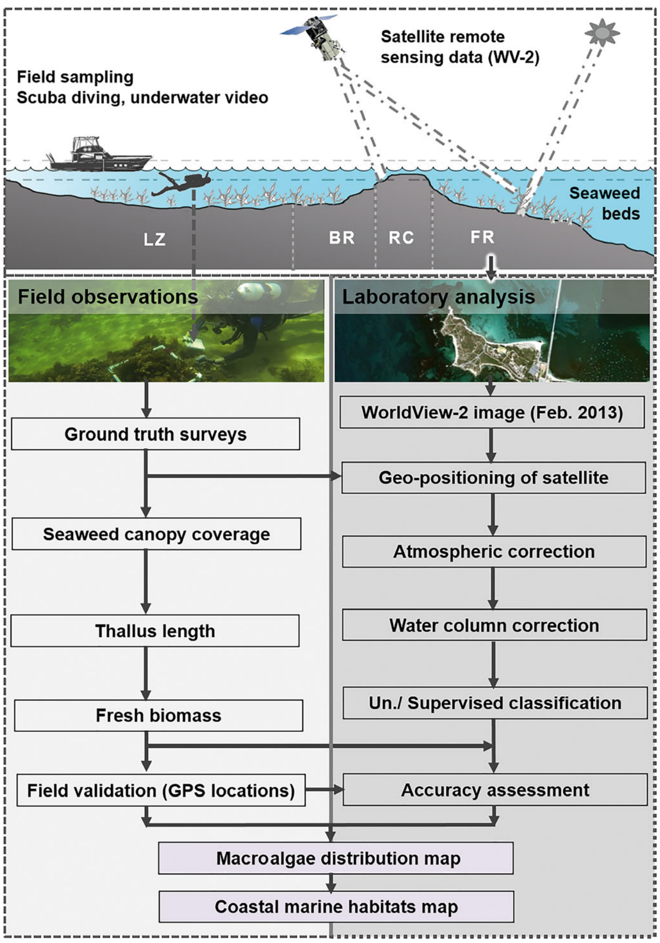

Fig. 2. Methodology used to map seaweed distribution and the associated benthic habitats at Point Peron using field survey data and high-spatial-resolution satellite imagery. Sites — LZ: lagoon zone; BR: back reef; RC: reef crest; FR: fore reef zone

Field sampling methods

Sampling frequency

The total duration of the trial was 2.5 yr, wherein summer and spring were represented 3 times and winter and autumn were represented twice. At least 1 sampling trip was carried out per season; however, we sampled twice during summer and spring seasons, which were then averaged out. During every trip, 4 transects (400 m long) were sampled. The average depth along each transect ranged from 0.3 to 2.5 m. For water quality analysis, 1 sample was collected from every transect. For canopy cover (CC), fresh biomass (FB) and mean thallus length (MTL) of *Sargassum* spp., every transect was further monitored from 4 reef zones by deploying random quadrats (0.5 × 0.5 m), 1 for each reef zone. The distance between the quadrats ranged from 20 to 80 m. The above protocol provided 4 samples for water quality analysis and 16 (4 transects × 4 quadrats) samples for *Sargassum* measurements per season.

Sampling description

The transects were selected based on the actual study site's topography and covering a range of different habitats. Using SCUBA survey techniques, we monitored and sampled *Sargassum* spp. along 4 predefined transects extending from the coastline to offshore. From each transect, the seawater samples were collected in a 1 l polyethylene bottle. The *Sargassum* spp. within each quadrat were collected, stored in labelled polyethylene bags and brought to the Curtin Aquatic Research Laboratory (CARL), Curtin University, Western Australia (WA). The locations of the sampling quadrats were recorded by a hand-held GPS (Garmin eTrex® 10). The collected *Sargassum* samples were retained in fibreglass tanks with seawater under natural sunlight. The samples were provided with constant aeration until further measurements were done. Fresh specimens were photographed immediately after arrival at the CARL. The holdfasts, blades, vesicles and receptacles were also examined and photographed. *Sargassum* specimens were identified based on taxonomic references (Noro et al. 1994, Phillips 1994, Garton 1997, Huisman 2000, Huisman et al. 2006, Guiry & Guiry 2015). A morphological study of *Sargassum* samples was undertaken on dried specimens. Herbarium specimens were stored at the CARL. Underwater video and photographs were captured along the monitored transects from 5 sampling trips in June and September in 2013, and January, March and July in 2014. These data were used for ground-truthing and classifying the marine habitats.

Meteorological data and physicochemical parameters

Meteorological data, including the maximum (MaxAT, °C), mean and minimum (MinAT, °C) air temperature, solar exposure (SE, MJ m^{-2}) and monthly rainfall for each season were acquired from the nearest Bureau of Meteorology weather station, at Garden Island (32° 14′ 24″ S, 115° 40′ 48″ E), 2 km north of Point Peron (BoM 2013). Euphotic depth (ED, m), sea-level pressure (SLP, hPa), the colored dissolved organic matter (CDOM) index, photosynthetically active radiation (PAR), sea-surface temperatures (SSTs), and chlorophyll *a* concentration (chl *a*, mg m^{-3}) in the study area (32° 12′–32° 17′ S, 115° 38′–115° 42′ E) were extracted from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data. The northward wind (NW, m s^{-1}) was extracted from the Modern Era Retrospective analysis for Research and Applications (MERRA) flat form in the Giovanni system, developed and maintained by the National Aeronautics and Space Administration (NASA) (Acker & Leptoukh 2007).

In situ seawater temperature (i-SST), conductivity and pH were measured in each season using a portable waterproof °C/mV/pH meter (CyberScan pH 300, Eutech Instruments). Salinity was measured using a hand-held refractometer (Atago® RHS-10ATC) in practical salinity units, and dissolved oxygen (DO) was determined with a digital DO meter (YSI®55, Perth Scientific). Seawater samples were collected during each sampling season for the analysis of nutrients: nitrate, nitrite, ammonium and phosphate. All samples were stored in 1 l polyethylene bottles and kept in a cold container (approximately 10°C) in the dark. Samples were transferred to the CARL for analysis within 48 h following collection according to the methods described in the Standard Methods for the Examination of Water and Wastewater (APHA 1998). Nitrate (NO_3^-) and nitrite (NO_2^-) were measured using a Hach DR/890 Colorimeter with the cadmium reduction method (Method 8171) and diazotization method (Method 8507), respectively (APHA 1998). Phosphate (PO_4^{3-}) concentration was analysed by the ascorbic acid method (Standard Method 4500-PE), and ammonium (NH_4^+) was determined by using Aquanal™ test kits (Sigma-Aldrich®) (see Table 1 for a list of symbols and acronyms).

Satellite remote-sensing data and processing

WorldView-2 satellite images at a 2 m spatial resolution were acquired on 7 February 2013 (austral summer), which was a period of high biomass and areal extent of *Sargassum* beds. Satellite remote-sensing WV-2 images were adjusted to pseudo-color composite images prior to the classification process, to enhance the image contrast for detecting *Sargassum* beds.

The acquired WV-2 images from DigitalGlobe® were registered into Georeferenced — the global geodetic system 1984 for latitude and longitude. The ground-truth data were acquired and confirmed using *in situ* field checks from 5 survey trips in 2013 and 2014. The ENVI® 4.7 environment for visualizing images was used to mask out the land area that was not used for classification at the study area (ENVI 2014). The method of K-means unsupervised classification was employed for image classification, as it is the most commonly used classifier in reef studies (Benfield et al. 2007, Hoang et al. 2015). A toolbox in ENVI® 4.7 was employed for classification and to count the number of pixels in the WV-2 satellite image that was used to detect the distribution of *Sargassum* beds. After classification, the data were converted from raster to vector format and were edited in geographical information system software packages. The complete diagrammatic processing imagery is presented in Fig. 2.

Table 1. List of symbols and acronyms used throughout the text

Acronym	Description and typical units
WA	Western Australia
SWA	Southwest Australia
DPaW	Department of Parks and Wildlife formerly named the Department of Environment and Conservation (DEC), Government of Western Australia
SPOT-4	Satellite Pour l'Observation de la Terre 4
WV-2	World View 2
LZ	Lagoon zone
BR	Back reef
RC	Reef crest
FR	Fore reef zone
BoM	Bureau of Meteorology, Australian Government
FB	Fresh biomass (g 0.25 m^{-2})
CC	Canopy cover (%)
MTL	Mean thallus length (cm)
APHA	American Public Health Association
GPS	Global Positioning System
CARL	Curtin Aquatic Research Laboratory
ED	Euphotic depth (m)
NW	Northward wind (m s^{-1})
MaxAT	Maximum air temperature (°C)
SE	Solar exposure (MJ m^{-2})
MinAT	Minimum air temperature (°C)
SLP	Sea-level pressure (hPa)
CDOM	Colored dissolved organic matter
PAR	Photosynthetically active radiation (Einstein m^{-2} d^{-1})
SSTs	Sea-surface temperatures (°C)
DO	Dissolved oxygen (mg l^{-1})
ENVI	Environment for visualizing image
ANOVA	Analysis of variance
PCA	Principal component analysis
MODIS	Moderate Resolution Imaging Spectro-radiometer
NASA	The National Aeronautics and Space Administration

Data analysis

Seaweed distribution and abundance data were processed using statistical software, IBM® SPSS Statistics 20 and Microsoft® Excel 2010. One-way analysis of variance (ANOVA) and general linear models were employed to test for significant differences between seasons in seawater quality. A 2-way ANOVA was carried out to test the effects of seasons and distribution sites on *Sargassum* CC and MTL. The multiple comparison, least significant difference (LSD) post hoc test, was also implemented to test for statistical significance among treatments. The statistical significance level was set at 0.05. Principal component analysis (PCA) was employed to evaluate the interaction between the physical, chemical and biological parameters and their effect on *Sargassum* spp. Results from the PCA were acquired based on the correlation matrix of the mean values of water quality parameters against sampling times. PCA was prepared by using the latest XLSTAT 2015.1.01 (Addinsoft™) package for Microsoft® Excel. All results are presented as means (±SE, standard error), unless otherwise stated.

RESULTS

Temporal variation in environmental conditions

The analysis of air temperature over the 3 study years (2012–2014) indicates that the monthly mean temperature was highest in the summer months (December–February). Temperatures then decreased in autumn (March–May) and were lowest in winter (June–August) and finally increased in spring (September–November). In the summer months, the maximum monthly mean temperature reached 28.2 ± 0.6°C and, in autumn, it reached 24.1 ± 0.9°C. In winter and spring, the maximum monthly mean temperatures were 18.5 ± 0.2 and 21.7 ± 1.3°C, respectively. In 2012, the mean air temperature reached a maximum in January (30.5°C) and was lowest in July (9.9°C) (Fig. 3a).

SSTs also showed a seasonal pattern, with values ranging from 12.9 to 24.1°C. There were significant (ANOVA, $F_{(9,37)}$ = 551.23, $p < 0.001$) differences in SSTs between seasons, except for between winter and spring (Fig. 3a). Rainfall and PAR usually showed an inverse pattern, and both showed strong seasonal variation. PAR reached its highest value in summer, at 58.5 ± 1.5 Einstein m^{-2} d^{-1} (a maximum in December 2013 of 63.2 Einstein m^{-2} d^{-1}). Although the monthly averaged rainfall for the months of Dec, Jan and Feb (the summer months) was only 2.6 mm, the average rainfall for summer seasons was 11.9 ± 6.4 mm. In contrast, PAR was lowest in winter months, at 22.8 ± 3.6 Einstein m^{-2} d^{-1} (17.5 Einstein m^{-2} d^{-1} in June 2013), and the highest mean rainfall value of 95.5 ± 11.9 mm was reached in winter (a maximum value of 151.6 mm in September 2013; Fig. 3b).

Seawater salinity in the study area ranged from 35.4 to 36.5 among seasons, but the differences were not significant (ANOVA, $F_{(9,37)}$ = 1.43, p = 0.224). The

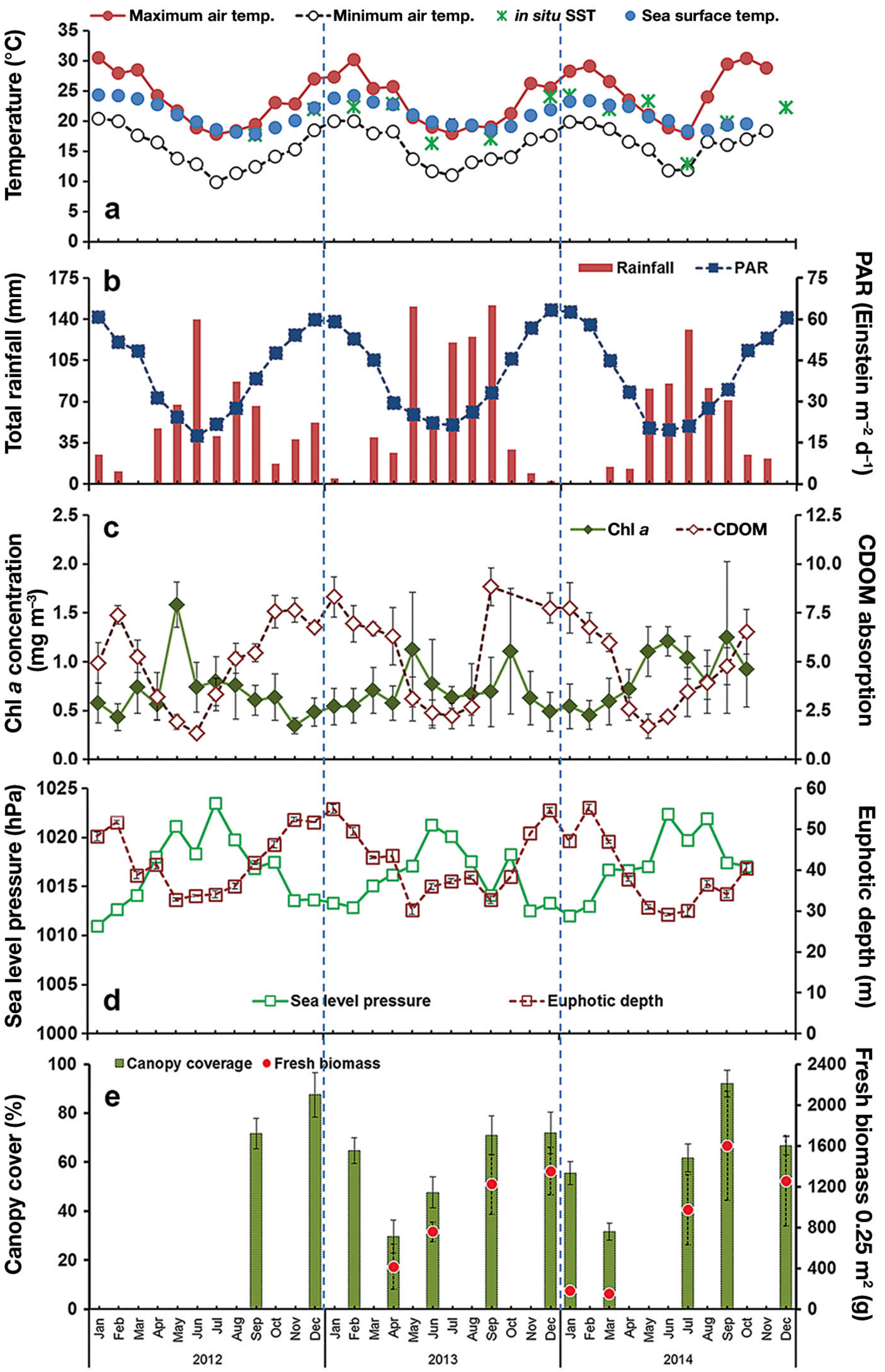

Fig. 3. Seasonal changes in (a) air temperature (maximum and minimum values) and sea-surface temperature (SST), (b) photosynthetically active radiation (PAR) and rainfall, (c) chlorophyll *a* (chl *a*) and colored dissolved organic matter (CDOM) index, (d) sea-level pressure and euphotic depth and (e) *Sargassum* canopy cover and fresh biomass at the study sites. *Sargassum* fresh biomass was not available from sampling trips in September 2012, December 2012, or February 2013. Air temperature and rainfall data were obtained from Garden Island weather station, Bureau of Meteorology, Australian Government. Euphotic depth, CDOM, PAR, SST, sea-level pressure and chl *a* in the study area (32° 12′–32° 17′ S, 115° 38′–115° 42′ E) were extracted from the Giovanni online data system, developed by NASA. Error bars are SE

electrical conductivity of seawater in the study area also differed significantly between sampled seasons (ANOVA, $F_{(9,37)}$ = 17.01, p < 0.001), with conductivity values ranging from −98.87 to −65.87 ECs. Dissolved oxygen (ANOVA, $F_{(9,37)}$ = 30.05, p < 0.001) and pH (ANOVA, $F_{(9,37)}$ = 3.32, p = 0.007) were significantly different between seasons and ranged from 5.39 to 8.27 mg l^{-1} and 7.82–8.21, respectively (Table 2).

Significant differences were observed in all nutrient levels among seasons during the study period at Point Peron as determined by 1-way ANOVA: NO_2^- (ANOVA, $F_{(3,36)}$ = 12.05, p < 0.05), NO_3^- (ANOVA, $F_{(3,36)}$ = 13.38, p < 0.05), NH_4^+ (ANOVA, $F_{(3,32)}$ = 5454, p < 0.05) and PO_4^{3-} (ANOVA, $F_{(3,36)}$ = 7.38, p = 0.001). In particular, the concentration of nitrite (NO_2^-) was relatively low, ranging from 2.2–17.4 µg l^{-1} during the study period. The nitrate (NO_3^-) concentration reached its highest value in spring 2014 (0.48 ± 0.06 mg l^{-1}) and lowest value in summer 2013 (0.02 ± 0.001 mg l^{-1}). The concentration of ammonium (NH_4^+) during the study period ranged from 0.6 to 2.0 mg l^{-1} and that of phosphate (PO_4^{3-}) ranged from 0.08 to 0.72 mg l^{-1} and reached its highest value in spring 2014 and lowest value in summer 2013. In general, nutrient concentrations were lowest in autumn and highest in spring throughout the study period (Table 3).

Seasonal pattern of *Sargassum* canopy cover

The mean values of *Sargassum* CC in selected quadrats at the 4 sites were higher in warmer months (spring and summer) than in cooler months (autumn and winter). The mean value of *Sargassum*

Table 2. Seasonality of physicochemical parameters observed at Point Peron, Western Australia. Means (±SE) in the same column with different superscripted letters are significantly different at the 0.05 level. Cond.: conductivity; SSTs: sea-surface temperatures; DO: dissolved oxygen; Spr: spring; Sum: summer; Aut: autumn; Win: winter

Month	Season	Salinity	pH	Cond. (mV)	SSTs (°C)	DO (mg l^{-1})
2012						
Sep	Spr	36.5 ± 0.29	8.1 ± 0.08^{ab}	−65.9 ± 2.89^{a}	17.6 ± 0.2^{d}	7.53 ± 0.28^{c}
Dec	Sum	35.8 ± 0.31	8.1 ± 0.05^{ab}	−98.8 ± 0.28^{d}	22.1 ± 0.1^{f}	6.07 ± 0.08^{b}
2013						
Apr	Aut	35.5 ± 0.20	8.1 ± 0.06^{ab}	−92.5 ± 6.13^{c}	22.8 ± 0.3^{h}	6.08 ± 0.02^{b}
Jun	Win	35.5 ± 0.29	8.0 ± 0.06^{b}	−87.8 ± 0.25^{bc}	16.3 ± 0.3^{b}	8.27 ± 0.13^{d}
Sep	Spr	35.8 ± 0.25	8.1 ± 0.11^{ab}	−88.0 ± 0.00^{bc}	17.0 ± 0.0^{c}	7.75 ± 0.25^{c}
Dec	Sum	35.7 ± 0.14	8.0 ± 0.02^{b}	−82.1 ± 2.79^{b}	24.1 ± 0.0^{z}	5.92 ± 0.40^{b}
2014						
Mar	Aut	35.8 ± 0.18	7.8 ± 0.14^{c}	−83.8 ± 2.95^{b}	22.6 ± 0.1^{gh}	5.99 ± 0.05^{b}
Jul	Win	35.5 ± 0.29	8.2 ± 0.01^{ab}	−87.0 ± 0.58^{bc}	12.9 ± 0.2^{a}	5.39 ± 0.01^{a}
Sep	Spr	35.4 ± 0.24	8.2 ± 0.01^{ab}	−69.7 ± 0.28^{a}	19.7 ± 0.1^{e}	5.84 ± 0.03^{ab}
Dec	Sum	35.8 ± 0.17	8.2 ± 0.02^{a}	−68.3 ± 0.50^{a}	22.2 ± 0.1^{fg}	7.33 ± 0.11^{cd}
	F	1.43	3.32	17.01	551.23	30.05
	p	0.224	0.007	<0.05	<0.05	<0.05

Table 3. Seasonality of the mean nutrient concentrations in collected seawater during the study period at Point Peron, south-western Australia. Data are presented as the means (±SE) of 4 replicates per sampling period. Different superscripted letters indicate significantly different means of physicochemical parameters at the 0.05 level within the same column. Spr: spring; Sum: summer; Aut: autumn; Win: winter; –: not available

Month	Season	NO_2^- (µg l^{-1})	NO_3^-(mg l^{-1})	PO_4^{3-}(mg l^{-1})	NH_4^+(mg l^{-1})
2012					
Sep	Spr	6.33 ± 1.86^{b}	0.33 ± 0.08^{cd}	0.45 ± 0.08^{c}	1.97 ± 0.12^{de}
Dec	Sum	13.25 ± 2.07^{c}	0.05 ± 0.02^{a}	0.14 ± 0.02^{a}	1.70 ± 0.13^{cd}
2013					
Apr	Aut	2.00 ± 0.41^{a}	0.02 ± 0.00^{a}	0.24 ± 0.03^{b}	0.73 ± 0.09^{a}
Jun	Win	4.50 ± 0.65^{ab}	0.02 ± 0.00^{a}	0.14 ± 0.02^{a}	1.55 ± 0.06^{c}
Sep	Spr	3.50 ± 0.65^{ab}	0.17 ± 0.00^{bc}	0.20 ± 0.01^{ab}	2.00 ± 0.06^{e}
Dec	Sum	10.50 ± 1.56^{c}	0.09 ± 0.01^{ab}	0.26 ± 0.03^{b}	1.11 ± 0.04^{b}
2014					
Mar	Aut	2.75 ± 0.48^{a}	0.02 ± 0.01^{a}	0.19 ± 0.02^{ab}	0.55 ± 0.10^{a}
Jul	Win	3.00 ± 0.58^{ab}	0.02 ± 0.00^{a}	0.22 ± 0.06^{ab}	1.53 ± 0.09^{c}
Sep	Spr	3.33 ± 0.33^{ab}	0.42 ± 0.04^{d}	0.72 ± 0.05^{d}	2.03 ± 0.09^{e}
Dec	Sum	5.00 ± 0.67^{ab}	0.28 ± 0.09^{c}	0.17 ± 0.03^{ab}	–
	F	12.05	13.38	7.38	54.54
	p	<0.05	<0.05	0.001	<0.05

CC for the whole area was highest (91.7 ± 2.6%) in spring 2014 and was lowest (29.7 ± 10.1%) in autumn 2013 at all sites. Thus, a 2-way ANOVA revealed that both seasons and reef sites affected *Sargassum* CC; this differed significantly between sampling seasons (ANOVA, $F_{(9,26)}$ = 9.88, p < 0.001) and reef sites (ANOVA, $F_{(3,26)}$ = 5.86, p = 0.03) from spring 2012 to summer 2014 (Fig. 4a).

Mean length of *Sargassum* thalli

The mean length of the seasonally harvested *Sargassum* thalli from randomized quadrats at each site is shown in Fig. 5. The longest thalli were found in months with higher temperatures (summer 2013 and spring–summer 2014). The MTL for all sampling sites was highest in spring 2014 (53.5 ± 9.6 cm). In a similar pattern of coverage, the MTL was also lowest in the cold months, when the mean length was 11.5 ± 1.5 and 13.6 ± 0.7 cm for autumn 2013 and 2014 winter, respectively (Fig. 4b).

In terms of spatial distribution, the BR sites had the longest *Sargassum* thalli during all seasons (31.3 ± 4.7 cm). The height of *Sargassum* thalli in the FR averaged 28.4 ± 6.9 cm in all seasons. The shortest thalli were present in the LZ (25.9 ± 4.3 cm). The 2-way ANOVA revealed that reef sites did not affect the *Sargassum* MTL (ANOVA, $F_{(3,26)}$ = 0.59, p = 0.628), but seasonal changes did have an effect (ANOVA, $F_{(9,26)}$ = 10.868, p < 0.001) from spring 2012 to summer 2014.

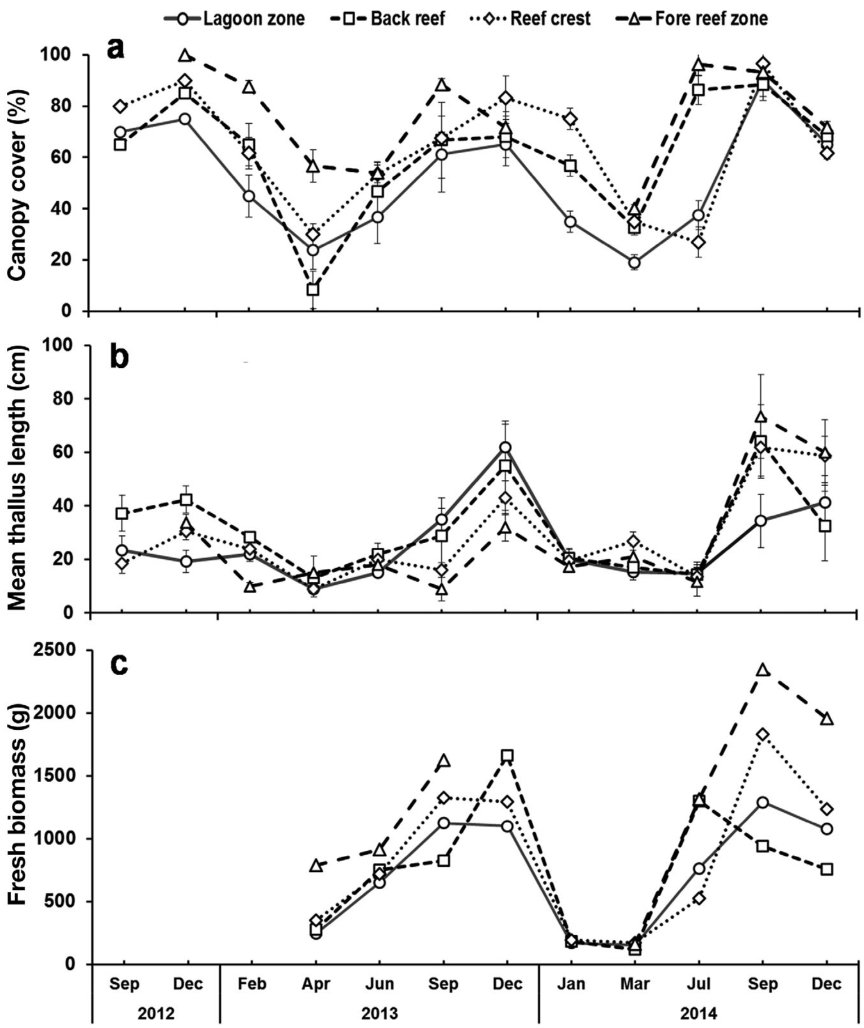

Fig. 4. Seasonality of (a) canopy cover, (b) mean thallus length and (c) fresh biomass of *Sargassum* observed in 4 different areas during spring 2012–2014. Data are means; error bars are standard errors. For canopy cover and mean thallus length of *Sargassum* spp., every transect was monitored from 4 reef zones by deploying random quadrats (0.5 × 0.5 m), 1 for each reef zone. Fresh biomass samples were measured at different reef zones of transect 4

Distribution of *Sargassum* beds and associated marine habitats

Sargassum CC was widely distributed around Point Peron. The highest coverage of *Sargassum* was recorded at the FR, followed by the RC, BR and LZ sites, with values of 75.9 ± 6.5, 63 ± 6.7, 61.4 ± 6.7 and 51.9 ± 6.4%, respectively (Table 4). However, no differences ($p > 0.05$) were found between reef sites. The surveyed data showed that 3 dominant *Sargassum* species were present in the study area: *S. spinuligerum, S. swartzii* and *S. confusum*. In addition, *S. longifolium* was less abundant in the FR zone than the other species.

The classification of benthic habitat was confirmed using WV-2 satellite images. *Sargassum* was mainly distributed on coral reefs and submerged limestone substrates from Gull Rock to Bird Island, White Rock and further west of Point Peron, extending to the area further south of Shoalwater Islands Marine Park. Field studies showed that the bottom depth of the *Sargassum* distribution area was relatively shallow (between 1.5 and 10 m). A sandy bottom and hard coral substrates were frequently found around *Sargassum* beds, and the boundaries between *Sargassum* and seagrass beds were detected with a high spatial resolution (2 m). Five bottom types were identified, including seaweed (*Sargassum* sp. and *Ecklonia* sp.) canopy, seagrass, sand, muddy sand and bare substrate, which were classified by the K-means unsupervised classification method (Fig. 5).

Multivariate analysis

PCA to establish multi-dimensional relationships among the studied parameters showed that the first 4 first principal components accounted for 88.6% of the total variation. The first principal component accounted for >43.3% of the total variation between sampling seasons, and consisted of the physicochemical parameters PAR, SSTs, SE, ED, MinAT, MaxAT, CDOM, salinity and NW. The second principal component accounted for 28.3% of the variation, and included nutrient parameters such as MLT, CC, NO_3^-, PO_4^{3-}, FB, conductivity, NH_4^+ and chl *a*. The third principal component explained 9.7% of the total variation, and included DO, NH_4^+, rainfall, NO_2^-, PAR and CC. The fourth principal component explained 7.4% of the total variation, and consisted of salinity, rainfall and conductivity parameters; 6.6% of the total variation was explained by the fifth principal component and 4.8% of the variation of sampling seasons by the sixth component.

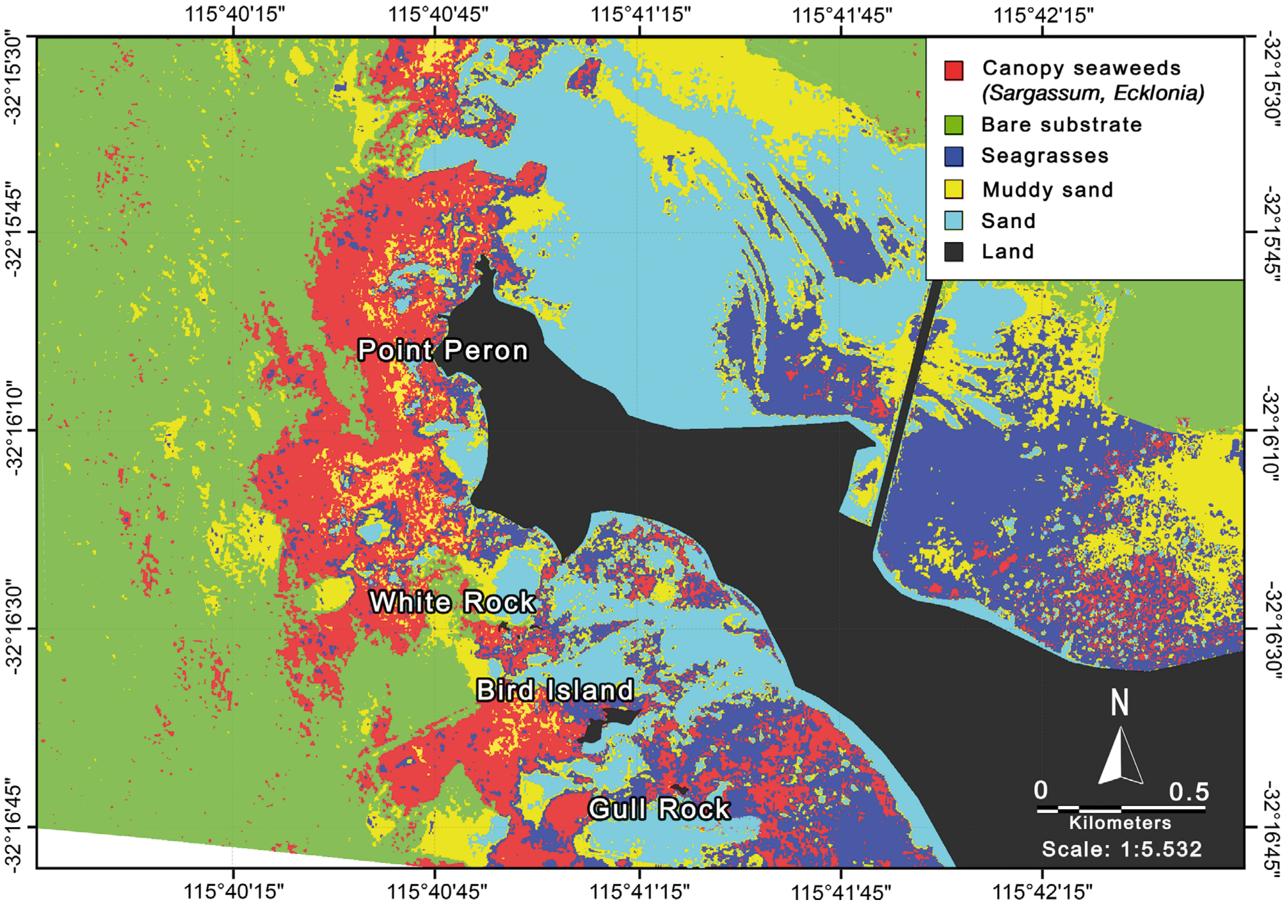

Fig. 5. Benthic habitat from satellite image classifications showing canopy seaweed beds (*Sargassum* spp.), their distribution and associated sub-littoral habitats (seagrass, sand and muddy sand) around Point Peron in summer (7 February 2013)

Table 4. Comparisons of canopy coverage (%) and thallus length (cm) between the sites

Sites	Canopy coverage (%) Mean	±SE	Thallus length (cm) Mean	±SE
Lagoon zone	51.9	6.4	25.9	4.3
Back reef	61.4	6.7	31.3	4.7
Reef crest	63.5	6.7	28.5	4.9
Fore reef zone	75.9	6.5	28.4	6.9

The bi-plot chart of the first and second components explained 71.6% of the total variation in physicochemical parameters during the sampling time. The results showed that nutrient composition (NO_3^-, PO_4^{3-} and NH_4^+) and *Sargassum* community structure (CC, FB and MTL) were encountered during spring sampling times. PAR, salinity and SSTs were key parameters during summer. The *Sargassum* population structure was typically explained by rainfall, SLP and pH parameters during winter months (Fig. 6).

DISCUSSION

Seasonal growth trends in *Sargassum* beds

This study investigated for the first time the ecology and seasonal growth trends in the brown algae *Sargassum* spp. at Point Peron in SWA. It was found that *Sargassum* biomass increased during winter and early spring, and stabilized during late spring and early summer, before decreasing during late summer and early autumn. This pattern of (1) increase, (2) stabilization and (3) reduction in biomass is linked to the 5 main stages of the *Sargassum* lifecycle, including recruitment and growth (increase in biomass), senescence and reproduction (stabilization of the biomass) and regeneration (reduction in biomass) (Gillespie & Critchley 1999). Here, we investigated which of the key physicochemical parameters, including SSTs, nutrient availability and irradiance, are responsible for regulating the timing of *Sargassum* lifecycle events (Fig. 7a).

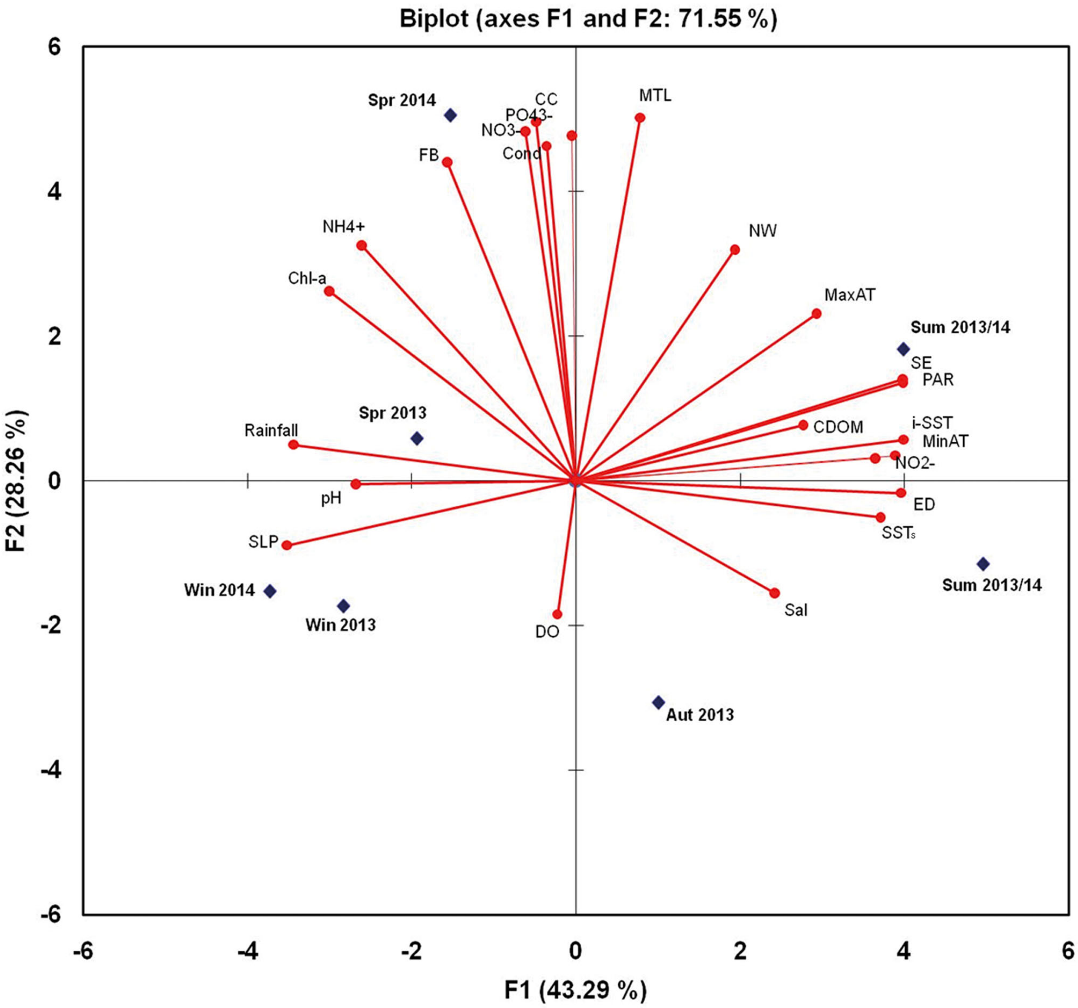

Fig. 6. Principal component analysis biplot showing the relationship between *Sargassum* sampling time (spr: spring; sum: summer; aut: autumn; win: winter), CC, MTL, fresh biomass and physicochemical parameters. Chl *a*: chlorophyll *a*; FB: fresh biomass (g 0.25 m^{-2}); Cond.: conductivity (mS m^{-1}); CC: canopy coverage (%); MTL: mean thallus length (cm); NW: northward wind (m s^{-1}); MaxAT: maximum air temperature (°C); SE: solar exposure (MJ m^{-2}); PAR: photosynthetically active radiation; CDOM: colored dissolved organic matter; i-SST: *in situ* sea-surface temperatures; MinAT: minimum air temperature (°C); ED: euphotic depth (m); SSTs: satellite-derived sea-surface temperatures (°C); Sal: salinity; DO: dissolved oxygen (mg l^{-1}); SLP: sea-level pressure (hPa)

1. Increase in biomass. This study showed that *Sargassum* biomass began to increase in early winter, from new recruits and remaining holdfasts, increased throughout winter and accelerated during spring. The highest nutrient concentrations, including NO_3^-, PO_4^{3-} and NH_4^+were measured during winter and early spring, which coincided with the increase in biomass and the highest growth rates. Considering that these high nutrient values occurred in winter and spring, which is a high rainfall season for SWA, rainwater run-off from the land probably played a vital role in the accelerated growth phase of *Sargassum* spp. Notably, this phase of high growth was negatively correlated with SSTs, i.e. the fastest growth rates occurred during the period with the lowest SSTs and irradiance (r = −0.43; Table 5), and only a weak correlation was observed between PAR and *Sargassum* spp. biomass; this trend has also been observed in other studies (Fulton et al. 2014, Sangil et al. 2015).

2. Stabilization of biomass. Following the growth phase, *Sargassum* biomass stabilized, with little or no observed change in MTL or CC between early spring (September) and mid-summer (January). This period is characterized by higher SSTs, longer day lengths and relatively high nutrient concentrations and primary productivity. Higher concentrations of ammonium were found at Point Peron during late spring, and were strongly correlated with the increase in CC and fresh biomass (r = 0.74 and 0.65, respectively).

3. Reduction in biomass. Following the reproductive stage, there was a reduction in *Sargassum* biomass beginning in late summer (February) and last-

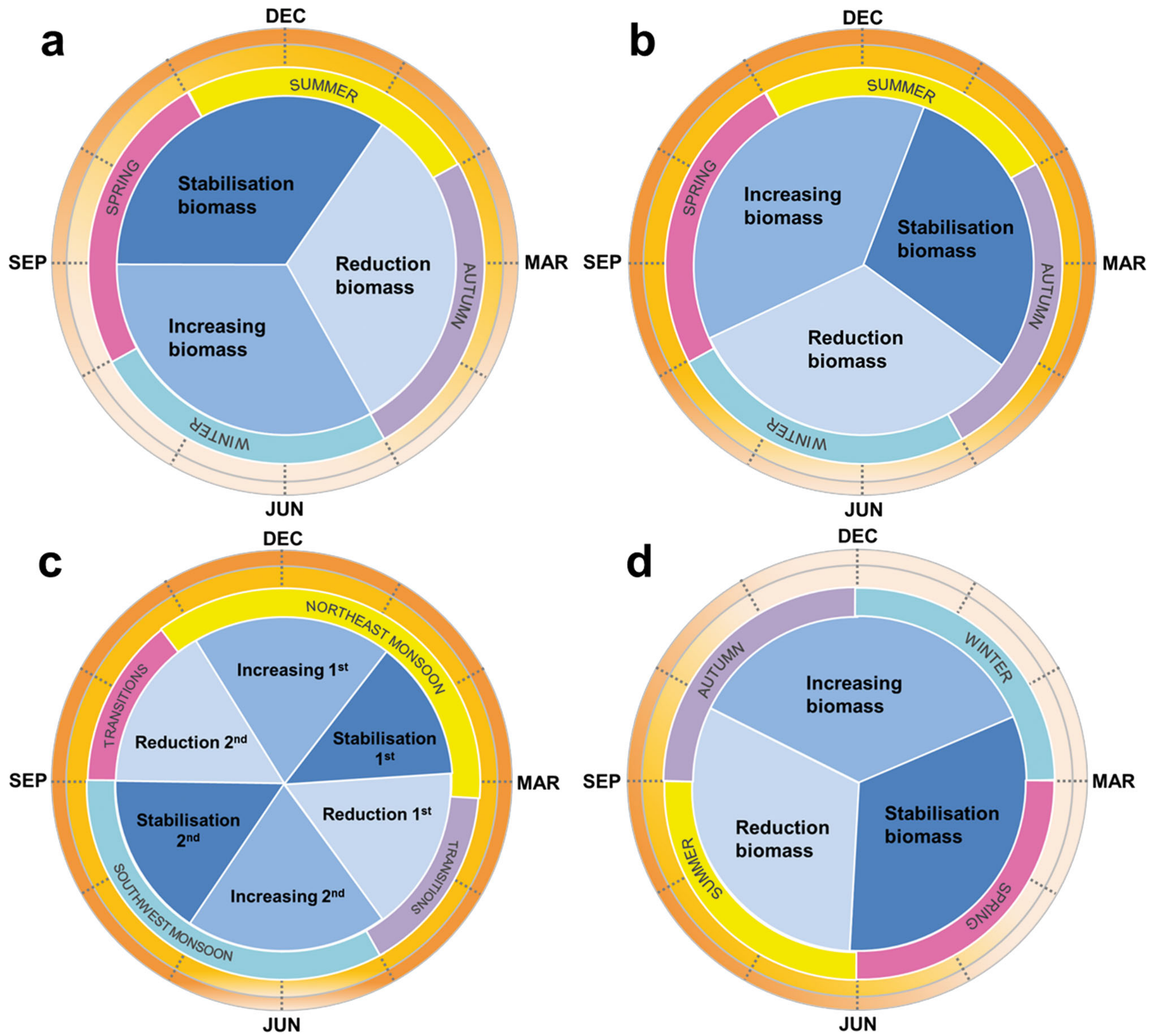

Fig. 7. Seasonal variation in *Sargassum* biomass in different climate zones across Australia and other geographical localities. (a) Point Peron, Western Australia, with a Mediterranean climate; (b) Magnetic Island, Australia, with a humid continental climate; (c) Pock Dickson, Malaysia, with a tropical rainforest climate; and (d) Cape Peñas, Spain, with an oceanic climate. The phase of increasing biomass includes recruitment and growth stages. The stabilization biomass phase includes the late-growth and reproduction stages. The reduction phase consists of senescence and regeneration periods. The outer ring and second ring represent sea-surface temperature and solar exposure, respectively. Light colors represent months with low temperatures; darker colors represent months with high temperatures. This figure was generated based on the present study in combination with published information from 3 other studies of different geographical regions. The previously published studies reported annual observatory data in their respective regions: Fig. 7b, Vuki & Price (1994); Fig. 7c, May-Lin & Ching-Lee (2013); Fig. 7d, Arenas & Fernández (2000)

ing through to the end of autumn (April–May). Die-off occurred towards the end of summer, which coincided with the highest water temperature, when some holdfasts remained and regenerated into new thalli in autumn and winter (Arenas et al. 1995). Decomposition of *Sargassum* thalli might lead to an increase in nitrite concentrations in summer and autumn months.

In general, the timing of the *Sargassum* lifecycle is synchronized so that full plant maturity is reached by late spring or early summer so the plant can take advantage of the highest levels of sunlight to redirect energy towards sexual reproduction. Towards the end of spring, the growth rates of *Sargassum* spp. begin to slow and cease as the algae enters its reproductive stage (Kendrick & Walker 1994). The repro-

Table 5. Correlation matrix between different physicochemical parameters and *Sargassum* at the study sites. See Table 1 for description of abbreviations

Variables	CC	MTL	FB	PAR	Rainfall	SST	Chl *a*	pH	DO	NO_2^-	NO_3^-	PO_4^{3-}	NH_4^+
CC	1												
MTL	0.82	1											
FB	0.83	0.76	1										
PAR	0.21	0.39	−0.10	1									
Rainfall	0.31	−0.18	0.42	−0.65	1								
SST	−0.23	0.08	−0.43	0.70	−0.72	1							
Chl *a*	0.55	0.34	0.53	−0.57	0.53	−0.49	1						
Sal	−0.18	−0.16	−0.35	0.54	−0.38	0.65	−0.38						
pH	−0.11	−0.02	0.40	−0.72	0.41	−0.37	0.33	1					
DO	−0.33	−0.43	−0.55	−0.11	−0.04	−0.27	−0.16	−0.43	1				
NO_2^-	0.05	0.21	−0.31	0.90	−0.73	0.58	−0.53	−0.87	0.15	1			
NO_3^-	0.80	0.82	0.70	0.02	0.16	−0.10	0.66	0.13	−0.21	−0.17	1		
PO_4^{3-}	0.73	0.90	0.69	0.11	−0.07	0.05	0.57	0.18	−0.37	−0.07	0.95	1	
NH_4^+	0.74	0.35	0.65	−0.34	0.75	−0.69	0.70	0.10	0.12	−0.42	0.66	0.43	1

ductive activity of *Sargassum* spp. occurs mainly in mid-summer via the release of ova and sperm into the water column (Gillespie & Critchley 1999).

Comparison in the seasonality of *Sargassum* biomass between Point Peron and other localities

To further understand how physicochemical parameters such as nutrients, SSTs and irradiance drive the *Sargassum* spp. growth cycle, we compared the seasonal results from Point Peron to other geographic regional studies in Australia and overseas (Table 6).

Point Peron and Magnetic Island in Australia's Great Barrier Reef region (Fig. 7b)

Magnetic Island is located 8 km off the North Queensland coast at about 22° S and experiences a tropical savanna-type climate, with a distinct wet summer and dry winter (opposite of the conditions in SWA). An increase in *Sargassum* biomass on Magnetic Island occurs at the beginning of spring to mid-summer, stabilization occurs between mid-summer and mid-autumn, and reduction occurs between mid-autumn and the start of spring (Vuki & Price 1994). The increasing biomass on Magnetic Island occurs during cooler SSTs towards the end of the dry season, and increasing irradiance, stabilization and growth of reproductive organs occur during the period of highest irradiance and SSTs. In contrast to Point Peron, reproduction on Magnetic Island occurs several months later, with the reduction in biomass occurring during high SSTs, whereas on Point Peron it occurs during the lowest SSTs and irradiance levels. *Sargassum* beds on Magnetic Island do not reach their highest MTL until autumn (Vuki & Price 1994). However, a similar relationship between CC and MTL was observed at both study sites. A positive correlation was found between CC and MTL for Magnetic Island (r = 0.73), and a strong correlation was also present in the Point Peron study (r = 0.82). When MTL was high, the *Sargassum* spp. in the selected quadrats also had a greater density, in turn, resulting in a high biomass.

The difference in the *Sargassum* growth cycle can be explained by high rainfall during the summer (December–February, 624.9 ± 275.3 mm), which coincides with high nutrient concentrations from runoff, providing optimum conditions for *Sargassum* growth (Vuki & Price 1994). The later growing stage of *Sargassum* beds on Magnetic Island might be caused by the irregular, high rainfall and the lower radiation in summer than in spring and winter, due to the higher cloud cover at this time, or a difference in *Sargassum* species composition.

Point Peron and Pock Dickson, Malaysia, with a tropical forest climate (Fig. 7c)

Tropical regions near the equator experience high SSTs and high rainfall throughout the whole year, with little difference between the wet and dry seasons. Several seasonality studies have been performed on *Sargassum* in tropical regions, such as Pock Dickson in Malaysia, the northern part of the Philippines and New Caledonia. Due to the effect of 2 strong monsoons, the *Sargassum* beds reveal 2

Table 6. Seasonal variation in *Sargassum* species and their correlation with physicochemical parameters reported in tropical and subtropical waters. Climate zones (according to Köppen-Geiger climate classification)—Af: tropical rainforest climate; Bwh: hot desert climate; Cfb: oceanic climate; Csa: Mediterranean climate; Cwa: humid subtropical climate; Dfb: humid continental climate; Spr: spring; Sum: summer; Aut: autumn and Win: winter (numbers within parentheses for all seasons are month) for oceanic climate and Mediterranean; Wet: wet months and Dry: dry months for the tropical climate zones; –: data not available; ? affected/correlated factors ($p < 0.05$); x: not correlated factors. Substrate types. S: sand-covered; Rb: rubble; CR: coral reef. Sources—(1): present study; (2): Kendrick & Walker (1994); (3): Fulton et al. (2014); (4): Vuki & Price (1994); (5): May-Lin & Ching-Lee (2013); (6): Ang (1986); (7): Ang (2007); (8): Mattio et al. (2008); (9): Arenas & Fernández (2000); (10): Sangil et al. (2015); (11): Ateweberhan et al. (2009); (12): McCourt (1984). Other abbreviations see Table 1

Study site	Country	Climate	Species	Max MTL	Peak FB	Max. CC	Nutrient	SST	PAR	Rainfall	Substrate	Depth (m)	Source
Point Peron	Australia	Csa	*Sargassum* spp.	Spr–Sum (9–12)	Spr–Sum (10–12)	Spr–Sum (10–1)	?	x	?	?	Rb, CR	1.5–10	(1)
Rottnest Island	Australia	Csa	*Sargassum* spp.	Spr (8–9)	Sum (1–2)	Sum (1–2)	–	–	–	–	S, Rb, CR	–	(2)
Ningaloo reef	Australia	Bwh	*Sargassum* spp.	–	Sum (2)	–	–	?	?	?	CR	1–5	(3)
Magnetic Island	Australia	Dfb	*Sargassum* spp.	Aut (3–4)	Spr (1)	Spr (10)	–	–	–	–	CR.	–	(4)
Port Dickson	Malaysia	Af	*S. binderi*	Wet	–	–	?	x	x	x	CR	–	(5)
			S. siliquosum	Dry (1–2)	–	–	?	x	x	x	CR	–	
The northern region	Philippines	Af	*Sargassum* spp.	–	–	Dry (10)	–	?	–	–	–	–	(6)
Tung-Ping Chan Marine Park	Hong Kong	Cwa	*Sargassum* spp.	Aut (11–2)	–	–	–	–	–	–	–	10	(7)
New Caledonia	N. Caledonia	Af	*Sargassum* spp.	Wet (12–3)	–	–	–	–	–	–	CR, Rb, S	20	(8)
Cape Peñas	Spain	Cfb	*S. muticum*	Win (12–1)	Spr–Sum (4–6)	–	–	–	–	–	Rb	–	(9)
La Palma Island	Spain	Bwh	*S. flavifolium*	Spr–Sum (5–7)	–	–	–	?	?	–	Rb, S	6–18	(10)
Massawa	Eritrea	Bwh	*Sargassum* spp.	Sum (2–3)	–	–	–	–	–	–	CR	–	(11)
Gulf of California	Mexico	Bwh	*Sargassum* spp.	–	Spr (4–5)	–	–	–	–	–	CR	–	(12)

periods of increasing biomass rates (January–February and June–July) and decreasing biomass rates (April and September) (May-Lin & Ching-Lee 2013). Thus, the growth cycle depends on seasonal changes in the monsoon, the species of *Sargassum* and the existing nutrient availability (Schaffelke & Klumpp 1998). The highest biomass can occur in the wet season for some species (e.g. *S. binderior*) or the dry season for others (e.g. *S. siliquosum*). In these tropical areas, the seasonality of *Sargassum* beds may be more dependent on changes in SSTs and rainfall (i.e. tropical monsoons).

A study in New Caledonia in the Indo-Pacific region showed that *Sargassum* spp. have a high MTL in summer months due to higher rainfall during this period, which causes an increased nutrient concentration and growth (Mattio et al. 2008). However, in the Philippines, *Sargassum* biomass is highest in the dry season, which possibly coincides with high SSTs (Ang 1986). Thus, equatorial climates can also experience a range of seasonal effects on *Sargassum* spp., although this might be less pronounced than in more temperate climates such as that at Point Peron.

Point Peron and studies in the Northern Hemisphere (Fig. 7d)

Cape Peñas (Asturias, Spain) is located at 43.4°N latitude, has a similar Mediterranean climate to Point Peron and experiences warm-dry summers and cool-wet winters. The summer season occurs from June to September, with a mean daily high air temperature >20°C. The increase in *Sargassum* biomass on Cape Peñas occurs from mid-autumn to late-winter, stabilization with peak biomass occurs between the end of winter and the end of spring, and reduction occurs between early summer and mid-autumn. Growth increases during the winter until spring, when higher SSTs increase photosynthesis and productivity and provide optimal growth conditions, followed by senescence from early summer to mid-autumn (Arenas & Fernández 2000). Seasonal changes in temperature are also thought to drive the growth of *Sargassum* spp. at La Palma, as well as on the Canary Islands, Spain. The biomass of *S. flavifolium* reaches its maximum in spring to summer and is similar to that of *Sargassum* spp. in this study, coinciding with an increase in SST and day length (irradiance) (Sangil et al. 2015). The growth and development of *Sargassum* at the study sites in Spain and SWA share a similar seasonal pattern, which can be explained by similar climate zones. However, they occur at different times of the year due to the reverse timing of seasons in the northern and southern hemispheres.

Spatial distribution of *Sargassum* spp. from both *in situ* and satellite observations

The distribution of *Sargassum* beds was restricted mainly to shallow water habitats, similar to the results of others (Hanisak & Samuel 1987, Mattio et al. 2008, Mattio & Payri 2011). Because the holdfasts grow on limestone rock substrates, the beds were widely distributed throughout these habitats; this was not so on sandy substrates, where seagrass was dominant. A similar study in New Caledonia found that *Sargassum* was dominant on rubble substrate and rocky bottoms, ranging from 2.5 to 12 m deep (Mattio et al. 2008). In this study, biomass increased as depth increased along the transects, and showed some variation in reef zones from the LZ to the FR. This represents a trend, suggesting that the biomass of *Sargassum* beds increases at greater depths, until light becomes a limiting factor (Rützler & Macintyre 1982, Ang 1986, Vuki & Price 1994).

The highest MTL of *Sargassum* in all seasons is related to its distribution area and was found in the BR zone, which is protected by the RC zone further offshore, where waves and currents are broken down and their kinetic energy is reduced before they approach the shoreline. The lowest MTL value was found in the LZ. The length of thalli in the LZ reflects the shallow depth there, as well as the high heat absorption from the sun, which causes higher SSTs than at other study sites. At Point Peron, the mean MTL of *Sargassum* species is similar to that found for *S. ilicifolium* and *S. subrepandum* in the southern Red Sea, which was 38.71 and 32.65 cm, respectively (Ateweberhan et al. 2009). The MTL here is also similar to that of a phenology study of *Sargassum* species in Tung Ping Chau Marine Park, Hong Kong (48.2 ± 29.9 cm) (Ang 2007). However, the MTL of *Sargassum* at Point Peron is shorter than that found in previous studies on Rottnest Island, SWA (10–95 cm) (Kendrick 1993), on the middle reef flat of Magnetic Island, north-eastern Australia (Vuki & Price 1994), and in other studies in Malaysia (Wong & Phang 2004, May-Lin & Ching-Lee 2013).

The present study was initially conducted using WV-2 satellite remote-sensing data to determine the spatial distribution of *Sargassum* and the associated marine benthic habitats in the study area. This study can be considered an original approach for the region, using more advantageous satellite remote-sensing data, with higher spatial and spectral resolutions, than the previous studies carried out in Thailand with ALOS-AVNIR 2 images (10 m spatial resolution) (Noiraksar et al. 2014) and New Caledonia with Landsat (30 m) and Quickbird (2.4 m) images (Mattio et al. 2008).

Thus, further studies could apply the recently archived results for identifying and mapping *Sargassum* beds in the SWA region (Hoang et al. 2015, Garcia et al. 2015). Results on the spatial distribution characteristics of *Sargassum* beds play an important role in providing information for regional natural resource management and a better understanding of the distribution characteristics, areas and seasonality of *Sargassum*, in terms of the highest biomass. However, a limitation does exist in this study, due to the lack of temporal satellite remote-sensing data that can be used to evaluate the distribution of brown canopy seaweeds. The current satellite remote-sensing image only reflects the distribution of brown canopy seaweeds (*Sargassum* and *Ecklonia*) during the peak biomass season — spring. However, if multiple satellite remote-sensing images were available for other seasons at the study region the seasonal variation in the distribution area could be illustrated.

In summary, this study provides primary and novel information on *Sargassum* spp. at Point Peron, using a combination of *in situ* and satellite remote-sensing observations. The *Sargassum* beds demonstrated a seasonal pattern of variation in CC and MTL, which was significantly influenced by nutrient concentrations (NO_3^-, PO_4^{3-}, NH_4^+) and rainfall ($p < 0.05$). This seasonal variation pattern is similar to that found in areas with temperate or Mediterranean climates, such as Rottnest Island, Australia, and Cape Peñas, Spain (Kendrick & Walker 1994, Arenas & Fernández 2000). The highest peaks in *Sargassum* biomass generally occurred between late spring and early summer. This seasonal pattern was also found in *Sargassum* CC and MTL. The seasonal variation in *Sargassum* biomass, CC and MTL at Point Peron was closely associated with seasonal changes in nutrient concentration and rainfall. These results provide essential information for coastal marine management and conservation, as well as for the sustainable utilisation of this renewable marine resource.

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