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Season 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 to investigate the effect of seasonality and the associated water quality changes on the distribution, canopy cover, mean thallus length and the biomass of *Sargassum* beds around Point Peron, Shoalwater Islands Marine Park, Southwest Australia. Samples of *Sargassum* and seawater were collected every three months from summer 2012 to summer 2014 from four 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 a strong seasonal variation in the environmental parameters, canopy cover, mean thallus length, and biomass of *Sargassum*, which were significantly ($P < 0.05$) influenced by the nutrient concentration (PO_4^{3-}, NO_3^-, NH_4^+) and rainfall. However, no variation in any studied parameter was observed among the four 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 coastal marine renewable resource.

KEY WORDS: Environmental 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* are commonly attached to rocks, but can also have floating life forms. In coastal areas and surrounding offshore islands, they form dominant communities playing vital ecological roles for marine ecosystems by providing feeding grounds for sea birds and sea lions and providing essential nursery habitats for invertebrates, larval and juvenile fish surrounding these islands (Wells & Rooker 2004, Tyler 2010). *Sargassum* also represents a living renewable resource that is used in medicines, and for the production of fertilisers, alginate, and bio-fuels (Chengkui et al. 1984, Arenas & Fernández 2000, Rivera & Scrosati 2006, Hong et al. 2007).

Approximately 46 *Sargassum* species are found along the Southwest Australian (SWA) coast (DPaW 2013) and the majority of these have been studied to determine their taxonomic affiliation, including the molecular basis of 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 on 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 influencing 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, affect the density of the 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, Tiit et al. 2006, Benfield et al. 2007, Vahtmäe & Kutser 2007, Casal et al. 2011a, Fearns et al. 2011, Maheswari 2013). However, the most clear and direct method for marine habitat mapping is visual observations, also termed ground-truthing, using either SCUBA or snorkel survey methods, which provides an essential input to remote-sensing observations (Komatsu et al. 2002). A methodology for mapping *Laminariales* (Kelp) in turbid waters of the Seno de Corcubión (Northwest Spain), using SPOT-4 satellite images was developed, 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 of the spatial distribution of *Sargassum* 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 (eight spectral sensors ranging from 400–1,040 nm) (Lee et al. 2011, DigitalGlobe 2013). However, a few detailed mapping studies of *Sargassum* have been performed using high-resolution satellite images, such as WV-2 (Hoang et al. 2015). In addition, a direct visual approach that is integrated into high spatial resolution remote-sensing observations could represent a robust approach to minimize costs and increase the accuracy of detection and distribution patterns of *Sargassum* shallow coastal waters. The aim of this study is to investigate the effects of seasonal changes in water quality on canopy cover, mean thallus length and the *Sargassum* biomass at a fringing limestone reef in Point Peron, SWA. We have 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 biomass of the *Sargassum* community and determined how these changes impacts the broader spatial distribution of *Sargassum*.

MATERIALS AND METHODS

Study sites

We selected our demonstration site 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 Rockingham city, 50 km south of Perth (Fig. 1). The point is approximately 930 m long and 1,450 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 study area includes a chain of limestone reefs approximately 450 m offshore (32°14'–32°17'S and 115°39'–115°42'E). The coastal area of Point Peron was divided into four zones: the Lagoon zone (LZ), Back reef (BR), Reef crest (RC) and Fore reef (FR) zone with the distance approximately 100 m between each zone (Rützler & Macintyre 1982) (Fig. 2). The field studies were carried out from September 2012 to December 2014 during four well-defined seasons; summer (December to February), autumn (March to May), winter (July to August), and spring (September to November) (BoM Australia 2013).

Field sampling methods

Sampling frequency

The total duration of the trial was two and half years wherein summer and spring were represented three times and winter and autumn were represented twice. At least one sampling trip was carried out per season, however, we could sample twice during summer and spring seasons which were then averaged out. During every trip, four 400 m long transects were sampled. The average depth along each transect ranged from 0.3 to 2.5 m. For water quality analysis, one 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 four reef zones by deploying random quadrats (0.5 × 0.5 m), one for each reef zone. The distance between the quadrats ranged from 20 to 80 m. The above protocol provided four 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 four 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 was 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 till further measurements. 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 2014). A morphological study of *Sargassum* samples was under taken on dried specimens. Herbarium specimens were stored at the CARL. Underwater video and photographs were captured along the monitored transects from five 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 environmental parameters

Meteorological data, including the maximum (MaxAT, ^{o}C), mean and minimum (MinAT, ^{o}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 Australia 2013). Euphotic depth (ED) (m), sea level pressure (SLP) (hPa), 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 the 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 ^{o}C/ mV/ pH meter (CyberScan pH 300, Eutech Instruments, Singapore). Salinity was measured using a hand-held refractometer (Atago® RHS-10ATC, Japan) in practical salinity units, and dissolved oxygen (DO) was determined with a digital DO meter (YSI®55, Perth Scientific, Australia). 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^{o}C) in the dark. Samples were transferred to the CARL for analysis within 48 h following collection and followed the methods described in 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 (Hach, Loveland, CO, USA) with the cadmium reduction method (Method 8171) and diazotization method (Method 8507), respectively (APHA 1998). Phosphate (PO_4^{3-}) concentration was analysed by Ascorbic acid method (Standard Method 4500-PE) and ammonium (NH_4^+) was determined by using Aquanal™ test kits (Sigma-Aldrich®, Germany) (see Table 1 for the 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 to detect the *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 five 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). 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 the classification and to count the number of pixels of 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 systems software packages. The complete diagrammatic processing imagery is presented in Figure 2.

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 two-way ANOVA was carried out to test the effects of seasons and distribution sites on the *Sargassum* CC and MTL. The multiple comparison, least significant difference (LSD's) post hoc test, was also implemented to test for the statistical significance among treatments. The statistical significance level was set at 0.05. Principle 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. Principle component analysis was prepared by using the latest XLSTAT 2015.1.01 (Addinsoft™, France) package for Microsoft® Excel. All the results were presented as means ± S.E. (standard error), unless otherwise stated.

RESULTS

Temporal variation in environmental conditions

The analysis of air temperature over the three study years (2012–2014) indicates that the monthly mean temperature was highest in the summer months (December to February). Temperatures then decreased in autumn (March to May) and were lowest in winter (June to August) and finally increased in spring (September to 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).

Sea surface temperatures 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 the seasons, except for between winter and spring (Fig. 3a). Rainfall and PAR usually showed an inverse pattern and both showed a strong seasonal variation. The PAR reached the highest value in the 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 rainfall was only 2.6 mm, mean summer rainfall was 11.9 ± 6.4 mm. In contrast, the PAR was the lowest in the 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 of 95.5 ± 11.9 mm was reached in winter (the maximum value of 151.6 mm was in September 2013 (Fig. 3b).

Seawater salinity in the study area ranged from 35.4 to 36.5 among the seasons, but the differences were not significant (ANOVA, $F(9, 37) = 1.43$, $P = 0.224$). The electrical conductivity of seawater in the study area also differed significantly between the 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 the 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 one-way ANOVA where 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, $F(3, 32) = 5454$, $P < 0.05$), 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 0.6–2.0 mg L^{-1} and that of phosphate (PO_4^{3-}) ranged from 0.08–0.72 mg L^{-1} and reached the highest value in spring 2014 and lowest value in summer 2013. In general, the 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 the selected quadrats at the four sites were higher during the warmer months (spring and summer) than in the cooler months (autumn and winter). The mean value of *Sargassum* 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 two-way ANOVA revealed that both seasons and reef sites did affect the *Sargassum* CC which 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).

The mean length of Sargassum *thalli*

The mean length of the seasonally harvested *Sargassum* thalli from randomized quadrats at each site is shown in Figure 5. The longest thalli were found in months with higher temperatures (summer 2013 and spring to 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 ranged from 11.5 ± 1.5 cm 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 two-way ANOVA revealed that reef sites did not affect the *Sargassum* MTL (ANOVA, $F(3, 26) = 0.59$, $P = 0.628$), but the seasonal changes did have an effect (ANOVA, $F(9, 26) = 10.868$, $P < 0.001$) from spring 2012 to summer 2014.

The distribution of Sargassum *beds and associated marine habitats*

The *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 three 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 the benthic habitat was confirmed using WV-2 satellite images. *Sargassum* was mainly distributed on the coral reefs and submerged limestone substrates from Gull Rock to Bird Island, White Rock and further west from Point Peron, extending to the area further south of the 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 seaweeds (*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

The principle component analysis (PCA) to establish multi-dimensional relationships among the studied parameters showed that there were four first principle components that accounted for 88.6 % of the total variation. The first principle component accounted for over 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 principle 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 principle component explained 9.7 % of the total variation, and included DO, NH_4^+, rainfall, NO_2^-, PAR, and CC. The fourth principle 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 principle component and 4.8% of the variation of the sampling seasons by the sixth component.

The bi-plot chart of the first and second components explained 71.6 % of the total variation in the environmental 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 at the spring sampling times. The PAR, salinity, and SSTs were key parameters during the summer. The *Sargassum* population structure was typically explained by rainfall, SLP, and pH parameters during the winter months (Fig. 6).

DISCUSSION

Seasonal growth trends in Sargassum beds

This study investigated the ecology and seasonal growth trends in the brown algae, *Sargassum* spp. at Point Peron, in the SWA for the first time. It was found that *Sargassum* biomass increased during the winter and early spring, and stabilized during late spring and early summer, before decreasing during the late summer and early autumn. This pattern of (*i*) increase, (*ii*) stabilization, and (*iii*) reduction in biomass is linked to the five 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 environmental parameters, including SSTs, nutrients availability, and irradiance are responsible for regulating the timing of the *Sargassum* lifecycle events (Fig. 7a).

i. 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 accelerates during spring. The highest nutrient concentrations, including NO_3^-, PO_4^{3-}, 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 the 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., and this trend has also observed in other studies (Fulton et al. 2014; Sangil et al. 2015).

ii. Stabilization of biomass: Following the growth phase, *Sargassum* biomass stabilized, with little or no observed change in MTL or CC between early spring (September) to 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 the late spring and were strongly correlated with the increase in CC and fresh biomass (r = 0.74 and 0.65, respectively).

iii. Reduction in biomass: Following the reproductive stage, there was a reduction in *Sargassum* biomass beginning in late summer (February) through the end of autumn (April to May). Die-off occurred towards the end of summer where coincide with the highest water temperature, when some holdfasts remained and regenerated into new thalli in autumn and winter (Arenas et al. 1995). The decomposition of *Sargassum* thalli might lead to an increase in nitrite concentrations in the summer and autumn months.

In general, the timing of the *Sargassum* lifecycle is geared so that full plant maturity is reached by late spring or early summer for the plant to 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 reproductive 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 environmental 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 experiences a tropical savanna-type climate, with a distinct wet summer and dry winter (opposite to the SWA). The 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 occurs 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 the high SSTs, whereas on Point Peron it occurs during the lowest SSTs and irradiance levels. *Sargassum* beds in Magnetic Island, Australia do not reach their highest MTL until autumn (Vuki & Price 1994). However, a similar relationship between CC and mean thallus length was observed at both study sites. A positive correlation was found between CC and MTL in Magnetic Island (r = 0.73), and a strong correlation was also present in the Point

Peron study (r = 0.82). When the 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 to February, 624.9 ± 275.3 mm), which coincides with high nutrient concentrations from run-off, which provide optimum conditions for *Sargassum* growth (Vuki & Price 1994). The later growing stage of *Sargassum* beds in Magnetic Island might be caused by the irregular, high rainfall and 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 season. 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 two strong monsoons, the *Sargassum* beds reveal two periods of increasing biomass rates (January to February and June to 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 can 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 the summer months due to higher rainfall at this time, 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 latitude 43.4ºN and 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 above 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 optimum 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, and in 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 the SST and day length (irradiance) (Sangil et al. 2015). The growth and development of *Sargassum* in 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, but not 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 (Ang 1986, Rützler & Macintyre 1982, 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 the waves and currents are broken down and their kinetic energy reduces 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 here, 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 cm and 32.65 cm, respectively (Ateweberhan et al. 2009). The MTL here is also similar to that from 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* in Point Peron is shorter than that found in previous studies in Rottnest Island, SWA (10–95cm) (Kendrick 1993), in 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 applied using WV-2 satellite remote sensing data to determine the spatial distribution of *Sargassum* and associated marine benthic habitats in the study area. This study can be considered as an original approach for the region when using more advantageous satellite remote sensing data, with higher spatial and spectral resolution, than the previous studies in Thailand with ALOS–AVNIR 2 images (10 m spatial resolution) (Noiraksar et al. 2014), New Caledonia with Landsat (30 m) and Quickbird (2.4 m) images (Mattio et al. 2008).

Thus, further studies could apply the recent archived results for identifying and mapping *Sargassum* beds for the SWA region (Hoang et al. 2015, Garcia et al. 2015). The results of spatial distribution characteristics of *Sargassum* beds play an important role in providing information on 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 sources in evaluating the brown canopy seaweeds distribution. The current satellite remote sensing image only reflects the distribution of brown canopy seaweeds (*Sargassum* and *Ecklonia*) in the peak biomass season, spring. However, if there were more than one satellite remote sensing images during another season available at the study region that would markedly illustrate the seasonal variation in the distribution area.

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 results show that the *Sargassum* beds demonstrated a seasonal variation pattern in CC and MTL, which was significantly influenced by the nutrient concentration (NO_3^-, PO_4^{3-}, NH_4^+), and rainfall ($P < 0.05$). This seasonal variation pattern is similar to that found in areas with a temperate or Mediterranean climate, such as Rottnest Island, Australia and Cape Peñas, Spain (Arenas & Fernández 2000, Kendrick & Walker 1994). 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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Table and Figure legends

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

Table 2. Seasonality of physicochemical parameters (mean ± S.E) observed at Point Peron, Western Australia. SSTs = Sea surface temperatures, DO = Dissolved oxygen.

Table 3. Seasonality of the mean nutrient concentrations in collected seawater during the study period at Point Peron, SWA.

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

Table 5. Correlation matrix between different physicochemical parameters and *Sargassum* at the study sites.

Table 6. The seasonal variation in *Sargassum* species and their correlation with the environmental parameters reported in tropical and subtropical waters.

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

Figure 2. Diagram presenting the methodology used to map seaweed distribution and the associated benthic habitats at Point Peron using high-spatial resolution satellite imagery and field survey data. Sites: LZ = Lagoon zone, BR = Back reef, RC = Reef crest, and FR = Fore reef zone.

Figure 3. Seasonal changes in (a) air temperature (maximum and minimum value) and sea surface temperature, (b) PAR and rainfall, (c) Chl-a and CDOM index, (d) Sea level pressure and Euphotic depth, (e) *Sargassum* canopy cover and fresh biomass at the study sites. *Sargassum* fresh biomass was not available for the sampling trips in September, December 2012 and February 2013. The air temperature and rainfall data were obtained from the Garden Island weather station, Bureau of

Meteorology, Australian Government. The 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.

Figure 4. Seasonality of percentage canopy cover (a), mean thallus length (b), and fresh biomass of *Sargassum* (c) observed in four different areas during spring 2012 to 2014. Each column for (a) and (b) present the mean and standard error. Four replicated quadrats (0.5 × 0.5 m) and four reef zones were measured for CC and MTL, respectively. The fresh biomass samples (c) were measured at difference reef zone.

Figure 5. Map of the benthic habitat from satellite image classifications showing the 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).

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

Figure 7. Diagram showing the 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 up 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 SST and solar exposure, respectively. The light color represents months with a low temperature and the darker color represents those with a high temperature. This figure was generated based on the present study and in combination with the published information from other three studies from different geographic regions. These previously published studies have reported the annual observatory data in their respective regions.

Table 1.

Acronym	Description and typical units
WA	Western Australia
SWA	Southwest Australia
DPaW	Department of Parks and Wildlife formerly named as 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 $0.25m^{-2}$)
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 (^{o}C)
SE	Solar exposure ($MJ\ m^{-2}$)
MinAT	Minimum air temperature (^{o}C)
SLP	Sea level pressure (hPa)
CDOM	Colored dissolved organic matter
PAR	Photosynthetically active radiation (Einstein $m^{-2}\ d^{-1}$)
SSTs	Sea surface temperatures (^{o}C)
DO	Dissolved oxygen ($mg\ L^{-1}$)
ENVI	Environment for visualizing image
ANOVA	Analysis of variance
PCA	Principle component analysis
MODIS	Moderate Resolution Imaging Spectroradiometer
NASA	The National Aeronautics and Space Administration

Table 2.

Year	Month	Season	Salinity	pH	Cond. (mV)	SSTs (ºC)	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

The mean in the same column with different superscript letter are significantly different at the 0.05 level.

Table 3.

Year	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

The data is presented as the mean ± S.E of four replicates per sampling period. The different superscript letters are significantly different means of environment parameters in the same column. The mean difference is significant at the 0.05 level.

Table 4.

Sites	Canopy coverage (%)		Thalli length (cm)	
	Mean	**± S.E**	**Mean**	**± S.E**
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

Table 5.

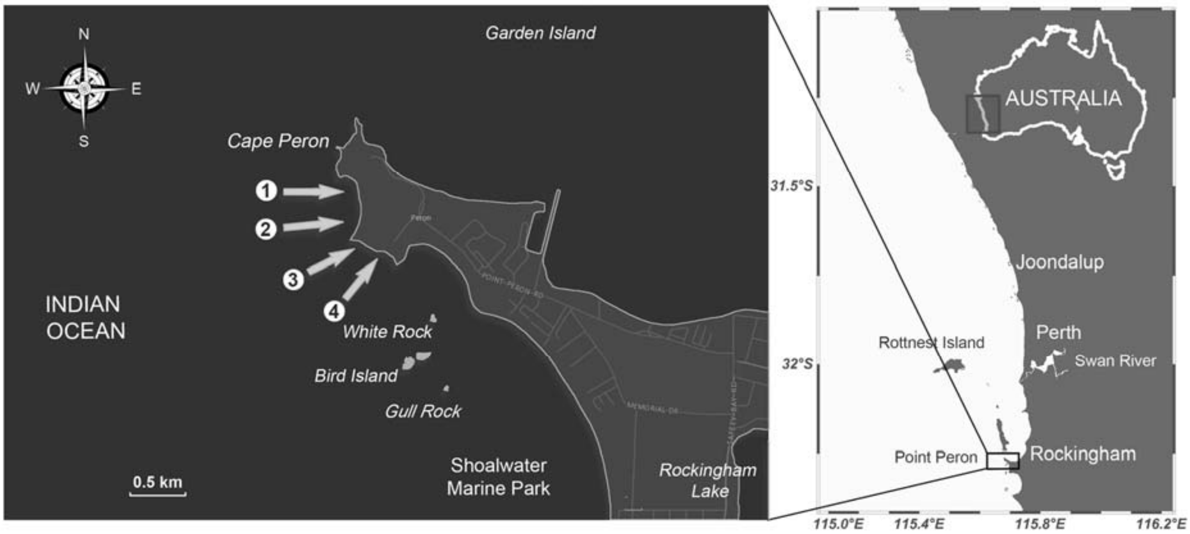
Variables	**CC**	**MTL**	**FB**	**PAR**	**Rain**	**SST**	**Chl**	**pH**	**DO**	**NO_2^-**	**NO_3^-**	**PO_4^{3-}**	**NH_4^+**
CC	**1**												
MTL	**0.82**	**1**											
FB	**0.83**	0.76	**1**										
PAR	0.21	0.39	-0.10	**1**									
Rain	0.31	-0.18	0.42	-0.65	**1**								
SST	-0.23	0.08	-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**

Table 6.

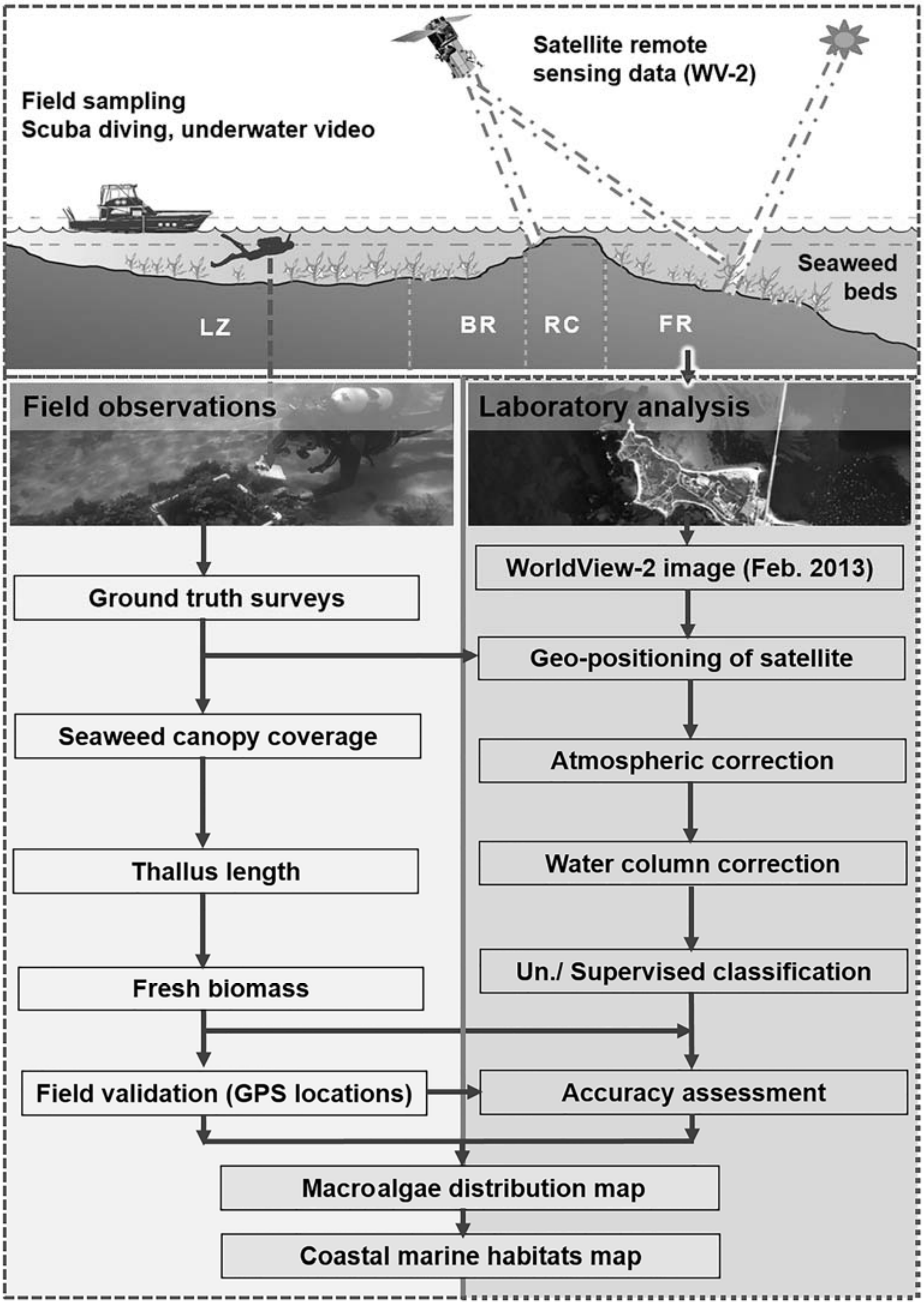
Study site	Country	Climate	Species	Max MTL	Peak FB	Max CC	Nutrient	SST	PAR	Rainfall	Substrate	Depth (m)	Ref.
Point Peron	Australia	Csa	*Sargassum spp.*	Sp.-Su. (9–12)	Sp.-Su. (10–12)	Sp.-Su. (10–1)	✓	x	✓	✓	Rb, CR	1.5-10	(1)
Rottnest Isl.	Australia	Csa	*S.* spp.	Sp. (8–9)	Su. (1–2)	Su. (1–2)	-	-	-	-	S, Rb, CR	-	(2)
Ningaloo reef	Australia	Bwh	*S.* spp.	-	Su. (2)	-	-	✓	✓	✓	CR	1-5	(3)
Magnetic Isl.	Australia	Dfb	*S.* spp.	Au. (3–4)	Sp. (01)	Sp. (10)	-	-	-	-	CR.	-	(4)
Port Dickson	Malaysia	Af	*S. binderi*	Wet (1–2)	-	-	✓	x	x	x	CR	-	(5)
			S. siliquosum	Dry (6–7)	-	-	✓	x	x	x	CR	-	
The Northern	Philippines	Af	*S.* spp.	-	-	Dry (10)	-	✓	-	-	-	-	(6)
Tung-Ping C.	Hong Kong	Cwa	*S.* spp.	Au. (11–2)	-	-	-	-	-	-	-	10	(7)
New Caledonia	N. Caledonia	Af	*S.* spp.	Wet (12–3)	-	-	-	-	-	-	CR, Rb, S	20	(8)
Cape Peñas	Spain	Cfb	*S. muticum*	Wi. (12–1)	Sp.-Su. (4–6)	-	-	-	-	-	Rb	-	(9)
La Palma Isl.	Spain	Bwh	*S. flavifolium*	Sp.-Su. (5–7)	-	-	-	✓	✓	-	P, Rb, S	6-18	(10)
Massawa	Eritrea	Bwh	*S.* spp.	Su. (2–3)	-	-	-	-	-	-	CR	-	(11)
Gulf of Cali.	Mexico	Bwh	*S.* spp.	-	Sp. (4–5)	-	-	-	-	-	CR	-	(12)

Note: 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. Sp. = spring (specific months), Su.= summer, Au.= autumn, Wi.= winter for oceanic climate and Mediterranean and Wet= wet months, Dry = dry months for the tropical climate zones. (-) = data not available, (✓) = affected/ correlated factors ($P < 0.05$), (x) = no correlated factors. Substrate types: C = cobbles, S = sand-covered, R = rock, Rb = rubble, CR = coral reef.
Ref.= References; (1) This 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 and Fernández 2000, (10) Sangil et al. 2015, (11) Ateweberhan et al. 2009, (12) McCourt 1984.

Figure 1


N
W
E
S
Garden Island
Cape Peron
1
2
3
4
INDIAN OCEAN
White Rock
Bird Island
Gull Rock
Shoalwater Marine Park
Rockingham Lake
0.5 km
AUSTRALIA
31.5°S
Joondalup
Perth
Swan River
Rottnest Island
32°S
Point Peron
Rockingham
115.0°E
115.4°E
115.8°E
116.2°E

5 **Figure 2**


Satellite remote sensing data (WV-2)
Field sampling
Scuba diving, underwater video
Seaweed beds
LZ
BR
RC
FR
Field observations
Laboratory analysis
Ground truth surveys
WorldView-2 image (Feb. 2013)
Geo-positioning of satellite
Seaweed canopy coverage
Atmospheric correction
Thallus length
Water column correction
Fresh biomass
Un./ Supervised classification
Field validation (GPS locations)
Accuracy assessment
Macroalgae distribution map
Coastal marine habitats map

6

7

Figure 3

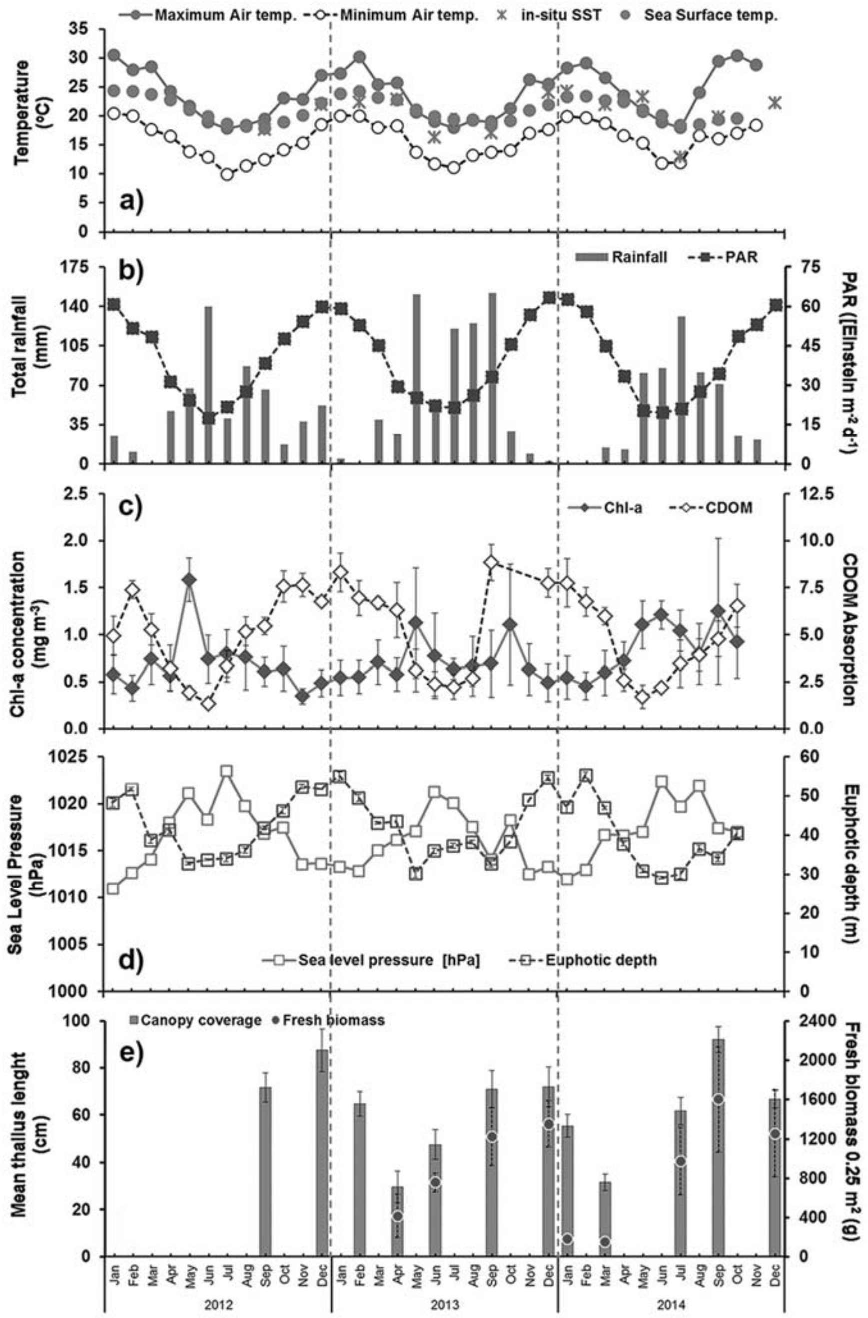

Maximum Air temp.
Minimum Air temp.
in-situ SST
Sea Surface temp.
Temperature (ºC)
a)
b)
Rainfall
PAR
Total rainfall (mm)
PAR ([Einstein m^{-2} d^{-1})
c)
Chl-a
CDOM
Chl-a concentration (mg m^{-3})
CDOM Absorption
d)
Sea level pressure [hPa]
Euphotic depth
Sea Level Pressure (hPa)
Euphotic depth (m)
e)
Canopy coverage
Fresh biomass
Mean thallus lenght (cm)
Fresh biomass 0.25 m^2 (g)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
2012
2013
2014

Figure 4

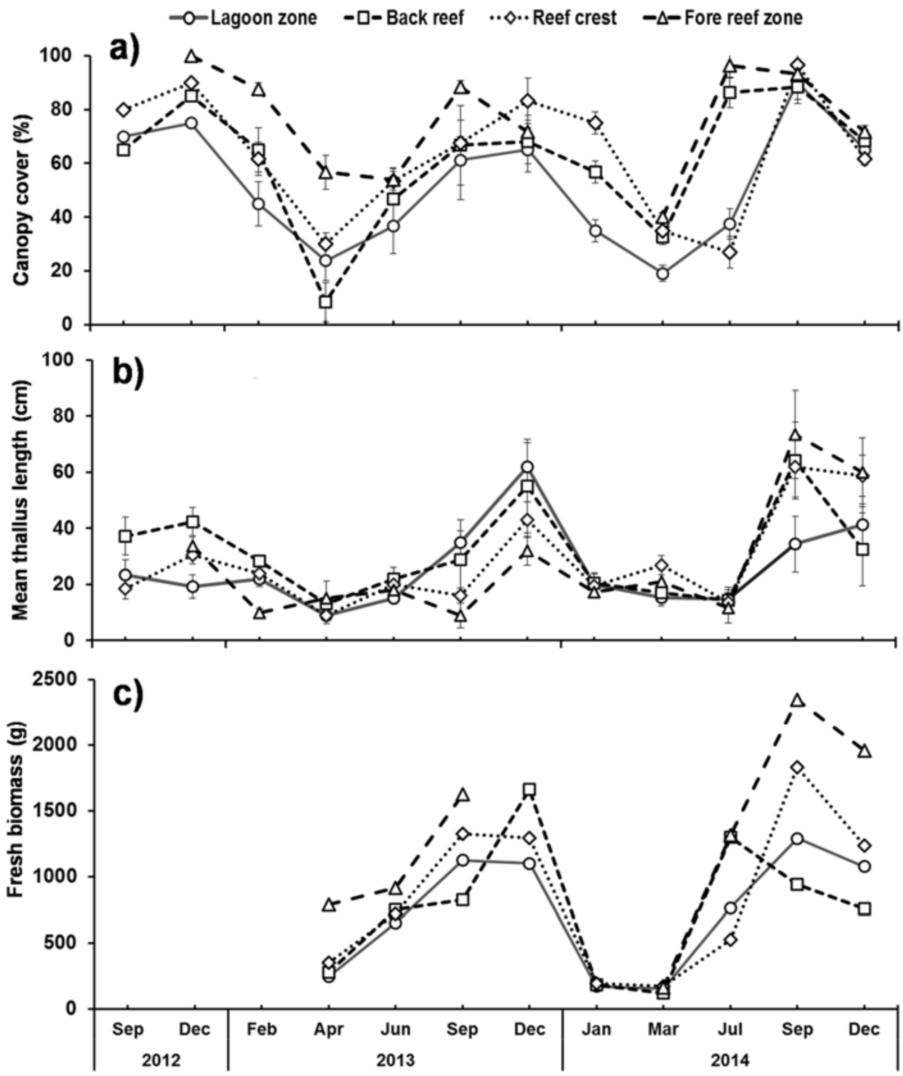

Lagoon zone
Back reef
Reef crest
Fore reef zone
a)
Canopy cover (%)
b)
Mean thallus length (cm)
c)
Fresh biomass (g)
Sep
Dec
Feb
Apr
Jun
Sep
Dec
Jan
Mar
Jul
Sep
Dec
2012
2013
2014

Figure 5

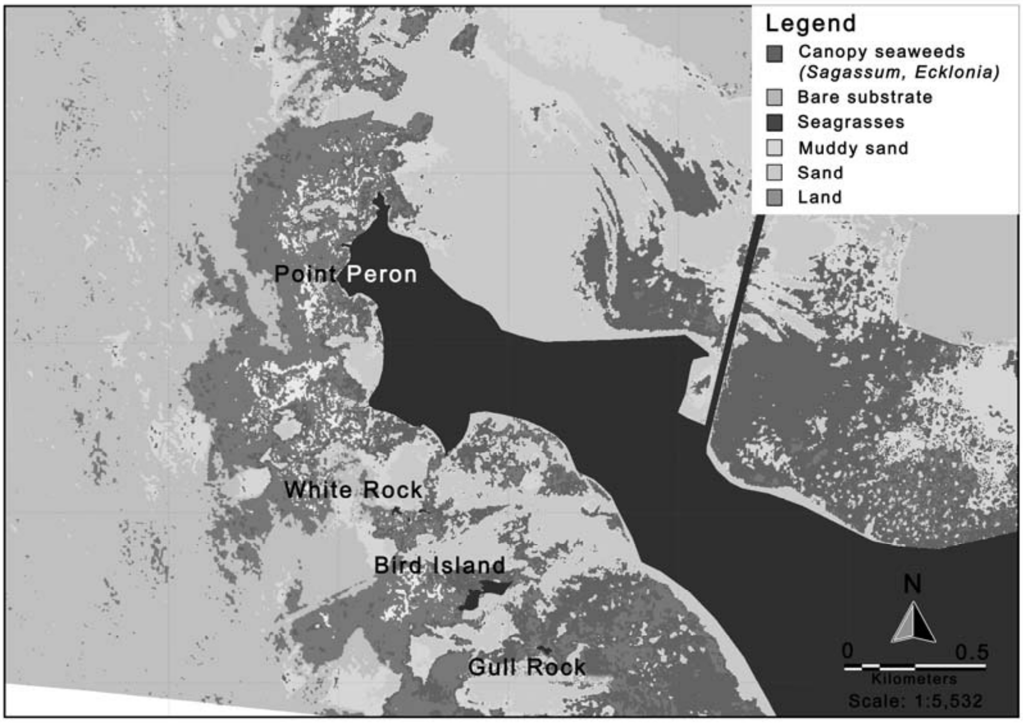
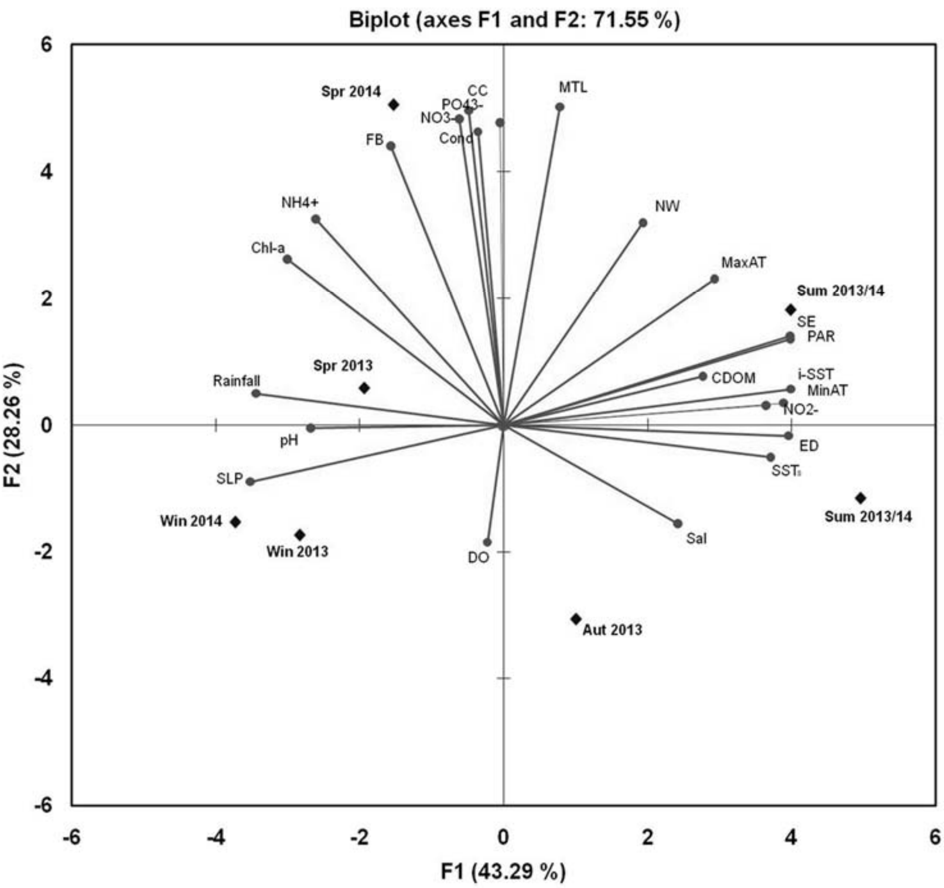
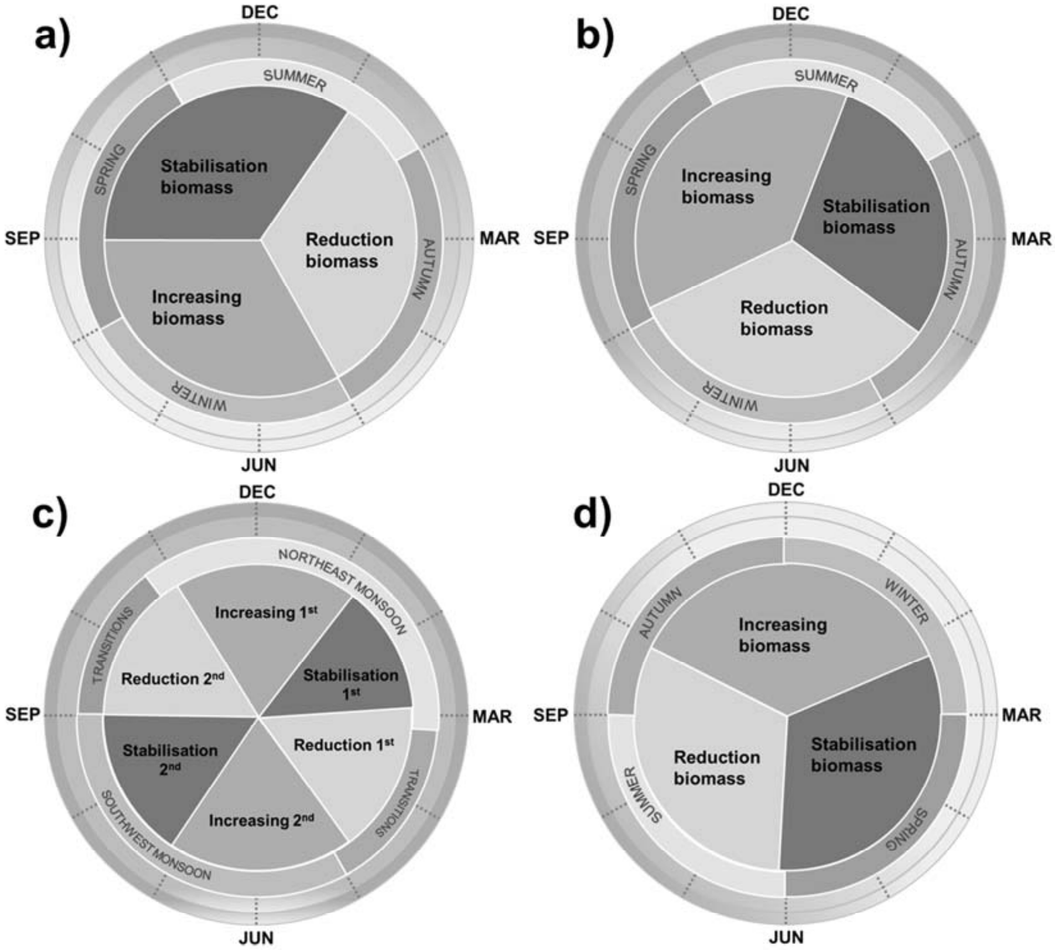

Legend
Canopy seaweeds
(Sagassum, Ecklonia)
Bare substrate
Seagrasses
Muddy sand
Sand
Land
Point Peron
White Rock
Bird Island
Gull Rock
N
0
0.5
Kilometers
Scale: 1:5,532

Figure 6



Biplot (axes F1 and F2: 71.55 %)
F2 (28.26 %)
F1 (43.29 %)
Spr 2014
CC
PO43-
NO3-
Cond
FB
MTL
NW
NH4+
Chl-a
MaxAT
Sum 2013/14
SE
PAR
CDOM
i-SST
MinAT
NO2-
Rainfall
Spr 2013
pH
ED
SLP
Win 2014
Win 2013
DO
Sal
Sum 2013/14
Aut 2013

Figure 7


a)
DEC
SUMMER
SPRING
AUTUMN
WINTER
SEP
MAR
JUN
Stabilisation biomass
Reduction biomass
Increasing biomass
b)
DEC
SUMMER
SPRING
AUTUMN
WINTER
SEP
MAR
JUN
Increasing biomass
Stabilisation biomass
Reduction biomass
c)
DEC
NORTHEAST MONSOON
TRANSITIONS
TRANSITIONS
SOUTHWEST MONSOON
SEP
MAR
JUN
Increasing 1st
Stabilisation 1st
Reduction 2nd
Reduction 1st
Stabilisation 2nd
Increasing 2nd
d)
DEC
AUTUMN
WINTER
SUMMER
SPRING
SEP
MAR
JUN
Increasing biomass
Reduction biomass
Stabilisation biomass