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Season changes in water quality and *Sargassum* biomass in Southwest Australia

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Running tittle: *Sargassum* beds 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*

4

92 observations and remote sensing methods to study the seasonal variation in physicochemical water

93 parameters with changes in mean thallus length, canopy cover, and biomass of the *Sargassum*

94 community and determined how these changes impacts the broader spatial distribution of

95 *Sargassum.*

96

MATERIALS AND METHODS

97 *Study sites*

99 We selected our demonstration site Point Peron, SWA, which is a small peninsula located

100 within the Shoalwater Islands Marine Park, an area of approximately 67 km^2, west of the

101 Rockingham city, 50 km south of Perth (Fig. 1). The point is approximately 930 m long and 1,450

102 m wide and is surrounded by a chain of limestone reefs and islands, including Garden Island to the

103 north. As part of the Shoalwater Islands Marine Park, Point Peron has a high diversity of marine

104 fauna and flora (DEC 2011).

105 The study area includes a chain of limestone reefs approximately 450 m offshore (32°14'–

106 32°17'S and 115°39'–115°42'E). The coastal area of Point Peron was divided into four zones: the

107 Lagoon zone (LZ), Back reef (BR), Reef crest (RC) and Fore reef (FR) zone with the distance

108 approximately 100 m between each zone (Rützler & Macintyre 1982) (Fig. 2). The field studies

109 were carried out from September 2012 to December 2014 during four well-defined seasons;

110 summer (December to February), autumn (March to May), winter (July to August), and spring

111 (September to November) (BoM Australia 2013).

112

113 *Field sampling methods*

114 *Sampling frequency*

115 The total duration of the trial was two and half years wherein summer and spring were

116 represented three times and winter and autumn were represented twice. At least one sampling trip

117 was carried out per season, however, we could sample twice during summer and spring seasons

118 which were then averaged out. During every trip, four 400 m long transects were sampled. The

119 average depth along each transect ranged from 0.3 to 2.5 m. For water quality analysis, one sample

120 was collected from every transect. For canopy cover (CC), fresh biomass (FB), and mean thallus

121 length (MTL) of *Sargassum* spp, every transect was further monitored from four reef zones by

122 deploying random quadrats (0.5 × 0.5 m), one for each reef zone. The distance between the

123 quadrats ranged from 20 to 80 m. The above protocol provided four samples for water quality

124 analysis and 16 (4 transects × 4 quadrats) samples for *Sargassum* measurements per season.

125 ***Sampling description***

126 The transects were selected based-on the actual study site's topography and covering a

127 range of different habitats. Using SCUBA survey techniques, we monitored and sampled

128 *Sargassum* spp. along four predefined transects extending from the coastline to offshore. From each

129 transect the seawater samples were collected in a 1-L polyethylene bottle. The *Sargassum* spp.

130 within each quadrat was collected, stored in labelled polyethylene bags and brought to the Curtin

131 Aquatic Research Laboratory (CARL), Curtin University, Western Australia (WA). The locations

132 of the sampling quadrats were recorded by a hand-held GPS (Garmin eTrex® 10). The collected

133 *Sargassum* samples were retained in fibreglass tanks with seawater under natural sunlight. The

134 samples were provided with constant aeration till further measurements. Fresh specimens were

135 photographed immediately after arrival at the CARL. The holdfasts, blades, vesicles, and

136 receptacles were also examined and photographed. *Sargassum* specimens were identified based-on

137 taxonomic references (Noro et al. 1994, Phillips 1994, Garton 1997, Huisman 2000, Huisman et al.

138 2006, Guiry & Guiry 2014). A morphological study of *Sargassum* samples was under taken on

139 dried specimens. Herbarium specimens were stored at the CARL. Underwater video and

140 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, ºC), mean and minimum (MinAT,

ºC) 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 ºC/ 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 10ºC) 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,

166 Loveland, CO, USA) with the cadmium reduction method (Method 8171) and diazotization method

167 (Method 8507), respectively (APHA 1998). Phosphate (PO_4^{3-}) concentration was analysed by

168 Ascorbic acid method (Standard Method 4500-PE) and ammonium (NH_4^+) was determined by

169 using Aquanal™ test kits (Sigma-Aldrich®, Germany) (see Table 1 for the list of symbols and

170 acronyms).

171

172 ### *Satellite remote-sensing data and processing*

173 WorldView-2 satellite images at a 2-m spatial resolution were acquired on 7 February 2013

174 (austral summer), which was a period of high biomass and areal extent of *Sargassum* beds. Satellite

175 remote-sensing WV-2 images were adjusted to pseudo-color composite images prior to the

176 classification process, to enhance the image contrast to detect the *Sargassum* beds.

177 The acquired WV-2 images from DigitalGlobe® were registered into Georeferenced−the

178 global geodetic system 1984 for latitude and longitude. The ground−truth data were acquired and

179 confirmed using *in situ* field checks from five survey trips in 2013 and 2014. The ENVI® 4.7

180 environment for visualizing images was used to mask out the land area that was not used for

181 classification at the study area (ENVI 2014). Method of K-means unsupervised classification was

182 employed for image classification as it is the most commonly used classifier in reef studies

183 (Benfield et al. 2007, Hoang et al. 2015). A toolbox in ENVI® 4.7 was employed for the

184 classification and to count the number of pixels of the WV-2 satellite image that was used to detect

185 the distribution of *Sargassum* beds. After classification, the data were converted from raster to

186 vector format and were edited in geographical information systems software packages. The

187 complete diagrammatic processing imagery is presented in Figure 2.

188

189 ### *Data analysis*

190   Seaweed distribution and abundance data were processed using statistical software, IBM®

191   SPSS Statistics 20 and Microsoft® Excel 2010. One-way analysis of variance (ANOVA) and

192   general linear models were employed to test for significant differences between seasons in seawater

193   quality. A two-way ANOVA was carried out to test the effects of seasons and distribution sites on

194   the *Sargassum* CC and MTL. The multiple comparison, least significant difference (LSD's) post hoc

195   test, was also implemented to test for the statistical significance among treatments. The statistical

196   significance level was set at 0.05. Principle component analysis (PCA) was employed to evaluate the

197   interaction between the physical, chemical and biological parameters and their effect on *Sargassum*

198   spp. Results from the PCA were acquired based on the correlation matrix of the mean values of

199   water quality parameters against sampling times. Principle component analysis was prepared by

200   using the latest XLSTAT 2015.1.01 (Addinsoft™, France) package for Microsoft® Excel. All the

201   results were presented as means ± S.E. (standard error), unless otherwise stated.

202

RESULTS

203

Temporal variation in environmental conditions

204

205   The analysis of air temperature over the three study years (2012–2014) indicates that the

206   monthly mean temperature was highest in the summer months (December to February).

207   Temperatures then decreased in autumn (March to May) and were lowest in winter (June to

208   August) and finally increased in spring (September to November). In the summer months, the

209   maximum monthly mean temperature reached 28.2 ± 0.6°C and in autumn, it reached 24.1 ± 0.9°C.

210   In winter and spring, the maximum monthly mean temperatures were 18.5 ± 0.2 and 21.7 ± 1.3°C,

211   respectively. In 2012, the mean air temperature reached a maximum in January (30.5°C) and was

212   lowest in July (9.9°C) (Fig. 3a).

213   Sea surface temperatures also showed a seasonal pattern, with values ranging from 12.9 to

214   24.1°C. There were significant (ANOVA, $F_{(9, 37)} = 551.23$, $P < 0.001$) differences in SSTs

9

215   between the seasons, except for between winter and spring (Fig. 3a). Rainfall and PAR usually

216   showed an inverse pattern and both showed a strong seasonal variation. The PAR reached the

217   highest value in the summer at 58.5 ± 1.5 Einstein m^{-2} d^{-1} (a maximum in December 2013 of 63.2

218   Einstein m^{-2} d^{-1}). Although the monthly rainfall was only 2.6 mm, mean summer rainfall was $11.9 \pm$

219   6.4 mm. In contrast, the PAR was the lowest in the winter months at 22.8 ± 3.6 Einstein m^{-2} d^{-1}

220   (17.5 Einstein m^{-2} d^{-1} in June 2013) and the highest mean rainfall of 95.5 ± 11.9 mm was reached in

221   winter (the maximum value of 151.6 mm was in September 2013 (Fig. 3b).

222   Seawater salinity in the study area ranged from 35.4 to 36.5 among the seasons, but the

223   differences were not significant (ANOVA, $F(9, 37) = 1.43$, $P = 0.224$). The electrical conductivity

224   of seawater in the study area also differed significantly between the sampled seasons (ANOVA,

225     $F(9, 37) = 17.01$, $P < 0.001$), with conductivity values ranging from -98.87 to -65.87 ECs.

226   Dissolved oxygen (ANOVA, $F(9, 37) = 30.05$, $P < 0.001$) and pH (ANOVA, $F(9, 37) = 3.32$, $P =$

227   0.007) were significantly different between the seasons and ranged from 5.39 to 8.27 mg L^{-1}, and

228   7.82–8.21, respectively (Table 2).

229   Significant differences were observed in all nutrient levels among seasons during the study

230   period at Point Peron as determined by one-way ANOVA where NO$_2^-$ (ANOVA, $F(3, 36) = 12.05$,

231     $P < 0.05$), NO$_3^-$ (ANOVA, $F(3, 36) = 13.38$, $P < 0.05$), NH$_4^+$ (ANOVA, $F(3, 32) = 5454$, $P < 0.05$),

232   PO$_4^{3-}$ (ANOVA, $F(3, 36) = 7.38$, $P = 0.001$). In particular, the concentration of nitrite (NO$_2^-$) was

233   relatively low, ranging from 2.2–17.4 µg L^{-1} during the study period. The nitrate (NO$_3^-$)

234   concentration reached its highest value in spring 2014 (0.48 ± 0.06 mg L^{-1}) and lowest value in

235   summer 2013 (0.02 ± 0.001 mg L^{-1}). The concentration of ammonium (NH$_4^+$) during the study

236   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

237   reached the highest value in spring 2014 and lowest value in summer 2013. In general, the nutrient

238   concentrations were lowest in autumn and highest in spring throughout the study period (Table 3).

239

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

264   The *Sargassum* CC was widely distributed around Point Peron. The highest coverage of

265   *Sargassum* was recorded at the FR, followed by the RC, BR and LZ sites, with values of 75.9 ± 6.5

266   %, 63 ± 6.7 %, 61.4 ± 6.7 %, and 51.9 ± 6.4 %, respectively (Table 4). However, no differences (*P*

267   > 0.05) were found between reef sites. The surveyed data showed that three dominant *Sargassum*

268   species were present in the study area: *S. spinuligerum, S. swartzii,* and *S. confusum*. In addition, *S.*

269   *longifolium* was less abundant in the FR zone than the other species.

270   The classification of the benthic habitat was confirmed using WV-2 satellite images.

271   *Sargassum* was mainly distributed on the coral reefs and submerged limestone substrates from Gull

272   Rock to Bird Island, White Rock and further west from Point Peron, extending to the area further

273   south of the Shoalwater Islands Marine Park. Field studies showed that the bottom depth of the

274   *Sargassum* distribution area was relatively shallow (between 1.5 and 10 m). A sandy bottom and

275   hard coral substrates were frequently found around *Sargassum* beds, and the boundaries between

276   *Sargassum* and seagrass beds were detected with a high spatial resolution (2 m). Five bottom types

277   were identified, including seaweeds (*Sargassum* sp. and *Ecklonia* sp.) canopy, seagrass, sand,

278   muddy sand, and bare substrate, which were classified by the K-means unsupervised classification

279   method (Fig. 5).

280

Multivariate analysis

282   The principle component analysis (PCA) to establish multi-dimensional relationships

283   among the studied parameters showed that there were four first principle components that

284   accounted for 88.6 % of the total variation. The first principle component accounted for over 43.3 %

285   of the total variation between sampling seasons and consisted of the physicochemical parameters

286   PAR, SSTs, SE, ED, MinAT, MaxAT, CDOM, salinity, and NW. The second principle component

287   accounted for 28.3 % of the variation and included nutrient parameters such as MLT, CC, NO_3^-,

288   PO_4^{3-}, FB, conductivity, NH_4^+, and Chl-a. The third principle component explained 9.7 % of the

289 total variation, and included DO, NH_4^+, rainfall, NO_2^-, PAR, and CC. The fourth principle

290 component explained 7.4 % of the total variation, and consisted of salinity, rainfall, and

291 conductivity parameters; 6.6 % of the total variation was explained by the fifth principle component

292 and 4.8% of the variation of the sampling seasons by the sixth component.

293   The bi-plot chart of the first and second components explained 71.6 % of the total variation

294 in the environmental parameters during the sampling time. The results showed that nutrient

295 composition (NO_3^-, PO_4^{3-}, and NH_4^+) and *Sargassum* community structure (CC, FB, and MTL)

296 were encountered at the spring sampling times. The PAR, salinity, and SSTs were key parameters

297 during the summer. The *Sargassum* population structure was typically explained by rainfall, SLP,

298 and pH parameters during the winter months (Fig. 6).

299

300

301 **DISCUSSION**

302 ***Seasonal growth trends in Sargassum beds***

303   This study investigated the ecology and seasonal growth trends in the brown algae,

304 *Sargassum* spp. at Point Peron, in the SWA for the first time. It was found that *Sargassum* biomass

305 increased during the winter and early spring, and stabilized during late spring and early summer,

306 before decreasing during the late summer and early autumn. This pattern of (*i*) increase, (*ii*)

307 stabilization, and (*iii*) reduction in biomass is linked to the five main stages of the *Sargassum*

308 lifecycle, including: recruitment and growth (increase in biomass), senescence and reproduction

309 (stabilization of the biomass), and regeneration (reduction in biomass) (Gillespie & Critchley

310 1999). Here, we investigated which of the key environmental parameters, including SSTs, nutrients

311 availability, and irradiance are responsible for regulating the timing of the *Sargassum* lifecycle

312 events (Fig. 7a).

13

313   *i. Increase in biomass*: This study showed that *Sargassum* biomass began to increase in early

314   winter from new recruits and remaining holdfasts, increased throughout winter and accelerates

315   during spring. The highest nutrient concentrations, including NO_3^-, PO_4^{3-}, NH_4^+ were measured

316   during winter and early spring, which coincided with the increase in biomass and the highest

317   growth rates. Considering that these high nutrient values occurred in the winter and spring, which is

318   a high rainfall season for SWA rainwater run-off from the land probably played a vital role in the

319   accelerated growth phase of *Sargassum* spp. Notably, this phase of high growth was negatively

320   correlated with SSTs, i.e., the fastest growth rates occurred during the period with the lowest SSTs

321   and irradiance ($r = –0.43$) (Table 5) and only a weak correlation was observed between PAR and

322   *Sargassum* spp., and this trend has also observed in other studies (Fulton et al. 2014; Sangil et al.

323   2015).

324   *ii. Stabilization of biomass:* Following the growth phase, *Sargassum* biomass stabilized, with

325   little or no observed change in MTL or CC between early spring (September) to mid-summer

326   (January). This period is characterized by higher SSTs, longer day lengths, and relatively high

327   nutrient concentrations and primary productivity. Higher concentrations of ammonium were found

328   at Point Peron during the late spring and were strongly correlated with the increase in CC and fresh

329   biomass ($r = 0.74$ and 0.65, respectively).

330   *iii. Reduction in biomass:* Following the reproductive stage, there was a reduction in *Sargassum*

331   biomass beginning in late summer (February) through the end of autumn (April to May). Die-off occurred

332   towards the end of summer where coincide with the highest water temperature, when some holdfasts

333   remained and regenerated into new thalli in autumn and winter (Arenas et al. 1995). The

334   decomposition of *Sargassum* thalli might lead to an increase in nitrite concentrations in the summer

335   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

361 Peron study ($r = 0.82$). When the MTL was high, the *Sargassum* spp. in the selected quadrats also

362 had a greater density, in turn resulting in a high biomass.

363 The difference in the *Sargassum* growth cycle can be explained by high rainfall during the

364 summer (December to February, 624.9 ± 275.3 mm), which coincides with high nutrient

365 concentrations from run-off, which provide optimum conditions for *Sargassum* growth (Vuki &

366 Price 1994). The later growing stage of *Sargassum* beds in Magnetic Island might be caused by the

367 irregular, high rainfall and lower radiation in summer than in spring and winter, due to the higher

368 cloud cover at this time, or a difference in *Sargassum* species composition.

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

370 Tropical regions near the equator experience high SSTs and high rainfall throughout the

371 whole year, with little difference between the wet and dry season. Several seasonality studies have

372 been performed on *Sargassum* in tropical regions, such as Pock Dickson in Malaysia, the northern

373 part of the Philippines, and New Caledonia. Due to the effect of two strong monsoons, the

374 *Sargassum* beds reveal two periods of increasing biomass rates (January to February and June to

375 July) and decreasing biomass rates (April and September) (May-Lin & Ching-Lee 2013). Thus, the

376 growth cycle depends on seasonal changes in the monsoon, the species of *Sargassum* and the

377 existing nutrient availability (Schaffelke & Klumpp 1998). The highest biomass can occur in the

378 wet season for some species (e.g. *S. binderior*) or the dry season for others (e.g. *S. siliquosum*). In

379 these tropical areas, the seasonality of *Sargassum* beds can be more dependent on changes in SSTs

380 and rainfall (i.e. tropical monsoons).

381 A study in New Caledonia in the Indo-Pacific region showed that *Sargassum* spp. have a

382 high MTL in the summer months due to higher rainfall at this time, which causes an increased

383 nutrient concentration and growth (Mattio et al. 2008). However, in the Philippines, *Sargassum*

384 biomass is highest in the dry season, which possibly coincides with high SSTs (Ang, 1986). Thus,

385 equatorial climates can also experience a range of seasonal effects on *Sargassum* spp., although this

386 might be less pronounced than in more temperate climates such as that at Point Peron.

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

388 Cape Peñas (Asturias, Spain) is located at latitude 43.4ºN and has a similar Mediterranean

389 climate to Point Peron, and experiences warm dry summers and cool wet winters. The summer

390 season occurs from June to September, with a mean daily high air temperature above 20°C. The

391 increase in *Sargassum* biomass on Cape Peñas occurs from mid-autumn to late-winter, stabilization

392 with peak biomass occurs between the end of winter and the end of spring, and reduction occurs

393 between early summer and mid-autumn. Growth increases during the winter until spring, when

394 higher SSTs increase photosynthesis and productivity and provide optimum growth conditions,

395 followed by senescence from early summer to mid-autumn (Arenas & Fernández 2000). Seasonal

396 changes in temperature are also thought to drive the growth of *Sargassum* spp. at La Palma, and in

397 the Canary Islands, Spain. The biomass of *S. flavifolium* reaches its maximum in spring to summer

398 and is similar to that of *Sargassum* spp. in this study, coinciding with an increase in the SST and

399 day length (irradiance) (Sangil et al. 2015). The growth and development of *Sargassum* in the study

400 sites in Spain and SWA share a similar seasonal pattern, which can be explained by similar climate

401 zones. However, they occur at different times of the year due to the reverse timing of seasons in the

402 Northern and Southern hemispheres.

403

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

405 The distribution of *Sargassum* beds was restricted mainly to shallow water habitats, similar to

406 the results of others (Hanisak & Samuel 1987, Mattio et al. 2008, Mattio & Payri 2011). Because

407 the holdfasts grow on limestone rock substrates, the beds were widely distributed throughout these

408 habitats, but not on sandy substrates, where seagrass was dominant. A similar study in New

409 Caledonia found that *Sargassum* was dominant on rubble substrate and rocky bottoms, ranging

410   from 2.5 to 12 m deep (Mattio et al. 2008). In this study, biomass increased as depth increased

411   along the transects, and showed some variation in reef zones from the LZ to the FR. This represents

412   a trend, suggesting that the biomass of *Sargassum* beds increases at greater depths, until light

413   becomes a limiting factor (Ang 1986, Rützler & Macintyre 1982, Vuki & Price 1994).

414   The highest MTL of *Sargassum* in all seasons is related to its distribution area and was found

415   in the BR zone, which is protected by the RC zone further offshore, where the waves and currents

416   are broken down and their kinetic energy reduces before they approach the shoreline. The lowest

417   MTL value was found in the LZ. The length of thalli in the LZ reflects the shallow depth here, as

418   well as the high heat absorption from the sun, which causes higher SSTs than at other study sites.

419   At Point Peron, the mean MTL of *Sargassum* species is similar to that found for *S. ilicifolium* and

420   *S. subrepandum* in the Southern Red Sea, which was 38.71 cm and 32.65 cm, respectively

421   (Ateweberhan et al. 2009). The MTL here is also similar to that from a phenology study of

422   *Sargassum* species in Tung Ping Chau Marine Park, Hong Kong (48.2 ± 29.9 cm) (Ang 2007).

423   However, the MTL of *Sargassum* in Point Peron is shorter than that found in previous studies in

424   Rottnest Island, SWA (10–95cm) (Kendrick 1993), in the middle reef flat of Magnetic Island,

425   North-Eastern Australia (Vuki & Price 1994) and in other studies in Malaysia (Wong & Phang

426   2004, May-Lin & Ching-Lee 2013).

427   The present study was initially applied using WV-2 satellite remote sensing data to determine

428   the spatial distribution of *Sargassum* and associated marine benthic habitats in the study area. This

429   study can be considered as an original approach for the region when using more advantageous

430   satellite remote sensing data, with higher spatial and spectral resolution, than the previous studies in

431   Thailand with ALOS–AVNIR 2 images (10 m spatial resolution) (Noiraksar et al. 2014), New

432   Caledonia with Landsat (30 m) and Quickbird (2.4 m) images (Mattio et al. 2008).

433   Thus, further studies could apply the recent archived results for identifying and mapping

434   *Sargassum* beds for the SWA region (Hoang et al. 2015, Garcia et al. 2015). The results of spatial

435 distribution characteristics of *Sargassum* beds play an important role in providing information on

436 regional natural resource management and a better understanding of the distribution characteristics,

437 areas, and seasonality of *Sargassum*, in terms of the highest biomass. However, a limitation does

438 exist in this study due to the lack of temporal satellite remote sensing data sources in evaluating the

439 brown canopy seaweeds distribution. The current satellite remote sensing image only reflects the

440 distribution of brown canopy seaweeds (*Sargassum* and *Ecklonia*) in the peak biomass season,

441 spring. However, if there were more than one satellite remote sensing images during another season

442 available at the study region that would markedly illustrate the seasonal variation in the distribution

443 area.

444   In summary, this study provides primary and novel information on *Sargassum* spp. at Point

445 Peron using a combination of *in situ* and satellite remote-sensing observations. The results show

446 that the *Sargassum* beds demonstrated a seasonal variation pattern in CC and MTL, which was

447 significantly influenced by the nutrient concentration (NO_3^-, PO_4^{3-}, NH_4^+), and rainfall ($P < 0.05$).

448 This seasonal variation pattern is similar to that found in areas with a temperate or Mediterranean

449 climate, such as Rottnest Island, Australia and Cape Peñas, Spain (Arenas & Fernández 2000,

450 Kendrick & Walker 1994). The highest peaks in *Sargassum* biomass generally occurred between

451 late spring and early summer. This seasonal pattern was also found in *Sargassum* CC and MTL.

452 The seasonal variation in *Sargassum* biomass, CC and MTL at Point Peron was closely associated

453 with seasonal changes in nutrient concentration and rainfall. These results provide essential

454 information for coastal marine management and conservation, as well as for the sustainable

455 utilisation of this renewable marine resource.

456

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631

632

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

656 Meteorology, Australian Government. The Euphotic depth, CDOM, PAR, SST, Sea level pressure,

657 and Chl-a in the study area (32°12'–32°17' S, 115°38'–115°42' E) were extracted from the Giovanni

658 online data system, developed by NASA.

659 Figure 4. Seasonality of percentage canopy cover (a), mean thallus length (b), and fresh biomass of

660 *Sargassum* (c) observed in four different areas during spring 2012 to 2014. Each column for (a) and

661 (b) present the mean and standard error. Four replicated quadrats (0.5 × 0.5 m) and four reef zones

662 were measured for CC and MTL, respectively. The fresh biomass samples (c) were measured at

663 difference reef zone.

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

665 seaweed beds (*Sargassum* spp.), their distribution and associated sub-littoral habitats (seagrass,

666 sand, and muddy sand) around Point Peron in summer (7 February 2013).

667 Figure 6. Principal component analysis biplot showing the relationship between *Sargassum*

668 sampling time, CC, MTL, fresh biomass, and the physicochemical parameters: FB represents fresh

669 biomass (g 0.25m^{-2}); Cond. represents conductivity (mS m^{-1}); CC represents canopy coverage (%);

670 MTL represents mean thallus length (cm); NW represents a northward wind (m s^{-1}); MaxAT

671 represents maximum air temperature (°C); SE represents solar exposure (MJ m^{-2}); CDOM

672 represents colored dissolved organic matter; i-SST represents *in situ* sea-surface temperatures;

673 MinAT represents minimum air temperature (°C); ED represents euphotic depth (m); SSTs

674 represents satellite-derived sea-surface temperatures (°C); Sal represents salinity; DO represents

675 dissolved oxygen (mg L^{-1}); SLP represents sea level pressure (hPa).

676 Figure 7. Diagram showing the seasonal variation in *Sargassum* biomass in different climate zones

677 across Australia and other geographical localities. (a) Point Peron, Western Australia with a

678 Mediterranean climate; (b) Magnetic Island, Australia with a humid continental climate; (c) Pock

679 Dickson, Malaysia with a tropical rainforest climate; and (d) Cape Peñas, Spain with an oceanic

680   climate. The phase of increasing biomass includes recruitment and growth up stages. The

681   stabilization biomass phase includes the late growth and reproduction stages. The reduction phase

682   consists of senescence and regeneration periods. The outer ring and second ring represent SST and

683   solar exposure, respectively. The light color represents months with a low temperature and the

684   darker color represents those with a high temperature. This figure was generated based on the

685   present study and in combination with the published information from other three studies from

686   different geographic regions. These previously published studies have reported the annual

687   observatory data in their respective regions.

688

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

692 **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

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

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696   **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

697   *The data is presented as the mean ± S.E of four replicates per sampling period. The different superscript letters are*

698   *significantly different means of environment parameters in the same column. The mean difference is significant at the*

699   *0.05 level.*

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703   **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

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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.
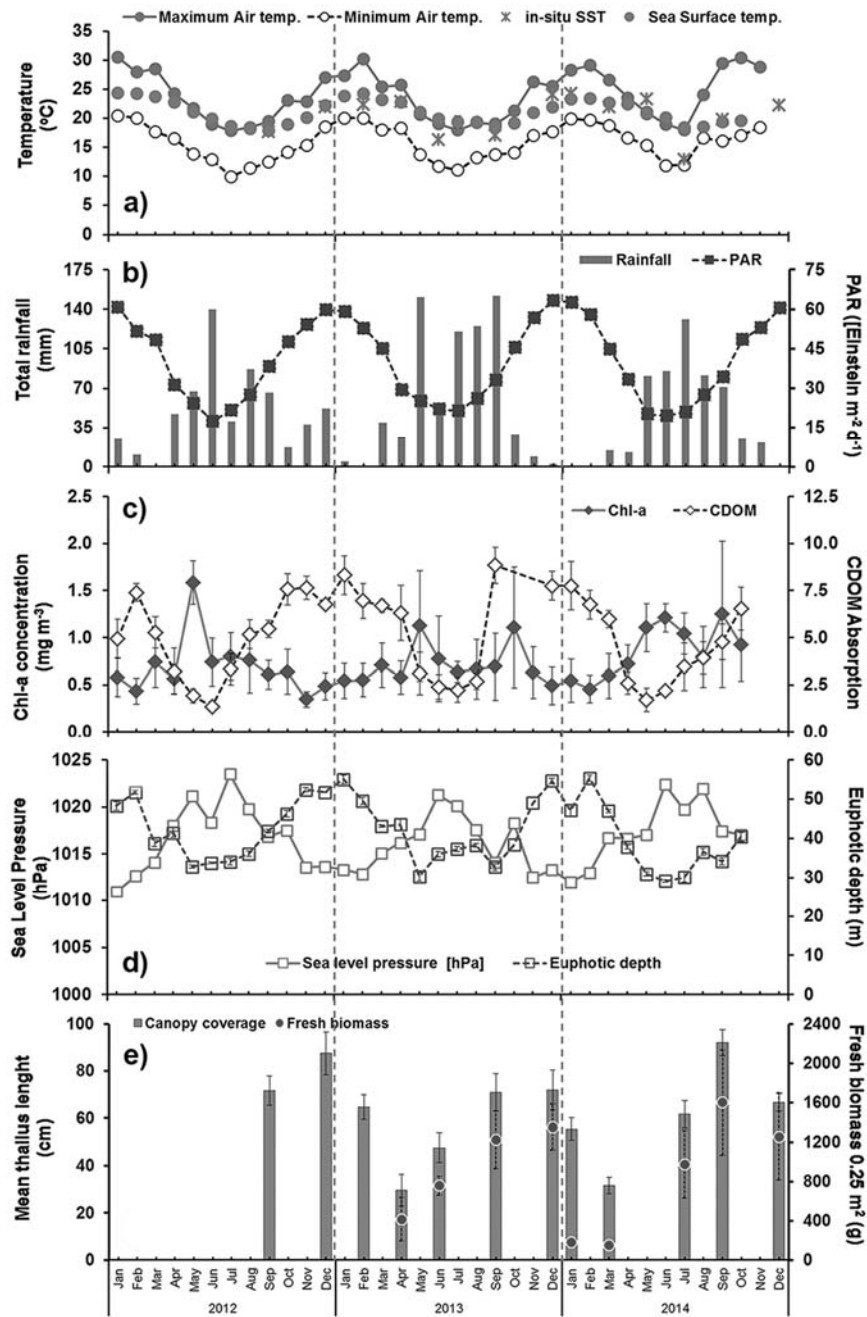
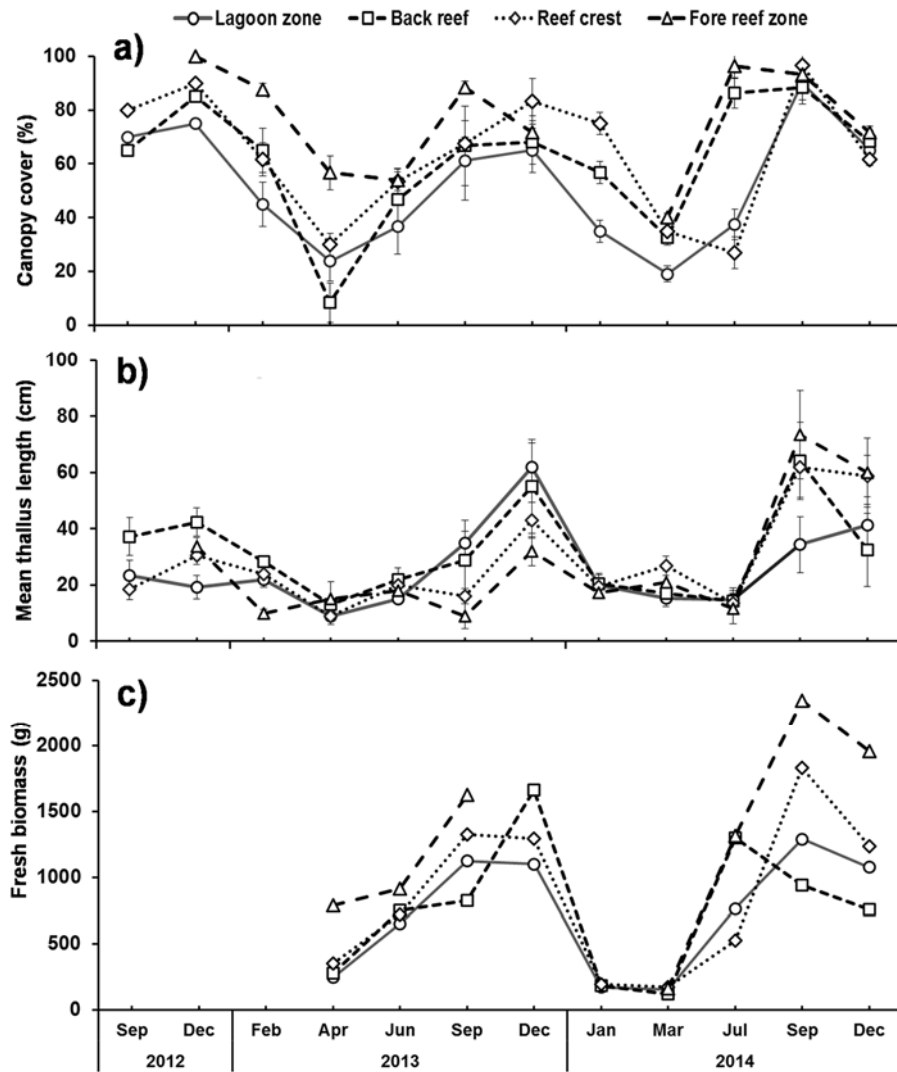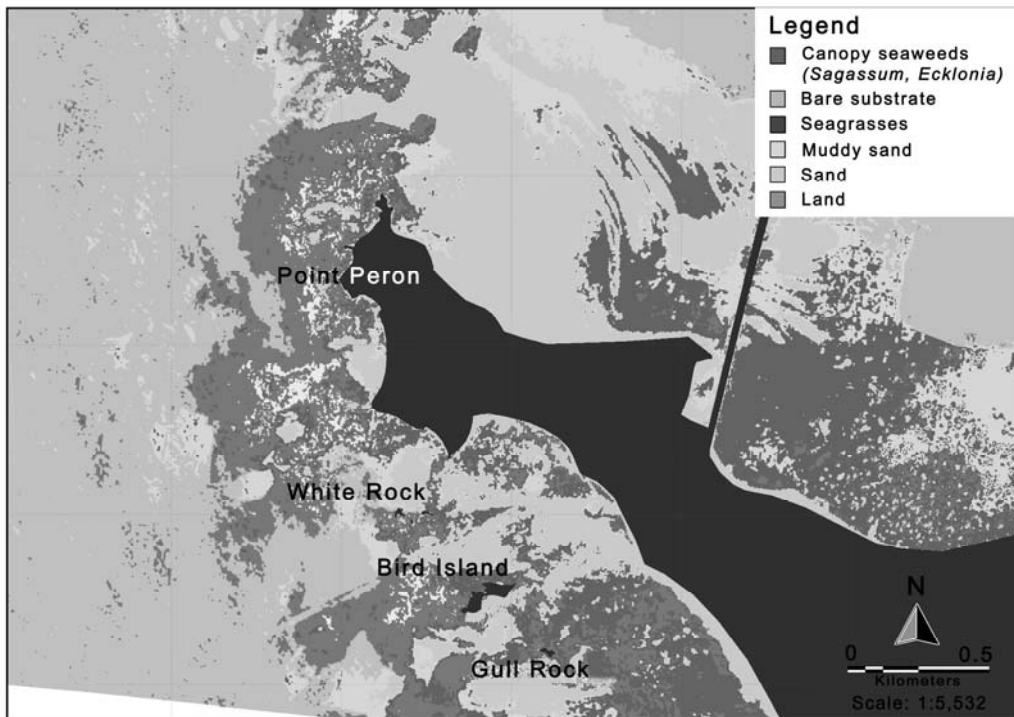1 **Figure 1**

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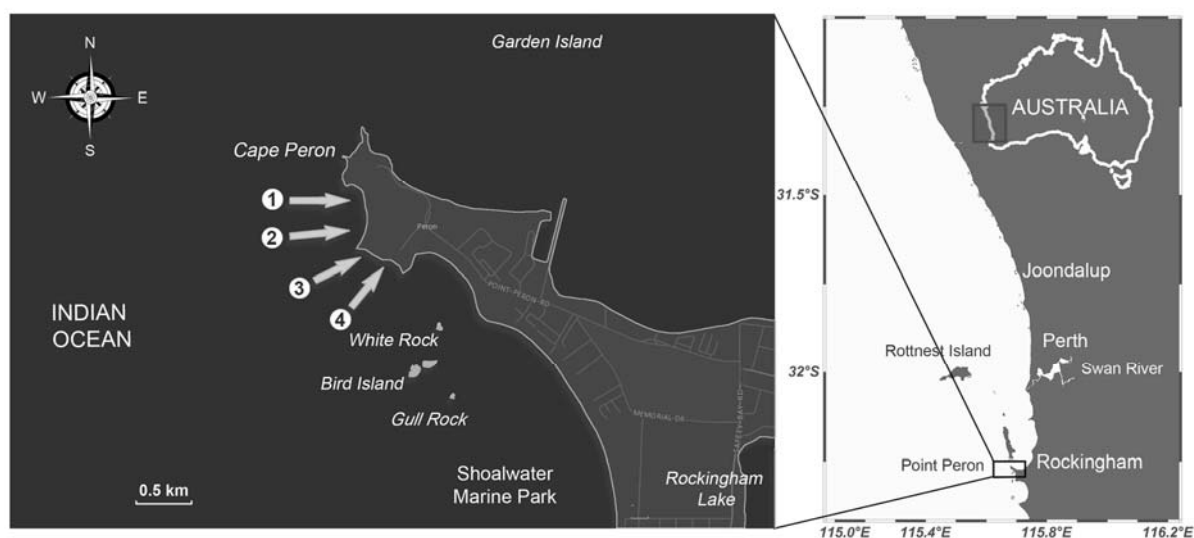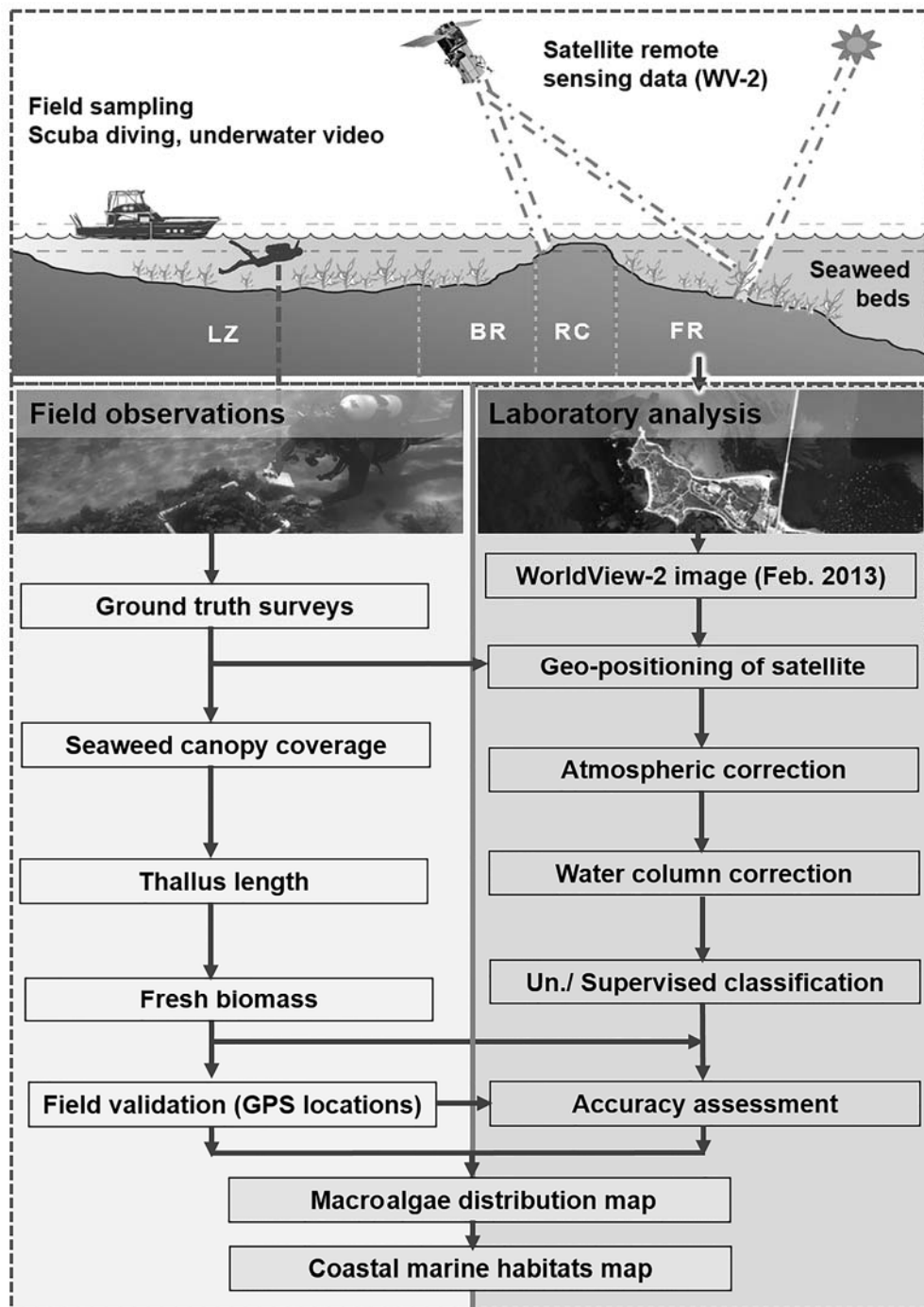
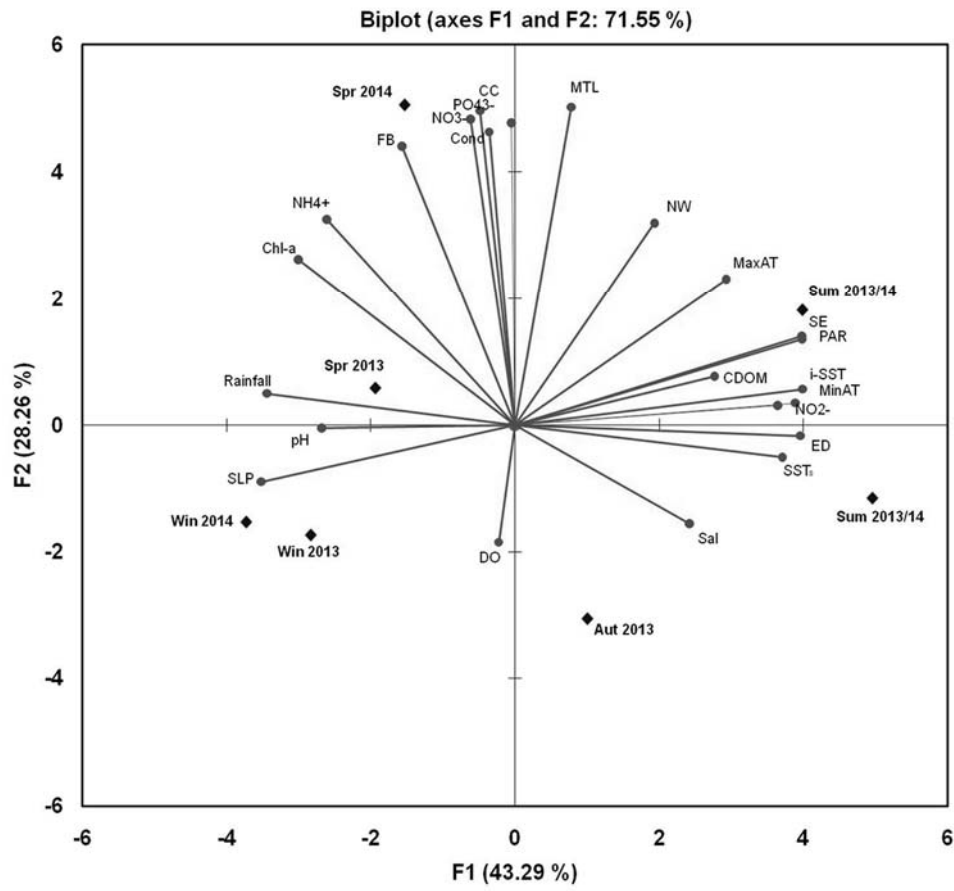5   **Figure 2**

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Biplot (axes F1 and F2: 71.55 %)

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20   **Figure 7**

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