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

6

7 Tin C. Hoang^{1*}, Anthony J. Cole¹, Ravi K. Fotedar¹, Michael J. O’Leary^{1,2}, Michael W. Lomas³
8 Shovonlal Roy⁴

9

10 ¹*Department of Environment and Agriculture, School of Science, Faculty of Science and*
11 *Engineering, Curtin University, Perth, WA 6102, Australia*

12 ²*Australian Institute of Marine Science, Crawley, WA 6009, Australia*

13 ³*Provasoli-Guillard National Centre for Marine Algae and Microbiota, Bigelow Laboratory for*
14 *Ocean Sciences, East Boothbay, Maine 04544, U.S.A.*

15 ⁴*Department of Geography and Environmental Science, The University of Reading, Whiteknights,*
16 *PO Box 227, Reading RG6 6AB, U.K*

17

18 *Corresponding author: tin.hoangcong@postgrad.curtin.edu.au

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20 **Running title: *Sargassum* beds in Southwest Australia**

21

22 **ABSTRACT**

23 *Sargassum* C. Agardh is one of the most diverse genera of marine macroalgae and
24 commonly inhabits shallow tropical and sub-tropical waters. This study aimed to investigate the
25 effect of seasonality and the associated water quality changes on the distribution, canopy cover,
26 mean thallus length and the biomass of *Sargassum* beds around Point Peron, Shoalwater Islands
27 Marine Park, Southwest Australia. Samples of *Sargassum* and seawater were collected every three
28 months from summer 2012 to summer 2014 from four different reef zones. A combination of *in situ*
29 observations and WorldView-2 satellite remote-sensing images were used to map the spatial
30 distribution of *Sargassum* beds and other associated benthic habitats. The results demonstrated a
31 strong seasonal variation in the environmental parameters, canopy cover, mean thallus length, and
32 biomass of *Sargassum*, which were significantly ($P < 0.05$) influenced by the nutrient concentration
33 (PO_4^{3-} , NO_3^- , NH_4^+) and rainfall. However, no variation in any studied parameter was observed
34 among the four reef zones. The highest *Sargassum* biomass peaks occurred between late spring and
35 early summer (from September to January). The results provide essential information to guide
36 effective conservation and management, as well as sustainable utilisation of this coastal marine
37 renewable resource.

38

39 **KEY WORDS:** Environmental parameters, *Sargassum* beds, Seasonality, Canopy cover, Mean
40 thallus length.

41

42

43 INTRODUCTION

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

53 Approximately 46 *Sargassum* species are found along the Southwest Australian (SWA)
54 coast (DPaW 2013) and the majority of these have been studied to determine their taxonomic
55 affiliation, including the molecular basis of identification (e.g. Kendrick 1993, Kendrick & Walker
56 1994, Goldberg & Huisman 2004, Dixon & Huisman 2010, Dixon et al. 2012, Rothman et al.
57 2015), and physiology (De Clerck et al. 2008, Huisman et al. 2009, Staehr & Wernberg 2009,
58 Kumar et al. 2011, Muñoz & Fotedar 2011). However, few studies have been carried out on the
59 impact of seasonality on *Sargassum* along the subtropical/temperate coastal zone of SWA
60 (Kendrick 1993, Kendrick & Walker 1994). Previous studies have shown that the growth,
61 development and distribution of *Sargassum* beds are strongly influenced by physicochemical water
62 parameters (Payri 1987, Ragaza & Hurtado 1999, Mattio et al. 2008), which play an important role
63 in influencing nutrient uptake via photosynthesis (Nishihara & Terada 2010). Seasonal variations in
64 the physicochemical parameters of seawater strongly influence changes in *Sargassum* canopy
65 structure, which in turn, affect the density of the local populations (Ang & De Wreede 1992,
66 Arenas & Fernández 2000, Rivera & Scrosati 2006, Ateweberhan et al. 2009).

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

83 The WorldView-2 (WV-2) satellite images provide one of the highest available spatial and
84 spectral resolutions (eight spectral sensors ranging from 400–1,040 nm) (Lee et al. 2011,
85 DigitalGlobe 2013). However, a few detailed mapping studies of *Sargassum* have been performed
86 using high-resolution satellite images, such as WV-2 (Hoang et al. 2015). In addition, a direct
87 visual approach that is integrated into high spatial resolution remote-sensing observations could
88 represent a robust approach to minimize costs and increase the accuracy of detection and
89 distribution patterns of *Sargassum* shallow coastal waters. The aim of this study is to investigate the
90 effects of seasonal changes in water quality on canopy cover, mean thallus length and the
91 *Sargassum* biomass at a fringing limestone reef in Point Peron, SWA. We have used *in situ*

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

97 **MATERIALS AND METHODS**

98 ***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 km², 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

141 September in 2013, and January, March, and July in 2014. These data were used for ground-
142 truthing and classifying the marine habitats.

143

144 ***Meteorological data and environmental parameters***

145 Meteorological data, including the maximum (MaxAT, °C), mean and minimum (MinAT,
146 °C) air temperature, solar exposure (SE) (MJ m⁻²), and monthly rainfall for each season, were
147 acquired from the nearest Bureau of Meteorology weather station, at Garden Island (32°14'24"S–
148 115°40'48"E), 2 km north of Point Peron (BoM Australia 2013). Euphotic depth (ED) (m), sea level
149 pressure (SLP) (hPa), colored dissolved organic matter (CDOM) index, photosynthetically active
150 radiation (PAR), sea surface temperatures (SSTs), and chlorophyll-a concentration (Chl-a) (mg m⁻³)
151 in the study area (32°12'–32°17'S, 115°38'–115°42'E) were extracted from the Moderate Resolution
152 Imaging Spectroradiometer (MODIS) satellite data. The northward wind (NW) (m s⁻¹) was
153 extracted from the Modern Era Retrospective-analysis for Research and Applications (MERRA)
154 flat form in the Giovanni system, developed and maintained by the National Aeronautics and Space
155 Administration (NASA) (Acker & Leptoukh 2007).

156 *In situ* seawater temperature (i-SST), conductivity and pH were measured in each season
157 using a portable waterproof °C/ mV/ pH meter (CyberScan pH 300, Eutech Instruments,
158 Singapore). Salinity was measured using a hand-held refractometer (Atago® RHS-10ATC, Japan)
159 in practical salinity units, and dissolved oxygen (DO) was determined with a digital DO meter
160 (YSI®55, Perth Scientific, Australia). Seawater samples were collected during each sampling
161 season for the analysis of nutrients; nitrate, nitrite, ammonium, and phosphate. All samples were
162 stored in 1-L polyethylene bottles and kept in a cold container (approximately 10°C) in the dark.
163 Samples were transferred to the CARL for analysis within 48 h following collection and followed
164 the methods described in Standard Methods for the Examination of Water and Wastewater (APHA
165 1998). Nitrate (NO₃⁻) and nitrite (NO₂⁻) 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

203 **RESULTS**

204 ***Temporal variation in environmental conditions***

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 $28.2 \pm 0.6^{\circ}\text{C}$ and in autumn, it reached $24.1 \pm 0.9^{\circ}\text{C}$.
210 In winter and spring, the maximum monthly mean temperatures were 18.5 ± 0.2 and $21.7 \pm 1.3^{\circ}\text{C}$,
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

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 $\text{m}^{-2} \text{d}^{-1}$ (a maximum in December 2013 of 63.2
218 Einstein $\text{m}^{-2} \text{d}^{-1}$). 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 $\text{m}^{-2} \text{d}^{-1}$
220 (17.5 Einstein $\text{m}^{-2} \text{d}^{-1}$ 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 $\mu\text{g L}^{-1}$ 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

240 **Seasonal pattern of *Sargassum* canopy cover**

241 The mean values of *Sargassum* CC in the selected quadrats at the four sites were higher
242 during the warmer months (spring and summer) than in the cooler months (autumn and winter). The
243 mean value of *Sargassum* CC for the whole area was highest (91.7 ± 2.6 %) in spring 2014 and was
244 lowest (29.7 ± 10.1 %) in autumn 2013 at all sites. Thus, a two-way ANOVA revealed that both
245 seasons and reef sites did affect the *Sargassum* CC which differed significantly between sampling
246 seasons (ANOVA, $F(9, 26) = 9.88$, $P < 0.001$) and reef sites (ANOVA, $F(3, 26) = 5.86$, $P = 0.03$)
247 from spring 2012 to summer 2014 (Fig. 4a).

249 **The mean length of *Sargassum* thalli**

250 The mean length of the seasonally harvested *Sargassum* thalli from randomized quadrats at
251 each site is shown in Figure 5. The longest thalli were found in months with higher temperatures
252 (summer 2013 and spring to summer 2014). The MTL for all sampling sites was highest in spring
253 2014 (53.5 ± 9.6 cm). In a similar pattern of coverage, the MTL was also lowest in the cold months,
254 when the mean length ranged from 11.5 ± 1.5 cm and 13.6 ± 0.7 cm for autumn 2013 and 2014
255 winter, respectively (Fig. 4b).

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

263 **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

281 **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).

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.

336 In general, the timing of the *Sargassum* lifecycle is geared so that full plant maturity is
337 reached by late spring or early summer for the plant to take advantage of the highest levels of
338 sunlight to redirect energy towards sexual reproduction. Towards the end of spring, the growth rates
339 of *Sargassum* spp. begin to slow and cease as the algae enters its reproductive stage (Kendrick &
340 Walker 1994). The reproductive activity of *Sargassum* spp. occurs mainly in mid-summer via the
341 release of ova and sperm into the water column (Gillespie & Critchley 1999).

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

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

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

348 Magnetic Island is located 8 km off the North Queensland coast at about 22°S experiences a
349 tropical savanna-type climate, with a distinct wet summer and dry winter (opposite to the SWA).
350 The increase in *Sargassum* biomass on Magnetic Island occurs at the beginning of spring to mid-
351 summer, stabilization occurs between mid-summer and mid-autumn, and reduction occurs between
352 mid-autumn and the start of spring (Vuki & Price 1994). The increasing biomass on Magnetic
353 Island occurs during cooler SSTs towards the end of the dry season, and increasing irradiance,
354 stabilization and growth of reproductive organs occurs during the period of highest irradiance and
355 SSTs. In contrast to Point Peron, reproduction on Magnetic Island occurs several months later, with
356 the reduction in biomass occurring during the high SSTs, whereas on Point Peron it occurs during
357 the lowest SSTs and irradiance levels. *Sargassum* beds in Magnetic Island, Australia do not reach
358 their highest MTL until autumn (Vuki & Price 1994). However, a similar relationship between CC
359 and mean thallus length was observed at both study sites. A positive correlation was found between
360 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 (Mattoo 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 43.4°N 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

404 ***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 Rottneest 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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469

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631

632

633 **Table and Figure legends**

634

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

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

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

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

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

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

645

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

648 Figure 2. Diagram presenting the methodology used to map seaweed distribution and the associated
649 benthic habitats at Point Peron using high-spatial resolution satellite imagery and field survey data.

650 Sites: LZ = Lagoon zone, BR = Back reef, RC = Reef crest, and FR = Fore reef zone.

651 Figure 3. Seasonal changes in (a) air temperature (maximum and minimum value) and sea surface
652 temperature, (b) PAR and rainfall, (c) Chl-a and CDOM index, (d) Sea level pressure and Euphotic
653 depth, (e) *Sargassum* canopy cover and fresh biomass at the study sites. *Sargassum* fresh biomass
654 was not available for the sampling trips in September, December 2012 and February 2013. The air
655 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 different 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.

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689 **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 (°C)
SE	Solar exposure (MJ m ⁻²)
MinAT	Minimum air temperature (°C)
SLP	Sea level pressure (hPa)
CDOM	Colored dissolved organic matter
PAR	Photosynthetically active radiation (Einstein m ⁻² d ⁻¹)
SSTs	Sea surface temperatures (°C)
DO	Dissolved oxygen (mg L ⁻¹)
ENVI	Environment for visualizing image
ANOVA	Analysis of variance
PCA	Principle component analysis
MODIS	Moderate Resolution Imaging Spectroradiometer
NASA	The National Aeronautics and Space Administration

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692 **Table 2.**

Year	Month	Season	Salinity	pH	Cond. (mV)	SSTs (°C)	DO (mg L ⁻¹)
2012	Sep	Spr.	36.5 ± 0.29	8.1 ± 0.08 ^{ab}	-65.9 ± 2.89 ^a	17.6 ± 0.2 ^d	7.53 ± 0.28 ^c
	Dec	Sum.	35.8 ± 0.31	8.1 ± 0.05 ^{ab}	-98.8 ± 0.28 ^d	22.1 ± 0.1 ^f	6.07 ± 0.08 ^b
2013	Apr	Aut.	35.5 ± 0.20	8.1 ± 0.06 ^{ab}	-92.5 ± 6.13 ^c	22.8 ± 0.3 ^h	6.08 ± 0.02 ^b
	Jun	Win.	35.5 ± 0.29	8.0 ± 0.06 ^b	-87.8 ± 0.25 ^{bc}	16.3 ± 0.3 ^b	8.27 ± 0.13 ^d
	Sep	Spr.	35.8 ± 0.25	8.1 ± 0.11 ^{ab}	-88.0 ± 0.00 ^{bc}	17.0 ± 0.0 ^c	7.75 ± 0.25 ^c
2014	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
	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}
		<i>F</i>	1.43	3.32	17.01	551.23	30.05
		<i>P</i>	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
2014	Dec	Sum.	10.50 ± 1.56 ^c	0.09 ± 0.01 ^{ab}	0.26 ± 0.03 ^b	1.11 ± 0.04 ^b
	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}	
		<i>F</i>	12.05	13.38	7.38	54.54
		<i>P</i>	< 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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706 **Table 5.**

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Variables	CC	MTL	FB	PAR	Rain	SST	Chl	pH	DO	NO₂⁻	NO₃⁻	PO₄³⁻	NH₄⁺
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				
NO₂⁻	0.05	0.21	-0.31	0.90	-0.73	0.58	-0.53	-0.87	0.15	1			
NO₃⁻	0.80	0.82	0.70	0.02	0.16	-0.10	0.66	0.13	-0.21	-0.17	1		
PO₄³⁻	0.73	0.90	0.69	0.11	-0.07	0.05	0.57	0.18	-0.37	-0.07	0.95	1	
NH₄⁺	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

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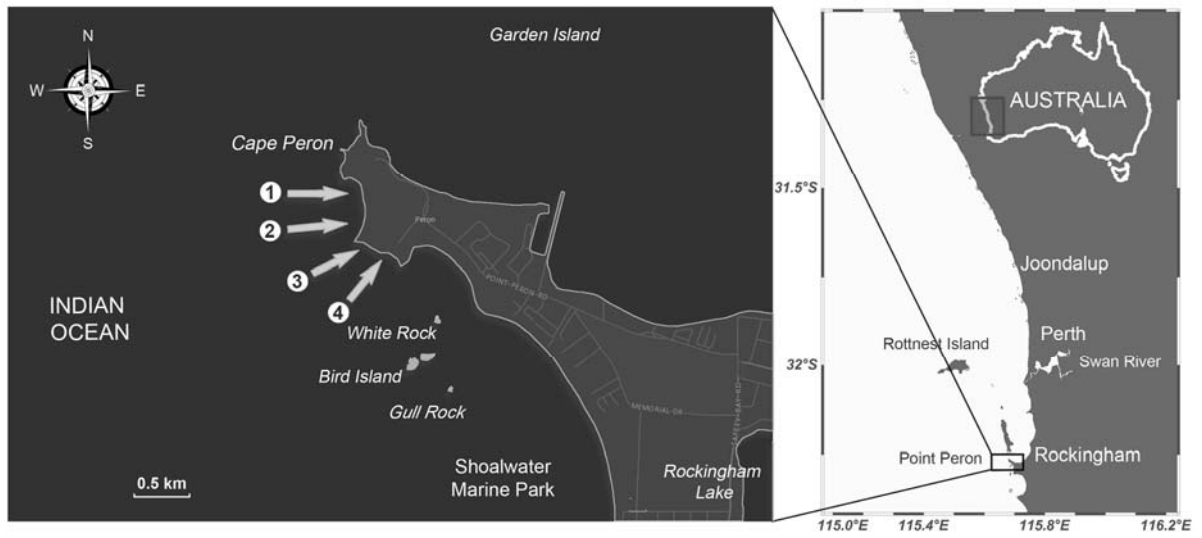
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Table 6.

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

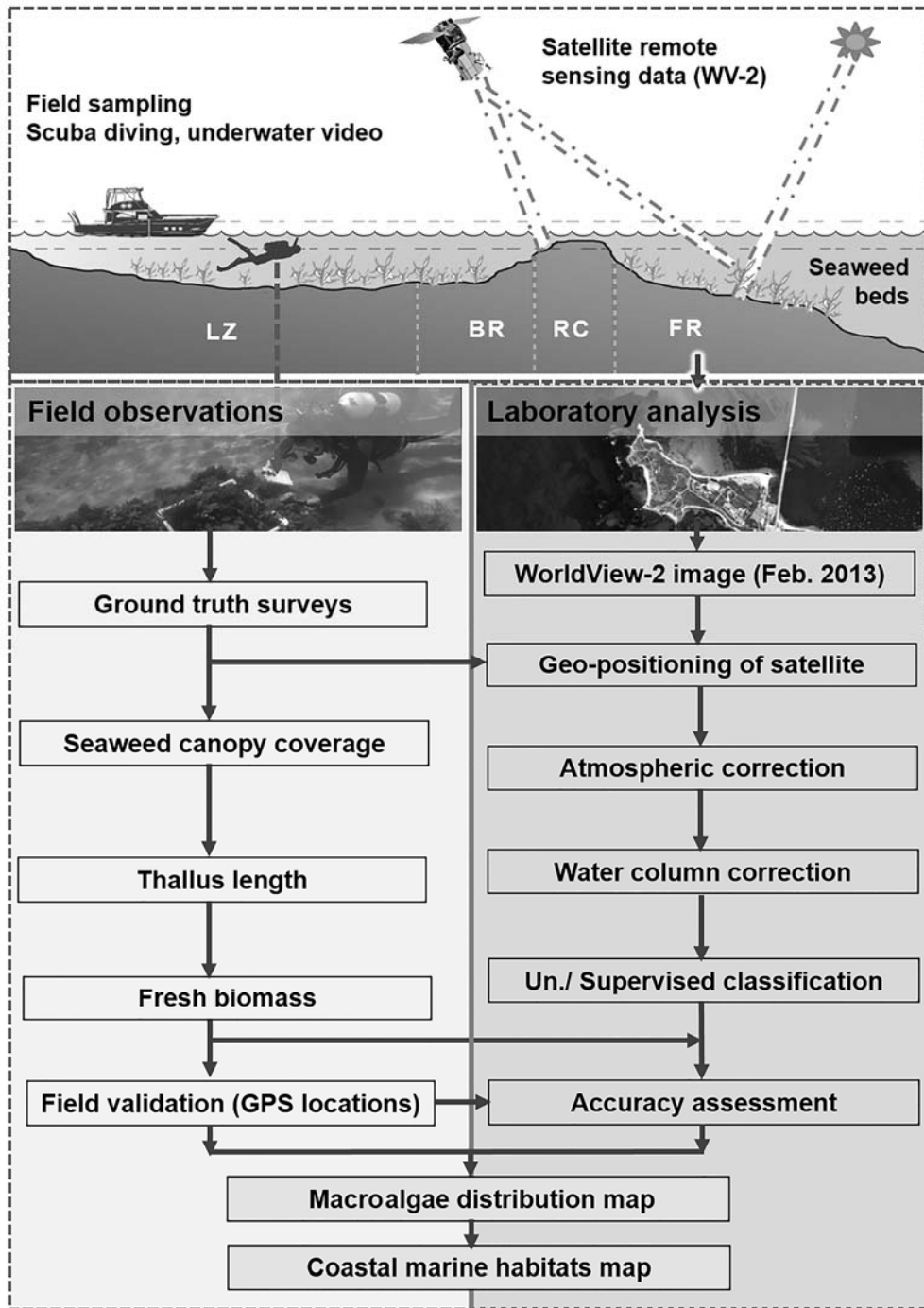
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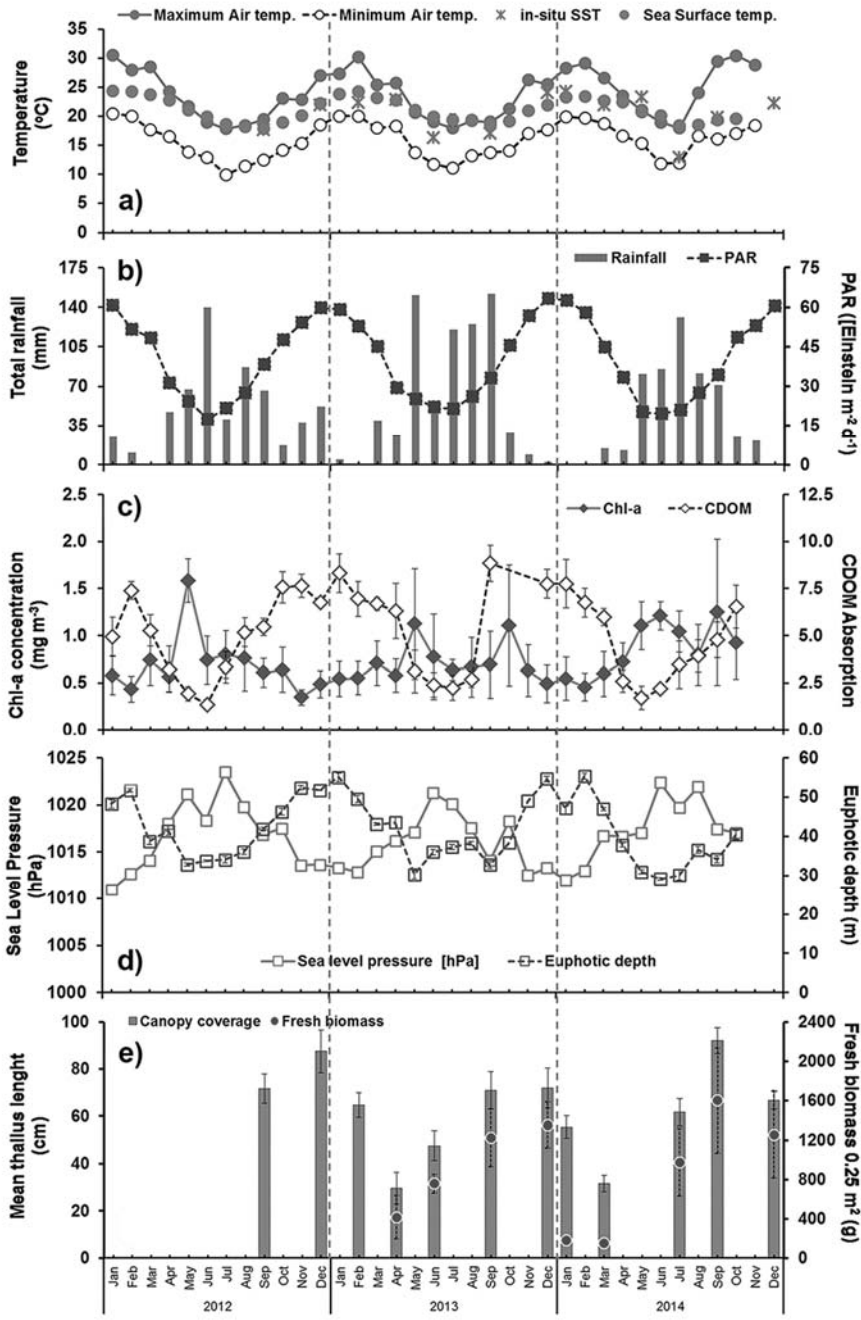
5 **Figure 2**



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8 Figure 3

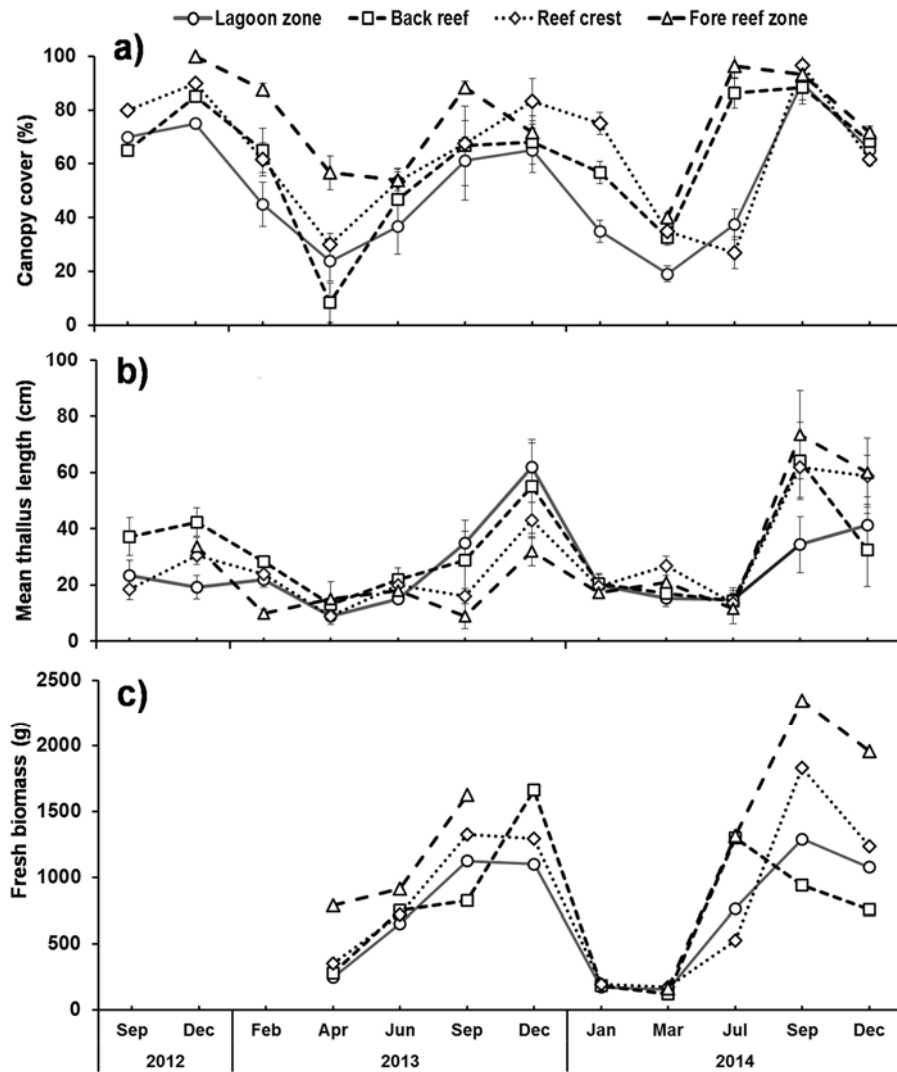


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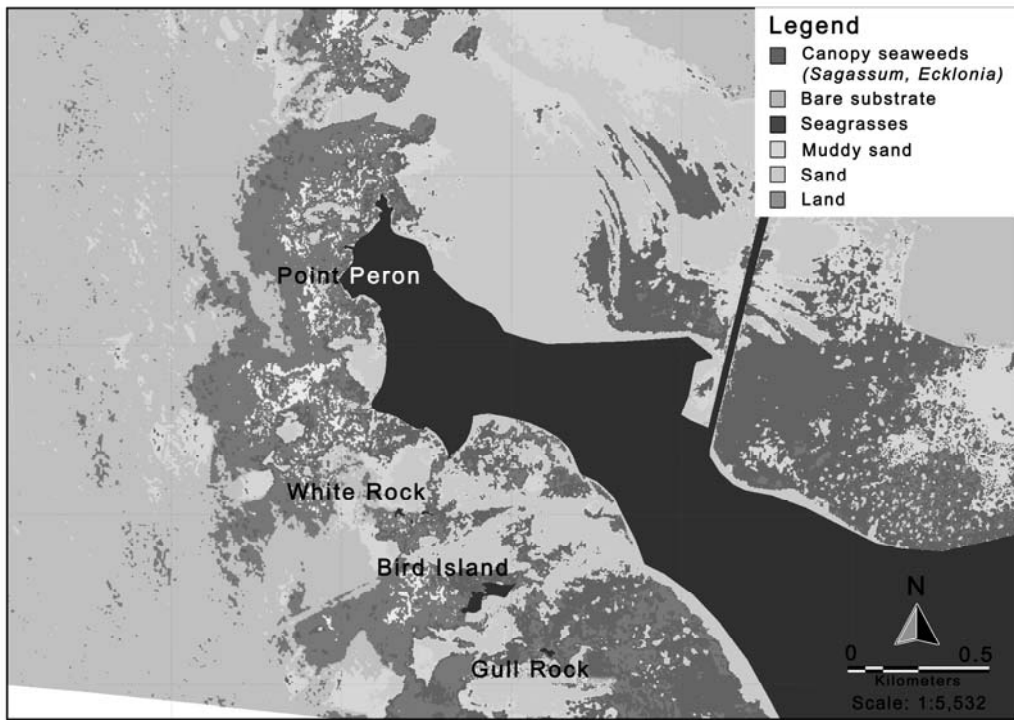
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11 Figure 4



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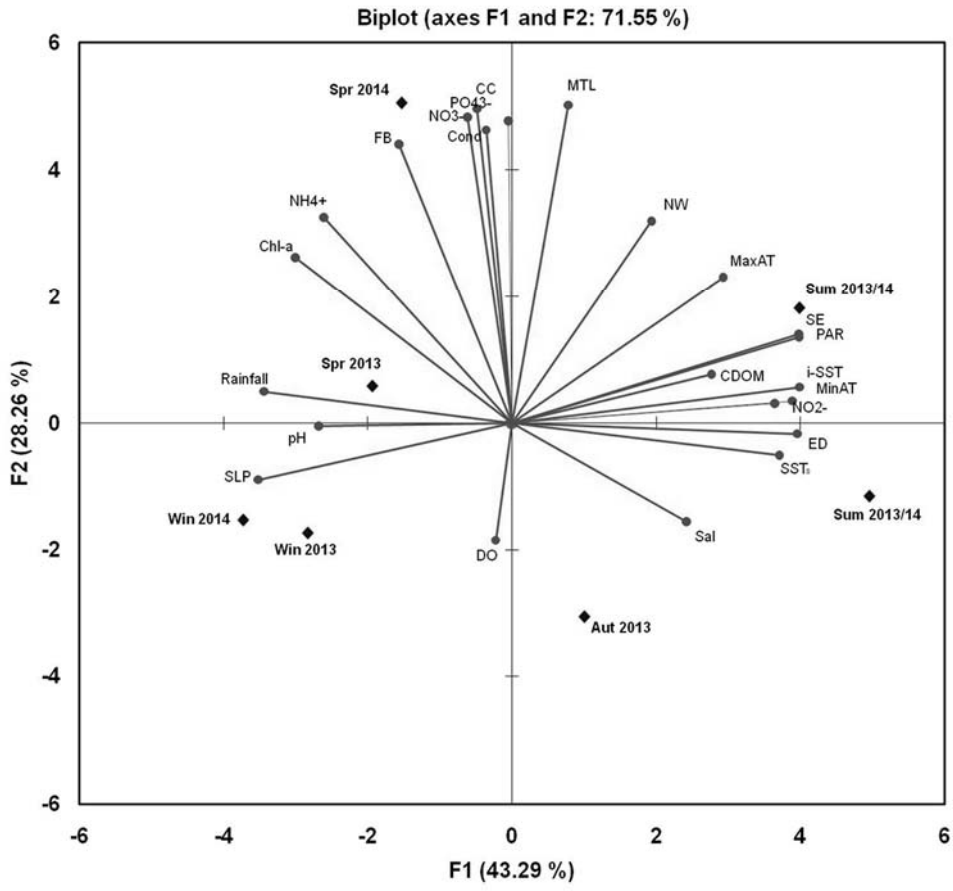
14 **Figure 5**

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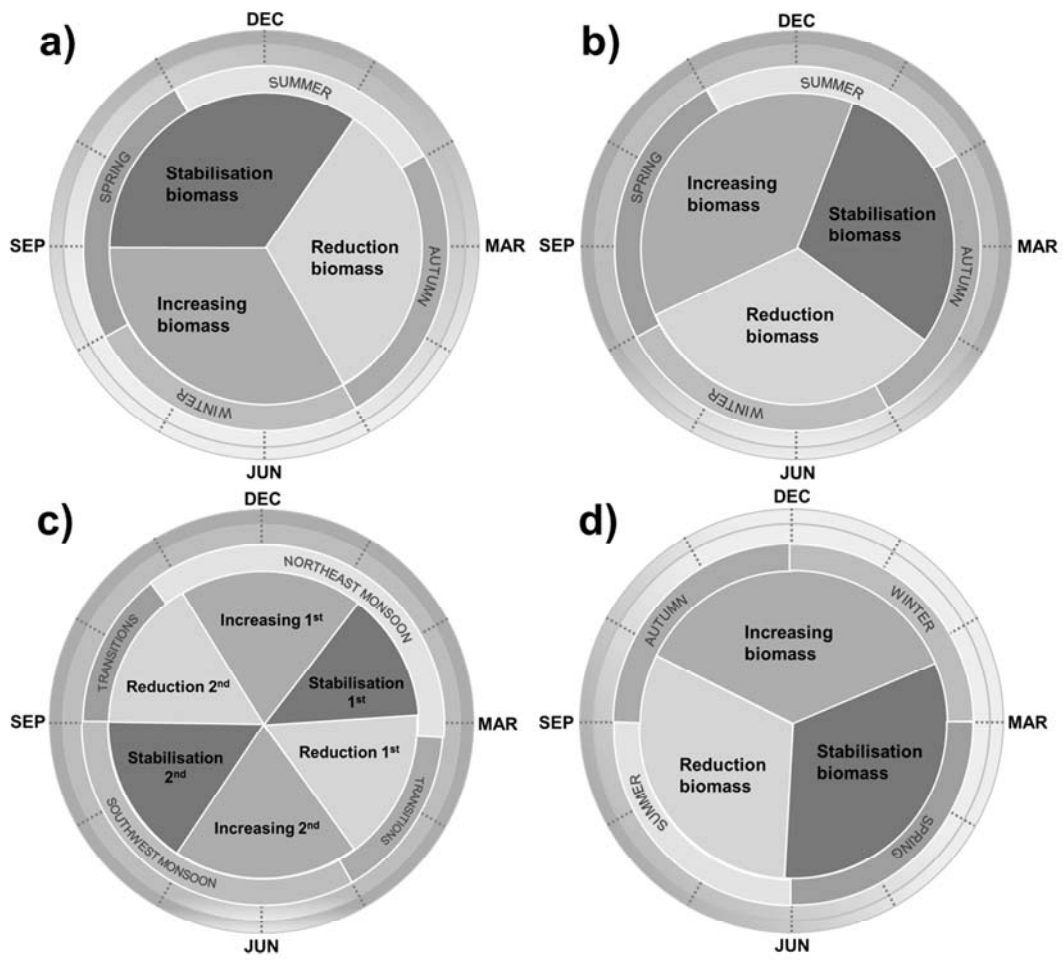
17 **Figure 6**



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20 **Figure 7**

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