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Dynamics and asexual reproduction of the jellyfish *Aurelia coerulea* benthic life stage in the Thau lagoon (northwestern Mediterranean)

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Abstract :

For many jellyfish, the magnitude and timing of medusae blooms are recognized to result from the benthic stage dynamics. However, information on the scyphistomae of jellyfish populations in the wild remains scarce. Here, bi-mensual underwater photoquadrat surveys were combined with scyphistomae sampling and observation to describe the annual (February 2017–January 2018) benthic stage dynamics and asexual reproduction strategy of *Aurelia coerulea* in the Thau lagoon (43°25'31.1"N; 03°42'0.9"E). Our results revealed unexpected seasonal patterns of variation: scyphistoma coverage peaked in the spring (11.6 ± 3.7% on 21st April) and was minimal in the summer and autumn (1.4 ± 1.3% on 10th October). The increase in scyphistoma coverage mainly resulted from an intense production of buds between February and April during the spring rise in water temperature (peak of 12,800 buds m⁻² on 21st April), but scyphistoma coverage appeared to be negatively influenced by the interaction of high summer temperatures and salinities. Strobilation was observed from November to April. It peaked on 17th November, with 33.1% of the scyphistomae strobilating and an average production of 19,100 strobila disks m⁻². However, the low scyphistoma coverage at this time of the year (< 2%) likely limited the intensity of ephyrae liberation and the subsequent medusae bloom. The final population size of *A. coerulea* thus results from a complex interaction of abiotic and biotic factors. Our results bring into question how the different populations of *Aurelia* spp. will respond to the predicted global warming scenarios.

40 **Introduction**

41 Seeming increases in the frequency of jellyfish blooms in some areas of the world
42 (Richardson et al. 2009; Brotz et al. 2012), together with their negative consequences on several
43 marine or littoral economic activities (Graham et al. 2014), have stimulated the scientific
44 interest on jellyfish ecology and bloom formation.

45 Climate change, overfishing, eutrophication, introduction of alien species and habitat
46 modifications have all been pointed out as factors that might boost jellyfish blooms (Purcell et
47 al. 2007; Richardson et al. 2009; Purcell 2012; Boero 2013). However, many blooming
48 jellyfish, mostly scyphozoans, have a complex life cycle, which complicates the identification
49 of the factors controlling the magnitude of their blooms. Previous studies suggested that ocean
50 warming might boost jellyfish benthic stage densities by increasing asexual reproduction and
51 scyphistoma survival, especially for temperate species (Purcell 2005, 2012; Purcell et al. 2007;
52 Richardson et al. 2009), which might originate larger and more frequent blooms.

53 Jellyfish from the *Aurelia* genus, are among the most common scyphozoans that form
54 blooms (Dawson and Martin 2001; Mills 2001). They are widely distributed in the
55 Mediterranean, where they occur mainly in coastal areas and semi-enclosed seas (Mills 2001).
56 Their life cycle comprises a sexual reproductive pelagic stage and an asexual reproductive
57 benthic stage (hereafter referred as pelagic and benthic populations, respectively). The adult
58 medusae reproduce sexually, releasing planulae which settle on natural and artificial hard
59 substrates (Holst and Jarms 2007; Hoover and Purcell 2009). After settlement, the planulae
60 metamorphose into scyphistomae which can display different asexual reproduction modes,
61 including different budding types (motile and non-motile) and podocysts (see Schiariti et al.
62 2014 for details). Under specific environmental conditions scyphistomae produce and release
63 great numbers of pelagic ephyrae, through the process of strobilation. These ephyrae grow in the
64 pelagic environment until they reach the adult medusa stage, ultimately causing pelagic
65 population pulses, that can sometimes result in outbreaks or the so-called jellyfish blooms
66 (Schiariti et al. 2014). The timing and magnitude of the *Aurelia* spp. blooms are therefore
67 dependent on the dynamics of their benthic populations and the environmental factors that
68 control it. Yet, this critical stage of the life cycle has been little investigated so far and very few
69 studies were performed on wild benthic populations of *Aurelia* spp. (Gröndahl 1988; Willcox et
70 al. 2008; Purcell et al. 2009; Malej et al. 2012; Hocesvar et al. 2018). Moreover, the *Aurelia*
71 genus comprises a complex of species, even within the Mediterranean (Dawson and Jacobs
72 2001; Dawson and Martin 2001; Scorrano et al. 2016). Among them, *Aurelia coerulea* has been
73 reported to occur in Japan, China, California, Australia, France and Italy (Dawson et al. 2005;
74 Scorrano et al. 2016). However, information on its wild populations is scarce (Watanabe and
75 Ishii 2001; Miyake et al. 2002; Ishii and Katsukoshi 2010; Makabe et al. 2014).

76 The Thau lagoon (NW Mediterranean) presents the rare particularity to harbor a
77 complete resident population of *Aurelia coerulea*, seemingly isolated from the Mediterranean
78 Sea (Bonnet et al. 2012; Marques et al. 2015a). In this lagoon, ephyrae first appear in the early
79 winter, to give rise to adult individuals at the beginning of spring, when temperature increases
80 (Marques et al. 2015b). Medusae remain in the water column until the late spring, when they
81 reproduce sexually before disappearing from the system. The benthic scyphistomae of *A.*
82 *coerulea* are found mainly on biofouling organisms covering man-made hard substrates. Their
83 local spatial distribution and preferential habitats in the Thau lagoon have been described
84 thoroughly (Marques et al. 2015a). However, their local seasonal population dynamics and their
85 asexual reproduction strategy are still unexplored.

86 Changes in jellyfish scyphistoma population size are regulated by the balance between
87 population growth (*i.e.* the increase in scyphistoma coverage and/or density) and mortality.
88 Population growth might result from the benthic recruitment of planulae, the excystment of
89 podocysts, the production of new scyphistomae by asexual reproduction and the dispersion of
90 detached scyphistomae or motile bud-like tissue particles (Lucas et al. 2012; Schiariti et al.
91 2015). Scyphistomae mortality might be induced by predation, inter- and intra-specific
92 interactions and physiological stress (Lucas et al. 2012). The influences of varied environmental
93 factors on planulae settlement and scyphistomae asexual reproduction have been studied for
94 several species of the *Aurelia* genus, mainly in laboratory experiments (*e.g.* Han and Uye 2010;
95 Purcell et al. 2012; Schiariti et al. 2014; Sokołowski et al. 2016; Hubot et al. 2017). The latter
96 studies suggest that temperature and food availability are likely critical factors controlling
97 benthic population dynamics in *Aurelia* spp., through an influence on the intensity of
98 scyphistoma asexual reproduction. However, the impacts of biotic and abiotic factors on the
99 wild benthic population dynamics of these jellyfish are complex and still poorly known
100 (Willcox et al. 2008; Malej et al. 2012; Hocevar et al. 2018). Density dependent factors,
101 predation and interspecific space competition were also stressed as important potential drivers
102 of scyphistoma densities, both from *in situ* (Miyake et al. 2002; Willcox et al. 2008; Feng et al.
103 2017; Dong et al. 2018) and laboratory studies (Hoover et al. 2012; Takao et al. 2014).

104 In this context, the present study aimed to (1) describe the seasonal dynamics of the
105 benthic population of *A. coerulea* and its annual asexual reproduction strategy in the Thau
106 lagoon and (2) link it with the annual variation of the main biotic and abiotic factors known to
107 affect jellyfish scyphistoma densities and physiology. This would allow identifying the main
108 drivers of *A. coerulea* scyphistoma population size in this lagoon and the importance of its
109 benthic population dynamics on the timing and intensity of its local pelagic medusae blooms.

110

111 **Material and Methods**

112 *Study site and sampling*

113 The Thau lagoon is a semi-enclosed, marine coastal lagoon which covers an area of 75
114 km² and is connected to the Mediterranean Sea by three narrow channels (Fig. 1). It is relatively
115 shallow, with mean and maximum depths of 4 and 10 m, respectively (with the exception of a
116 localized depression of 24 m). The monitoring area chosen for this study (43°25'31.1"N;
117 03°42'0.9"E) is among those with the biggest shaded continuous surfaces (underside surface of a
118 half-submerged fiberglass boat) and, therefore, highest coverage of *A. coerulea* scyphistomae in
119 Thau (Marques et al. 2015a). It is located in the eastern part of the lagoon, where the maximum
120 depth is of 7 m. Seasonal changes in the dynamics and asexual reproduction strategy of the
121 scyphistomae of *Aurelia coerulea* were studied there over one entire year, by 23 SCUBA diving
122 surveys, scheduled every two weeks from February 2017 to January 2018.

123

124 *Environmental parameters*

125 For each sampling date, environmental parameters (temperature, salinity, chlorophyll *a*
126 concentration and mesozooplankton abundance) were monitored. Temperature and salinity were
127 measured with a probe (EC 300 VWR international/ WTW model 350i), right above the
128 scyphistoma monitoring site, at about 0.5 m depth. Chlorophyll *a* concentration and
129 mesozooplankton abundance were determined from samples collected at a nearby site
130 (43°23'59.1''N; 03°36'37.2''E, Fig. 1). Chlorophyll *a* concentration was measured from 150 ml
131 water samples, collected in triplicate. Water was filtered on Whatman GF/F filters and stored at
132 -30°C until pigment extraction in acetone and chlorophyll *a* concentration measurement by
133 spectrofluorimetry (LS 50B Perkin Elmer). Mesozooplankton samples were collected near the
134 surface, by horizontal towing, using a modified WP2 plankton net (1.2 m long, 50 cm opening
135 area and 200-µm mesh). Samples were immediately preserved in 4% buffered formaldehyde
136 until further analysis in the laboratory. Mesozooplankton abundance was determined by visual
137 counting of organisms under dissecting microscope (Olympus SZX7 – ILLT).

138

139 *Dynamics of the benthic stage*

140 The temporal dynamics of the benthic stage of *A. coerulea* on the study site was
141 estimated at a depth of 2 – 4 m, by measuring the scyphistoma coverage (%) using an
142 underwater photoquadrat method. For this, four distinct zones of 15 × 15 cm (hereafter called
143 photoquadrats) were selected on the surface of the wreck, according to four criteria: a minimum
144 distance of 2 m between photoquadrats and, within each of them, a flat surface area, the absence
145 of large biofouling organisms (*e.g.* mussels, oysters, sponges, etc.) and the presence of at least a
146 small patch of *A. coerulea* scyphistomae. Their respective positions were identified by
147 scratching the surface of the wreck. Underwater photographs of all four zones were taken at
148 each survey date using a Canon PowerShot G16 camera with Ikelite Canon G16 Compact
149 Housing non-TTL case and a Riff TL-WW light. For this, a PVC structure forming a square of

150 15 × 15 cm was adapted to the camera case in order to keep a constant distance between the
151 camera and the analysed surface. Only the same central square area of 11 × 11 cm (121 cm²)
152 was analysed in each photoquadrat to avoid shaded areas. Photographs were pre-treated with
153 Gimp 2.8.22 to improve contrast and analysed using a purpose-built image analysis software in
154 MATLAB (IZS: Image Zone Selector, Tremblay, unpublished). The IZS uses the different
155 colour channels of the images in order to identify, select and determine the percent coverage of
156 the scyphistomae (Fig. 2). All images were also visually inspected and corrections were made
157 when necessary. To avoid the bias linked to software limitations in individual scyphistomae
158 identification, six photographs per photoquadrat, from different times of the year (embracing
159 minimum, maximum and intermediate values of scyphistoma coverage), were re-analysed and
160 scyphistomae were visually counted. The number of scyphistomae in the photographs were
161 plotted against the corresponding value for scyphistoma coverage and a linear regression line
162 was fitted (Fig. 3). The regression equation was used to estimate the number of scyphistomae in
163 all photographs. Scyphistoma densities (in ind cm⁻²) in each photoquadrat (121 cm²), were then
164 estimated over the entire study period following the equation

165 (eq.1)
$$Density = \frac{88.5 + 6542.1 * Scyphistoma\ coverage\ (\%) * 100^{-1}}{121}$$

166 Where 88.5 and 6542.1 are the y-intercept and slope of the regression line, respectively.

167 When determining scyphistoma coverage by image analysis, one biofouling species, the
168 red algae *Peyssonnelia* sp., was identified as an important substrate for scyphistoma fixation,
169 with potential influence on the dynamics of the benthic population of *A. coerulea*. Therefore,
170 the IZS was also used to assess its coverage (%), by changing the values of the colour channels.
171 All images were visually inspected and corrected when necessary.

172

173 *Asexual reproduction strategies*

174 To investigate the reproductive activity of the benthic population of *A. coerulea* at each
175 survey date, three samples of scyphistomae, attached to the underside surface of oyster or
176 mussel shells, were collected in the monitoring site. Sampling was done on the same half-
177 submerged fiberglass boat, at depths between 2 and 6 m, at few meters away from the
178 photoquadrats. Scyphistomae were brought alive to the laboratory and counted under a
179 dissecting microscope (Olympus SZ40; Olympus KL 1500 LCD), using a small mesh net (mesh
180 0.65 cm²) as a counting grid. Since density dependent effects were previously demonstrated to
181 influence population growth of *Aurelia* scyphistomae (e.g. Melica et al. 2014; Schiariti et al.
182 2015), the effect of density was reduced by selecting only the most dense area of each sample
183 for asexual reproduction assessment (i.e. 3 to 22 sections of the counting grid with a mean
184 density of 44.4 ± 16.6 scyphistomae cm⁻², to obtain a minimum of 100 scyphistomae per
185 sample). Asexual reproduction modes were identified after Schiariti et al. (2014), using needles

186 to inspect each individual scyphistoma and recording the following data for each sample: the
 187 total number of scyphistomae, their density (ind cm⁻²), the percentage of non-reproductive
 188 scyphistomae, the percentage of scyphistomae producing non-motile buds (NMB, specifying the
 189 percentage of scyphistomae producing 1, 2 or more buds), the number of podocysts per
 190 scyphistoma, the percentage of strobilae and the number of disks per strobila. The percentage of
 191 scyphistomae producing non-motile buds (NMB) comprises three reproductive modes: typical
 192 lateral budding, lateral budding by means of stolons and reproduction from parts of
 193 stolons/stalks (see Schiariti et al. 2014 for details). We pooled them since their distinction is
 194 often difficult in wild samples and they have an equivalent impact on scyphistomae population
 195 dynamics (Schiariti et al. 2014), as they all produce sessile buds right beside the mother
 196 scyphistoma and appear to respond to the same environmental clues (Schiariti et al. 2015).

197

198 *Asexual reproduction effort*

199 The asexual production (*AP*) of buds or strobila disks per surface area (m²) was
 200 estimated for each sampling date (*t_i*) as:

201 (eq.2)
$$AP(t_i) = \frac{p * n * d * 10^3}{100}$$

202 Where *p* is the percentage of the scyphistomae exhibiting each asexual reproduction
 203 strategy (*i.e.* production of NMB or strobilation), *n* is the mean number of reproductive outputs
 204 (*i.e.* buds or strobila disks) produced per scyphistoma and *d* is the mean density of scyphistomae
 205 estimated from the four photoquadrats (eq.1). The total number of ephyrae released (ind m⁻²)
 206 from the study site during the whole study period (assuming a continuous strobilation period
 207 between November and April), was estimated based on Ishii and Katsukoshi (2010) and
 208 Makabe et al. (2014). The ephyrae liberation at each sampling date (*EL_{t_i}*, ind m⁻²) was
 209 calculated as:

210 (eq.3)
$$EL_{t_i} = AP(t_i) * R^{-1}$$

211 Where *R* is the residence time of ephyrae (days). *R* is dependent on temperature (*T*) and was
 212 estimated based on *in situ* temperatures in Thau, using the equation obtained by laboratory
 213 experiments on *A. coerulea* from Japan, performed by Makabe et al. (2014), as:

214 (eq.4)
$$R = 109 * e^{-0.221 * T}$$

215 The number of ephyrae released (ind m⁻²) from the study site between *t₀* and *t₁* was then
 216 estimated as:

217 (Eq.5)
$$EL_1 = (EL_{t_0} + EL_{t_1}) * (t_1 - t_0) * 2^{-1}$$

218 And that during the whole study period was estimated as:

219 (Eq.6)
$$TEL = EL_1 + EL_2 + \dots + EL_n$$

220

221 *Statistical analysis*

222 For biological variables (scyphistoma coverage, percentage of scyphistomae adopting
223 each reproductive strategy, number of buds and disks produced per scyphistoma and number of
224 podocysts per scyphistoma) differences among sampling months and photoquadrats (for
225 scyphistoma coverage) were tested by one-way ANOVAs, when variables presented normal
226 distribution and homogeneity of variances (tested by Shapiro and Bartlett tests). Otherwise,
227 Kruskal-Wallis tests were used and *post hoc* tests were carried out using Dunn's test for
228 multiple comparisons. Temporal and spatial autocorrelations were tested by examination of
229 ACF plots and by Mantel tests from *ade4* package (Dray and Dufour 2007). Although
230 scyphistoma coverage of *A. coerulea* differed significantly between the four photoquadrats
231 (ANOVA, $F(3, 83) = 5.33$, $P = 0.002$), temporal or spatial autocorrelations were not detected
232 so the data from all photoquadrats was grouped for temporal trend analyses. Generalized linear
233 models (GLM, using linear and logistic regressions) were employed to assess the contribution
234 of temperature, salinity, chlorophyll *a* concentration and mesozooplankton abundance
235 (explanatory variables) on the scyphistoma coverage, NMB and podocysts per scyphistoma
236 (response variables). The minimal adequate model was achieved by a stepwise deletion of the
237 least significant terms from the maximal model, with interactions included. For each fitted
238 model, we calculated AIC and selected the model presenting the lowest AIC. The final models
239 were validated by examination of plots of residuals versus fitted values for the entire model
240 (Harrison et al. 2018). The influence of the environmental parameters on the strobilation activity
241 was assessed by Hurdle models from *pscl* package (Zeileis et al. 2008), due to the presence of
242 many zeros in the dataset. Spearman correlations tests were used to investigate the relationship
243 between the scyphistoma percent coverage with the NMB and the number of podocysts per
244 scyphistoma. The presence of the red algae was observed in photoquadrats 1, 2 and 3. The
245 relationship between scyphistoma and red algae coverages in these three photoquadrats was
246 studied by Pearson correlation test. All statistical analyses were performed using the software R
247 Studio Version 1.0.143 (R Core Team 2017) and taking $\alpha < 0.05$ as the limit for statistical
248 significance.

249

250 **Results**

251 *Environmental conditions in the Thau lagoon*

252 The annual pattern of temperature variation in Thau followed the normal trend in
253 temperate regions, with lower values in the winter and higher values in the summer (Fig. 4).
254 During the study period, temperature at the study site ranged from 7.6 °C (on December 13th
255 2017 and January 29th 2018) to 25.8 °C on June 27th 2017. Salinity varied between 35.0 (on
256 February 24th 2017) to 39.6 (on November 09th 2017), with a drastic decrease at the end of the
257 study period, where salinity dropped to 33.9 (on January 29th 2018). The concentration of
258 chlorophyll *a* and the abundance of mesozooplankton were highly variable over the year.

259 Chlorophyll *a* concentration ranged from 0.5 $\mu\text{g L}^{-1}$ (on January 10th 2018) to 2.8 $\mu\text{g L}^{-1}$ (on
260 February 24th 2017) without any clear seasonal pattern, while mesozooplankton abundance
261 varied between 94 and 166 607 ind m^{-3} (on April 21st 2017 and June 27th 2017, respectively),
262 with an intermediate peak of abundance at 10 524 ind m^{-3} (on March 10th 2017). Due to logistic
263 constraints, chlorophyll *a* concentration and mesozooplankton abundance were not measured in
264 August 2017.

265

266 *Dynamics of the benthic stage*

267 Scyphistoma coverage in the photoquadrats varied between a minimum of 0.3% and a
268 maximum of 18% of the photographed area (both observed in photoquadrat 2, Fig. 5), which
269 corresponds to a range in density of 0.25 to 10.3 scyphistomae cm^{-2} . The overall mean of
270 scyphistoma coverage on the study site fluctuated significantly during the study period
271 (ANOVA, $F(1, 21) = 11.2$, $P = 0.003$), with a minimum average value ($1.4 \pm 1.3\%$, $n = 4$) on
272 October 10th 2017 and a maximum one ($11.6 \pm 3.7\%$, $n = 4$) on April 21st 2017. Temporal
273 variations differed slightly among photoquadrats: scyphistoma coverage peaked in April in
274 photoquadrats 1, 3 and 4 and in May – June in photoquadrat 2. However, all photoquadrats
275 presented low scyphistoma coverage between September and November. Scyphistoma coverage
276 for this period was below 1%, with the exception of photoquadrat 4, where it remained above
277 3% during all the study period.

278

279 *Asexual reproduction strategy*

280 During the whole study period, the mean percentage of scyphistoma reproducing
281 asexually varied between 2.2 ± 1.5 to $33.5 \pm 4.9\%$ ($n=3$, per sampling date) (Fig. 6).
282 Scyphistoma-to-scyphistoma reproduction (NMB) was the most important asexual reproduction
283 mode observed. The percentage of scyphistomae producing buds varied between sampling
284 dates (Kruskal-Wallis test, $H_{24} = 53.5$, $P < 0.001$). It was maximum between March and May
285 2017, when 15.0 ± 6.7 to $19.4 \pm 5.2\%$ ($n = 3$, per sampling date) of the scyphistomae were
286 producing buds. The asexual production (AP_{ii}) of buds was higher in this period, with a peak on
287 the April 21st when 12 800 buds m^{-2} were produced (Fig. 7). The percentage of scyphistomae
288 producing buds was then highly variable until November (4.6 ± 1.1 to $25.2 \pm 7.3\%$, $n = 3$, per
289 sampling date), with noticeable peaks above 19% in July, September and October (Fig. 6).
290 During the study period, most of the budding scyphistomae ($92.8 \pm 17.3\%$, $n = 69$) produced
291 just one bud at a time, but simultaneous production of several buds per scyphistoma was
292 observed all year round (except in January 2018). The maximum number of buds observed for a
293 given scyphistoma (4), was registered in September. However, the production of buds observed
294 per scyphistoma was highest in October: among the budding scyphistoma, $13.7 \pm 5.3\%$ ($n = 3$,
295 per sampling date) produced two buds and $4.2 \pm 4.5\%$ ($n = 3$, per sampling date) produced 3 or

296 more buds. In November, the percentage of scyphistomae producing buds decreased sharply and
297 reached its lowest value ($0.4 \pm 0.7\%$, $n = 3$) on November 17th, when the production of buds
298 was also minimum (70 ind m^{-2} , Fig. 7). This percentage remained low ($< 9\%$) until the end of
299 the study period (in January 2018).

300 The average number of podocysts per scyphistoma ranged from 0 to 0.5 ± 0.4 ($n = 3$,
301 per sampling date), showing high variability between samples from the same date. No
302 significant difference was observed among sampling dates for this reproduction mode (Kruskal-
303 Wallis test, $H_{22} = 24.8$, $P = 0.3$).

304 Strobilation was observed from February to April 2017 and from November 2017 to
305 January 2018 suggesting that, ephyrae production by *A. coerulea* scyphistoma likely occurs
306 from late autumn to early spring in the Thau lagoon (Fig. 6). During this period, the percentage
307 of scyphistomae strobilating varied significantly between sampling dates (Kruskal-Wallis test,
308 $H_{24} = 56.7$, $P < 0.001$): less than 5.5% of the population strobilated irrespective of the month,
309 except in November when this percentage increased to $33.1 \pm 4.2\%$ ($n = 3$, on November 17th).
310 During the strobilation period, the maximum number of disks produced per strobila was of 11,
311 with a general mean of 3.7 ± 1.4 ($n = 16$) disks per scyphistoma. No significant differences
312 between sampling dates were recorded in the number of disks formed per scyphistoma
313 (Kruskal-Wallis test, $H_7 = 9.9$, $P = 0.2$). As a result, the estimated asexual production (AP_{it}) of
314 strobila disks presented a short but conspicuous peak in November 17th 2017 ($19\,100 \text{ disks m}^{-2}$),
315 but was also high in spring, due to high scyphistoma density (Fig. 7). During this season, it
316 peaked at $11\,800 \text{ disks m}^{-2}$ on February 24th 2017 and decreased afterwards to $1\,500 \text{ disks m}^{-2}$
317 on April 7th 2017, in parallel with an increase of buds production. Assuming a continuous
318 strobilation period between November and April, the total number of ephyrae liberated (TEL)
319 from the study site during the whole study period was estimated at $82\,301 \text{ ind m}^{-2}$.

320

321 *Drivers of the dynamics and asexual reproduction*

322 Scyphistoma coverage was positively influenced by temperature (GLM, $P = 0.03$) but
323 responded negatively to joint increases in temperature and salinity (GLM, $P = 0.03$) (Table 1).
324 No significant correlation was found with the other environmental variables tested. The
325 coverage of *A. coerulea* scyphistomae and that of the red algae (*Peyssonnelia* sp.) were
326 positively correlated (Pearson correlation, $t_{19} = 5.06$, $P < 0.01$).

327 With regards asexual reproduction modes, scyphistoma coverage was significantly
328 correlated only with the number of podocysts per scyphistoma (Spearman correlation, $S =$
329 853.7 , $P = 0.004$), which was similarly affected by temperature (positive correlation, GLM, $P =$
330 0.02) and by the interaction of temperature and salinity (negative correlation, GLM, $P = 0.02$)
331 (Table 1). Although NMB was the highest before April, *i.e.* before the peak of scyphistoma
332 coverage, it was not correlated with the latter variable (Spearman correlation, $S = 1746$, $P =$

333 0.53). Indeed, scyphistoma coverage dropped from spring to summer, while NMB remained
334 high and even peaked when scyphistoma coverage was at its minimum. Moreover, none of the
335 environmental variables tested was significantly correlated with the variability in NMB.

336 Strobilation intensity was found to be affected only by temperature (Zero Hurdle model,
337 $P = 0.046$), with the probability of a scyphistoma to strobilate increasing by 0.75 times for each
338 decreasing °C (Table 2). Indeed, the high peak of strobilation observed in November followed a
339 sharp decrease in temperature (of 8.3 °C) from October 20th to November 17th (Fig. 4).

340

341 **Discussion**

342 *Dynamics of the Aurelia coerulea benthic stage*

343 Extensive patches of *Aurelia coerulea* scyphistomae cover a variety of anthropogenic
344 submerged substrates in the Thau lagoon (Marques et al. 2015a), which allowed *in situ*
345 evaluation of the intra-annual dynamics of its population at the benthic stage. Estimated
346 densities in this study varied between 0.25 to 10.3 scyphistomae per cm⁻², in accordance with
347 previous estimations for the same species in Japan, of 0.005 to 18 scyphistomae per cm⁻²
348 (Miyake et al. 2002; Ishii and Katsukoshi 2010), but also for other species of the *Aurelia* genus,
349 for which mean densities of 7.3 ± 0.6 and 31.3 ± 1.3 scyphistomae cm⁻² were registered in two
350 sites in Tasmania (Willcox et al. 2008), and of 6 to 27 scyphistomae cm⁻² in the Adriatic Sea
351 (Malej et al. 2012; Hocevar et al. 2018). Nonetheless, comparisons among sites are to be
352 considered with caution, because scyphistomae are usually distributed in patches, so the density
353 value changes according to the total area assessed (Miyake et al. 2002) and the substrate type
354 considered. In this study, for instance, scyphistoma density estimates from the photoquadrat
355 survey were much lower than those in the samples used to assess asexual reproduction strategies
356 (9.9 to 78.8 scyphistomae cm⁻²). Still, these latter values are in accordance with those (88
357 scyphistomae cm⁻²) reported by studies assessing the micro-distribution of scyphistomae on
358 bivalve shells (Miyake et al. 2002).

359 The intra-annual pattern of demographic variation for *A. coerulea* scyphistomae in Thau
360 is characterized by a peak in coverage in spring, followed by a decrease until minimum values
361 are reached in the summer and autumn and a progressive recovery over the winter. This trend is
362 not in agreement with previous observations made for *A. coerulea* (Ishii and Katsukoshi 2010;
363 Makabe et al. 2014) and other *Aurelia* spp. (*e.g.* Gröndahl 1988; Willcox et al. 2008; Malej et
364 al. 2012; Hocevar et al. 2018): scyphistomae densities in the *Aurelia* genus usually peak from
365 spring to summer and are at their lowest in both the autumn and winter months. These
366 differences are surprising because temperature appeared to positively affect the population size
367 of scyphistoma in the wild (Willcox et al. 2008; Hocevar et al. 2018) and this study was
368 conducted in an enclosed coastal habitat with a temperature range (7.6 to 25.8°C) similar to
369 those where investigations were made for *A. coerulea* in Japan (9°C to 29°C, Ishii and

370 Katsukoshi 2010; Makabe et al. 2014) or, for example, for *A. aurita* in the Adriatic (6.3 °C to
371 27.4 °C, Hocevar et al. 2018). Although scyphistoma coverage was positively correlated with
372 temperature in Thau, the interaction of high temperatures with high salinities appeared to be
373 detrimental to *A. coerulea* scyphistoma. Indeed, the salinity range observed in our study site
374 (35.0 to 39.6) was above that reported for the studies conducted in Japan (up to 33, Ishii and
375 Katsukoshi 2010; Makabe et al. 2014), but similar to that reported in the Adriatic (32.8 to ca.
376 38, Hocevar et al. 2018), where the negative influence of salinity on scyphistoma density was
377 also pointed out. So far, no clear negative effect of salinity was ever found on *Aurelia* spp.
378 scyphistoma survival (Willcox et al. 2007; Holst and Jarms 2010; Widmer et al. 2016) nor
379 somatic growth (Willcox et al. 2007; Hubot et al. 2017), except when reaching freshwater
380 conditions (Holst and Jarms 2010). However, most laboratory studies so far, focused on the
381 influence of fresh water inputs (*e.g.* Holst and Jarms 2010; Amorim et al. 2018) and were
382 therefore performed at low salinities (<37) *i.e.* lower than the values registered in our study,
383 especially in the summer (ca. 39). Still, Hubot et al. (2017) assessed the influence of relatively
384 high salinities on the asexual reproduction and somatic growth of *Aurelia coerulea* from the
385 Adriatic Sea and reported a decrease in physiological performances between 24 and 37 in
386 salinity. To our knowledge, laboratory experiments on the effect of salinities > 37 have never
387 been performed with *A. coerulea* but our results suggest that high summer salinity associated
388 with high temperature conditions might be detrimental to its scyphistomae, contributing to the
389 benthic population dynamics observed in the Thau lagoon.

390 Food availability is often pointed as one of the most important drivers of jellyfish
391 population growth, boosting the production of new scyphistomae (Han and Uye 2010; Schiariti
392 et al. 2014; Ikeda et al. 2017). During this study however, mesozooplankton abundance did not
393 statistically influenced scyphistoma coverage nor NMB. The few existing studies so far on the
394 diet of *Aurelia* spp. scyphistomae suggested that they feed on microzooplankton (Kamiyama
395 2011, 2013) and small mesozooplankton species (*e.g.* copepods, cladocerans, gelatinous
396 zooplankton; Östman 1997) . Therefore, only a portion of the potential prey of *A. coerulea*
397 scyphistomae was surveyed in the present work. To improve our understanding of the influence
398 of food availability on the *in situ* dynamics of the benthic stage of this species, further
399 investigations on scyphistoma diet associated with micro-, mesozooplankton and epibenthic
400 prey abundance *in situ* are still required.

401 Apart from the already discussed impact of temperature and salinity on scyphistoma
402 coverage, other interspecific interactions, such as predation and room for expansion, can also
403 play an important role in reducing the density of jellyfish benthic populations (*e.g.* Willcox et
404 al. 2008; Takao et al. 2014; Feng et al. 2017). Different species of benthic organisms are able to
405 feed on *Aurelia* spp. scyphistomae. Some of these predators might even consume more than 600
406 scyphistomae per day (*e.g.* the crab *Hyastenus diacanthus*) (Takao et al. 2014). In Thau, several

407 potential predators were identified in the photoquadrats (sea stars of the genus *Asterina*,
408 gasteropods: *Ocenebra erinaceus* and *Hexaplex trunculus*, nudibranchs: *Felimare villafranca*
409 and sea urchins: *Paracentrotus lividus*), but the consumption of scyphistomae by these
410 organisms has never been reported so far. Fishes feeding on benthic prey might also consume *A.*
411 *coerulea* scyphistomae, through direct or indirect predation (*i.e.* targeting their fixation
412 substrate, like bivalves). Their predation pressure might be high enough to significantly affect
413 scyphistomae coverage, as shown in predation experiments involving the sparid *Sparus aurata*
414 (Marques et al. 2016). The exact importance of predation in controlling the population of *A.*
415 *coerulea* scyphistomae in the Thau lagoon however remains to be assessed.

416 Biofouling organisms compete for space with jellyfish scyphistomae, so their densities
417 frequently have negative effects on scyphistoma population growth (Watanabe and Ishii 2001;
418 Willcox et al. 2008; Makabe et al. 2014; Feng et al. 2017). Nevertheless, *Aurelia* spp. appear to
419 be more resilient than other scyphozoans, mainly due to their asexual reproduction modes (Feng
420 et al. 2017, 2018): their scyphistomae can adhere to the surface of different organisms by
421 producing different types of budding, stolons, and can even detach themselves from the
422 substrate and drift to another one (Schiariti et al. 2015). Colonization of other benthic organisms
423 by jellyfish scyphistomae is frequent (Miyake et al. 2002; Willcox et al. 2008; Toyokawa et al.
424 2011) and even suggested as a promoter of settlement and proliferation for *A. coerulea*
425 scyphistomae in China (Dong et al. 2018). In Thau, scyphistomae of *A. coerulea* were
426 recurrently found attached to red algae (*Peyssonnelia* sp.): in three out of the four photoquadrats
427 surveyed in the present work but also in surrounding areas where scyphistomae were
428 particularly abundant (Marques R., personal observation). The decline of this algae observed in
429 the study site in the summer might have contributed to the concomitant reduction of the benthic
430 population of *A. coerulea*. These results corroborate the importance of interspecific interactions
431 and settling substrates availability in the population dynamics of *Aurelia* spp.. Future studies on
432 the *in situ* demography of the benthic stage of jellyfish should, therefore, be designed to
433 embrace the variability of their settling substrates and the potential role on the population
434 dynamics of certain biofouling organisms that provide adequate fixation substrate for their
435 scyphistomae.

436

437 *Contribution of the asexual reproduction*

438 The growth of jellyfish benthic population, results from both the production of new
439 scyphistomae by asexual reproduction (*e.g.* via the production of non-motile buds or the
440 excystment of podocysts) and the recruitment of pelagic planulae to the sea floor (Schiariti et al.
441 2015).

442 In the Thau lagoon, *A. coerulea* planulae are usually produced between May and June
443 (Bonnet et al. 2012), when they swim to the bottom and settle on the substrate. Pelagic life

444 duration before settlement is usually short (typically less than 4 days, Lucas et al. 2012),
445 probably to decrease planulae vulnerability to predation in the pelagic environment (Lucas et al.
446 2012). Thus, we expected an increase of scyphistoma coverage after planulae release in 2017,
447 which was not detected. Instead, scyphistoma coverage started to decrease in May 2017, when
448 the first medusae with planulae about to be released were spotted in the lagoon (Marques R.,
449 personal observation). Therefore, the recruitment of new scyphistomae by planulae fixation
450 does not contribute most to the observed benthic population dynamics, at least at our study site.
451 In *Aurelia* spp., planulae are thought to play an important role in the expansion of populations
452 to new habitats through pelagic dispersion (Holst and Jarms 2007; Lucas et al. 2012). This is
453 probably the case in Thau, where the presence of *A. coerulea* scyphistomae over the entire
454 lagoon area might result from the dissimination of planulae, together with the widespread
455 availability of suitable settling substrates and favourable hydrographic characteristics in the
456 lagoon (Marques et al. 2015a).

457 Although podocysts excystment was suggested to play an important role in bloom
458 formation for some jellyfish species (*e.g. Nemopilema nomurai*; Kawahara et al. 2013), its
459 impact on scyphistoma density was very limited in the population of *A. coerulea* investigated so
460 far (*e.g.* Thein et al. 2012). In this species, podocysts appear to lie in ensuring the survival of
461 the benthic population under unfavourable conditions and providing protection from predators
462 (Arai 2009; Thein et al. 2012; Hubot et al. 2017). In our study, the number of podocysts per
463 scyphistoma was significantly correlated with scyphistoma coverage and it appears to follow the
464 same environmental forcing, which may suggest a significant contribution of podocysts for the
465 increasing of the benthic stage. Nevertheless, until the exact production, excystment and
466 residency time are assessed for the species in the wild, it is impossible to tell whether there were
467 more scyphistomae at our study site because more podocysts were produced or *vice-versa*. For
468 this reason, the significance of the contribution of podocysts excystment to the increase of
469 scyphistoma coverage of *A. coerulea* in Thau remains elusive.

470 The production of NMB, on the contrary, could be the main responsible for local
471 increases of scyphistoma coverage. Although the temporal trend of NMB and scyphistoma
472 coverage were not significantly correlated (with a mismatch during the summer), a high
473 percentage of scyphistomae produced buds in March and April. Estimates for bud production
474 intensity on the study site matched the peak of scyphistoma coverage, supporting the hypothesis
475 that the bud production is the main asexual mode responsible for benthic population increases in
476 Thau. During the end of spring and beginning of summer, both NMB and scyphistoma coverage
477 decrease, but more than 10% of the scyphistomae produced continuously at least one bud per
478 scyphistoma, and it even peaked in September, when scyphistoma coverage was very low.
479 Although in laboratory experiments, the production of buds is boosted by high temperatures and
480 food availability (*e.g.* Han and Uye 2010; Schiariti et al. 2014; Hubot et al. 2017; Ikeda et al.

481 2017), none of the environmental variables tested were significantly correlated with NMB at our
482 study site. Still, we suspect that high salinities in Thau lagoon during the summer might be
483 unfavourable to the production of buds, as demonstrated by Purcell (2007) and Hubot et al.
484 (2017). However, additional information on the intraannual availability of scyphistoma prey in
485 the lagoon, together with a long-term survey, is needed to reach a more complete understanding
486 of the drivers of this asexual reproduction mode followed by *A. coerulea* in the Thau lagoon.

487

488 *Strobilation*

489 In Thau, the strobilation period for *A. coerulea* appears to span from the end of the
490 autumn (November) and the beginning of the spring (April), with a peak in November (33% of
491 the population strobilated in November 2017). This result is in accordance with the previously
492 reported period for ephyrae presence in the lagoon, from early winter to early spring (Marques
493 et al. 2015b), and with the strobilation periods described so far in other areas for *A. coerulea*
494 (Toyokawa et al. 2000; Watanabe and Ishii 2001; Miyake et al. 2002; Uye and Shimauchi 2005)
495 and for *A. aurita* (Hocevar et al. 2018). As previously suggested by Holst (2012), the
496 strobilation onset in our study seems to have been triggered by a sharp drop (of 8.3°C) in water
497 temperature, as temperatures in Thau fell to 10°C over a few days in November 2017. Water
498 temperatures below 15°C have been shown to induce physiological changes in the scyphistomae
499 of *A. coerulea*, probably to prepare them for metamorphosis (Han and Uye 2010; Feng et al.
500 2018). This is possibly what happened in the *A. coerulea* scyphistomae of Thau in November
501 2017.

502 The magnitude of most jellyfish blooms is tightly reliant on the density of
503 scyphistomae, but also on their strobilation strategy as this later directly determines the
504 magnitude of the initial production of the pelagic individuals responsible for the blooms. The
505 number of ephyrae released depends on the number of disks produced per strobila combined
506 with the number of strobilating scyphistomae. In Thau, an average of 3.7 ± 1.4 disks per
507 scyphistoma were produced by *A. coerulea* over the strobilation period, which is in accordance
508 with previous observations (3.2 – 7.7 disks per scyphistoma) made for *Aurelia* spp. (Holst 2012;
509 Makabe et al. 2014; Feng et al. 2018). Despite the low percentage of scyphistomae strobilating
510 in February (< 5.5%) the estimated production of disks was relatively high (11 800 disks per
511 m²), due to the high density of scyphistomae at this time of the year (> 30 000 ind per m²).
512 However, the main period of *A. coerulea* strobilation was observed in November with a
513 production of circa 19 100 disks per m². If our study was representative of a complete
514 strobilation season (*i.e.* from November to April in the same year), the number of ephyrae
515 released (of 82 301 ephyrae per m²), at our study site would be much higher than previous
516 estimations for *A. coerulea* in Japan (131 ephyrae per m²) by Ishii and Katsukoshi (2010), but
517 close to that (86 806 ephyrae m²) from Makabe et al. (2014). This production, though, was

518 limited by the low densities of scyphistomae in this season, especially in November. Therefore,
519 the magnitude of *A. coerulea* blooms in Thau is limited, not only by the mortality of ephyrae
520 during the winter (Fu et al. 2014), but also by the important mortality of scyphistomae over the
521 summer.

522

523 **Conclusion**

524 While climate change and the consequent ocean warming are currently expected to
525 cause larger and more frequent jellyfish blooms, our results prompt the question if all
526 populations of one of the most blooming genus, the *Aurelia*, will respond likewise. In this
527 temperate lagoon the seasonal dynamics of the benthic stage of *A. coerulea* in 2017 contrasted
528 those previously described for *Aurelia* genus, mainly because of a combination of high
529 temperatures and salinities in the summer that appear to be detrimental to scyphistomae of *A.*
530 *coerulea*. The resulting decrease in scyphistomae density undoubtedly reduced the outcome of
531 the late-autumn strobilation peak in Thau, thereby limiting the intensity of the subsequent
532 pelagic bloom of *A. coerulea*. Because warm and dry summers are expected to be more
533 frequent in the coming decades in the Mediterranean area (IPCC 2014), we may assist to a
534 decrease in the benthic population size and in the intensity of the blooms of this jellyfish, at
535 least in Thau. However, the short-term of this study hampers substantiated conclusions and
536 further investigations, based on long-term studies, are still required to corroborate such
537 suspicion.

538 Consequently, there is an urgent need for widespread *in situ* studies on the benthic
539 population dynamics of scyphozoans and their local environmental drivers. In jellyfish, benthic
540 population dynamics is an outcome of complex biotic and abiotic interactions which apparently
541 act differently in each ecosystem. Our results show that predicting it needs comprehensive
542 understanding of the interspecific relationships that might regulate scyphistoma abundance.
543 Long-term *in situ* studies, involving different species of jellyfish and encompassing diverse
544 localities and habitats are crucial if we want to understand the formation of jellyfish blooms and
545 their fate in the face of the predicted climate change.

546 **Compliance with Ethical Standards**

547 Conflict of interest: The authors declare that they have no conflict of interest.

548 Ethical approval: All applicable international, national, and/or institutional guidelines for the
549 care and use of animals were followed. The jellyfish *Aurelia coerulea* is an invertebrate which
550 is not endangered or protected species and therefore, no permits were needed for sampling their
551 scyphistomae. All bivalves with attached scyphistomae were released alive after laboratory
552 observation.

553

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561

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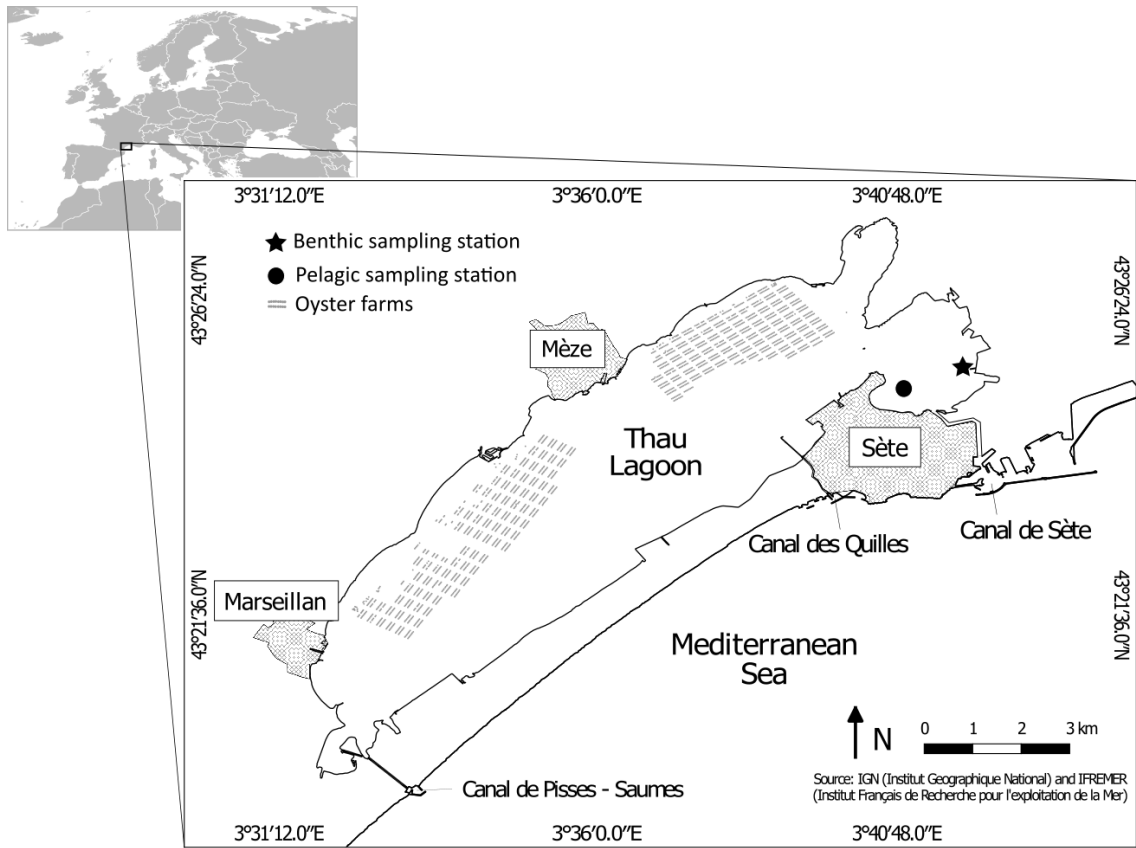
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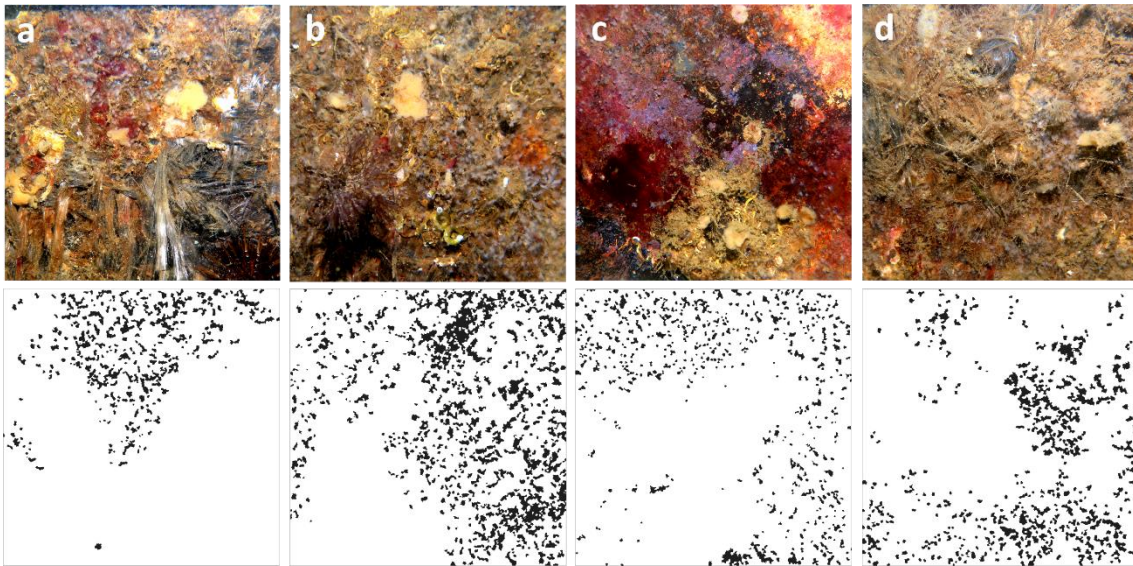
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741 **Fig. 1** Map of the Thau lagoon showing the location of the benthic (star) and pelagic (circle)

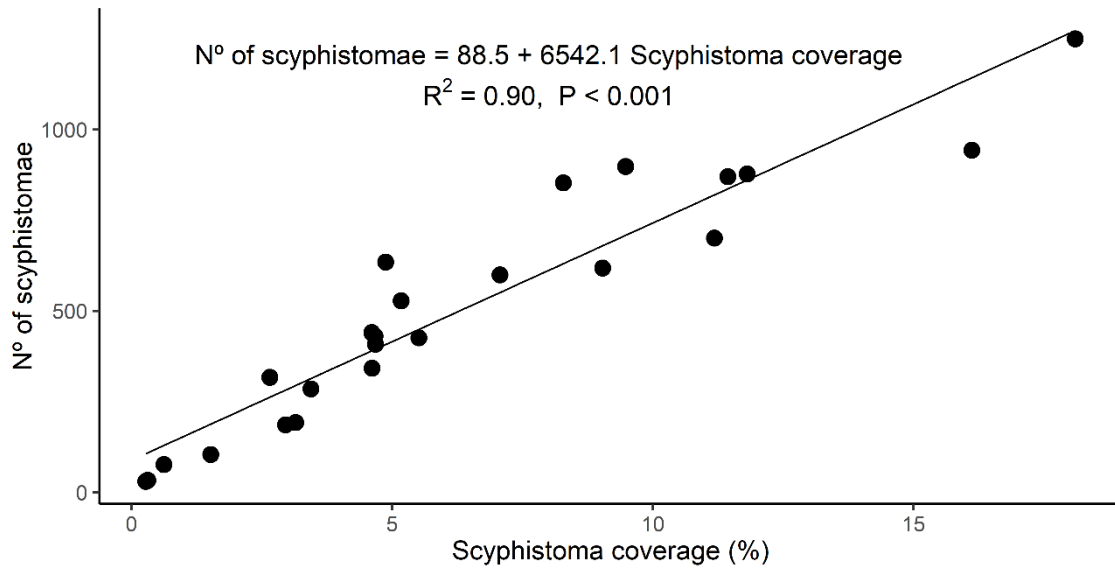
742 sampling sites for this study. Shaded areas represent urban areas



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745 **Fig. 2** Example of the photoquadrats (top) and the respective IZS output (bottom). a)
746 photoquadrat 1 (6.10 % coverage), b) photoquadrat 2 (16.1 % coverage), c) photoquadrat 3
747 (6.64 % coverage), c) photoquadrat 4 (9.93 % coverage).

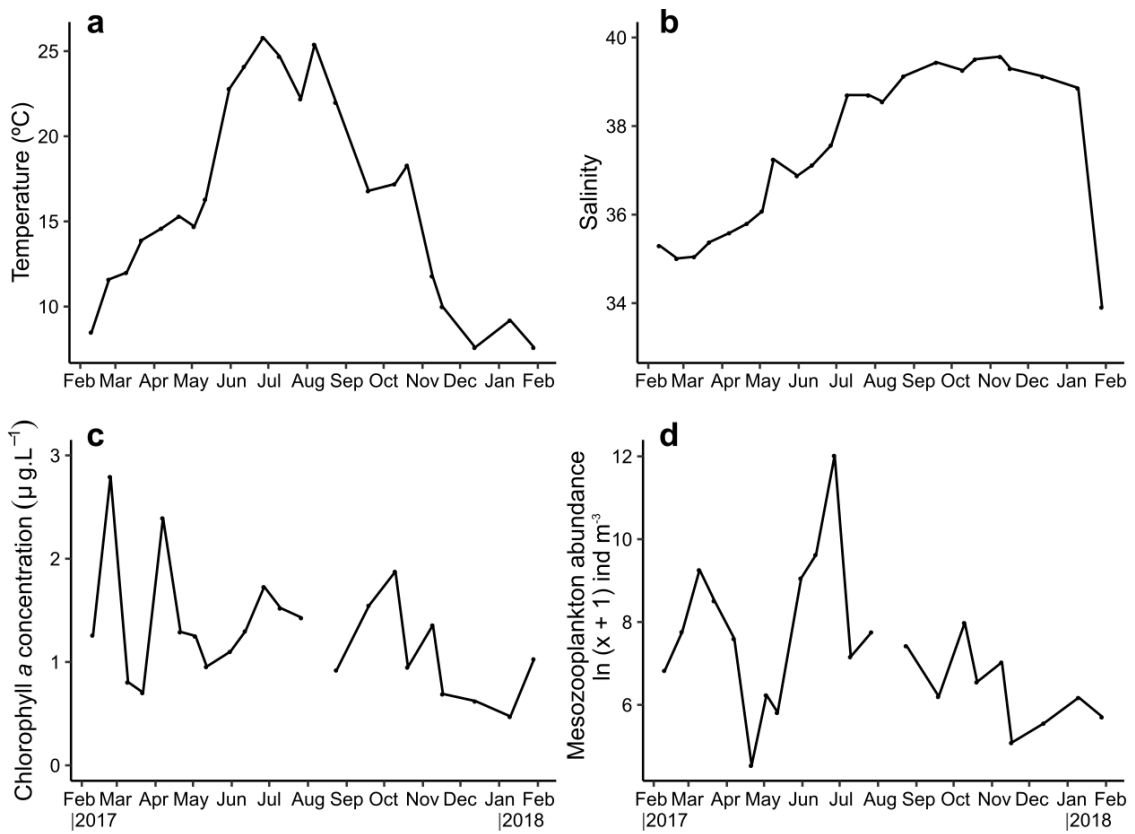
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750 **Fig. 3** Relationship between number of scyphistomae and scyphistoma coverage (%) in the
 751 photoquadrats (121 cm²). The resulting equation was used to estimate scyphistoma density in
 752 the study site (eq. 1)

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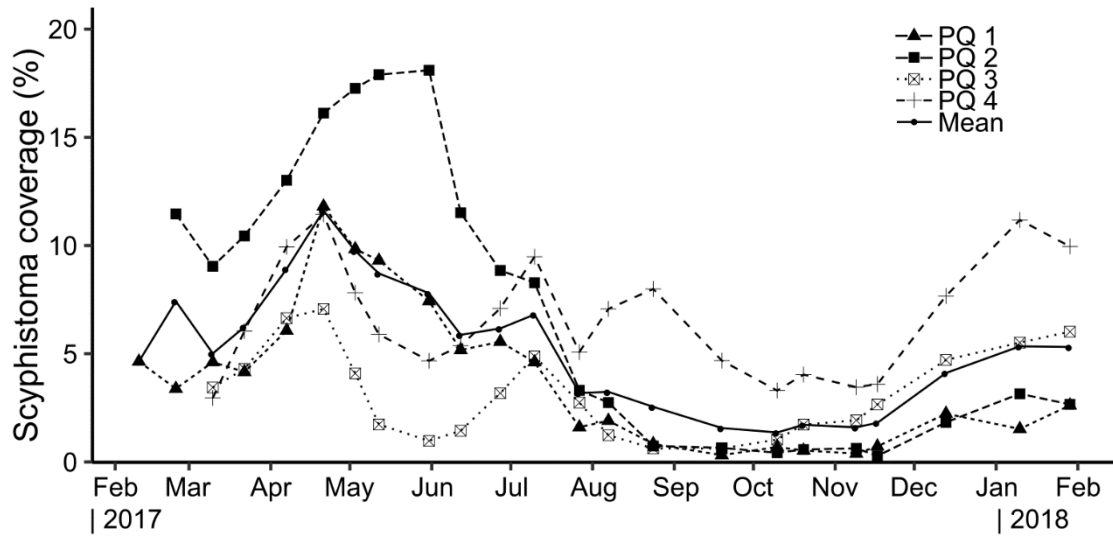


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756 **Fig. 4** Variation of the environmental variables in the Thau lagoon, during the study period: a)
 757 temperature, b) salinity, c) chlorophyll *a* concentration and d) mesozooplankton abundance

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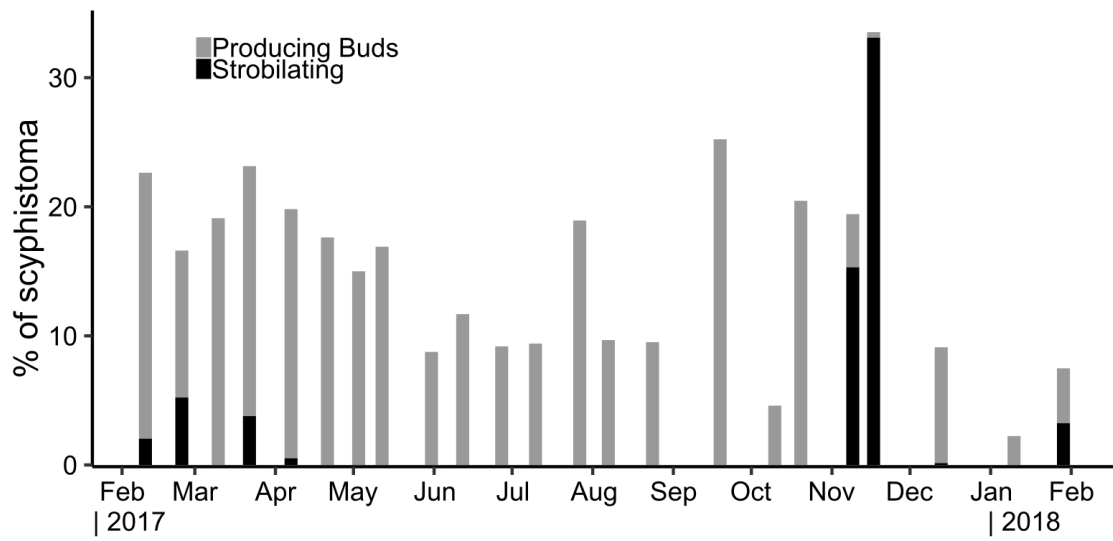
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761 **Fig. 5** Variation of *A. coerulea* scyphistoma coverage in each photoquadrats (PQ) and the mean

762 of all photoquadrats, during the study period

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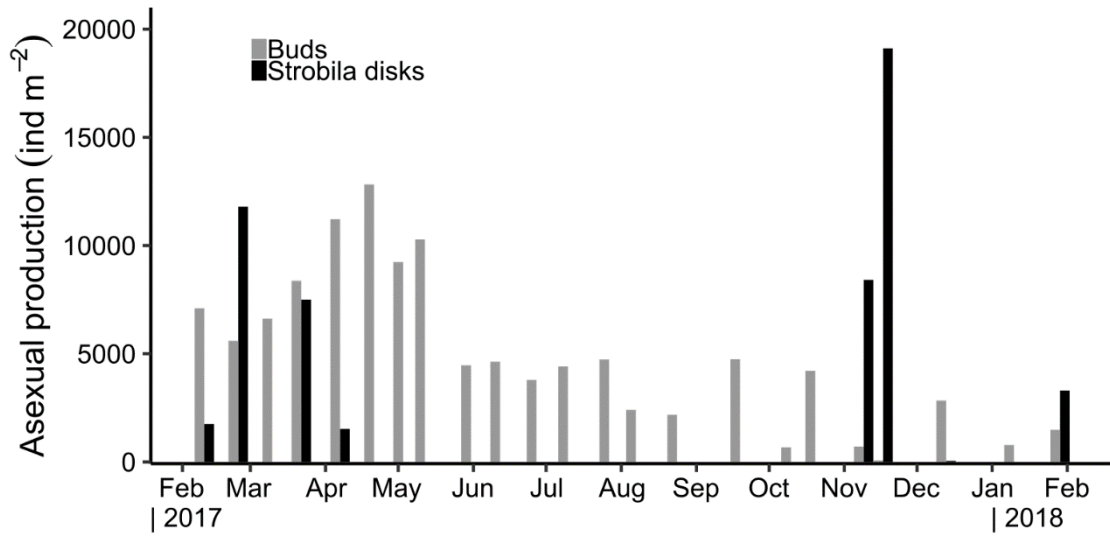


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766 **Fig. 6** Annual asexual reproduction strategy of *A. coerulea* scyphistoma in the Thau lagoon over
767 the study period. Each bar represents the percentage of the population producing non-motile
768 buds (grey) and strobilating (black) at each sampling time

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772 **Fig. 7** Asexual Production (AP_{t_i}) in the Thau lagoon over the study period. Each bar represents
773 the estimated production of non-motile buds (grey) and strobila disks (black) by the population
774 of *A. coerulea* scyphistoma, at each sampling time (t_i), at the study site

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778 **Tables**

779 **Table 1** Parameters of the final General Linear Models used to assess correlations between each
 780 of the biological variables (scyphistoma coverage, percentage of scyphistomae producing non-
 781 motile buds (NMB) and podocysts per scyphistoma) and environmental variables in the lagoon.
 782 Temp: temperature (°C), Sal: salinity; Chla: chlorophyll *a* concentration ($\mu\text{g L}^{-1}$), logZAb:
 783 mesozooplankton abundance ($\ln(x + 1)$ ind m^{-3}). Significant correlations ($P < 0.05$) are
 784 indicated in bold.

Scyphistoma coverage (%)	Estimate	Std. Error	t value	<i>P</i>
(Intercept)	-1.78	1.22	-1.46	0.17
Temp	0.23	0.09	2.47	0.03
Sal	0.05	0.03	1.50	0.16
logZAb	0.21	0.19	1.09	0.29
Temp:Sal	-0.01	0.00	-2.43	0.03
Temp:logZAb	-0.02	0.01	-1.62	0.13
Sal:logZAb	-0.01	0.01	-1.12	0.28
Temp:Sal:logZAb	0.00	0.00	1.62	0.13
NMB (%)				
(Intercept)	179.57	221.44	0.81	0.42
Temp	-12.97	14.69	-0.88	0.38
Sal	-5.32	5.80	-0.92	0.36
MChla	-231.26	240.37	-0.96	0.34
logZAb	-20.53	28.22	-0.73	0.47
Temp:Sal	0.37	0.38	0.96	0.34
Temp:MChla	13.17	15.31	0.86	0.39
Sal:MChla	6.63	6.35	1.04	0.30
Temp:logZAb	1.46	1.88	0.78	0.44
Sal:logZAb	0.61	0.74	0.83	0.41
MChla:logZAb	28.57	31.26	0.91	0.36
Temp:Sal:MChla	-0.37	0.40	-0.92	0.36
Temp:Sal:logZAb	-0.04	0.05	-0.86	0.39
Temp:MChla:logZAb	-1.53	1.99	-0.77	0.44
Sal:MChla:logZAb	-0.83	0.83	-1.00	0.32
Temp:Sal:MChla:logZAb	0.04	0.05	0.83	0.41
Podocysts per scyphistoma				
(Intercept)	-2.56	1.47	-1.75	0.10
Temp	0.29	0.11	2.61	0.02
Sal	0.07	0.04	1.76	0.09
Temp:Sal	-0.01	0.00	-2.54	0.02

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789 **Table 2** Hurdle model coefficients used to assess the influence of environmental variables on
790 strobilation intensity. Temp: temperature (°C), Sal: salinity; Chla: chlorophyll *a* concentration
791 ($\mu\text{g L}^{-1}$), logZAb: mesozooplankton abundance ($\ln(x + 1)$ ind m^{-3}). Significant correlations ($P <$
792 0.05) are indicated in bold.

Count model coefficients (truncated negbin with log link):	Estimate	Std. Error	z value	<i>P</i>
(Intercept)	-1.79	11.73	-0.15	0.88
Temp	0.27	0.47	0.57	0.57
Sal	0.19	0.30	0.64	0.52
Chla	0.10	0.60	0.17	0.87
logZAb	-0.62	0.89	-0.71	0.48
Log(theta)	-0.19	0.60	-0.31	0.76
Zero hurdle model coefficients (binomial with logit link):				
(Intercept)	-2.23	12.40	-0.18	0.86
Temp	-0.29	0.15	-2.00	0.05
Sal	0.08	0.31	0.24	0.81
Chla	0.83	0.90	0.92	0.36
logZAb	0.23	0.45	0.52	0.60
Exponentiated coefficients		Count model	Zero hurdle model	
(Intercept)		0.17		0.11
Temp		1.31		0.75
Sal		1.21		1.08
Chla		1.11		2.29
logZAb		0.54		1.26

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