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6 HOW EXPERIMENTAL PHYSIOLOGY AND ECOLOGICAL NICHE MODELLING

7 CAN INFORM THE MANAGEMENT OF MARINE BIOINVASIONS?

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23 ABSTRACT

24   Marine bioinvasions are increasing worldwide by a number of factors related to the

25   anthroposphere, such as higher ship traffic, climate change and biotic communities' alterations.

26   Generating information about species with high invasive potential is necessary to inform

27   management decisions aiming to prevent their arrival and spread. *Grateloupia turuturu,* one of the

28   most harmful invasive macroalgae, is capable of damaging ecosystem functions and services, and

29   causing biodiversity loss. Here we developed an ecological niche model using occurrence and

30   environmental data to infer the potential global distribution of *G. turuturu*. In addition,

31   ecophysiological experiments were performed with *G. turuturu* populations from different

32   climatic regions to test predictions regarding invasion risk. Our model results show high suitability

33   in temperate and warm temperate regions around the world, with special highlight to some areas

34   where this species still doesn't occur. Thalli representing a potential temperate region origin, were

35   held at 10, 13, 16, 20 and 24ºC, and measurements of optimal quantum field (Fv/Fm) demonstrated

36   a decrease of photosynthetic yield in the higher temperature. Thalli from the population already

37   established in warm temperate South Atlantic were held at 18, 24 and 30°C with high and low

38   nutrient conditions. This material exposed to the higher temperature demonstrated a drop in

39   photosynthetic yield and significant reduction of growth rate. The congregation of modelling and

40   physiological approach corroborate the invasive potential of *G. turuturu* and indicate higher

41   invasion risk in temperate zones. Further discussions regarding management initiatives must be

42   fostered to mitigate anthropogenic transport and eventually promote eradication initiatives in

43   source areas, with special focus in the South America. We propose that this combined approach

44   can be used to assess the potential distribution and establishment of other marine invasive species.

45

46   Keywords: *Grateloupia turuturu*, invasive marine algae, populational ecology,

47   ecophysiology, anthropogenic impacts.

48

49   1. INTRODUCTION

50   Marine bioinvasions are receiving great attention as many of them are producing negative

51   socio-environmental-economic impacts worldwide (Katsanevakis et al., 2014). Offshore oil

52   exploitation, aquaculture activities and ballast water are major vectors responsible for growing

53   events of non-indigenous species arrival and spread (Creed et al., 2017; Hulme, 2009). Climate

54   change further facilitates the dispersal of marine organism by increasing the frequency and

55   intensity of extreme climatic/oceanographic events (Sissini et al., 2017, 2014; Ummenhofer and

56   Meehl, 2017). A diverse and abundant array of vectors for the transport of organisms across

57   biogeographic boundaries coincides with disrupted native communities of marine organisms,

58   caused by both global (ocean acidification and warming) and local stressors (coastal pollution,

59   overfishing) (Shea, 2002), which is facilitating the establishment of non-indigenous species on

60   coastlines all around the world (Occhipinti-Ambrogi 2007). Williams and Smith (2007) estimated

61   that there are 277 introduced seaweed species around the globe, with the Mediterranean and the

62   North-East Atlantic being the most highly invaded regions. The geographical distribution of

63   marine macroalgae is determined by their physiological tolerance to environmental conditions

64   (Breeman, 1988; Hoek, 1982), enabling the prediction of suitable habitats for invasive species

65   (Elith et al., 2006; Marcelino and Verbruggen, 2015). Ecological Niche Models (ENM) relate

66   occurrence data with environmental gradients to produce habitat suitability maps (Peterson, 2003).

67   An ability to assess the risk of invasion and the threats posed by foreign organisms helps managers

68   and stakeholders put preventive measures in place and optimize biosecurity monitoring (Marcelino

69   and Verbruggen, 2015). Eradication of established populations is costly and usually ineffective

70   (Bax et al., 2001; D'Antonio and Meyerson, 2002). The known occurrence of species informs

71   predictive distribution models, which can be misleading since this depends on sampling effort and

72   identification expertise which varies widely depending on the species and regions investigated

73   (Verbruggen et al., 2009). ENM do not consider the physiological traits of species when modelling

74   distributions, likely missing valuable information about the mechanisms and processes allowing

75   the presence and establishment of populations (Marcelino and Verbruggen, 2015). Therefore,

76   physiological information can be used to validate and further improve ENMs to create a more

77   accurate prediction of habitat suitability (Martínez et al., 2015).

78   Considering species traits related with dispersal, establishment and ecological impact, the

79   fifth most dangerous invasive alga in a global perspective is *Grateloupia turuturu* Yamada (1941)

80   (Nyberg and Wallentinus, 2005), commonly known as the "Devil's tongue weed" (Mulas and

81   Bertocci, 2016). *G. turuturu* can displace native species in rocky intertidal habitats (Freitas et al.,

82   2016; Mulas and Bertocci, 2016), has advantage establishing in recently perturbed environments,

83   where native assemblages are disrupted (Mulas and Bertocci, 2016), and has been reported for

84   reducing the abundance and richness of invertebrates (Janiak and Whitlatch, 2012; Jones and

85   Thornber, 2010). Native to Japan, *G. turuturu* has been documented as an invasive species in the

86   United States (Balcom and Yarish, 1994; Mathieson et al., 2008), Mexico (Aguilar-Rosas et al.,

87   2012), New Zealand (D'Archino et al., 2007), France (Simon et al., 2001), Italy (Cecere et al.,

88   2011), Portugal (Araújo et al., 2011), Australia (Saunders and Withall, 2006), and Israel (Tsiamis

89   et al., 2015). This species was recently registered for the coast of South Brazil, being the first

90   record of this species in the South Atlantic (Azevedo et al., 2015). The transport of oyster for

91   aquaculture and ballast water are the main probable vectors of *G. turuturu* introduction in the

92   Atlantic and Mediterranean (Araújo et al., 2011; Harlin and Villalard-Bohnsack, 2001). Important

93   dispersion vectors may also be yacht and ship hulls, as specimens have been found attached to

94   such boats in France (Simon et al., 2001). *G. turuturu* has been described to tolerate a wide range

95   of temperature (from 4 to 28ºC), salinity (from 15 to 37), nutrients (Simon et al., 2001) and can be

96   found down to a depth of 7m (Sweet 2011). Liu and Pang (2010) described lower photosynthetic

97   activity in *G. turuturu* when exposed to freezing, which further explains why this species is mostly

98   found, until now, in temperate regions. However, even with the description of *G. turuturu* being

99   tolerant to a great spectrum of environmental conditions in the North Atlantic and Pacific, there is

100   no descriptions of the South Atlantic population tolerance to the local oceanographic conditions,

101   nor experiments that describe the biochemical processes of its ecophysiological performance. For

102   this reason, ecophysiological experiments are necessary to better understand the influence of

103   temperature and nutrients in *G. turuturu* physiology and assess its probability of success in regions

104   with conditions similar to the native range.

105   In this study we developed an ENM to estimate the global potential distribution of *G.*

106   *turuturu.* In addition, we determined the ecophysiological thresholds of *G. turuturu* as a tool to

107   infer about the species resilience and temperature tolerance. Our hypothesis is that *G. turuturu* will

108   present higher habitat suitability and physiological performance in temperate regions. By

109   combining ENMs and the physiological thresholds evaluation, we desire to propose this associated

110   approach to foster coastal management strategies related not only to *G. turuturu* bioinvasion, but

111   also to invasions by other marine species.

112

113   2. MATERIALS AND METHODS

114   2.1 Ecological Niche Modelling

115   To develop the ENM for *G. turuturu*, six environmental benthic data layers (i.e., along the

116 bottom of the ocean) were extracted from Bio-ORACLE (Assis et al., 2017b; Tyberghein et al.,

117 2012) based on the biological relevance of macroalga (Assis et al., 2017a, 2014; Neiva et al., 2015)

118 (environmental predictors used in the model are described in Table 1). Depth was not included as

119 a predictor as it has no direct biological meaningfulness in the ecophysiological response of

120 macroalgae, and many previous works modelling marine macroalgae also do not include it

121 (Jueterbock et al., 2016, 2013; Tyberghein et al., 2012). Bio-ORACLE data has been widely used

122 for marine ecological modelling (Marcelino and Verbruggen, 2015) since it contains climatic and

123 geophysical data with a global spatial resolution of 0.08º (9.2 km). Detailed georeferenced

124 occurrence data from both invaded and native ranges was obtained from the public Global

125 Biodiversity Information Facility (GBIF, 2018), and literature data (available in the supplementary

126 material ESM1) (e.g. Tyberghein et al. 2012; Escobar et al. 2016). The inclusion of the invaded

127 range in the model increases model accuracy, as models trained using data only from the native

128 range usually fail to predict the full invasion extent of a species (Beaumont et al., 2009;

129 Broennimann and Guisan, 2008). Duplicated occurrences, outside marine range or too close to

130 each other (5 km²) were excluded to prevent biases and reduce spatial autocorrelation in the

131 analyses, remaining 106 records (Figure 1). The radius of 5 km² was chosen as an conservative

132 distance of about half of the resolution of the climatic data used in the model, seeking spatial

133 independence between the environmental data of occurrences (Phillips et al. 2009; Kramer-Schadt

134 et al. 2013). The modelling approach combined multiple cross-validation interactions using

135 independent datasets with Boosted Regression Trees (BRT), a statistical algorithm able to fit

136 complex non-linear relationships between a response (occurrence records) and predictor variables

137 (environmental data), while avoiding overfitting through optimized parameterization procedures

138 and specific forcing of monotonic responses (Elith, Leathwick, & Hastie, 2008). BRT algorithm

139 is known for high predictive performance (De'ath, 2007; Neiva et al., 2014), improving its

140 performance by combining many models for prediction, which makes it a more accurate algorithm

141 when compared to other regression methods (Elith, Leathwick, & Hastie, 2008). In the lack of

142 absence data, presence-only modelling requires the generation of pseudo-absences or background

143 information (e.g., Maxent; Phillips et al. 2006). This information was produced using the method

144 developed by Senay et al. (2013) for improved ecological modelling, which comprise the

145 calculation of environmentally dissimilar regions to the presence points and the random selection

146 of pseudo-absences in clustered climatic predictors to reduce the use of redundant information. To

147 account for likely sources of sampling bias, pseudo-absences were chosen from a kernel

148 probability surface developed with the records of occurrence over a grid with the same resolution

149 of environmental data (e.g., Phillips et al. 2009; Assis et al. 2018a)

150   Cross-validation interactions were developed by partitioning species records (i.e.,

151 presences and also pseudo-absences) into 10 independent longitudinal bands to evaluate the

152 performance of models (Wenger and Olden, 2012). Models fitted with one withheld band at a time,

153 and True skill statistics (TSS) compared this data to the outcomes of a predicted surface of

154 distribution reclassified to reflect presence and absences (binomial) with a threshold maximizing

155 TSS. Over-fitting in the models was reduced by tuning the algorithm parameters (i.e., learning

156 rate, number of trees and tree complexity; see Elith et al. 2008; Assis et al. 2016, 2018a for details)

157 and also by forcing monotonic responses (positive for minimum nutrients, salinity, light and

158 temperature; negative for maximum temperatures). Final predictions using optimal parameters

159 were reclassified to binomial responses and its final accuracy was reported with AUC (Area Under

160 the receiver operating characteristic Curve, Fielding and Bell 1997), sensitivity (true positive rate)

161 and TSS (True Skill Statistics, Allouche et al. 2006). The significance of models was determined

162 by inferring the relative contribution of each environmental predictor to the performance of the

163 models (Elith et al., 2008). Physiological limits points (maximum and minimum, depending on the

164 predictor) were determined by extracting the individual fitting function of each predictor alone,

165 while fixing the alternative predictors in their average (Elith et al., 2008; Marcelino and

166 Verbruggen 2015).

167 ENM analyses were performed with R (R Development Core Team, 2017) using the

168 packages dismo, gbm, parallel, raster, SDMTools, and sm.

169

170 2.2 Ecophysiological experiments

171 Two populations of *G. turuturu* were ecophysiologically evaluated considering different

172 acclimatization histories. A warm temperate adapted population (WAP) was sampled

173 (approximately 100 g of fresh weight (FW)) on August 22nd, 2016 from the intertidal zone of

174 Itapirubá beach (28°20'14.32"S, 48°42'4.87"W), in the city of Imbituba, Santa Catarina, Southern

175 Brazil. A temperate adapted population (TAP), approximately 60 g FW, was also sampled in Saint

176 Malo beach (48°39'32.8"N 2°00'24.6"W), France, on February 20th, 2017, region representing a

177 possible source of *G. turuturu* germlings through oyster seeds or ballast water. Since a determined

178 biomass of *G. turuturu* was collected, which included individual blades and blades attached

179 together by a holdfast, all samples were separated in individual blades. The sampled blades of both

180 populations presented around 6 cm height and 2 cm in width, were not fertile, collected in winter,

181 immediately transported in plastic containers with seawater to the lab, and manually cleaned from

182 epiphytes or associated fauna after sampling.

183   To determine the control conditions for each of the experimental designs, we considered

184   the different adaptation conditions of each population. Therefore, the temperate and warm

185   temperate populations were exposed to conditions observed in their respective occurrence regions

186   (~10ºC in France in February (Dubois et al., 2007), and ~18ºC in Imbituba in August (Gouvêa et

187   al., 2017)). Both populations were cultivated in 250 mL Erlenmeyer flasks, in UV sterilized

188   seawater enriched with Von Stosch medium in a 50% concentration, without EDTA chelating salt

189   (adapted from Edwards 1972) until the beginning of the experiment. To prevent the lack of

190   essential nutrients water was replaced daily. Aeration was provided individually in the flasks, also

191   stirring the water in each flask to disrupt the diffusive boundary layer. The temperature was

192   adjusted by heaters (Radical 1 HP, Brazil) positioned in trays with water, where the treatment

193   flasks were kept in a water bath. Each tray contained one data logger (HOBO Pendant

194   Temperature/Light Data Loggers, Onset, Bourne, USA) that recorded the water temperature every

195   10 minutes. A 12-hour light/dark photoperiod was used, and irradiance was provided by

196   fluorescent lamps with an average of 65 ± 5 μmol photons $m^{-2}\,s^{-1}$.

197   The experimental design performed in Brazil had as main purpose to observe short-term

198   ecophysiological effects of temperature and nutrients, key environmental drivers selected

199   according to conditions found in adjacent tropical environments where the species has not been

200   reported yet (Gouvêa et al., 2017). The WAP sampled blades were brought to the laboratory, and

201   acclimated for 21 days to laboratory irradiance, maintaining field temperature (18ºC). Initial and

202   final 1g FW samples were frozen with liquid nitrogen for the analysis of biochemical descriptors.

203   The experiment lasted for seven days. The experimental setup in Brazil utilized three temperatures

204   (18, 24 and 30ºC) and two nutrient conditions: one without medium culture (Low Nutrient

205   Concentration – LNC) and another with 50% of Von Stosch (VS) medium (High Nutrient

206 Concentration – HNC), resulting in 6 factorial treatments. Each treatment contained 10 replicas (*n*

207 = 10), consisting of individual blades of *G. turuturu* weighted to sum 1g FW per Erlenmeyer flask.

208   The experiment performed with the temperate adapted population, a potential source of *G.*

209 *turuturu*, has as main purpose the investigation of the short-term ecophysiological effects of

210 temperature, an environmental driver traditionally related with the distribution constraints of

211 marine algae (Hoek, 1982). The chosen temperature values used in the experiment are present in

212 the region of the North Atlantic where the algae were sampled (Dubois et al., 2007), expect for the

213 higher temperature used. The higher temperature used was chosen to overlap with conditions

214 observed in the warm temperature region, providing the necessary scenario for the evaluation of

215 the potential ecophysiological continuum, contribution to the discussion about invasive potential

216 of *G. turuturu.* For the TAP experiment realized in France, *G. turuturu* blades were acclimated for

217 three days at 10ºC, temperature observed in the water of the sampling location. *G. turuturu* was

218 exposed for 60 hours to 5 different temperatures: 10 (control), 13, 16, 20 and 24ºC. Each treatment

219 contained 6 replicas (*n* = 6), also consisting of individual blades of *G. turuturu* weighted to sum

220 1g FW. The experiment duration was limited by laboratory structure and the availability at Saint

221 Malo. Figure S1 on the supplementary material ESM2 illustrates the different experimental designs

222 of both populations.

223

224   2.3 Physiological analyses

225   Physiological analysis performed in both populations were measurements of optimal

226 quantum field (Fv/Fm). Growth rate and photosynthetic pigments were only evaluated in the WAP

227 experiment, as the biomass sent to Brazil lost minimum preservation conditions due to

228 transportation delay. Considering the relevance of Fv/Fm as a descriptor, we chose to keep the

229 results obtained in the TAP experiment.

230

231   2.3.1 Photosynthetic yield

232   In the WAP experiment, effective quantum yield (Fv/Fm) was estimated by the

233 fluorescence of *in vivo* chlorophyll *a*. Three measurements of Fv/Fm were made in each replica in

234 different parts of the thallus, resulting in 3 subreplicas of each one of the 10 replicas. Measurements

235 of Fv/Fm were taken with a pulse-amplitude modulated chlorophyll *a* fluorometer (Diving PAM

236 – Walz Germany) after acclimation in the dark for 20 minutes in the first day, then every two days,

237 and in the last day of the experiment (for further explanation of the methodology followed, see: de

238 Ramos et al., 2018; Figueroa et al., 2006). For the TAP experiment, measurements of Fv/Fm were

239 made in the dark only in the end of the 60 hours.

240

241   2.3.2 Pigment extraction

242   At the end of the experiment, all the replicates from the WAP experiment were frozen and

243 used for pigments quantification. Each replica was divided in 3 portions of 100 mg, allowing the

244 reading of 3 subreplicas, which resulted in 30 extractions for each treatment. The extraction

245 followed Schubert et al. (2011), where phycobiliproteins, chlorophyll *a* and total carotenoids were

246 extracted from the same 100 mg biomass sample grinded in liquid nitrogen. Phycobiliproteins were

247 extracted first with phosphate buffer (pH 6.8) and kept in the dark at 4ºC for 2 hours until

248 centrifugation for 4 minutes at 13000 rpm in the MiniSpin centrifuge (Eppendorf) at room

249 temperature. Subsequently, the supernatant was used to determine the concentration of

250 phycobiliproteins according to Beer and Eshel (1985). Afterwards, methanol 100% was placed on

251   the same biomass and kept in the dark at 4ºC overnight, and then centrifuged as stated before.

252   Then, chlorophyll and total carotenoids were quantified according to Torres et al. (2014).

253   Absorbance was determined in the SpectraMax Paradigm Multi-Mode Microplate Reader

254   (Molecular Devices), of the Laboratório Multiusuário de Estudos em Biologia (LAMEB).

255

256   2.3.3 Growth rate (GR)

257   To determine the daily growth rate (GR), replicates were spun for 15 seconds in a salad

258   spinner to reduce the excess of water, and then weighted in an analytical balance. The replicates

259   were weighted in the first and last days to determine the GR by the following equation (Lignell

260   and Pedersén, 1989):

261                $$GR\ (\%.\,day^{-1}) = \left[\left(\frac{Wt}{Wi}\right)^{1/t}\right] \times 100\%$$ (1)

262   Where Wi and Wt are respectively the initial and final fresh weight after t days (t = 7 days).

263

264   2.4 Statistical analysis

265   For the WAP experiment, the independent variables considered were time (beginning and

266   end), nutrient concentration (HNC and LNC) and temperature (18, 24 and 30ºC). For Fv/Fm, time

267   was considered for the 1st, 3rd, 5th and 7th day. For significant differences, post-hoc test of Tukey

268   was used to identify significantly different groups ($p<0.05$). The TAP experiment had as variables

269   only the different temperatures, 10, 13, 16, 20 and 24ºC, with 6 replicates ($n=6$).

270   Each treatment of the WAP experiment had 10 replicates ($n=10$), which were used for the

271   analysis of GR. However, in the reading of pigments and Fv/Fm, some of the replicas presented

272   negative values or values too close to zero, representing errors in the readings. This required the

273   removal of 3 replicas in each treatment (resulting in a $n=7$), to maintain the same number of

274 replicates for statistical analysis. Before analysis, data were tested for normality and residuals for

275 half-normality. Statsoft Statistica 13.0 was used to perform multifactorial Analysis of Variance

276 (ANOVA, $p<0.05$). Due to the removal of outliers, the data did not require transformation, as it

277 attained the normality requirements for the ANOVA parametric tests calculated.

278

279   3. RESULTS

280   3.1 Ecological Niche Modelling

281   The final predictive model had high performance (AUC: 0.96; Sensitivity: 0.95; TSS: 0.93)

282 and showed that *G. turuturu* has great habitat suitability in temperate regions of Northern Pacific,

283 Northern Atlantic, South America, Australasia (Oceania) and a small portion of Southern Africa

284 (Fig. 2). Light at bottom and maximum ocean temperature were the most important predictors to

285 the ecological niche of *G. turuturu*, while nutrients (as nitrates and phosphates) were the least

286 important (Table 1). Response curves showed habitat suitability with light above 4.4 E . m^{-2} . yr^{-1}

287 and ocean temperature bellow 26.55ºC, however, with a starting drop at 21.23ºC (Fig. 3). Response

288 curves of the other variables used in the model are available in the supplementary material ESM2

289 (Figures S2, S3, S4, S5 and S6).

290

291   3.2 Ecophysiological experiments and physiological analyses

292   3.2.1   Photosynthetic yield

293   In the WAP experiment, there was significant interaction ($p<0.05$) between temperature,

294 time and nutrient concentration for Fv/Fm (Table 2). A decline in Fv/Fm was noticeable as the

295 temperature increases and through the experiment time in WAP (Fig. 4). The treatment of 30ºC

296 with HCN showed the lowest values in the fifth and seventh day of treatment in comparison with

297   the treatments with lower temperatures. For 30ºC with LNC, there was a smaller decline in Fv/Fm,

298   but still presented Fv/Fm values lower than the treatments of 24 and 18ºC. Similarly, there was a

299   contrast between the LNC and HNC treatments at 24ºC, with lower values of Fv/Fm observed at

300   HNC. In France, statistical analysis of TAP experiment results of Fv/Fm showed significant

301   difference between temperatures (Table 2). The response of *G. turuturu* to the short-term exposure

302   in the TAP experiment to different temperatures was of lower Fv/Fm in the treatment of 24ºC (Fig.

303   5).

304

305   3.2.2   Photosynthetic pigments

306   No significant interaction ($p>0.05$) was found for both GR and pigments with time,

307   temperature, and nutrient concentration (i.e., no three-factorial interaction for GR and pigments).

308   However, regarding chlorophyll *a*, total carotenoids and GR, when the effects of nutrient

309   concentration are taken out, the interaction between time and temperature was significant ($p<0.05$).

310   For phycoerythrin and chlorophyll *a* the interaction between the effects of time and nutrient

311   concentrations was significant (Table 3). For chlorophyll, the treatments of 24ºC and 30ºC in the

312   end of the experiment were statistically distinct from the samples of the beginning and 18ºC (Fig.

313   6a). The higher concentration of chlorophyll was found in 30ºC, followed by 24ºC. Similarly, the

314   higher concentration of total carotenoids was found in the last day at 30ºC, and all the other

315   treatments had the same lower concentration (Fig. 6b). Additionally, for chlorophyll there was

316   statistical difference between different nutrient concentrations. On the end of the experiment, the

317   HNC treatment presented higher values of chlorophyll, as in LNC the concentration remained

318   close to the one in the beginning of the experiment (Fig. S7 on the supplementary material ESM2).

319   On the other hand, there was a decrease in phycoerythrin concentration in the last day in LNC,

320 while at the treatment of HNC remained constant throughout the experiment (Fig. 7).

321 Concentration of phycocyanin was not detectable.

322

323   3.2.3   Growth rate

324   For daily growth rate, only temperature and time were significant (Table 3). The algae

325 exposed to 30ºC showed lower GR when compared to the algae in lower temperatures (Figure 6c).

326

327   2.4   DISCUSSION

328   The investigation of the potential geographic distribution through ENM and physiological

329 thresholds tested through experiments of *G. turuturu* indicated higher habitat suitability of this

330 invasive species in temperate and warm-temperate regions around the world. Experimental results

331 demonstrated a decrease in photosynthetic yield in algae exposed to higher temperatures, along

332 with a stress response observed in pigments and growth rate. At the same time, ENM showed a

333 possible expansion of the distribution of *G. turuturu* to new countries around the globe, especially

334 in regions with temperatures close to the ones that the algae better adapted in the experiments.

335   The variables that most contributed to explain the distribution of *G. turuturu* were the

336 availability of light at bottom and maximum ocean temperatures. Light at bottom is determined

337 with an exponential decay function of photosynthetic active radiation, diffuse attenuation

338 coefficient and depth (Assis et al., 2017b) and allows restricting the species vertical distribution.

339 Indeed, the 4.04 E. m^{-2}. yr^{-1} threshold is comparable with the minimum annual irradiance inferred

340 for other species of algae (Gattuso et al., 2006). The limitation of 26.55ºC maximum temperature

341 inferred in ENM was also in line with previous descriptions of Simon et al. (2001) for the species

342 occurrence in Brittany (France), where waters can reach up to 28ºC in summer. The relative

343 discrepancy in these values can arise from the short term variations of temperature in the water

344 pools where Simon et al. (2001) described the occurrences, which are not captured in the averaged

345 climatic layers used for modelling. In fact, our experiment results show, the warm temperate

346 population of *G. turuturu* can maintain its photosynthetic yield for at least three days in this

347 temperature, demonstrating that this alga can survive to short-time exposure to high temperatures.

348 In addition, the temperate population experiment demonstrated *G. turuturu* similar Fv/Fm

349 responses to temperature as the response curve from the model, with higher photosynthetic yield

350 in 10, 13, 16 and 20ºC. The experiment with the blades collected in Brazil also showed higher

351 Fv/Fm in the lower temperature used. These results indicate that both populations of *G. turuturu*

352 present better physiological performance in regions with mild temperatures, i.e. temperate

353 climates. Interestingly, in higher temperatures the two populations responded differently. As stated

354 above, the WAP population presented tolerance to a short-time exposure to 30ºC, and to 24ºC for

355 the duration of the experiment (LNC only), while the TAP population had a significant drop in

356 performance in 24ºC. Although the different responses may be relative to the fact that these are

357 two distinct invasive populations (Allendorf and Lundquist, 2003), both demonstrated the

358 tendency to experience a drop in Fv/Fm in higher temperatures. The higher temperature used in

359 the warm temperate experiment demonstrated that *G. turuturu* will also present reduced growth

360 rate in regions with average temperatures around 30ºC. Even with the higher chlorophyll content,

361 *G. turuturu* was not able to maintain its photosynthetic yield in 30ºC. Furthermore, the higher

362 concentration of total carotenoids showed a stress response of the algae to the higher temperature

363 but did not prevent the reduction of growth. However, previous studies of the species demonstrated

364 that younger stages of *G. turuturu*'s life cycle have a wider temperature tolerance range than older

365 stages, with germiling growth being the same at 15ºC and 30ºC (Kraemer et al., 2017). For this

366 reason, juvenile stages and/or spores may be more aggressive in a bioinvasion process if

367 transported by an oceanographic vector. And once in a new habitat, the acclimation conditions

368 during the invasive process may be determinant in the success of establishment, when temperature

369 limits are between the ones here evaluated for adult blades.

370 The ecophysiological experiment in Brazil showed that *G. turuturu* can tolerate a wider

371 range of nutrient concentration without reducing its photosynthetic yield in 18ºC, which was

372 expected based on previous descriptions of this algae (Simon et al., 2001). The region where the

373 species is found in southern Brazil is characterized by the presence of upwelling of colder, nutrient-

374 rich waters from the South Atlantic Central Water, and during winter receives influence from the

375 nutrient-rich La Plata river plume and the cold waters of the Sub-Antartic currents (Pereira et al.,

376 2009). Simultaneously, Martins et al. (2012) reported the algae diversity decrease in southern

377 Brazil caused by urbanization and coastal pollution, damaging the resilience of the benthic

378 community. Consequently, the local conditions of this region meet the suitable conditions

379 demonstrated by the experiment and the model for the establishment and expansion of *G. turuturu*

380 occurrence. Hence, countries with similar coastal characteristics with no register of the species

381 must be aware and act to prevent the arrival and establishment of *G. turuturu.*

382 Our results allow the affirmation that non-fertile adult blades of *G. turuturu* will likely not

383 have success in expanding its niche to regions with an average temperature around 30ºC or survive

384 to heatwaves (short periods with an average of 5 days of anomalous warming of the ocean)

385 (Hobday et al., 2016) in regions with milder temperatures. As for temperate and warm-temperate

386 regions, our model predicts habitat suitability for *G. turuturu* for temperatures reaching up to

387 approx. 26ºC, and the WAP experiment results demonstrated that this alga can maintain its

388 photosynthetic yield and growth at 24 ºC. However, if in 24ºC an event of introduction of a higher

389 amount of nutrients in the water column occurs, *G. turuturu* may suffer a drop in photosynthetic

390 yield depending on the exposure period. Consequently, the invasive potential of this alien species

391 in regions with an average temperature around 24ºC may be smaller than its potential in colder

392 water regions, as noted in the 18ºC treatment, where *G. turuturu* had no response to the higher

393 nutrient concentration.

394   Temperature was chosen as one of the variables in the experiments and model due to its

395 importance in determining the geographic distribution of macroalgae (Hoek, 1982). The changes

396 in the average sea surface temperature caused by climate change are characterized as a global

397 stressor to autochthonous communities. *G. turuturu*, as demonstrated in this study, can have

398 advantage in such scenario, expanding its distribution to locations with predicted regional cooling

399 (e.g. northern Chile and South Africa, Falvey and Garreaud 2009; Bolton and Anderson 2012) or

400 warming of cold-water regions (Poloczanska et al., 2013; Vergés et al., 2014). Models as the one

401 here used are the best approach to translating future climatic changes into ecological responses,

402 guiding strategies of conservation and management (Wiens et al., 2009). Moreover, the effects of

403 a local stressor, higher nutrient concentration, were assessed in *G. turuturu* through ecophysiology

404 evaluation. By combining both approaches, we could determine the possible geographic expansion

405 of *G. turuturu* under both local and global stressors.

406   Habitat models for invasive seaweeds need a high transferability, expanding predictions to

407 regions where the species could potentially invade. Verbruggen et al. (2013) demonstrated that for

408 global predictions the most important procedure to increase model transferability is choosing fewer

409 predictors with high ecological significance for the species. Furthermore, the use of

410 ecophysiological knowledge about the species is highly advisable to assess the significance of

411 predictions (Araújo and Guisan, 2006). Accordingly, we used ENM and fewer variables to model

412 the global distribution of *G. turuturu* together with the evaluation of its ecophysiology.

413 With increasing environmental changes and availability of transport vectors, it is essential

414 the use and improvement of approaches capable of predicting possible new events of bioinvasion,

415 as done in this work. Invasive species represent great harm to ecosystem services, with provision

416 services being the most affected by them, such as food provision and genetic variability (Vilà et

417 al., 2010). It becomes clear that these predicting tools and the knowledge of invasive species and

418 their habitats must be used as the foundation of international regulatory agreements, pursuing the

419 protection of natural resources and biodiversity (Hulme et al., 2008). The results found in this

420 study enable stakeholders and policymakers to discuss and foster management actions regarding

421 prevention or eradication in case of *G. turuturu* expanding its distribution to new regions,

422 especially for South America where there are few registers of its occurrence (Azevedo et al., 2015).

423 Therefore, the present work takes place as an important tool of bioinvasions management in a

424 scenario of quick changes in environmental conditions and dispersion patterns, in which the delay

425 of response by international and local governments can cost the planet ecosystem functions and

426 services that it relies upon.

427

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718   Figure captions

719   **Fig. 1** Map of *G. turuturu* occurrences used in the model. Sampling locations are represented in

720   white diamonds, whilst black dots represent occurrences in the known introduced range and grey

721   dots represent occurrences in the native range. A close-up was made in South America to show

722   more clearly the introduced and sampled locations in this region.

723   **Fig. 2** Map of *G. turuturu* habitat suitability in the planet (a), with zoom in South America (b),

724   and Europe/North Africa (c). Regions in black represent regions suitable for the occurrence of *G.*

725   *turuturu,* whilst regions in light grey represent regions with unsuitable environmental conditions

726   for *G. turuturu.* Land is represented in dark grey, and zones without environmental data are

727   represented in white (no data).

728   **Fig. 3** Response curve of *G. turuturu* to maximum ocean temperature. Decline point is set at

729   21.23°C and the limiting point at 26.55°C, demonstrating low habitat suitability of *G. turuturu* to

730   higher temperatures.

731   **Fig. 4** Average ± standard deviation (*n*=7) of Optimal Quantum Yield (Fv/Fm) for all

732   temperatures (18, 24 and 30°C) and nutrient conditions (low nutrient condition – LNC, and high

733   nutrient concentration – HNC) in the first, third, fifth and seventh day of the warm temperate

734   adapted population (WAP) experiment. Letters indicate Tukey's test significantly different

735   groups (*p*<0.05).

736   **Fig. 5** Average ± standard deviation (*n*=6) of Optimal Quantum Yield (Fv/Fm) in the temperate

737   adapted population (TAP) experiment in the beginning of the experiment (initial control), then

738   the values of each treatment after three days at 10 (control), 13, 16, 20 and 24°C. Letters indicate

739   Tukey's test significantly different groups (*p*<0.05).

740   **Fig. 6** Response of *G. tururu* (warm temperate adapted population - WAP) to different

741   temperatures in treatments. Different letters represent Tukey's test significantly (*p*<0.05)

742   different groups. Bars represent average ± standard deviation. (a) Chlorophyll *a* concentration

743   (µg chlorophyll-*a* per g of fresh weight) in the experiment's beginning and end (*n*=7). (b) Total

744   Carotenoids concentration (µg total carotenoids per g of fresh weight) in experiment's beginning

745   and end (*n*=7). (c) Percentage of *G. tururu* daily growth rate during the experiment (*n*=10).

746   **Fig. 7** Average ± standard deviation (*n*=7) of phycoerythrin concentration (µg phycoerythrin per

747   g of fresh weight) at different nutrient conditions (warm temperate adapted population - WAP).

748   Letters indicate Tukey's test significantly different groups (*p*<0.05).

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750   Supplementary material

751   **ESM1:** Excel file with all the occurrences and their sources used in the Ecological Niche Model.

752   **ESM2:** Word document with additional figures, such as the experimental design setup, response

753   curves of the model and chlorophyll concentration in each nutrient condition (WAP experiment).

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