

2020-01-15

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<http://hdl.handle.net/10026.1/15272>

10.1016/j.scitotenv.2019.134692

Science of The Total Environment

Elsevier BV

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1 This is the author's accepted manuscript. The final published version of this work (the version of record) is
2 published by Elsevier in *Science of the Total Environment*. The manuscript was made available online on the
3 20 December 2019 at: <https://www.sciencedirect.com/science/article/pii/S0048969719346832> This work
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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 24°C, 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 28°C), 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 0.08° (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 (~10°C in France in February (Dubois et al., 2007), and ~18°C 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 $65 \pm 5 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

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 (18°C). 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 30°C) 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), except 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 10°C, 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 24°C. 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 yield (F_v/F_m). 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 4°C 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 4°C 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):

$$261 \quad \text{GR (\% \cdot day}^{-1}\text{)} = \left[\left(\frac{W_t}{W_i} \right)^{1/t} \right] \times 100\% \quad (1)$$

262 Where W_i and W_t 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 30°C). 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 24°C, 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 $4.4 \text{ E} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$
287 and ocean temperature below 26.55°C , however, with a starting drop at 21.23°C (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 30°C
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 30°C with LNC, there was a smaller decline in Fv/Fm,
298 but still presented Fv/Fm values lower than the treatments of 24 and 18°C. Similarly, there was a
299 contrast between the LNC and HNC treatments at 24°C, 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 24°C (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 24°C and 30°C in the
312 end of the experiment were statistically distinct from the samples of the beginning and 18°C (Fig.
313 6a). The higher concentration of chlorophyll was found in 30°C, followed by 24°C. Similarly, the
314 higher concentration of total carotenoids was found in the last day at 30°C, 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 30°C 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 $4.04 \text{ E. m}^{-2} \cdot \text{yr}^{-1}$ threshold is comparable with the minimum annual irradiance inferred
340 for other species of algae (Gattuso et al., 2006). The limitation of 26.55°C 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 28°C 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 20°C. 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 30°C, and to 24°C for
355 the duration of the experiment (LNC only), while the TAP population had a significant drop in
356 performance in 24°C. 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 30°C. Even with the higher chlorophyll content,
361 *G. turuturu* was not able to maintain its photosynthetic yield in 30°C. 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 germinating growth being the same at 15°C and 30°C (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 18°C, 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-Antarctic 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 30°C 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. 26°C, and the WAP experiment results demonstrated that this alga can maintain its
388 photosynthetic yield and growth at 24 °C. However, if in 24°C 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 24°C may be smaller than its potential in colder
392 water regions, as noted in the 18°C 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

428 ACKNOWLEDGEMENTS

429 We would like to thank Eduardo de Oliveira Bastos and Lidiane Pires Gouvêa for help in
430 experiments. We also thank the Laboratório Multiusuário de Estudos em Biologia (LAMEB) of
431 the Federal University of Santa Catarina (UFSC) for the availability of equipment.

432

433 FUNDING

434 This work was financed by National Council for Scientific and Technological
435 Development (CNPq), Sustainable prospection in ocean islands: biodiversity, chemistry, ecology
436 and biotechnology (PROSPECMAR-Islands), Instituto Nacional de Ciência e Tecnologia para as
437 Mudanças no Clima (INCT-MC), Rede nacional de pesquisa em biodiversidade marinha
438 (SISBIOTAMar), Foundation support research and innovation in the State of Santa Catarina
439 (FAPESC), Fundação Boticário, and Coordenação de Aperfeiçoamento de Pessoal de Nível
440 Superior (CAPES). This study was supported by the Pew Foundation and the Foundation for
441 Science and Technology (FCT) of Portugal through the postdoctoral fellowship
442 SFRH/BPD/111003/2015 and project CCMAR/Multi/04326/2013, and by the Centre Mondial
443 d’Innovation, Roullier Group. Gabrielle Koerich received a scholarship (CSF 88888.884790/2014-
444 00) and a fellowship from CAPES.

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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 \pm 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 \pm 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. turuturu* (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 \pm 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. turuturu* daily growth rate during the experiment ($n=10$).

746 **Fig. 7** Average \pm 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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