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A modelling approach to explore the critical environmental parameters influencing the growth and establishment of the invasive seaweed *Undaria pinnatifida* in Europe

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21 **Abstract:**

22 A key factor to determine the expansion dynamics and future distribution of non-native
23 species is their physiological response to abiotic factors and their changes over time. For this
24 study we developed a spatially explicit, agent-based model of population growth to represent
25 the complex population dynamics of invasive marine macroalgae with heteromorphic
26 biphasic life cycles. The model framework represents this complex life cycle by treating the
27 individual developmental stages (gametophytes/sporophytes) as autonomous agents with
28 unique behaviour/growth parameters. It was parameterised to represent a well-documented
29 invasive algal species, the Asian kelp *Undaria pinnatifida*, and validated against field results
30 from an *in situ* population in Brittany, France, showing good quantitative agreement in terms
31 of seasonal changes in abundance/recruitment and growth dynamics. It was then used to
32 explore how local environmental parameters (light availability, temperature and day length)
33 affect the population dynamics of the individual developmental stages and the overall
34 population growth. This type of modelling approach represents a promising tool for
35 understanding the population dynamics of macroalgae from the bottom-up in terms of the
36 individual interactions between the independent life history stages (both microscopic and
37 macroscopic). It can be used to trace back the behaviour of the population as a whole to the
38 underlying physiological and environmental processes impacting each developmental stage
39 and give insights into the roles these play in invasion success.

40

41 **Keywords:**

42 Macroalgae; agent-based model; individual-based model; invasive species; seaweed; kelp;
43 *Undaria pinnatifida*

44

45

46 **1. Introduction:**

47 The introduction and establishment of non-native plant and animal species can have a
48 broad range of impacts on native species and community structure as well as economic
49 consequences through the disruption of ecosystem services (Simberloff et al., 2013; Vilà et
50 al., 2009). However, it is often difficult to predict the actual (and future) invasive behaviour
51 under changing environmental conditions, since it is seldom possible to determine the source
52 of an introduction with certainty, especially in marine environments (Rius et al., 2015). A
53 further level of complexity comes from the fact that the response of introduced species to
54 environmental factors may differ between the native and introduced ranges, as a consequence
55 of trait plasticity (Davidson et al., 2011). A recent study of plant invaders pointed out an
56 increased physiological tolerance of successful introduced species (Higgins and Richardson,
57 2014). Niche shift may thus be more common than previously assumed, which may
58 complicate ecological-niche modelling efforts (Parravicini et al., 2015).

59 Seaweeds account for 20-29% of all non-native marine species in Europe and they are
60 an important concern because of their role as primary producers in coastal ecosystems
61 (Engelen et al., 2015; Schaffelke and Hewitt Chad, 2007; Schaffelke et al., 2006). One
62 example of a notable invasive species on a global scale is the brown kelp *Undaria pinnatifida*
63 (Harvey) Suringar, 1873 (Phaeophyceae: Laminariales). This has traditionally been cultivated
64 in its native range of eastern Asia, including Japan, Korea and China (Ohno and Matsuoka,
65 1993; Shao-jun and Chao-yuan, 1996). However, in recent decades it has arisen as an
66 invasive threat in Europe, North America and New Zealand among other places, due to
67 human-mediated transport (Castric-Fey et al., 1993; Fletcher and Farrell, 1998; Floc'h et al.,
68 1991; Grulois et al., 2011; Hay and Luckens, 1987; Silva et al., 2002; Voisin et al., 2005).

69 The order Laminariales (kelp) is characterised by a heteromorphic life history that
70 consists of two distinct phases: a haploid gametophyte stage and a diploid sporophyte stage

71 (see Fig. 1) (Bessho and Iwasa, 2010; Clayton, 1988). Each stage has specific environmental
72 requirements for optimal growth and development, in particular with respect to water
73 temperature, light intensity and photoperiod (daily light:dark ratio) (Floc'h et al., 1991).

74 One key outcome of biological invasion studies has been to point out the role played
75 by match-mismatch between the physiological requirements of the introduced species and the
76 local environmental conditions. It is important to define the conditions under which
77 introduced species expand (locally or spatially) in order to predict their fate. However, in
78 many marine species, it is difficult to make predictions due to their complex life cycle and
79 substantial variation in physiological traits. The purpose of this study was thus to propose a
80 modelling approach that takes into account both the individual stages of the life cycle and
81 their specific environmental requirements, when modelling the overall population dynamics.

82 An agent-based (or individual-based) modelling approach was chosen in order to be
83 able to integrate data on the basic physiological properties of *U. pinnatifida* individuals into
84 an overall model of population growth. This allows the individual life history stages
85 (gametophytes/sporophytes) to be represented as autonomous agents and their
86 behaviour/interactions to be explicitly described. This so-called bottom-up approach means
87 that the emergent dynamics, at the population level, can be traced back to the individual
88 components (Denny and Benedetti-Cecchi, 2012; Grimm and Railsback, 2005).

89 The main challenge in building an agent-based model of a complex biological system
90 such as this is the ability to parameterise it. For this reason, a thorough review of the
91 literature was first carried out in order to gather empirical data on the basic responses of the
92 individual life stages of *U. pinnatifida* from a mechanistic point of view. We then tested the
93 model for accuracy and robustness by comparing it with an empirical data set from a natural
94 population in Brittany, France (Voisin, 2007). This step was critical as phenotypic plasticity
95 is often assumed to be an important characteristic of invasive species. Finally, we used the

96 model to explore how some of the critical environmental parameters influence the population
97 dynamics of the test species.

98 This type of low-level insight can help us to understand the role that climatic
99 conditions play in the invasion dynamics of *U. pinnatifida* and other invasive macroalgae.
100 The aim of this research was to develop a framework for exploring how direct and indirect
101 effects on the life cycle and individual life history stages of macroalgae determine their
102 population dynamics and invasive potential. This could enable better predictions about the
103 potential future spread and range distribution of invasive seaweeds under changing climatic
104 conditions. Furthermore, the agent-based approach means that heterogeneities in local
105 environmental conditions, and between individual life history stages, can be explicitly
106 accounted for in order to be able to predict the potential emergent dynamics at the population
107 level.

108

109 **2. The Model**

110 The model was built upon a generic agent-based framework called CoastGEN, built in
111 the C++ programming language, which has been developed to simulate populations of
112 biological entities in a discrete two-dimensional environment (Murphy and Johnson, 2015).
113 The advantages of this framework are that it is fully parallelisable (using domain
114 decomposition and the Message Passing Interface) to take advantage of distributed
115 computing architectures and it represents a robust and adaptable tool to simulate spatially and
116 temporally heterogeneous phenomena (Gropp et al., 1996).

117 A detailed individual-based model of the life history of *U. pinnatifida* (including
118 distinct microscopic gametophyte and macroscopic sporophyte stages) was built upon this
119 basic framework for the purposes of this study. The input parameters used for the simulations
120 in this paper are summarised in Table 1. Additional stochasticity is introduced into the model

121 by adding random individual variability when initialising each agent's parameters, using the
122 Mersenne twister pseudo-random number generator (Matsumoto and Nishimura, 1998).

123

124 *2.1. The environment*

125 The coastal environment is represented as a discrete, two-dimensional grid with each
126 grid element corresponding to 0.25 m² of surface area and periodic boundary conditions. This
127 allows for heterogeneity in the environmental conditions and spatial distribution of
128 organisms, as opposed to assuming a completely homogeneous, mixed environment. The
129 maximum number of agents (gametophytes/sporophytes) that may occupy a lattice position
130 can be specified by the user. For the purposes of the simulations in this paper, this value was
131 set to 10⁴, which was selected in order to avoid space limitations affecting the growth curves
132 over the timescales involved in the simulations in this paper. To investigate the role of space
133 limitations and competition in the natural environment, a more detailed model of frond
134 structure and competition for light will need to be incorporated in future versions.

135 The availability of light in the water column is a function of the light attenuation
136 coefficient for photosynthetically available radiation (K_{dPAR}) (Saulquin et al., 2013). This
137 represents light attenuation in the water column due to backscattering of light caused by
138 suspended matter and absorption by dissolved organic matter. Estimates of surface irradiance
139 together with the K_{dPAR} are used to calculate the residual energy (I) available for
140 photosynthesis at a given depth:

$$141 \quad I = E(z) = E(0)e^{-zK_{dPAR}} \quad (1)$$

142 where z is depth (m), $E(0)$ is surface irradiance, and $E(z)$ is the irradiance energy
143 available for photosynthesis at depth z . The average depth for the test simulations in this
144 paper was set to 1.0 m. This was chosen in order to match the conditions from field surveys

145 of a natural population in Brest harbour which involved installing sampling panels that were
146 suspended approximately a metre below the floating pontoons (Voisin, 2007).

147 At lower depths, growth becomes inhibited due to light limitation and peak
148 recruitment is expected to decrease as a function of depth. This is why floating pontoons
149 represent appropriate substrates for early colonisation by *U. pinnatifida* since they are
150 maintained at a constant depth relative to the surface. Future work will involve more detailed
151 analyses of the effects of depth and light attenuation on the growth of the various life history
152 stages. However, for the purposes of this study, the depth was maintained at a constant value
153 in order to represent optimal conditions for growth.

154

155 2.2. Gametophyte agents

156 Gametophytes are the microscopic haploid stages of the *U. pinnatifida* life cycle (see
157 Fig. 1). In the model, their relative daily growth rate is calculated as a function of the water
158 temperature, solar radiation, and number of day light hours. Experimental data is available in
159 the literature for *U. pinnatifida* gametophytes growing under different temperature regimes
160 (Morita et al., 2003a). To represent the effect of temperature on growth, a thermal
161 performance curve (Stevenson et al., 1985) was fitted to this data (Fig. 2a, $R^2 > 0.99$):

$$RGR_{GT} = S \left[\frac{1}{(1 + K_1 e^{-K_2(T_w - CT_{min})})} \right] \times [1 - e^{K_3(T_w - CT_{max})}] \quad (2)$$

162 where RGR_{GT} is the relative growth rate in response to temperature, T_w is the current
163 water temperature K_1 , K_2 and K_3 are constants, CT_{min} and CT_{max} are the lower and upper
164 critical temperature limits respectively, and S is a scaling factor.

165 Furthermore, it has been shown in studies that the growth rate of gametophytes is
166 sensitive to changes in both solar irradiance and day length (Choi et al., 2005). This data set
167 was used to generate a photosynthesis-irradiance curve by fitting the hyperbolic equation of

168 Jassby and Platt (1976) to empirical measurements of *U. pinnatifida* gametophytes by Choi et
169 al. (2005) (Fig. 2b, $R^2 > 0.99$):

$$REG_{G_I} = P_{max} \cdot (1 - \exp \left[-\alpha \cdot \frac{I - I_c}{P_{max}} \right]) \quad (3)$$

170 where REG_{G_I} is the relative effect of irradiance on the growth rate of the
171 gametophyte agent, I is the current irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$, calculated for a given depth by
172 Equation 1 above), P_{max} is the maximum rate of photosynthesis, α is the slope of the curve
173 and I_c is the compensation point (Jassby and Platt, 1976). Note that REG_{G_I} is expressed
174 relative to a baseline condition (where irradiance = $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ and day light (DL) hours
175 = 12). The hyperbolic equation of Jassby & Platt was chosen because it has been extensively
176 tested and applied to different species of marine organisms, including *U. pinnatifida*
177 (Campbell et al., 1999; Harrison et al., 1985).

178 The data from Choi et al. (2005) was also used to calculate the relationship between
179 day length (d , or day light hours) and the parameters P_{max} and α of the photosynthesis-
180 irradiance curve. For α , there is a positive linear relationship with day length ($R^2 > 0.99$),
181 whereas an exponential function was used to fit the data for P_{max} as a function of day length
182 ($R^2 = 0.95$):

$$\alpha = 0.029d - 0.198 \quad (4)$$

$$P_{max} = 0.292e^{0.11d} \quad (5)$$

183 By incorporating these equations into the model it allows us to estimate the relative
184 daily growth rate of the gametophyte agents (RGR_G) at any point in time as a function of
185 the current temperature, irradiance and day length conditions:

$$RGR_G = RGR_{G_T} \times REG_{G_I} \quad (6)$$

186

187

188 2.3. *Gametogenesis*

189 The maturation and production of gametes (or gametogenesis) by gametophytes, and
190 the subsequent fertilisation to form new sporophytes are important processes influenced by
191 external environmental cues. Experimental tests have demonstrated that there is a relationship
192 between day length/water temperature and the maturation of female gametophytes of *U.*
193 *pinnatifida* (Choi et al., 2005; Morita et al., 2003a).

194 The effect of temperature on the fertility of female gametophytes of *U. pinnatifida*
195 over the range 10-25°C was explored by Morita et al. (2003a). They demonstrated a peak in
196 fertility at 10-15°C with an approximately exponential decrease in fertility above that. A
197 simple logistic function was chosen to represent this as it showed a good fit against the data
198 over the temperature range explored (Fig. 2c, $R^2=0.97$):

$$RF_T = 1 - \left[\frac{1}{(1 + e^{-k(t-t_0)})} \right] \quad (7)$$

199 where RF_T is the relative fertility of the gametophytes in response to temperature, k is
200 the steepness of the curve, t is the current water temperature, and t_0 is the temperature at the
201 midpoint of the sigmoid.

202 The fertility of female gametophytes was also recorded by Choi et al. (2005) under
203 different day length regimes (8, 12 and 16 hours). A Weibull curve was fitted to this data
204 ($R^2>0.99$) in order to represent the effect of day length on the relative fertility (RF_{DL}) of the
205 gametophyte agents (Fig. 2d). This curve was chosen because of its relative simplicity and
206 flexibility (for example, it does not require any prior assumptions about symmetry in the
207 data).

208

209 2.4. *Sporophyte agents*

210 Sporophyte agents are modelled from their initial microscopic cellular scale up to an
211 eventual size of 1-3 metres (frond length), with growth represented as the relative daily

212 increase in the total length of the frond structure. This represents a particular modelling
 213 challenge due to the range of scales involved. Therefore, it was necessary to model the
 214 relative growth rate as a function of the length of the sporophyte. Studies from the literature
 215 were used to calculate the growth rate of sporophytes in different size classes (from
 216 microscopic sporophytes in culture to mature sporophytes 79 cm in length) (Choi et al., 2007;
 217 Pang and Lüning, 2004; Shao-jun and Chao-yuan, 1996). A power law functional relationship
 218 between the relative growth rate and the length of the sporophyte was estimated by fitting to
 219 this data (Fig. 3a, $R^2=0.97$):

$$RGR_{S_{base}} = 3.615l^{-0.407} \quad (8)$$

220 where l is the length of the sporophyte. This equation is used to calculate a baseline
 221 relative growth rate for sporophyte agents ($RGR_{S_{base}}$) under “default” environmental
 222 conditions (irradiance = $40 \mu\text{mol m}^{-2} \text{s}^{-1}$, temperature = 15°C and day light (DL) hours = 12).

223 Furthermore, to account for the change in photosynthetic efficiency with increasing
 224 frond length (i.e. due to increasing thallus complexity/density and the proportion of
 225 differentiated cell types) the input parameters for the photosynthesis-irradiance curve of
 226 Jassby & Platt (Eq. 3) are expressed as functions of sporophyte length (Eq. 8-10). These
 227 functions were derived by fitting to data from Campbell et al. (1999) on macroscopic
 228 sporophytes and Choi et al. (2005) on microscopic gametophytes ($R^2>0.99$ for all three
 229 curves).

$$P_{max} = 0.4 \ln(l) - 0.596 \quad (9)$$

$$\alpha = 0.5l^{-0.328} \quad (10)$$

$$I_c = 2.5 \ln(l) - 19.92 \quad (11)$$

230 To estimate the initial photosynthetic efficiency of microscopic sporophytes (i.e.
 231 immediately following fertilisation when the proportion of differentiated cell types is still
 232 low), data from studies of gametophytes had to be used. Nevertheless, this should be a

233 relatively good estimator of photosynthetic efficiency for the purposes of this model since the
234 dry weight to fresh weight ratio of microscopic gametophytes and sporophytes would be
235 expected to be similar due to the lack of differentiated cell types. The availability of
236 equivalent data on cultured sporophytes would be preferable however.

237 Data from Pang and Lüning (2004) was used to characterise the effect of day length
238 on the growth rate of sporophytes. They measured the time in weeks to maturity for
239 sporophytes grown under different day length regimes and this was used to estimate the
240 relative differences in growth rates. A hyperbolic curve (see Eq. 3) was then fitted to this data
241 to predict the relative effect of day length on the growth rate ($REG_{S_{DL}}$) (Fig. 3b, $R^2 > 0.99$).

242 For temperature, a thermal performance curve was fitted to experimental data on
243 sporophytes grown in water temperatures between 5-20°C by Morita et al. (2003b), using the
244 same approach described for the gametophyte agents above (see eq. 2). Figure 3c shows the
245 results of fitting the curve to Morita's data through least squares regression ($R^2 = 0.99$) in
246 order to represent the relative effect of temperature on the growth rate (REG_{S_T}). Finally, Fig.
247 3d shows an example of the photosynthesis-irradiance curve (REG_{S_I}) for an *U. pinnatifida*
248 sporophyte as calculated directly by Campbell et al. (1999).

249 The relative daily growth rate of each sporophyte agent (RGR_S) is thus a function of
250 the baseline growth rate and the relative effects of temperature, light and day length:

$$RGR_S = RGR_{S_{base}} \times REG_{S_T} \times REG_{S_I} \times REG_{S_{DL}} \quad (12)$$

251

252 In order to test the growth algorithm described above, some initial validation tests
253 were carried out on the predicted growth rates for sporophytes of different lengths versus
254 observations from the literature. For example, in cultivation experiments (irradiance=100
255 $\mu\text{mol m}^{-2} \text{s}^{-1}$, temp=15°C, DL=12h), Pang & Lüning (2004) recorded average growth rates
256 (measured as an increase in frond length) of 6-10 % per day among 3-4 week old sporophyte

257 recruits (length unspecified). Under similar conditions, the model predicts growth rates of
258 5.8-7% per day for 3-4 week old sporophytes (10-16 cm long). Similarly, Choi et al. (2007)
259 recorded a relative growth rate (frond length) of 7.2% per day among a population of
260 sporophytes with an average length of 79.06 cm. This compares to a model predicted growth
261 rate of 6.9% (79 cm long, assuming light-saturated conditions).

262 Sporophytes agents die away naturally after reaching maturity and releasing all of
263 their spores. However, the premature loss of sporophytes may also occur through potential
264 random events (e.g. storms, grazers) which result in detachment/death. In fact, field studies in
265 Brest harbour, France, have indicated that as much as 70% of all sporophyte recruits do not
266 survive past their first month (Voisin, 2007). To account for this, an age to mortality curve
267 (Weibull function) was calculated and fitted to the data from Brest harbour to determine the
268 probability of premature death as a function of the age of the sporophyte (Fig. 4a).

269

270 2.5. Spore Release

271 Mature sporophytes are characterised by a distinct sporophyll structure at the base of
272 their stipe in which the spores are formed. The mean size at maturity calculated for a
273 population in Brest harbour, France was 32.66 cm (Voisin, 2007). This is used in the model
274 to determine the mean minimum size at which spore release can occur. The release of spores
275 by mature sporophytes is thought to be a temperature-dependent event (Saito, 1975). Suto
276 (1952) recorded the average (10-day) sea water temperatures and the presence/absence of
277 shedding among *U. pinnatifida* sporophytes in Japan (Suto, 1952). We used their original
278 data to plot the frequency of spore release versus temperature and fitted a logistic function to
279 this (Fig. 4b, $R^2 > 0.99$).

280 For the test simulations in this paper, the mean spore release rate per individual
281 sporophyte agent was set to 2.0×10^7 spores hour^{-1} and total spore production in a season is

282 10^{10} spores sporophyte⁻¹. This is within the range of estimates for the rate of spore release
283 ($1.0 \times 10^7 - 1.4 \times 10^8$ spores h⁻¹) and the total spore production ($>10^9$) for *U. pinnatifida* from
284 the literature (Schaffelke et al., 2005; Suto, 1950). Once released, they are represented as
285 simple particles subject to a discretised implementation of Fick's First Law of diffusion for
286 dispersal across a lattice environment (Ginovart et al., 2002). Water currents are not explicitly
287 simulated, but in terms of local population dynamics a simple diffusion algorithm is thought
288 to be sufficient due to the short lifespan of spore particles in the water column (Thiébaud et
289 al., 1998).

290 Experimental studies have shown that *U. pinnatifida* spores can lose their fixing
291 ability within hours of release and stop swimming within 3 days (Forrest et al., 2000; Suto,
292 1950). Therefore, they were assigned a relatively short half-life of 24 hours in the
293 simulations. A gametophyte agent is formed when a spore comes into contact with a suitable
294 substrate for attachment. In the model, this process is represented as a simple stochastic
295 process where the probability of recruitment of new gametophytes (P_{recruit}) is a function of the
296 number of spores occupying the lattice position ij (s_{ij}) at that point in time and a user-defined
297 probability of attachment/germination on the substrate (A_{substr}):

$$P_{\text{recruit}} = A_{\text{substr}} s_{ij} \quad (13)$$

298

299

300 **3. Results & Discussion:**

301 *3.1. Model validation*

302 Simulations were carried out using environmental parameters (light, temperature and
303 day length) representative of Brest harbour, France, in order to validate the model against
304 real-world data collected by researchers at the Station Biologique de Roscoff, France. Surface
305 water temperature data for the port of Brest (2003-06) were obtained from a SOMLIT

306 (Service d'Observation en Milieu Littoral, INSU-CNRS, Brest, [http://somlit-db.epoc.u-](http://somlit-db.epoc.u-bordeaux1.fr)
307 [bordeaux1.fr](http://somlit-db.epoc.u-bordeaux1.fr)) buoy situated a few hundred metres from the marina (Voisin, 2007).
308 Meanwhile, sample mean global solar irradiance data for the region were obtained using the
309 CalSol online application (Institut National de L'Energie Solaire, CEA-CNRS).

310 Figure 5 shows model predictions for the overall sporophyte population growth of an
311 *U. pinnatifida* invasion in a harbour setting (for raw data, see Table 1, (Murphy et al.,
312 (submitted))). The model displays an annual pattern of growth and decay characteristic of *U.*
313 *pinnatifida* populations in nature, in response to seasonal variations in light and temperature
314 levels. For validation purposes, this was compared to real-world field results from the port of
315 Brest in France during the 2005/06 growing season (Voisin, 2007): During this field
316 experiment, 64 aluminium panels were set-up one metre below the surface, a depth optimal
317 for the recruitment of the study species, and the settlement and length of each individual was
318 recorded every month.

319 The raw data was first normalised to express the monthly abundance/recruitment
320 values for the sporophytes relative to their peak annual abundance/recruitment respectively
321 (see Tables 2-3, (Murphy et al., (submitted))). This means that all monthly abundance values
322 for a growing season (Aug-July) were expressed relative to the peak abundance in that year
323 (usually in April). This was done in order to avoid bias in the results due to differences in
324 population size and to focus on the relative seasonal variation in abundance/recruitment due
325 to environmental effects.

326 The model results and field data were then plotted against each other in terms of
327 overall abundance data and monthly recruitment rates (Fig. 6a & b). The R^2 values were 0.84
328 and 0.85 when comparing the model predictions and the real-world measurements for total
329 abundance and monthly recruitment respectively over the course of the 12 months. Some
330 variation from the real-world results is to be expected since factors such as competition and

331 self-shading were not taken into account. Future work will involve extending the base model
332 to incorporate intra- and inter-specific competition for light/space.

333 Figure 6b shows the monthly recruitment rate (i.e. appearance of new sporophytes >5
334 cm in length) for Brest harbour compared with the model predictions. The model matches
335 closely the seasonal pattern of growth observed in the real-world populations. The one
336 exception is in November when the model over-predicts the rate of recruitment. Possible
337 explanations for this include seasonal changes in the turbidity of the water affecting the
338 growth of young sporophytes or increased mortality due to winter storm activity that year.

339 The predicted life expectancy and age to maturity for *U. pinnatifida* sporophytes were
340 also compared with field records from Brest (Fig. 7). There is good quantitative agreement
341 between the model predictions and field measurements for life expectancy, age to maturity
342 and duration of the mature phase respectively. This indicates that the physiological responses
343 to environmental factors of the local population of *U. pinnatifida* match closely with
344 predictions based on studies of individuals in its native range of eastern Asia.

345 Voisin (2007) also investigated the important relationship between water temperature
346 and the recruitment of sporophytes. Previous studies in California, USA, had identified
347 recruitment pulses in *U. pinnatifida* populations associated with drops in ocean temperature 2
348 months prior to the recruitment (Thornber et al., 2004). Therefore, to investigate if the model
349 reproduced this pattern the predicted rate of recruitment was plotted against the water
350 temperature two months prior, and compared with similar field results from Brest. As can be
351 seen in Figure 8, there is good overlap between model predictions and the real-world data (for
352 raw data, see Table 4, (Murphy et al., (submitted))). They both show increased recruitment at
353 lower temperatures, which agrees with data from the literature indicating significantly higher
354 recruitment of sporophytes at temperatures below 15°C (Thornber et al., 2004; Voisin, 2007).

355 It must be noted that apart from the use of a scaling factor, no attempt to fit the model
356 parameters to the Brest population was made. The model input parameters were solely based
357 on experimental records from various studies in the literature often involving geographically
358 disparate populations of *U. pinnatifida* in their native range. Interestingly, the fact that the
359 Brest population behaves similarly to the model predictions may indicate that relatively
360 limited phenotypic adaptation has occurred in the local Brittany populations as compared to
361 its native range, meaning that this species may be pre-adapted to a large set of environmental
362 conditions, for the factors considered here. In this case, abiotic factors seem to be the
363 dominant factor in influencing the local population dynamics. However, since *U. pinnatifida*
364 is a recent introduction to Brittany, there is the possibility that future adaptation to the new
365 environment may play an important role in determining its continued spread in the region.

366

367 *3.2. Response to environmental parameters*

368 The next step was to explore the underlying system dynamics and critical parameters that
369 contribute to the observed patterns of growth predicted by the model. To achieve this, the
370 responses of the various developmental stages of *U. pinnatifida* to three key environmental
371 parameters (light, temperature, and day length) were investigated using the model. Figures 9-
372 11 represent the raw simulation output expressed in terms of these three environmental
373 variables. All the plots come from an identical simulation run over the course of 56 months in
374 order to exclude any variation due to differences in the initial conditions. By dissecting the
375 model output like this, it is possible to gain insights into the underlying mechanisms for the
376 observed patterns of population growth.

377 Figure 9 plots the relationship between water temperature and the growth/fertility of
378 *U. pinnatifida* agents in the model. In the case of both the gametophyte and sporophyte stages
379 of the life cycle, the growth rate is moderately positively correlated with water temperature

380 (Fig. 9a-b, $R^2=0.65$ & 0.7 respectively). However, temperature does not appear to play an
381 important role in influencing gametophyte fertility, with a minor negative correlation
382 predicted (Fig. 9c, $R^2=0.4$). This is because the water temperature in Brest harbour rarely
383 exceeds a value that would be expected to inhibit the maturation of gametophytes ($>21^\circ\text{C}$).
384 However, this may play a greater role in influencing the population dynamics under scenarios
385 of increasing sea water temperatures in the study area (Brittany) in the future (Gallon et al.,
386 2014). Finally, spore release by mature sporophytes primarily occurs at higher water
387 temperatures $>10^\circ\text{C}$ (Fig. 9d). This agrees with field studies from the literature which
388 suggested a critical minimum temperature value for spore release of approximately $12\text{-}14^\circ\text{C}$
389 (Saito, 1975; Suto, 1952).

390 In the case of day light hours and solar radiation, these also play a key role in
391 influencing the population dynamics of *U. pinnatifida* (Fig. 10 & 11). The model results
392 indicate a positive correlation between day light hours/solar radiation and the growth rate of
393 gametophytes (Fig. 10a & 11a: $R^2=0.82$ & 0.74 respectively). Similarly, for sporophytes,
394 there is a moderate positive correlation (Fig. 10b & 11b: $R^2=0.6$ & 0.62 respectively). In
395 contrast, the fertility of gametophytes is negatively correlated with day length and light
396 availability (Fig. 10c & 11c: $R^2=0.87$ & 0.77 respectively). These results suggest that
397 gametogenesis and new sporophyte formation is adapted to occur during the shorter days of
398 winter. Conversely, there is no clear relationship between spore release and either day length
399 or solar radiation ($R^2<0.1$, Figs. 10d & 11d). This is because the model does not assume any
400 relationship between these variables and spore release as there is no clear data from the
401 literature of a direct causal relationship.

402 The different patterns of response to environmental parameters between the life
403 history stages (particularly gametophyte fertility, gametophyte growth rates and sporophyte
404 growth rates) in response to the environmental parameters is an important consideration when

405 attempting to explain the patterns of growth observed in populations of *U. pinnatifida* in the
406 field. It is necessary to take into account these complex interactions in order to build up an
407 accurate view of the invasion dynamics but this is often overlooked in population studies that
408 focus on the macroscopic stages of the life cycle alone. Furthermore, these types of
409 interactions are common in other species of macroalgae that exhibit dimorphic life cycles.
410 Therefore, a modelling approach which explicitly takes into account the differing responses
411 of the individual life stages may be a useful tool for understanding the complex non-linear
412 dynamics of macroalgal populations in general.

413 The results in this paper illustrate how the characteristic seasonal growth patterns
414 observed among populations of *U. pinnatifida* in Brest harbour are dictated by the differing
415 responses of the individual life history stages to environmental parameters: Gametophytes
416 mature and reproduce to form new sporophytes during the shorter days of the winter when
417 light availability is lowest. They reach maturity in the spring and release their spores in the
418 early summer when light availability is at its peak, before dying out gradually during the
419 spring and summer months. The population dynamics of the gametophyte stages in field
420 populations are less well understood. However, the model predicts that the density of
421 gametophytes is expected to peak in the summer months but there is a delay before maturity
422 is reached during the autumn when appropriate conditions (day length/solar irradiance) are
423 present.

424 The individual-based modelling approach allows us to make quantitative predictions
425 about the temporal and spatial dynamics affecting this seasonal schedule using basic
426 physiological data on the species. It has been suggested that the heteromorphic life cycle of
427 macroalgal species such as *U. pinnatifida* may have evolved in response to seasonal changes
428 in temperate climates (Bessho and Iwasa, 2009). Therefore, it is important to take into

429 account the ecophysiological responses of the individual life history stages when attempting
430 to make predictions about the responses of the population as a whole.

431 The individual-based approach allows us to treat the life history stages as independent
432 entities and to connect the local interactions at the individual-scale to the overall population
433 dynamics. A greater understanding of the mechanistic basis for these responses could allow
434 predictions about how populations will respond to changing environmental conditions in the
435 future (such as increasing sea water temperatures) and the potential for future range
436 expansion in Europe and other regions of the world. There is an extra computational burden
437 associated with the IBM approach and it is more dependent on empirical knowledge
438 compared to simpler state variable modelling approaches. However, by using appropriate
439 aggregation of parameters in order to simplify the model, and cognizant of its limitations, it
440 can be a useful approach to supplement, rather than supplant, existing theoretical approaches,
441 such as metapopulation models, when local interactions play an important role (McCauley et
442 al., 1993).

443 In addition, the IBM approach provides a framework to understand how processes at
444 the individual level and local interactions affect invasion success. It allows spatial
445 heterogeneity (or patches) to be generated both “internally”, by the interactions and
446 movements of the organisms, as well as imposed “externally” (for example, by specifying the
447 structure of a harbour with different substrates, currents etc.). This allows the effects of local
448 rules, for migration or diffusion between or among patches, on population dynamics to be
449 assessed. It also allows one to differentiate the responses of the gametophyte and sporophyte
450 stages and to isolate the key factors that limit/promote the population growth/fitness under a
451 given set of environmental conditions. This can help to inform strategies for
452 control/eradication of invasive populations by identifying susceptible stages in the life cycle

453 schedule and the timing of intervention, or to assess the risk for spread and establishment of
454 the species in a region.

455

456 **4. Conclusions & Future Work:**

457 We present a novel agent-based modelling framework for simulating marine
458 macroalgal species taking into account their complex biphasic life histories. Initial validation
459 results indicate that the model can accurately predict the growth dynamics of an *in situ*
460 population of invasive seaweed (*U. pinnatifida*, in Brest harbour, France) and give insights
461 into the underlying population dynamics that contributed to its establishment. This type of
462 modelling approach represents a promising tool for understanding the effects of changing
463 environmental conditions (both temporal: e.g. climate change; and spatial: e.g. by range
464 expansion) on the growth dynamics and distribution of invasive seaweed species. Moreover,
465 through building a mechanistic representation of the important life history stages of the
466 species, and modelling their basic interactions at an individual level, it is possible to build up
467 a more complete understanding of the underlying dynamics driving their spread and
468 establishment. This can have applications in terms of informing control strategies for invasive
469 populations and risk assessment for the potential spread and establishment of non-native
470 species.

471 Future work will involve extending the model to represent more complex spatial and
472 temporal patterns of invasion in order to be able to explore the impact of these factors on
473 invasion dynamics. A detailed competition model will be incorporated to represent the
474 potential interactions between different algal species and local ecosystem dynamics. This
475 individual-based approach could also enable investigations into more long term processes
476 such as the role of phenotypic/genotypic variation and evolutionary selective pressures on
477 invasion dynamics.

478

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487

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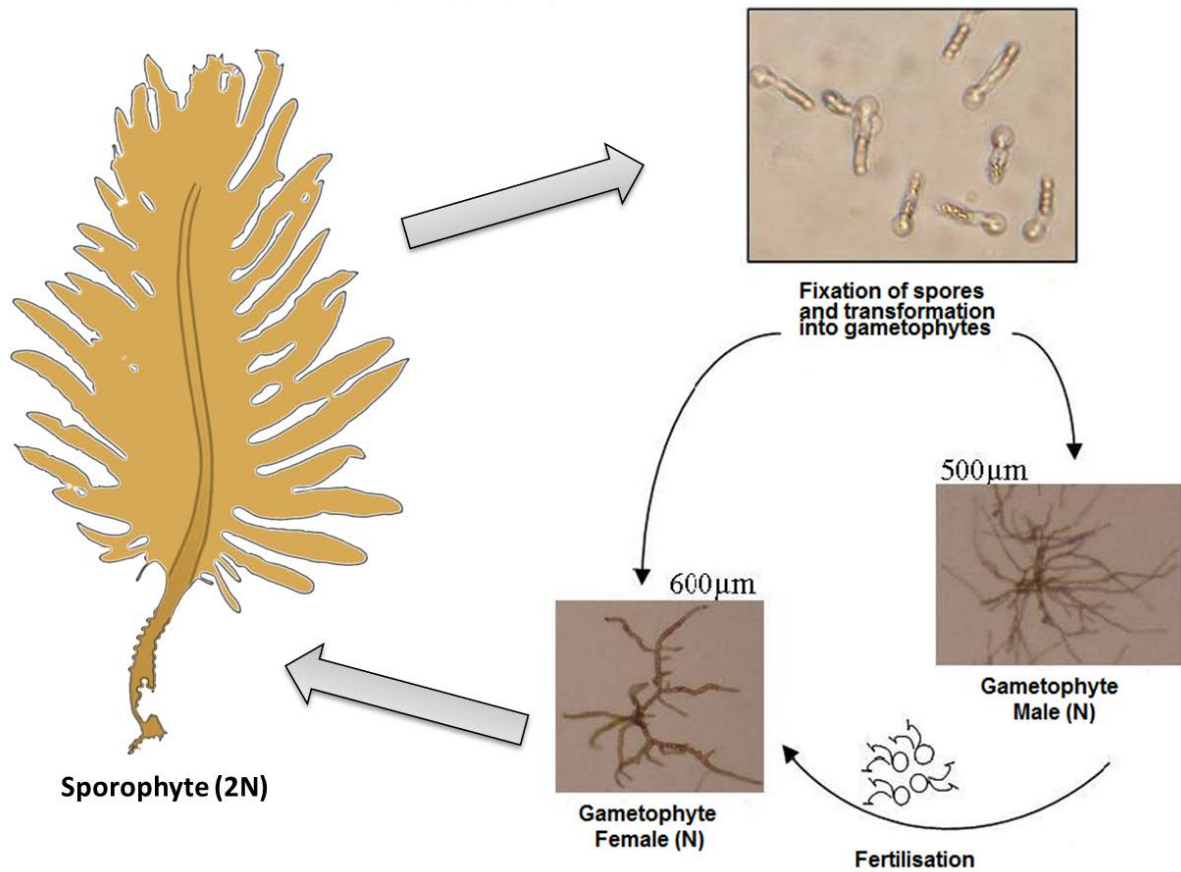
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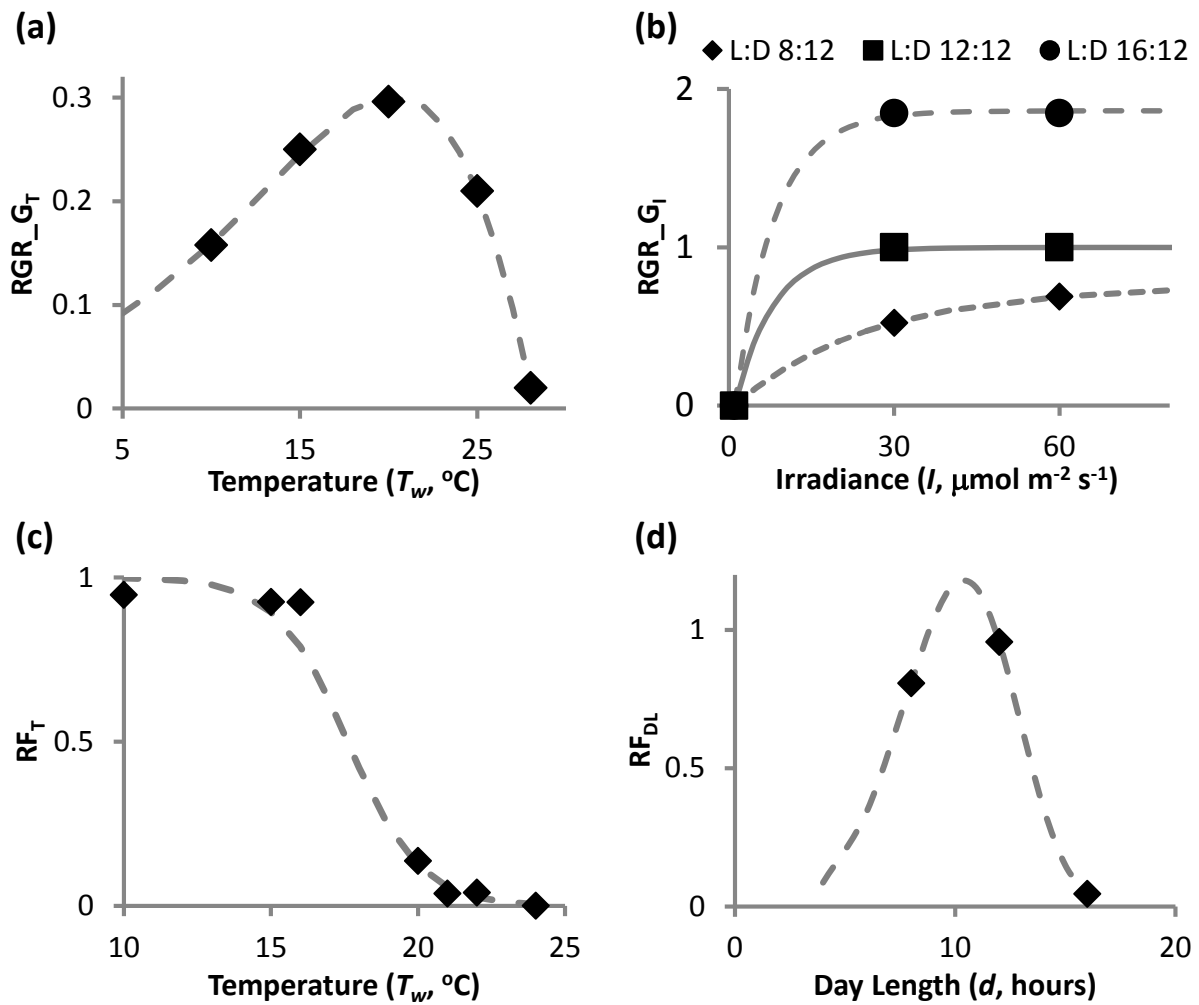
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636

637 **Fig. 1:** Heteromorphic life cycle of *Undaria pinnatifida* consisting of microscopic haploid
 638 (N) gametophyte stages which reproduce sexually to form the diploid (2N) sporophyte stage
 639 (1-3 m in length). Photos: Daphné Grulois-Station Biologique Roscoff.

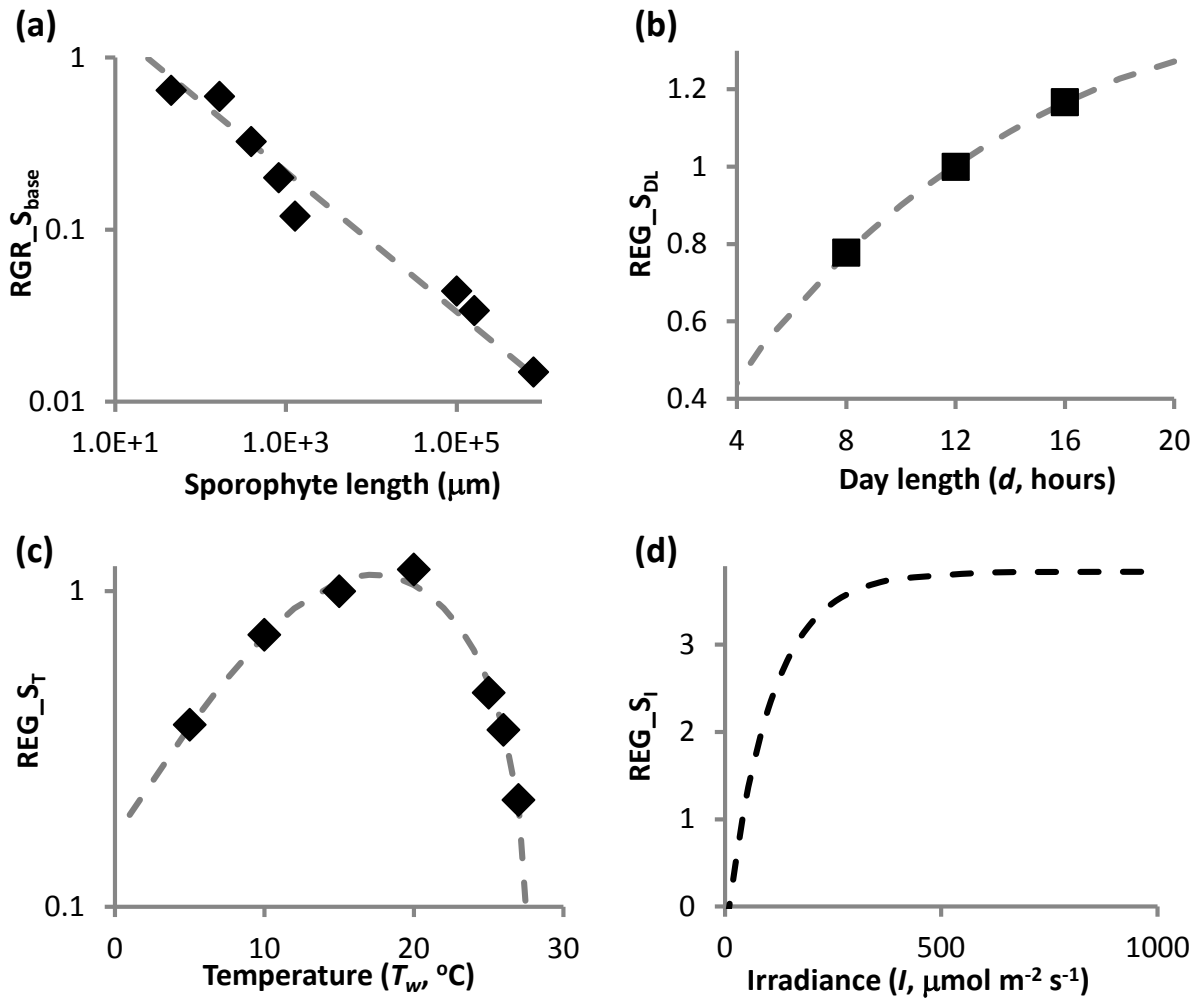
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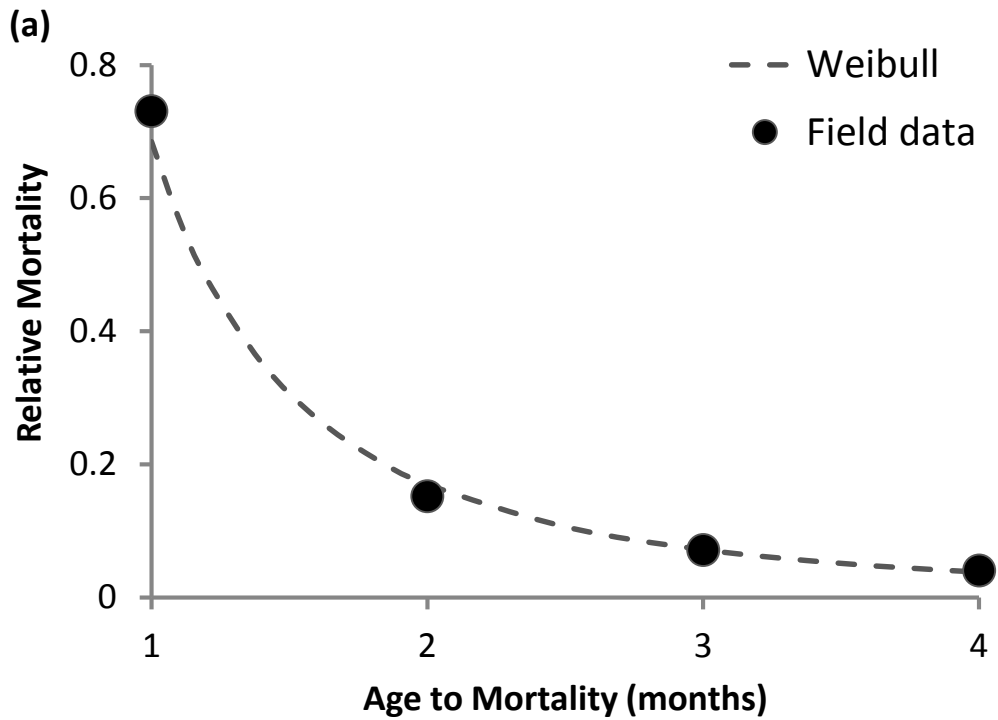
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643 **Fig. 2:** Response of gametophyte agents to environmental parameters. (a) Relative growth
644 rate in response to temperature (RGR_{G_T}). Thermal performance curve fitted to data from
645 Morita et al. (2003) ($R^2 > 0.99$). (b) Relative effect of solar irradiance and day length (day
646 light hours) on growth rate (REG_{G_I}): Hyperbolic function fitted to data from Choi et al.
647 (2005) ($R^2 > 0.99$ for all curves). (c) Relative effect of temperature on fertility (RF_T): Logistic
648 function fitted to data from Morita et al. (2003) and Choi et al. (2005) ($R^2 = 0.97$). (d) Relative
649 effect of day length on fertility (RF_{DL}): Weibull distribution fitted to data from Choi et al.
650 (2005) ($R^2 = 1.0$).

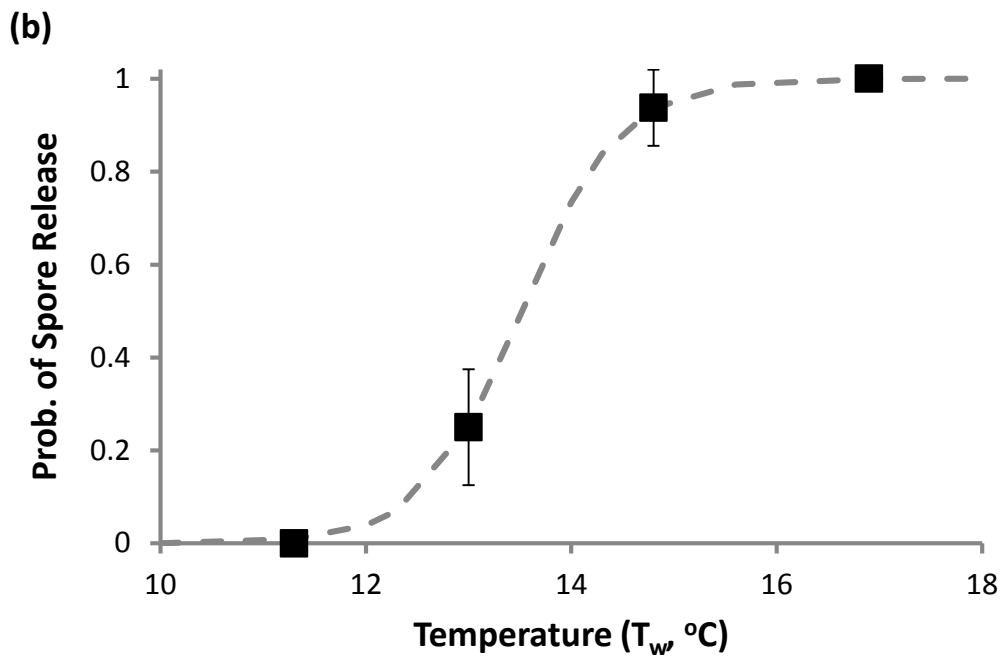
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652
 653 **Fig. 3:** Input data from the literature on the effects of sporophyte length and environmental
 654 parameters (day light hours, water temperature and solar irradiance) on the relative growth
 655 rate of *U. pinnatifida* sporophytes. (a) Power law relationship ($r^2=0.97$) between sporophyte
 656 length and relative daily growth rate of sporophytes ($RGR_{S_{base}}$) (Pang & Wu, 1996) (b)
 657 Relative effect of changes in day light hours on the growth rate of sporophytes ($REG_{S_{DL}}$)
 658 (Pang & Luning, 2004). Hyperbolic equation fitted to data ($R^2>0.99$) (c) Relative effect of
 659 changes in water temperature on the growth rate (REG_{S_T}) of sporophytes (log scale).
 660 Thermal performance fitted to data from Morita et al. (2003) ($r^2>0.99$). (d) Relative effect of
 661 solar irradiance on the growth rate of sporophytes (REG_{S_I}) based on photosynthesis-
 662 irradiance curve data from Campbell et al. (1999).



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665

666 **Fig. 4:** (a) Field data on the age to mortality of immature sporophytes (n=198) growing in

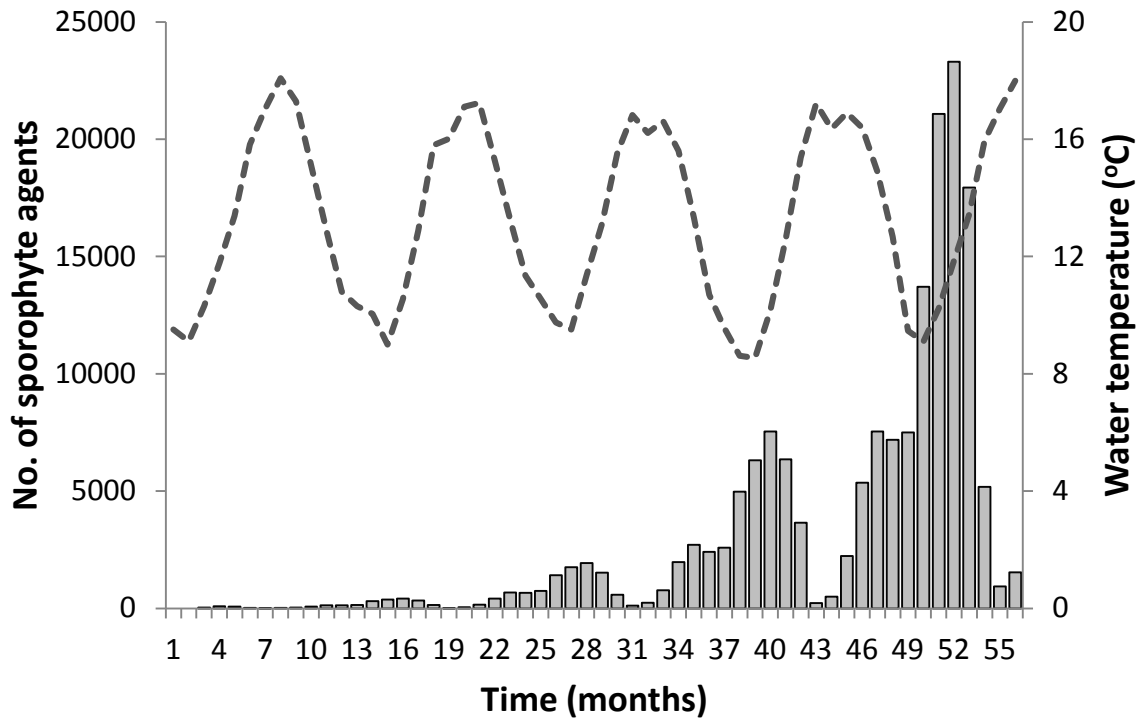
667 Brest harbour surveyed in the year 2004 (Voisin, 2007). A Weibull distribution ($k=0.1635$,

668 $\lambda=8.2E-06$) was fitted to the data ($R^2>0.99$). (b) Impact of water temperature on the

669 probability of spore release from mature *U. pinnatifida* sporophytes. Logistic function fitted

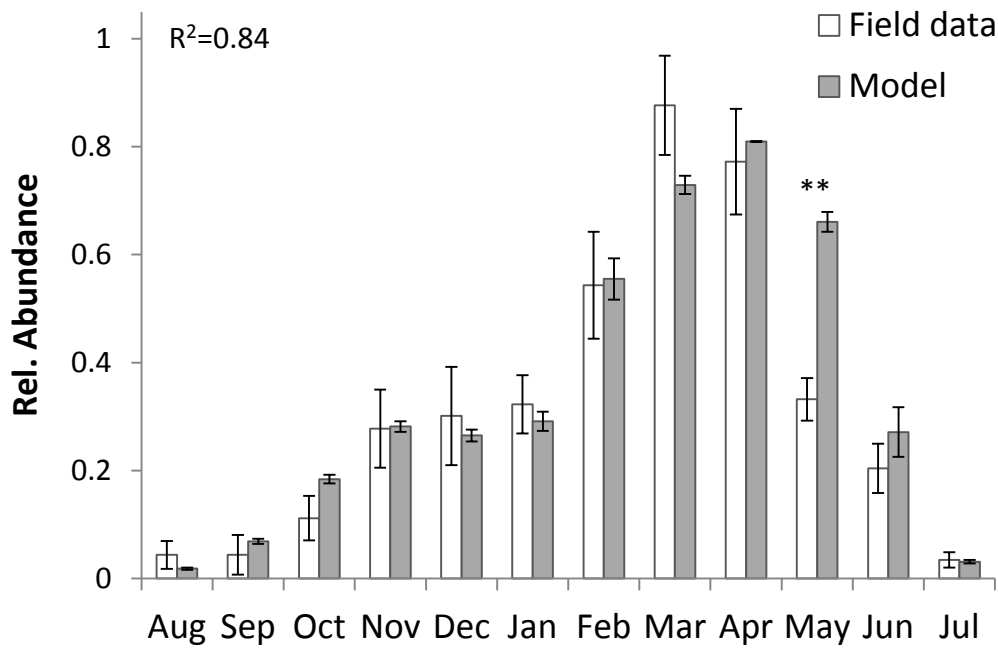
670 to data from Suto (1952) ($R^2>0.99$).

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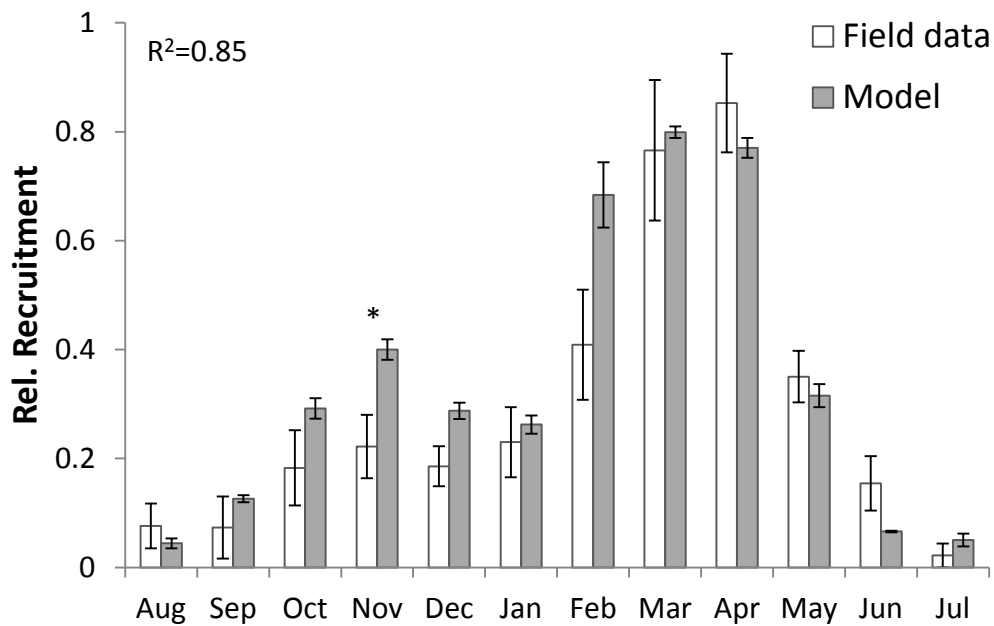


672
 673 **Fig. 5:** Simulation Results: Predicted development of population of *U. pinnatifida*
 674 sporophytes over the course of five seasons in environmental conditions representative of
 675 Brest harbour, France. Abundance values for sporophytes are plotted on a monthly basis (bar
 676 chart). Line chart represents sea water surface temperature input data (SOMLIT, Brest).
 677

678 (a)



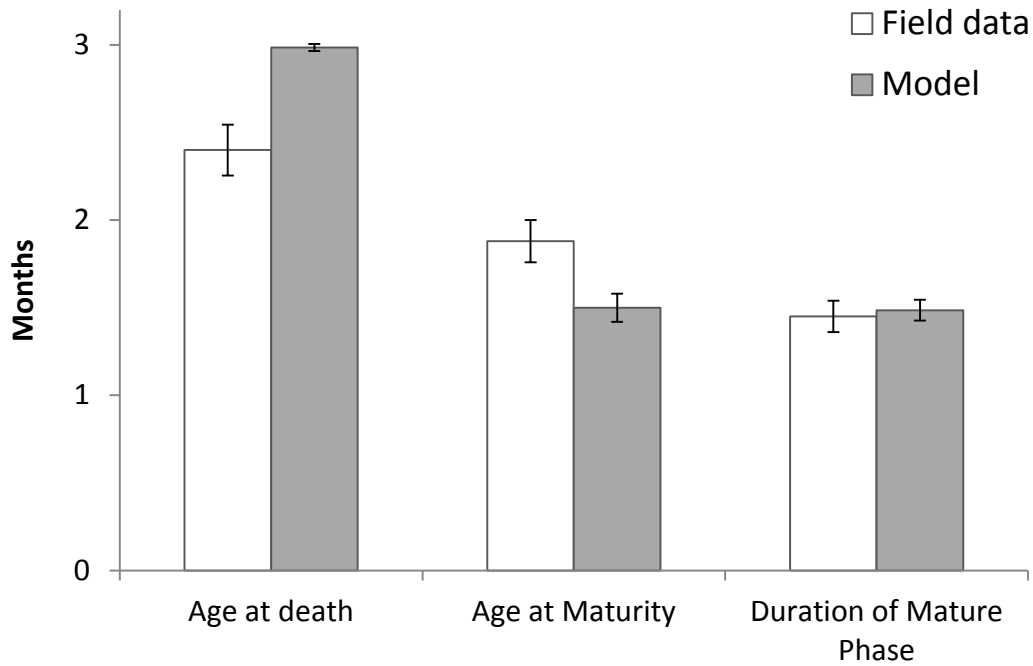
679 (b)
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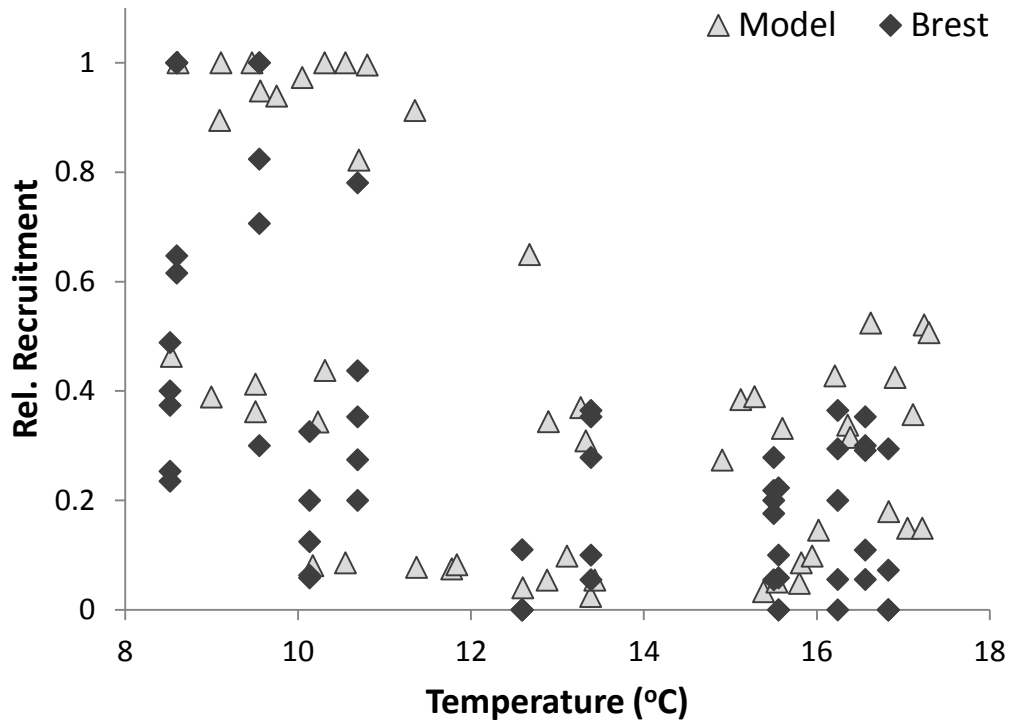
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683 **Fig. 6:** (a) Predicted relative abundance and (b) relative rate of recruitment of *U. pinnatifida*
684 sporophytes *versus* field data from a real-world population in Brest harbour, France. Model
685 values are the means (\pm SE) of four simulated years. Field values are the means (\pm SE) from
686 five colour-coded sets of plates, installed in different locations in Brest harbour, for the
687 period Aug 2005 – Jul 2006 (Voisin, 2007).

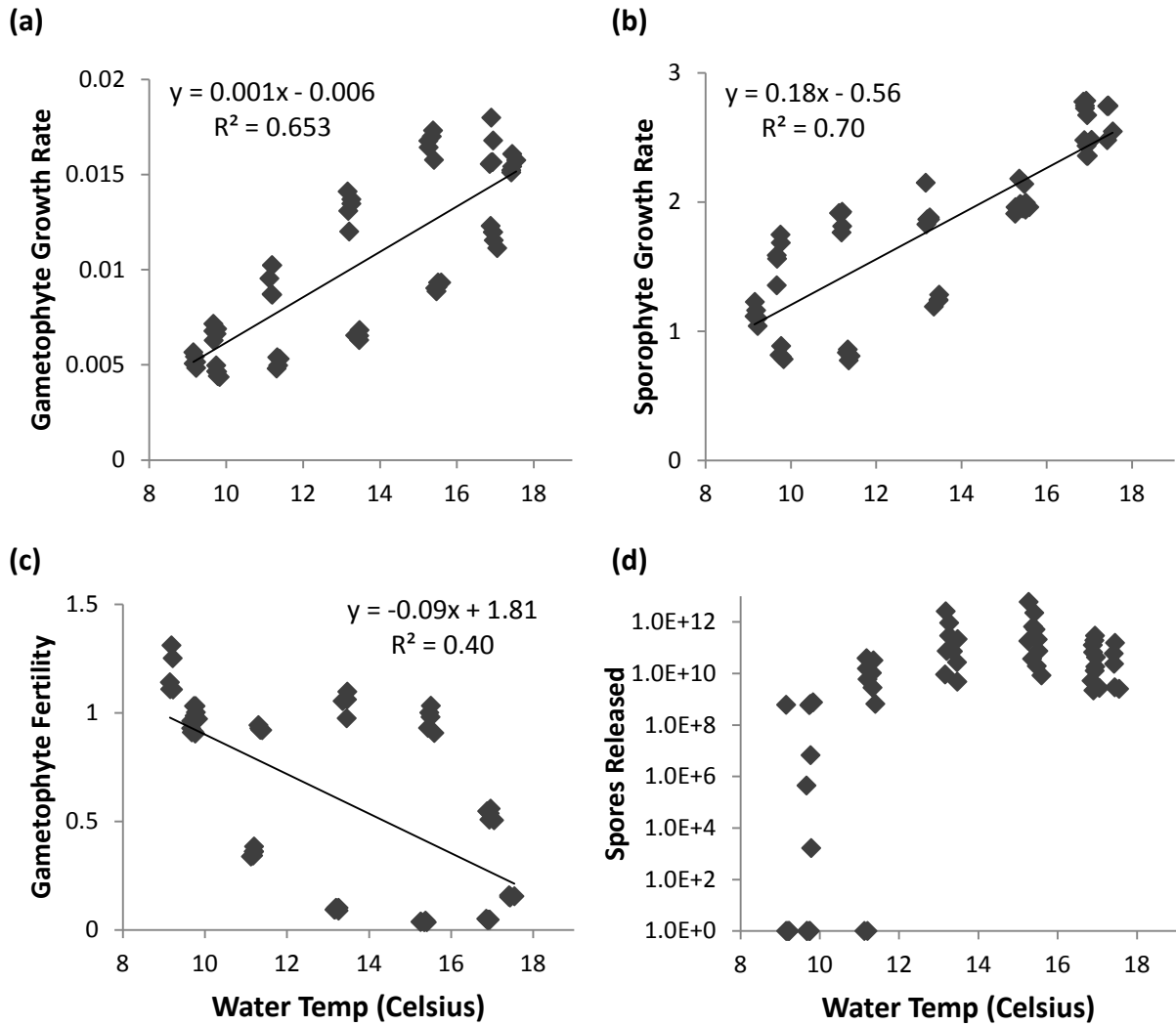
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689
 690 **Fig. 7:** Comparison between the predicted life expectancies of mature *U. pinnatifida*
 691 sporophytes and results from field studies of a population sampled (n=94) in Brest harbour
 692 over the period 2003-2006 (Voisin, 2007). The mean age at death, mean age at sexual
 693 maturity (i.e. formation of sporophylls), and the number of months sexually mature (\pm SE) are
 694 compared.
 695



696 **Fig. 8:** Plot of the relationship between recruitment events (appearance of new sporophytes)
 697 and water temperature for simulated *U. pinnatifida* populations. Comparison between field
 698 data for the years 2003-06 (diamonds) in Brest harbour, France, and model predictions
 699 (triangles).
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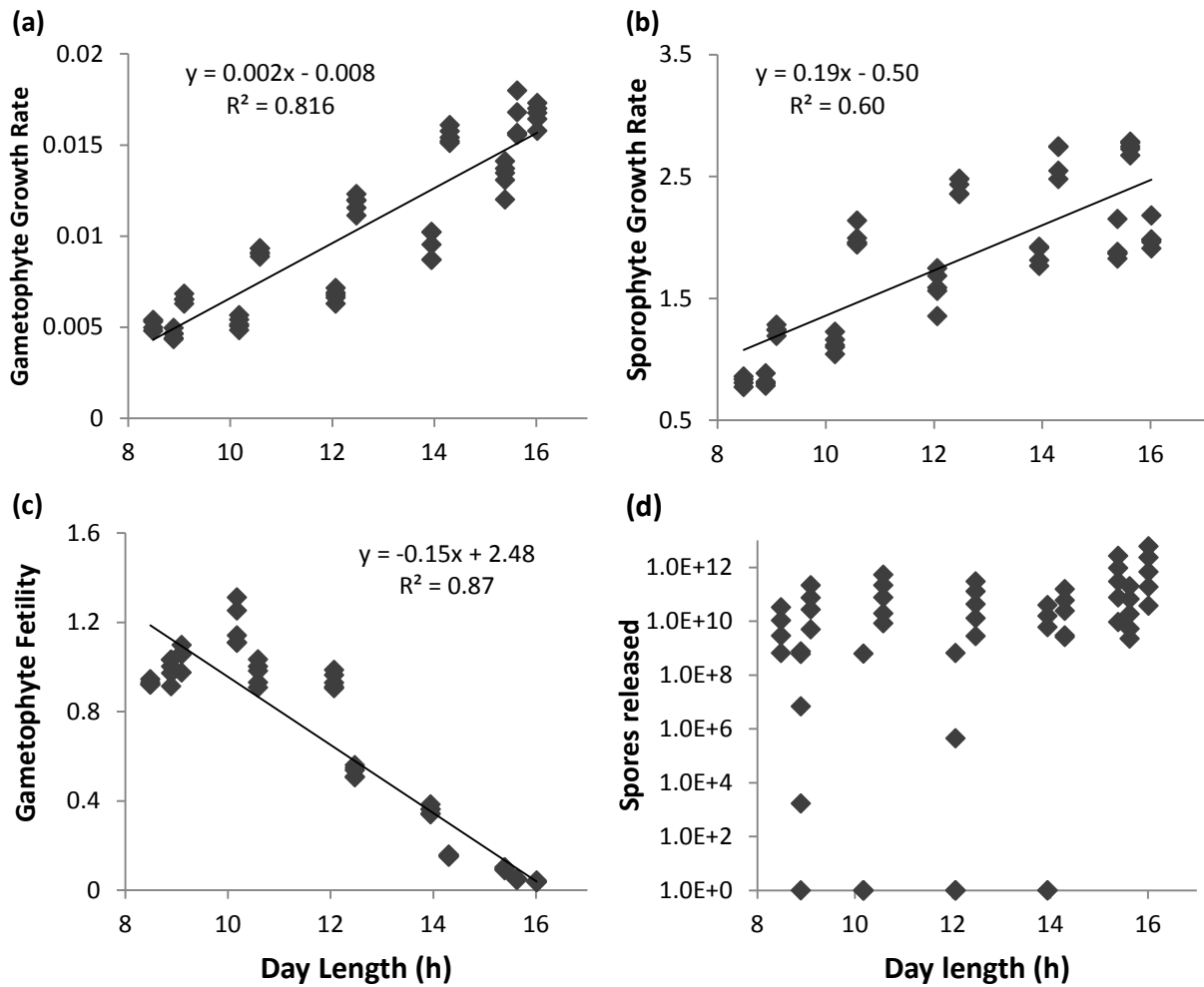
703 **Fig. 9:** Exploration of the effects of temperature on the system dynamics of the model.

704 Relationship between water temperature and: (a) gametophyte growth rate, (b) relative

705 sporophyte growth rate, (c) relative gametophyte fertility, (d) spores released by mature

706 sporophytes (log scale).

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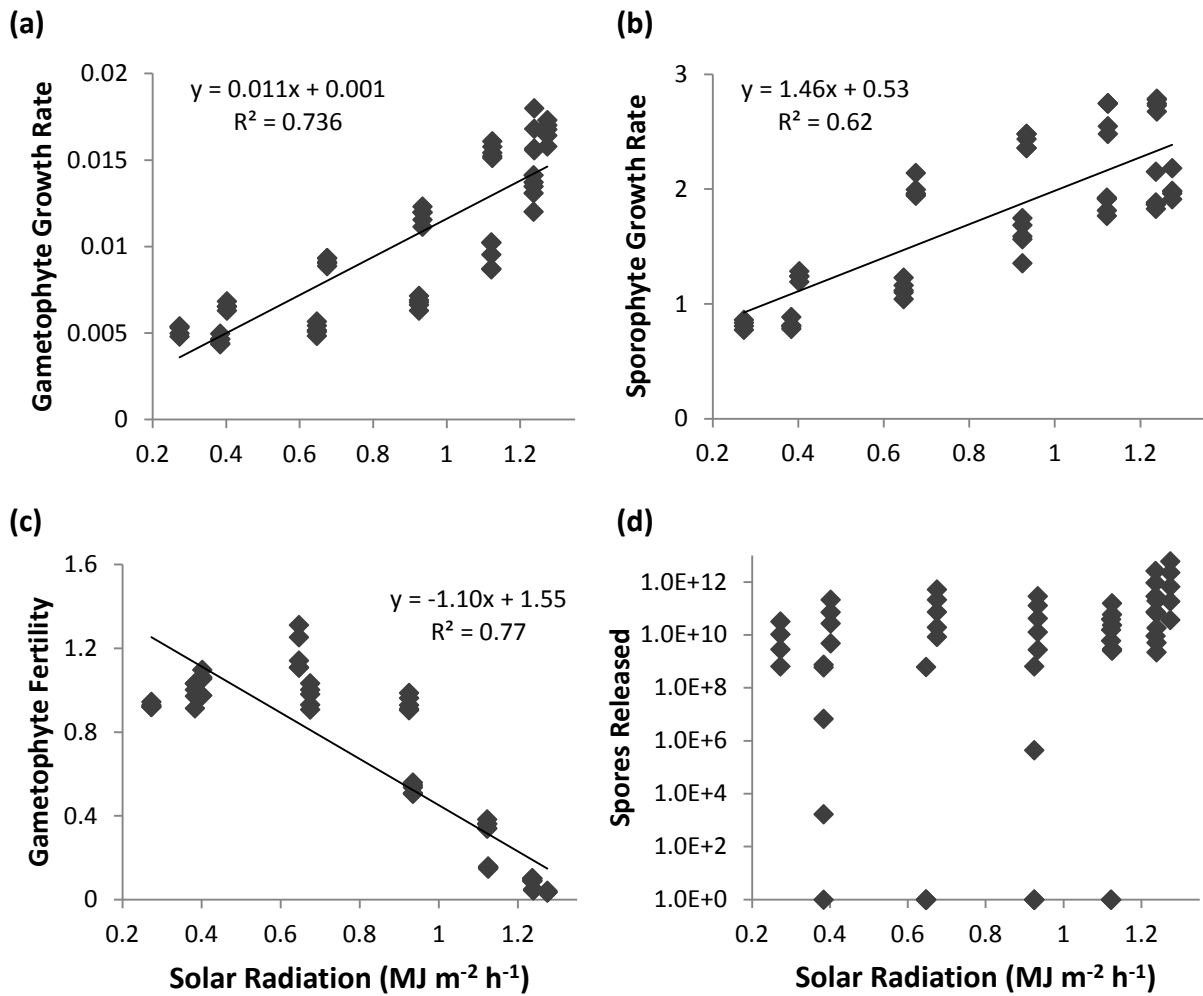
709 **Fig. 10:** Exploration of the effects of day light hours on the system dynamics of the model.

710 Relationship between day light hours and: **(a)** gametophyte growth rate, **(b)** relative

711 sporophyte growth rate, **(c)** relative gametophyte fertility, **(d)** spores released (log scale) by

712 mature sporophytes.

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 715 **Fig. 11:** Exploration of the effect of solar radiation (Megajoules m⁻² hour⁻¹) on the system
 716 dynamics of the model. Relationship between day light hours and: **(a)** gametophyte growth
 717 rate, **(b)** relative sporophyte growth rate, **(c)** relative gametophyte fertility, **(d)** spores released
 718 (log scale) by mature sporophytes.

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721 Table 1: Input parameters for CoastGEN simulations of *Undaria pinnatifida* in 2D simulated
 722 coastal environment. l = sporophyte length (μm), d = day light hours, $loop$ = simulation loop.

Parameter Type	Parameter (units)	Input Value
General	Length of Simulation Loop (hours)	1
	Environment Size (No. of Cells)	514 x 482
	Cell Area (m^2)	0.25
	Substrate depth in water (m)	1.0
	Attenuation coefficient (K_{dPAR})	0.6
Sporophyte agents	Initial length, l_0 (μm)	20.0
	Base growth rate	$3.615 l^{-0.407}$
	Day length response (hyperbolic curve):	
	P_{max}	1.56
	a	0.13
	I_c	0.0
	Thermal performance curve :	
	K_1	21.09
	K_2	0.213
	K_3	0.006
CT_{min}	1.62	
CT_{max}	28.28	
$Scale$	3031	
Photosynthesis-irradiance curve:		
P_{max}	$0.4\ln(l) - 0.596$	
a	$0.5l^{-0.33}$	
I_c	$2.5\ln(l) - 19.9$	
Mean length at maturity (cm)	32.66	
Gametophyte agents	Thermal performance curve :	
	K_1	35.67
	K_2	0.158
	K_3	0.015
	CT_{min}	4.45
	CT_{max}	28.24
$Scale$	10.63	

	Photosynthesis-irradiance curve: P_{max} a I_c	$0.29e^{0.11d}$ $0.029d - 0.2$ 0.0
	Prob. of fertilisation (loop ⁻¹)	0.0002
Gametogenesis	Temperature response curve (log): x_0 k	17.6 0.82
	Day length response (Weibull): α β	4.5 10.96
Spores	Half-life (hours)	24
	Release rate (agent ⁻¹ loop ⁻¹)	2.0×10^7
	Spore stock (agent ⁻¹)	10^{10}
	Diffusion coefficient	0.15
	Prob. of germination (loop ⁻¹)	10^{-9}