1 **Modeling the growth and sporulation dynamics of the macroalga *Ulva* in mixed-age**

2 **populations in cultivation and the formation of green tides**

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Abstract

Ulva is a widespread green algal genus with important ecological roles and promising potential as a seagriculture crop. One of the major challenges when cultivating *Ulva* is sudden biomass disappearance, likely caused by uncontrolled and unpredicted massive sporulation. However, the dynamics of this process are still poorly understood. In this study, we propose a mathematical model describing the biomass accumulation and degradation of *Ulva,* considering the potential impact of sporulation inhibitors. We developed a differential equation model describing the time evolution of *Ulva* biomass. Our model simulates biomass in compartments of different *Ulva* 'age' classes, with varying growth and sporulation rates. Coupled with these classes is a differential equation describing the presence of a sporulation inhibitor, produced and secreted by the algae. Our model mimics observed *Ulva* dynamics. We present *Ulva´*s biomass accumulation under different initial algae population age distributions and sporulation rates. Furthermore, we simulate water replacement, effectively depleting the sporulation inhibitor, and examine its effects on *Ulva´*s biomass accumulation. The model developed in this work is the first step towards understanding the dynamics of *Ulva* growth and degradation. Future work refining and expanding our results should prove beneficial to the ecological research and industrial growth of *Ulva.*

Keywords: *Ulva*, sporulation, sporulation inhibitor, modeling, green tides, gametogenesis, aging, aquaculture management**.**

1. Introduction

The genus *Ulva* (Ulvales, Chlorophyta) comprises a group of green macroalgae, which are cosmopolitan species, both ecologically and economically. Its highly adaptive nature allows it to flourish in various environments, as can be seen from its widespread presence from the Arctic and Antarctic seas to the Equator. In natural populations, *Ulva* spp. are very common in littoral and sublittoral areas. As *Ulva* in nature is a holobiome, its ecological role is vast and includes multiple interactions with other players of the marine ecosystems, such as protista, fungi, bacteria, viruses and various marine fauna. *Ulva* is highly relevant for aquaculture due to its fast growth rates and potential food, feed, materials, chemicals and energy applications. Hence, *Ulva* is considered as a potential crop for controlled biomass production, onshore and offshore (Fernand et al., 2017). Multiple reports in the last decade addressed *Ulva* aquaculture alone or in multitrophic systems. In addition, *Ulva* biorefinery-enabling processes and technologies have made immense progress in producing of starch, protein, cellulose, ulvan, salts, methane, biocrude, biodiesel, bioethanol, and polyhydroxyalkanoates, just to mention a few. Over the years, various systems including plastic sleeves, raceway ponds, tanks, dripping, ropes, nets, rafts and aerated cages have been proposed for *Ulva* biomass cultivation. The variation of cultivation systems ranges from closed, artificial and seawater, onshore systems with fresh seawater to near shore and far offshore production. Yet, one of the significant risks in *Ulva* cultivation is the sudden biomass loss when the algal tissue disintegrates and bleaches, most probably caused by uncontrolled and unpredicted massive sporulation.

Opposite to the controlled cultivation, *Ulva* green tides are massive, rapid natural accumulations of unattached green macroalgae biomass usually associated with eutrophicated marine environments. Various *Ulva* species (e.g., *U. prolifera*, *U. compressa*, *U. linza*) are commonly linked to the formation of green tides which eventually reach coastal marine areas. Green tides seriously damage the coastal marine environment on occasions modifying the shoreline structure, or affecting biodiversity and damaging ecosystem services such as navigation, fishery and recreation. In addition, decaying seaweed biomass causes anoxia yielding hydrogen sulfide at toxic levels in coastal waters and on the shores (Nedergaard et al., 2002)(Nedergaard et al., 2002; Castel et al., 1996; Viaroli et al., 1995).

Various explanations have been proposed for the rapid accumulation and simultaneous collapse of *Ulva* dominated green tides. Favorable environmental conditions for *Ulva* habitats, such as temperature, salinity, hydrodynamics and nutrient levels affect the rapid biomass growth. In addition, recent studies showed that blooming leads to the selection of rapidly growing strains (Fort et al., 2020) with potentially differentially expressed genetic signatures (He et al., 2021). Furthermore, for *Ulva prolifera*, a strain

61 dominating the Yellow Sea bloom, 91.6–96.4 % of the released spores developed into young seedlings,

62 suggesting that 1 gFW thallus was able to produce about 2.8×10^{8}–2.7×10^{9} new younger seedlings, of

63 free-floating biomass (Zhang et al., 2013).

64 *Ulva* sp. has a complex reproduction strategy with alternation of generations in which both isomorphic

65 gametophytes and sporophytes coexist. The gametophytes produce biflagellated haploid gametes through

66 mitosis while the sporophytes produce quadriflagellated haploid zoids through meiosis (Wichard 2015).

67 The initiation of a green tide requires simultaneous sporulation and release of gametes of multiple thalli.

68 How this sporulation is achieved and controlled at the initial population is still a puzzling question. The

69 simultaneous release of zoids and gametes in large numbers over a short period, combined with favorable

70 environmental conditions, would provide the prerequisites for the formation of green tides. Indeed,

71 mechanical or other factors, fragmentation of *Ulva* thalli would produce large amounts of spores giving

72 rise to the rapid proliferation of the seaweed under field conditions. This explanation likely supports the

73 rapid accumulation of the vast biomass of *U. prolifera* in the green tide that occurred in Qingdao, 2008

74 (Gao et al., 2010) .

75 Ecological studies indicate that sporulation in *Ulva* is seasonal, and when it occurs a significant amount of

76 parental biomass contributes to the massive production of swarmers (Amsler and Searles, 1980; Littler

77 and Littler, 1980; Niesenbaum, 1988). It has been also shown that the formation and release of swarmers

78 is inhibited by "sporulation-inhibiting substances" excreted into the growth medium by the whole thalli,

79 or their fragments (Nilsen and Nordby, 1975). A later study identified two sporulation inhibitors in both

80 *Ulva mutabilis* and *Ulva linza*. The first sporulation inhibitor 1 (SI-1), is a glycoprotein isolated from the

81 thalli media or the cell wall' and the second sporulation inhibitor 2 (SI-2), is a small molecular weight

82 compound that was isolated from the inner space between the two blade cell layers (Stratmann et al.,

83 1996; Jónsson et al., 1985; Kessler et al., 2018; Vesty et al., 2015). It was also shown that the production

84 rate of the SI-1 decreases with the maturation of the thallus and the production rate of SI-2 is constant

85 (Stratmann et al., 1996).

86 Furthermore, it was discovered that the formed gametes were only released slowly and asynchronously in

87 the presence of another substance known as a swarming inhibitor, the removal of which resulted in nearly

88 immediate and complete swarming (Stratmann et al., 1996; Wichard and Oertel, 2010). This precise

89 control of swarmer formation and release suggests that *Ulva* developed a tightly regulated mechanism to

90 guarantee simultaneous release of swarmers to the environment, observed initially by Smith at the Pacific

91 coast (Smith, 1947), probably to maximize the likelihood of sexual reproduction. Indeed, most recent

92 studies on the floating *Ulva prolifera* showed that all tested thalli were sporophytes with sexual

93 reproductive patterns (Zhao et al., 2019). Additional studies showed that if the thalli are ageing (i.e. no

94 growth) they become insensitive to the artificially added sporulation inhibitor and release swarmers even

95 in its controlled presence in the growing media (Alsufyani et al., 2017).

96 Mathematical models are essential tools to study and predict the behavior of complex biological systems.

97 Several models have been developed to predict seaweed biomass growth and decomposition, the behavior

98 of harmful green tides and the seaweed biomass production in seagriculture. Indeed, long-term ecological

99 models that predict macroalgal productivity and seasonal blooms in prone ecosystems (Martins and

100 Marques, 2002; Solidoro et al., 1997; Ren et al., 2014; Martins et al., 2007; Port et al., 2015; Brush and

101 Nixon, 2010; Aldridge and Trimmer, 2009; Lavaud et al., 2020; Seip, 1980; Aveytua-Alcázar et al., 2008;

102 Duarte and Ferreira, 1997) or culture models that focus mostly on onshore photobioreactors (Friedlander

103 et al., 1990; Oca Baradad et al., 2019) and offshore cultivation(Broch and Slagstad, 2012; Petrell et al.,

104 1993; Hadley et al., 2015) were developed. These models, which pursue a basic understanding of the

105 thermodynamics of individual algae thalli and photobioreactors (Zollmann et al., 2018), provide

106 important tools to predict the productivity and seasonal environmental effects on the seaweed population

107 dynamics. However, such models treat the macroalgae population as a bulk and do not differentiate

108 between ages of individual thalli within the population. As discussed above, thalli age is an important

109 factor affecting the activity of sporulation inhibitors in the alga and the ultimate release of swarmers.

110 Furthermore, these models do not consider the possible interthalli chemical interactions, some of which

111 can be based on SI-1 secreted to the environment. The production and secretion to the environment of

112 molecules such as SI-1 could provide insights into the molecular mechanisms behind the synchronization

113 of massive spore release at the population level - a phenomenon crucial for both green tide formation and

114 sudden biomass disappearance in *Ulva* seagriculture.

115 This paper aims to introduce a novel framework for the description of population dynamics and collective

116 thalli behavior of *Ulva* biomass, presumably controlled by shared sporulation inhibitors. We propose that

117 various environmental and internal biological changes on the single thallus level predetermine the ability

118 of the individual thallus to produce, and to donate to and receive from the population environment, factors

119 that regulate the synchronized formation and release of swarmers. A natural tool to describe this process

120 is offered by population dynamics models, often employed to describe bacterial and animal population

121 dynamics (Succurro and Ebenhöh, 2018; Friedman and Gore, 2017).

122 In the following sections we develop and simulate such a mathematical model in an attempt to

123 characterize the dynamics of *Ulva* biomass formation and degradation.

2. Methods

125 The model presented below consists of n+1 ordinary differential equations (ODEs), where n is set as the
126 number of cultivation days (also equal to the number of age group equations). ODEs *0... n-1* describe the
127 rate of change of biomass of n discrete age classes of *Ulva* thalli, denoted a_i , and additional *n+1*
128 equations for the rate of change of the inhibitor *I*. As described previously, there are at least three types of
129 inhibitors involved in the process of *Ulva* swarmers release: SP-1, SP-2 and a swarming inhibitor (SWI).
130 We aggregate these inhibitors into a single quantity that controls the simultaneous swarmers' release from
131 thalli, followed by the biomass decrease.

132 The *n* ODEs follow a simple discretized version of a partial differential equation of *m(a,t)* where *m* is the
133 biomass of *Ulva* in controlled volume (a bioreactor or a given sea volume, for example), *a* is the age of
134 algae, and *t* is time. As previously shown, the growth rate for thalli decreases with age(Alsufyani et al.,
135 2017).

136 The following equations specify the dynamics of the biomass of each age class a_i, coupled with the
137 dynamics of the inhibitor *I*, in the growth environment:

138
$$\frac{da_i}{dt} = r_i \left(1 - \frac{\sum\limits_{i}^{a} a_i}{K} \right) + \lambda_i a_{i-1} - \lambda_{i+1} a_i - \sigma \, a_i f_i(I) \quad i = 1, 2 \ldots n \tag{1}$$

139
$$\frac{dI}{dt} = \sum\limits_{i}^{n} a_i (\theta_i) - I(\sum\limits_{i}^{n} \mu_i a_i) - \xi I + \gamma_I \tag{2}$$

140 **Table 1:** model parameters, their interpretation, and values.

Parameter	Meaning	Value
r_i	Growth rate of algae age a_i	$0.45(0.1 + e^{-i \cdot log(2)/30})$
$f(I)$	Limiting factor due to inhibitor concentration, I	$1 - (1 + e^{-10(I-0.5)})^{-1}$
σ	Degradation constant	0.3
ξ	Inhibitor loss function to the environment (for example, water replacement)	$0.45(0.1 + e^{-i \cdot log(2)/120})$

θ_i	Age-dependent inhibitor generation function	$0.45(0.1 + e^{-i \cdot log(2)/120})$
μ_i	Age-dependent inhibitor uptake	$0.45(0.05 + e^{-i \cdot log(2)/120})$
γ_I	Constant inhibitor addition or extraction	0.0 - 0.1 (varies in the figures)

141 The model assumes a logistic growth of biomass with a growth rate parameter r_i for each algae age class
142 a_i and a carrying capacity K, defined as the maximum *Ulva* biomass density in the growth environment.
143 Biomass moves between compartment a_i to a_{i+1} at rates λ_i , defining the "natural aging" of algae. At each
144 age class a_i, biomass is degraded at a rate $\sigma_i f(I)$, where σ_i is the maximal destruction rate, and $f(I)$ is a
145 monotonically decreasing function of the inhibitor I , scaled between zero and one. Furthermore, we
146 define μ_i as the SI1 uptake rate of each age class a_i; ξ the leakage or injection of the inhibitor I , that
147 can be managed externally to the system (e.g., washing the algae, destroying the algae, injection
148 nutrients); and γ is the nutrient supply flux in the units of inhibitor concentration. Model parameters are
149 also summarised in Table 1.

150 3. Results and Discussion

151 Here we study the *Ulva* biomass population dynamics, controlled by sporulation inhibitor production and
152 absorption, by stimulating the biomass accumulation under various scenarios for mixed-age populations,
153 for 100 days (Stratmann et al., 1996; Alsufyani et al., 2017). In all the following simulations, we assumed
154 the initial density of seaweed in the cultivation media is a_{in} = 0.2 kg m^{-3} and at the maximum carrying
155 capacity, the biomass can reach a density of 10 kg m^{-3} (a_{imax}). In addition, for the initial population
156 conditions, we denoted young thalli as a population with a_i = 0 at t = 0 and old thalli as a population with
157 a_i = 120 days at t = 0. From a physiological point of view, young thalli are those thalli, whose cell
158 differentiation is controlled by SI and old thalli are those thalli, which are insensitive to SI and do not
159 produce it.

160 In the following plots, we simulated the behavior of populations with a mixed-age composition. Each
161 population was labeled by the percentage of young and old thalli at initial population. Thus, for example,
162 100/0 labels an entirely young initial population (0.2 kg m^{-3} of thalli with ai = 0 at t = 0); 0/100 labels a
163 completely old initial population (0.2 kg m^{-3} of thalli with a_i = 120 days at t = 0); and 50/50 represents an
164 initial population comprised of equal parts of old and young algae (0.1 kg m^{-3} of thalli with a_i=0 at t=0
165 and 0.1 kg m^{-3} of thalli with a_i = 120 days at t = 0).

166   The biomass yield (density increase due to growth; i.e. initial density subtracted from final density) over

167   time for various mixed-age populations is shown in **Fig. 1a**. The growth of mixed aged populations with

168   100/0, 80/20 and 50/50 population mix of old and young thalli showed a typical sigmoidal growth,

169   reaching 90% of the maximum biomass density (9 kg m^{-3}) at 27 , 30 and 37 days, respectively.

170   Populations with predominantly old biomass at the beginning (20/80) showed a long lag phase but

171   exhibited positive growth, reaching 90% of the maximum biomass density at day 87 (**Fig. 1b**). The

172   population with only old algae (0/100) at the beginning of the cultivation showed degradation of the

173   biomass from day 1 and never showed positive growth (**Fig. 1b**). The population with a 10/90 mix of

174   initial ages showed a small growth (positive yield) during the first 40 days but then showed biomass

175   degradation and never reached 90% of the maximum density (**Fig. 1a,b**).

176   As simulated in our model, such dynamics of the biomass growth could be explained by the dynamics of

177   the production of the sporulation inhibitor (**Fig. 1c**). For populations 100/0, 80/20, 50/50 and 20/80 the

178   rate of sporulation inhibitor generation is positive and increases over time, while for the 10/90 and 0/100

179   populations, although initial production of the sporulation inhibitor is observed, it is reduced over time

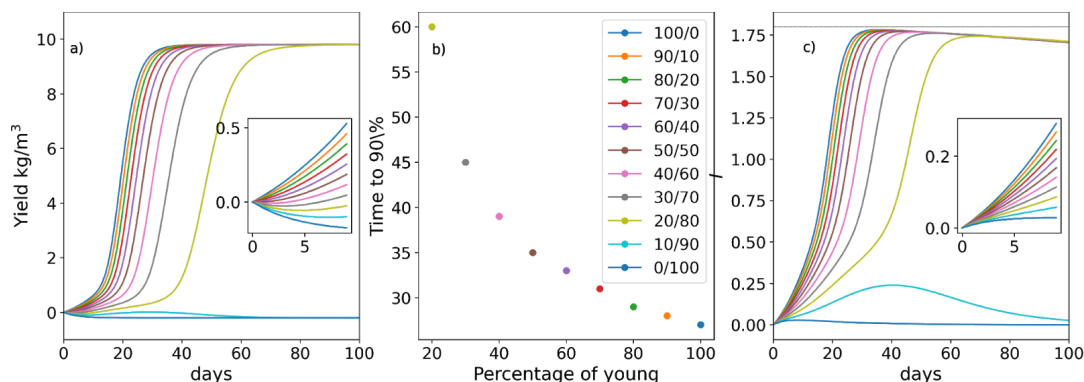
180   (**Fig. 1c**). These findings show that sporulation inhibitor production by a small (20% in our simulations)

181   young population could potentially provide enough inhibitor to prevent the old algae population from

182   biomass loss, thus leading to overall positive biomass production. Additionally, the rate of biomass

183   accumulation increases with the increased fraction of the young thalli in the initial population.

184   Nevertheless, the maximum inhibitor production decreases with time in all populations as all thalli age

185   (**Fig. 1c**).

186 **Figure 1. a.** Yield (biomass gain in kg/m³ up to the limit of 10 kg/m³ in a bioreactor with a starting density of 0.2

187 kg/m³) for populations with various initial age mixes. **b**. *Ulva* biomass growth kinetics as a function of the initial age

188 distribution of thalli in the population. Values of the 0/100, and 10/90 populations are not presented as they did not

189 reach 90% of the maximal carrying capacity. **c**. Inhibitor production in the population over time.

190 As seaweeds rarely grow in closed bodies of water, where the inhibitor could accumulate continuously in

191 the environment, we sought to stimulate the impact of inhibitor removal from the seaweed environment

192 by water replacement. We assume that each event of water replacement completely removes the inhibitor

193 produced by the seaweed during the time interval from the previous water replacement. **Figure 2a** shows

194 the dynamics of various initial age mixed populations yields when the inhibitor is removed by water

195 replacement. In the scenario where water is replaced every 14 days, only few, relatively "young"

196 populations (100/0, 90/10, 80/20 and 70/30) achieved the 90% of the maximum yield. Moreover, the time

197 to reach this yield level increased from 27-30 days (without replacement for these four age groups) to

198 37-40 days, in the 100/0, 90/10, 80/20 and 70/30 populations, respectively (**Fig. 2b**). The growth yield

199 shows fluctuating dynamics, showing in the initial overall growth for populations with predominantly

200 young thalli during the first 60 cultivation days, followed by the overall reduction of the yield in the aging

201 populations. Interestingly, these fluctuating yield dynamics were previously reported by us during a

202 12-month offshore cultivation work with *Ulva* harvesting every week (Chemodanov et al., 2018). It could

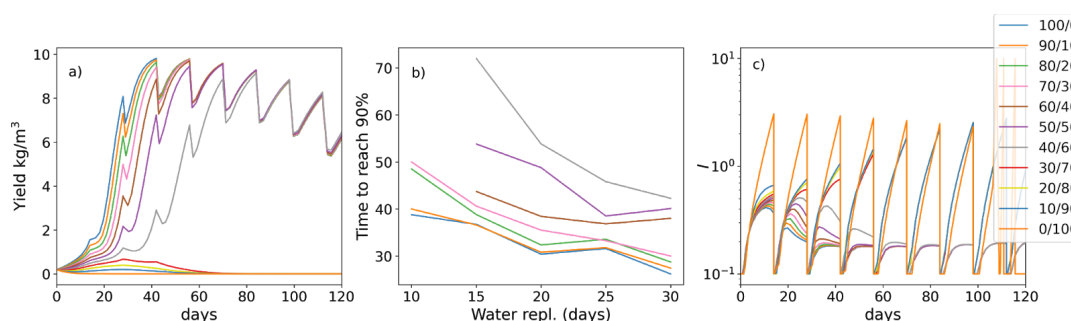
203 happen that the weekly removal of the whole seaweed biomass from the sea and cages for weighting also

204 removed the sporulation inhibitor accumulated in the boundary layer near the thalli. This suggestion, of

205 course, requires further detailed experiments investigating the ability to monitor the dynamics of

206 sporulation inhibitors production and accumulation/diffusion in the thalli environment. Increasing the

207 frequency of water exchange, and thus inhibitor removal (**Fig. 2c**), reduced the ability of populations with

208 a large portion of old algae to show positive yield during the whole cultivation period (**Fig. 2a**).

209 **Figure 2. a.** Yield (biomass gain in kg/m³ up to the limit of 10 kg/m³ in a bioreactor with a starting density of 0.2

210 g/m³) for populations with various initial age mixes with 14 days water replacement frequency. **b.** *Ulva* biomass

211 growth kinetics as a function of the initial age distribution of thalli in the population with various frequencies of

212 water replacement. **c.** Inhibitor production in the population of the time with 14 days of water replacement

213 frequency.

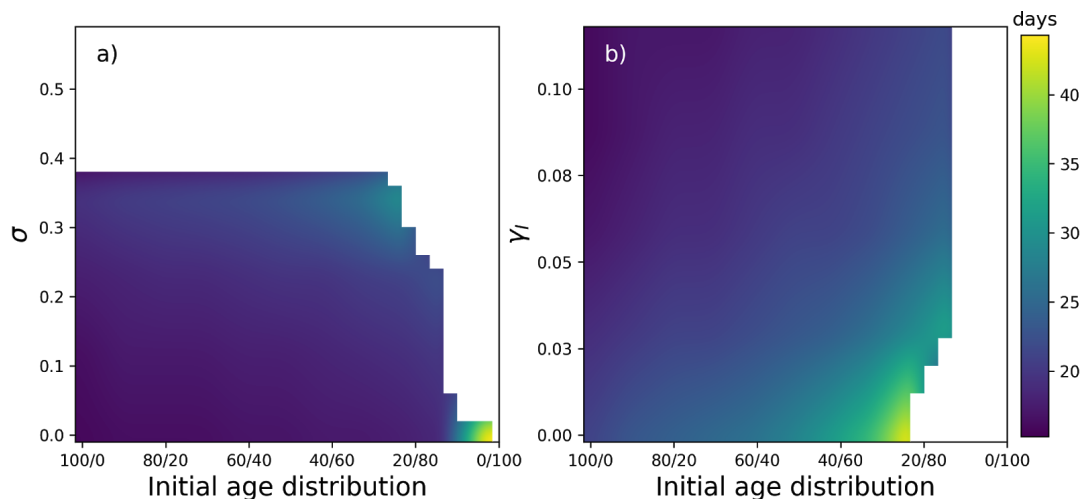
214 As seaweed in the natural environment usually live in high energy conditions, we also studied the coupled

215 effects of mechanical destruction (σ) and population age distribution on the ability of the population

216 biomass yield (**Fig. 3a**). Higher rates of mechanical destruction prevent positive yields in all mixed-age

217 populations. Lower mechanical destruction affects a smaller portion of the population with higher initial

218 portions of young thalli (**Fig. 3a**) showing again the regenerative ability of the populations with high

219 growth (lower sporulation) capabilities.

220 **Figure 3**. a. Time to achieve 90% of the maximum carrying capacity as a heatmap (color represents the time in

221 days) depending on the initial age distribution (x-axis) and the mechanical destruction parameter σ_i (y-axis). **b.**

222 Time to 90% as a heatmap (color represents the time in days) depending on the initial age distribution (x-axis) and

223 the addition of the external inhibitor γ (y-axis). White color means that the population never achieves 90% of the

224 maximum carrying capacity.

225 Finally, after confirming experimentally that direct application of SI-1 prevents gametogenesis in *U.*
226 *mutabilis* (**Supplemental Information and Fig S1**), we investigated the impact of direct addition of the
227 sporulation inhibitor to the seaweed growth media computationally.

228 Adding an external sporulation inhibitor (up to 0.1) reduced the time to achieve 90% of the maximum
229 yield from 27 days (without inhibitor addition) to 21 days for 100/0 group, 29 days (without inhibitor
230 addition) to 24 for 80/20 group, from 35 days (without inhibitor addition) to 28 for the 50/50 group and
231 from 60 (without inhibitor addition) to 45 days for the 20/80 group. No effects at this maximum
232 concentration have been observed for the 0/100 group.

233 4. Conclusions

234 In this study, we aimed to further understand the growth and sporulation dynamics of *Ulva* using a
235 mathematical model. We found that successful accumulation of *Ulva* biomass depends on the age
236 distribution of the algae population, where older starter populations produce lower yields. However, this
237 age-dependent effect can be mitigated, leading to prolonged maintenance of *Ulva*'s aquacultures, by
238 external addition of sporulation inhibitors.
239 Indeed, the sporulation phenomenon creates unique constraints on the age structure of *Ulva* populations.
240 In higher plants, sexual reproduction and vegetative propagation compete for nutrients, but the
241 competition may be mitigated by separating these processes through time (Evans and Black, 1993).
242 However, in *Ulva*, the whole thallus can be transformed into gametangia and sporangia while flowering
243 plants assign only a specific portion of biomass to reproductive structures. *Ulva* thus requires a strict
244 regulation of sporulation, e.g. through the age-dependent production of SI. Only if the SI-1 synthesis
245 ceases during the *Ulva*'s development cycle and its concentration falls below a critical threshold
246 concentration, gametogenesis is induced at positions of the blade where the SI-2 concentration between
247 the cell layers is also sufficiently low (Stratmann et al., 1996). Our findings thus imply that the more SI
248 provided by young algae in mixed cultures, the higher the growth rate and biomass yields. As purified SIs
249 are not yet widely available in large quantities, the use of mixed-aged cultures can be an important tool to
250 maintain them at adequate nutrient levels e.g. in integrated multi trophic aquaculture. The modeling of
251 *Ulva*´s growth indicates the importance of SI-producing algae for sustainable and successful
252 seagricultures, and paves the way for a better understanding of the green tide formation in coastal areas.

5. Code availability

The model creation process is explained in detail in the Methods. Code for creating the figures is available upon request.

6. Author contributions

AG and AL conceived the initial idea for the study; UO, AG and AL designed the study and the mathematical model; AL produced the results; TW produced the experimental results; All authors interpreted the results and wrote the manuscript.

7. Acknowledgements

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8. Competing interests

The authors declare that they have no conflict of interest.

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