Furthering knowledge on seaweed growth and development to facilitate sustainable aquaculture

Charrier, Bénédicte; Abreu, Maria Helena ; Rita, Araujo; Bruhn, Annette; Coates, Juliet; De Clerck, Olivier; Katsaros, Christos; Robaina, Rafael; Wichard, Thomas

DOI:

[10.1111/nph.14728](https://doi.org/10.1111/nph.14728)

License:

None: All rights reserved

Document Version

Peer reviewed version

Citation for published version (Harvard):

Charrier, B, Abreu, MH, Rita, A, Bruhn, A, Coates, J, De Clerck, O, Katsaros, C, Robaina, R & Wichard, T 2017, 'Furthering knowledge on seaweed growth and development to facilitate sustainable aquaculture', *New Phytologist*, vol. 216, no. 4, pp. 967-975. <https://doi.org/10.1111/nph.14728>

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

This is the peer reviewed version of the following article: Charrier, B., Abreu, M. H., Araujo, R., Bruhn, A., Coates, J. C., De Clerck, O., Katsaros, C., Robaina, R. R. and Wichard, T. (2017), Furthering knowledge of seaweed growth and development to facilitate sustainable aquaculture. *New Phytol.* doi:10.1111/nph.14728, which has been published in final form at 10.1111/nph.14728. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

New Phytologist

**Furthering knowledge on seaweed growth and development
to facilitate sustainable aquaculture.**

Journal:	<i>New Phytologist</i>
Manuscript ID	NPH-V-2017-23688.R1
Manuscript Type:	V - Viewpoint
Date Submitted by the Author:	n/a
Complete List of Authors:	Charrier, Benedicte; Centre National de la Recherche Scientifique, Station Biologique Abreu, Helena; ALGApplus Lda, SME Araújo, Rita; European Commission, Joint Research Centre, Directorate for Sustainable Resources, Water and Marine Resources Unit; Universidade do Porto Centro Interdisciplinar de Investigacao Marinha e Ambiental, CIIMAR Bruhn, Annette; Aarhus Universitet, Bioscience Coates, Juliet; University of Birmingham, School of Biosciences; De Clerck, Olivier; Ghent University, Onderzoeksgroep Algologie Katsaros, Christos; National and Kapodistrian University of Athens, Department of Biology Robaina, Rafael; Universidad de Las Palmas de Gran Canaria, Ciencias del Mar Wichard, Thomas; Friedrich Schiller University of Jena, Institute for Inorganic and Analytical Chemistry
Key Words:	aquaculture, development, macroalga, marine, reproduction, seaweed, morphogenesis, biomass

SCHOLARONE™
Manuscripts

1 **Viewpoint**

2 **Title :**

3 **Furthering knowledge on seaweed growth and development to facilitate sustainable**
4 **aquaculture.**

5 **Authors:**

6 Bénédicte Charrier¹, Maria Helena Abreu², Rita Araujo³, Annette Bruhn⁴, Juliet C. Coates⁵, Olivier
7 De Clerck⁶, Christos Katsaros⁷, Rafael R. Robaina⁸, Thomas Wichard⁹

8 **Affiliations:**

9 ¹ Morphogenesis of Macroalgae, UMR8227, CNRS-UPMC, Station Biologique, 29680 Roscoff,
10 France. ² ALGApplus Lda, Travessa Alexandre da Conceição 3830-196 Ílhavo, Portugal. ³ European
11 Commission, Joint Research Centre - Directorate for Sustainable Resources, Water and Marine
12 Resources Unit, Ispra, Italy. ⁴ Aarhus University, Department of BioScience, Vejlsøvej 25, 8600
13 Silkeborg, Denmark. ⁵ School of Biosciences, University of Birmingham, Birmingham B15 2TT,
14 United-Kingdom. ⁶ Department of Biology, Ghent University, Krijgslaan 281 S8, 9000 Ghent,
15 Belgium. ⁷ Morphogenesis of Macroalgae, National and Kapodistrian University of Athens,
16 Department of Biology, Athens, 157 84, Greece. ⁸ Facultad de Ciencias del Mar. Universidad de
17 Las Palmas de Gran Canaria. ⁹ Friedrich Schiller University Jena, Institute for Inorganic and
18 Analytical Chemistry, Lessingstr. 8, 07743 Jena, Germany.

19 Author for correspondence:

20 *Bénédicte Charrier*

21 Tel: 33-2-98-29-56-53

22 email: benedicte.charrier@sb-roscoff.fr

23 **Keywords:** development, macroalgae, life cycle, morphogenesis, reproduction, seaweeds.

Total word count (excluding summary)	3080	No. of Figures	4 (all in colour)
Summary	167	No. of Table	0
Paragraph 1: Ecological and societal position of macroalgae	609	No. of Supporting Information Files	0
Paragraph 2: Mastering genetics through the control of the life cycle	798	Open Access	Yes
Paragraph 3: Early and microscopic stages of development	388		
Paragraph 4: Controlled growth and organogenesis factors: towards biomass production monitoring	332		
Paragraph 5: Current technological requirements	655		
Paragraph 6: Conclusion	267		
Acknowledgements	20		

24 **Abstract**

25 Macroalgae (seaweeds) are the subject of increasing interest for their potential as a source of
 26 valuable, sustainable biomass in the food, feed, chemical and pharmaceutical industries. Compared
 27 to microalgae, the pace of knowledge acquisition in seaweeds is slower despite the availability of
 28 whole-genome sequences and model organisms for the major seaweed groups. This is partly due to
 29 specific hurdles related to the large size of these organisms and their slow growth. As a result, this
 30 basic scientific field is falling behind, despite the societal and economic importance of these
 31 organisms. Here, we argue that sustainable management of seaweed aquaculture requires
 32 fundamental understanding of the underlying biological mechanisms controlling macroalgal life
 33 cycles - from the production of germ cells to the growth and fertility of the adult organisms - using
 34 diverse approaches requiring a broad range of technological tools. This viewpoint highlights
 35 several examples of basic research on macroalgal developmental biology that could enable the
 36 step-changes which are required to adequately meet the demands of the aquaculture sector.

37 **Ecological and societal position of macroalgae**

38 Macroalgae are macroscopic aquatic organisms belonging to three distinct and distantly-related
 39 eukaryotic lineages (commonly named green, red, and brown algae). Their unicellular ancestors
 40 diverged more than 1.6 billion years ago (Parfrey *et al.*, 2011) implying independent acquisitions of
 41 multicellularity, and leading to a bewildering diversity of life cycles, fertilization processes and
 42 morphogenetic strategies. At the ecological level, macroalgae fulfil important roles as key habitat-
 43 structuring agents and primary producers in coastal ecosystems. The goods and services seaweeds
 44 (marine macroalgae) support are varied (Figure 1), and include elevated secondary production,

45 nutrient cycling, energy capture and flow, and coastal defence (Steneck *et al.*, 2002). They can also
 46 significantly contribute to carbon sequestration at a level exceeding that of angiosperm marine
 47 coastal vegetation (up to 1.5 times as much as seagrass meadows, salt marshes and mangroves and
 48 up to 2% of the annual anthropogenic emission; Krause-Jensen & Duarte, 2016 and references
 49 therein). In addition, macroalgae support complex food webs in coastal zones and provide habitats
 50 and food for associated organisms, from apex predators to invertebrates (Reisewitz *et al.*, 2006).
 51 Macroalgal communities also enable transfer of biomass between ecosystems (Krumhansl &
 52 Scheibling, 2012), removal of dissolved nutrients from coastal waters and coastal protection from
 53 erosion (Arkema *et al.*, 2013). De Groot *et al.* (2012) estimated the value of coastal ecosystem
 54 services provided by macroalgae to be over 28,000 intl.\$·ha⁻¹·year⁻¹.

55 Seaweeds are also an alternative/additional source of food, feed, fuel, biomolecules and livelihood
 56 for humans. Over 80% of macroalgal production and harvesting is at present destined for human
 57 consumption directly (Abreu *et al.*, 2014) or as hydrocolloids (thickeners, gelling agents, etc)
 58 (Rebours *et al.*, 2014). Macroalgae are also used as fertilizers and animal feed (Makkar *et al.*,
 59 2016). In addition, the industrial sector uses seaweed biomass for nutraceuticals, cosmetics,
 60 biotechnological and pharmaceutical applications, thus propelling the growth of seaweed
 61 biotechnology (Mazarrasa *et al.*, 2013). Currently, ~28 million tonnes of seaweeds per year (wet
 62 weight) are produced and, as a proxy for the growth of the biotechnology-market of seaweed-
 63 derived products, seaweed-related patent applications increased at a rate of 11% per year since
 64 1990 (Mazarrasa *et al.*, 2014).

65 While in Asia 99% of seaweed production is sourced from cultivation (accounting for 93% of the
 66 global production in 2013) (FAO, 2016), the dominant practice of non-Asian countries is still
 67 harvesting natural stocks. However, the availability of wild stocks under the current scenario of
 68 global change needs to be assessed, while management plans for seaweed exploitation must be
 69 adapted to the natural population dynamics of commercially important species. Increasing demands
 70 for high-quality seaweed biomass may therefore affect the long-term sustainability of seaweed

71 exploitation. Seaweed cultivation is the alternative to cope with industry's demand for biomass,
 72 concomitantly protecting natural resources (Fig. 1). Unlike terrestrial crops, they do not compete
 73 for arable land, fertilizer and freshwater resources. Furthermore, the development of Integrated
 74 Multi-Trophic Aquaculture (IMTA: co-cultivation of seaweeds with fin/shell fishes) enables
 75 recapture of excessive inorganic nutrients released in coastal areas by fish farms, thereby
 76 improving their sustainability (Holdt & Edwards, 2014). Beyond aquaculture proper, seaweed
 77 cultivation could also function as a general instrument for circular resource management (Seghetta
 78 *et al.*, 2016), treatment of waste-water produced by land-based farming and municipal treatment
 79 plants (Neveux *et al.*, 2016), heavy metal biosorption (He & Chen, 2014) and recolonisation of
 80 artificial reefs (Fig. 1). As a response to this assessment, the European seaweed aquaculture sector
 81 has progressively expanded, accounting for 12% of total European biomass production in 2013
 82 (FAO, 2016). Further expansion calls for advances in seaweed production technology, which rely
 83 on a better knowledge of both the environmental and the intrinsic factors controlling the
 84 development of macroalgae.

85 **How could developmental biology help solve bottlenecks in seaweed aquaculture?**

86 *Mastering genetics through the control of the life cycle*

87 Most seaweeds have complex, biphasic life cycles, involving free-living haploid gametophyte and
 88 diploid sporophyte generations (Coelho *et al.*, 2007) (Box 1). Either phase of the life cycle can be
 89 exploited, depending on the seaweed species. The harvestable biomass of kelps consists of
 90 sporophytes up to several meters long (45 m in *Macrocystis*), while in nori (*Pyropia* and
 91 *Porphyra*), the life stage of interest is the haploid gametophyte. Other exploited seaweeds e.g.
 92 *Gracilaria* and *Chondrus* (red algae) have isomorphic life-cycles, with both sporophyte and
 93 gametophyte developing macroscopic exploitable thalli. Currently, clonal propagation (e.g. red alga

94 *Kappaphycus*) and recourse to a limited number of parent genotypes (kelp) account for the
 95 production of most commonly cultivated seaweeds. The resulting impoverishment of genetic
 96 diversity increases seaweed susceptibility to diseases and decreases their fitness within their
 97 cultivation environment (Loureiro *et al.*, 2015). For example, the continuous vegetative
 98 propagation of the carrageenophyte *Kappaphycus* in intensively cultivated areas has increased its
 99 vulnerability to diseases (e.g. bacterial mediated “ice-ice” disease), thereby dramatically impacting
 100 the production in various countries (Largo *et al.*, 1995). This problem requires counteraction by the
 101 selection of new breeding strains, potentially through artificial hybrids (Gupta *et al.*, 2015), but
 102 more optimally through crossings, as somatic hybridisation usually results in severe and unstable
 103 phenotypic alteration (Charrier *et al.*, 2015). However, whilst in some seaweeds the promotion of
 104 sexual reproduction still requires development (e.g. *Gracilariopsis*; Zhou *et al.*, 2013), the loss of
 105 the genetic patrimony resulting from cross-fertilisation might be detrimental to maintaining specific
 106 and valuable genotypes resulting from decades of selection. Therefore, manipulating the different
 107 steps of the seaweed life cycles would allow a balance between the maintenance of given
 108 genotypes of interest and controlled breeding. Progress in basic research opens possible paths to
 109 bypass steps of the life cycle, thereby allowing to reach this goal (Box 1).

110 *Manipulating the sexual life cycle.*

111 Most cultivated seaweeds reproduce sexually (kelps, red algae *Porphyra* ssp.), placing both time
 112 and genetic constraints on seaweed farmers. Physiological studies have long been establishing
 113 protocols for maintaining seaweeds in a vegetative stage or shifting them to the next phase using
 114 specific temperature and light conditions, or even by tissue ablation. This allows year-round
 115 production of juveniles and increases the cultivated net biomass (Pang & Lüning, 2004). Several
 116 illustrations of these practices applied to exploited seaweeds are displayed in Box 1. Recent
 117 fundamental studies propose potential alternatives. Treatments with algal phytohormones could be
 118 used to control the vegetative-to-reproductive transition and speed up reproduction, as illustrated in

119 the red alga *Grateloupia imbricata* upon addition of methyl jasmonate (García-Jiménez *et al.*,
120 2016).

121 *Promoting parthenogenesis.*

122 Other seaweeds propagate vegetatively from a single life phase through parthenogenesis, mainly by
123 apogamy but also by apomeiosis. The flexibility is high and is a valuable feature for aquaculture, as
124 it allows the maintenance of a specific genotype in potentially morphologically different organisms
125 (Box 1, left side). Parthenogenesis can be induced by hybridisation (e.g. *Caloglossa*
126 tetrasporophytes; Kamiya & West, 2008) or through chemical treatments preventing gamete
127 motility (e.g. formaldehyde in brown algae Ectocarpales; Gwo & Chen, 1999). The lab-based
128 identification of endogenous factors controlling seaweed parthenogenesis might provide more
129 natural alternatives to regulate or manipulate parthenogenesis in aquaculture. Recently, Han *et al.*
130 (2014) identified three mitochondrial proteins involved in the control of parthenogenesis in
131 *Scytosiphon lomentaria* (brown alga Ectocarpales). In parallel, Arun *et al.* (2013) showed that algal
132 chemical factors (so far unidentified) secreted by the parthenosporophyte of *Ectocarpus siliculosus*
133 (brown alga Ectocarpales) control the fate of the released zoospores (Box 1). Coelho *et al.* (2011)
134 showed that the whole parthenosporophytic stage itself was controlled by a single genetic locus.
135 The characterisation of these factors could lead to the development of additional strategies to
136 control parthenogenesis.

137 Finally, Li *et al.*, (2014) produced *Undaria pinnatifida* (brown alga) gametophytes that made only
138 male gametes from both oogonia and antheridia (Shan *et al.*, 2015). These gametes are able to self-
139 cross and to produce homozygous male diploid sporophytes. This example illustrates that crosses
140 are controlled by the morphological identity of the reproductive organs rather than by their
141 genotypes, emphasizing the importance of a control over morphogenesis.

142 In parallel to these improvements for seaweeds cultivated off-shore (Fernand *et al.*, 2017),
143 standardized protocols should also be developed specifically for not-yet cultivated, high-value
144 seaweeds amenable to on-shore cultivation. This includes seaweeds producing high-value

chemicals, or seaweeds in high demand on the food market, such as *Ulva*, *Palmaria*, *Porphyra*, *Cystoseira*, *Himanthalia*, *Codium*, *Polysiphonia* and *Asparagopsis* (Abreu *et al.*, 2014), as well as the red macroalgae *Ochtodes* and *Portieria* cultivated in photobioreactors (Rorrer & Cheney, 2004).

Altogether, basic research into the development and reproduction of macroalgae will likely provide alternative means of manipulating seaweed reproduction, which will be very valuable for future breeding programmes and aquaculture practices (Cottier-Cook *et al.*, 2016).

Early and microscopic stages of development

Seaweed growth starts with the formation and development of juveniles, which originate from the release and germination of single cells (zygotes or spores). They subsequently attach to marine substrata to initiate their sessile development (bloom-forming algae are usually free-living). Deciphering the early and microscopic developmental stages of seaweeds is an important requirement for future integrative management of their cultivation (Fig. 2). Exploitation of seaweed biomass concentrates on the macroscopic life-cycle stage, which is the sporophyte in the most predominantly exploited brown algae (*Ecklonia*, *Laminaria*, *Saccharina*, *Undaria*), together with the gametophyte in red seaweeds (*Gracilaria*, *Kappaphycus*, *Eucheuma*) and in some isomorphic green (*Ulva*) seaweeds. Optimizing fertilisation success could help control the rate of production of seaweed embryos in hatcheries, which, when too high, impedes the quality of sporophyte juveniles (Fig. 2 and 3). Environmental cues inducing fertility and spore/gamete release have been determined for tens of seaweed species (photoperiod, irradiance, temperature and nutrient concentration; previous section and Box 1). However, the paucity of molecular studies regarding e.g. the periodicity of gamete release, attraction of gametes to opposite sex or mating type, and cell-cell recognition (Fig. 3) stands in a stark contrast to the wealth of eco-physiological and biochemical studies that predate the molecular era. As an illustration, in certain *Ulva* species,

169 gametogenesis and subsequent gamete release can be artificially induced by removal of sporulation
170 and swarming inhibitors (Vesty *et al.*, 2015 and references therein), but so far, neither these
171 inhibitors nor the signalling pathways inducing gametogenesis have been characterised. Similar
172 cases could be made for pheromone signalling in brown seaweeds (Boland, 1995) and glycoprotein
173 recognition between opposite-sex gametes (Schmid *et al.*, 1994).

174 Many macroalgal zygotes experience polarisation prior to the growth and development of the
175 embryo (Fig. 3), similarly to land plants and metazoans. Whether polarisation is necessary for
176 proper development, and the identity of polarisation cues and regulatory factors, are unknown for
177 most macroalgae: only Fucales and Dictyotales (brown algae) zygotes have allowed the
178 identification of detailed polarisation cues (light direction and location of sperm entry; Brownlee *et*
179 *al.*, 2001; Bogaert *et al.*, 2017) and of specific cell cycle checkpoints (Bothwell *et al.*, 2008).
180 Bogaert *et al.* (2017) recently described in *Dictyota* a unique two-phase polarisation mechanism,
181 thereby illustrating the importance of seaweeds to decipher fundamental developmental processes
182 in the tree of life.

183 *Controlled growth and organogenesis factors: towards biomass production monitoring,*

184 Production of large seaweed biomass with specific features of industrial interest (polysaccharides,
185 proteins and pigments) depends both on seaweed net growth and seaweed capacity to grow organs
186 and tissues with specific structures and compositions. Indeed, the quantity and quality of key
187 compounds vary within the algal body (beta-glucan in *Durvillaea*: Bobadilla *et al.*, 2013;
188 phytohormones in *Sargassum*: Li *et al.*, 2016), and cells with thicker walls, storage organelles and
189 vacuoles might be more resistant to dehydration, chemical exposure, eutrophication, and pathogen
190 attacks, and hence be of high interest. Unfortunately, macroalgal cell fate specification is one of the
191 least-understood areas of macroalgal biology. Undoubtedly, both endogenous (e.g. bacteria:
192 Spoerner *et al.*, 2012; circadian rhythm: Cunningham & Guiry, 1989) and abiotic environmental

193 factors (light, temperature, sea currents) are required (Fig. 3), but the intrinsic signalling pathways
 194 are largely unknown. To understand how to manipulate hatchery culture conditions to give
 195 juveniles the best start in life in tune with aquaculture demands, additional studies assessing the
 196 molecular impact of the surrounding physical and chemical environment (light, nutrients, salinity,
 197 water movement) are required. In some seaweeds, complex interactions with bacteria are a
 198 prerequisite for proper cell growth and differentiation into specific tissues (Goecke *et al.*, 2010).
 199 This has been well-illustrated in green seaweeds (*Ulva* and *Monostroma* - Matsuo *et al.*, 2005;
 200 Spoerner *et al.*, 2012), as well as in brown algal species where bacteria might control their life
 201 cycle (Tapia *et al.*, 2016) and their morphology in waters with different salinities (Dittami *et al.*,
 202 2014). It is tempting to hypothesize that controlling macroalgal development with bacteria will
 203 direct the chemical composition of the macroalga and its value as cash crop. This is mainly relevant
 204 for land-based aquaculture starting with a defined seed-stock (axenic germlings) and a synthetic
 205 microbiome, which could influence the production of primary and secondary metabolites.
 206 However, further work determining macroalgal-bacterial interactions throughout algal life-cycles is
 207 necessary to discriminate between mutualistic, beneficial or pathogenic interactions.

208 **Current technological requirements**

209 Reliable, cost-effective and long-term maintenance of genetic resources is a major requirement to
 210 ensure the sustainability of the quality of the exploited traits (biomass yield, quality of extracted
 211 polysaccharides, texture and taste of species for human consumption; Chapman *et al.*, 2015). Both
 212 sub-culturing of macroalgal explants and cryopreservation of macroalgal omnipotent cells are
 213 current techniques to vegetatively propagate macroalgae over time. However, sub-cultivation is
 214 time-consuming and re-iteration of the protocol over years is a source of bacterial or fungal
 215 contamination. Long-term preservation (through refrigeration or liquid-nitrogen freezing) of
 216 commercially important seaweed explants has therefore received increasing attention and several

217 protocols are now available. Techniques depend on the species (e.g. gametophytic filaments of
 218 *Macrocystis*; Barrento *et al.*, 2016; pieces of *Ulva* thalli; Lee & Nam, 2016; and apical meristems
 219 of *Gracilaria*: Lalrinsanga *et al.*, 2009) and a better knowledge of both the mitotic activities within
 220 the thallus and the underlying molecular mechanisms governing cell proliferation *versus* cell
 221 differentiation would accelerate the assessment of the regenerative potential of these seaweeds and
 222 the necessary development of adequate protocols (Stacey & Day, 2014) (Fig. 3). Basic research has
 223 revealed specificities in brown seaweeds, specifically in the *Fucus* embryo, where cell division is
 224 subject to distinct control mechanisms compared to other eukaryotes (Corellou *et al.*, 2001). As
 225 bacteria play a crucial role in many algal developmental processes (Goecke *et al.*, 2010),
 226 macroalgal preservation should also consider cryopreservation of algae with their natural
 227 microbiome rather than axenic explants. Therefore, development of seaweed biobanking
 228 procedures may be pivotal to meet future aquaculture demands.

229 Beyond cryopreservation, while some techniques are easily transferable from land plants to
 230 macroalgae, others require species-specific optimization. The impact of the sea water medium on
 231 the ionic concentration of buffers used in standard lab protocols and the different polysaccharide
 232 compositions of red and brown algal cell walls (Deniaud-Bouët *et al.*, 2014; Popper *et al.*, 2011)
 233 require different cell wall enzymolytic treatments in cytology protocols (Joubert & Fleurence,
 234 2008). At the genetic level, the sequence of reporter genes commonly used in other organisms
 235 require modification for transgene expression, because of differing codon usages, as shown in red
 236 and green seaweeds (Uji *et al.*, 2014; Oertel *et al.*, 2015). The growing interest of the evolutionary
 237 developmental biology (“evo-devo”) community in macroalgae would help phycologists develop
 238 these techniques further.

239 In addition to the requirement for cell biology and genetic adjustments, ‘OMICS’ technology must
 240 be adapted to the level of analysis required to tackle developmental mechanisms taking place at the
 241 microscopic and early developmental stages (Fig. 2 and 3). Several transcriptomic (Wang *et al.*,
 242 2015), proteomic (Qian *et al.*, 2016) and metabolomic (Kumar *et al.*, 2016 and references therein)

243 studies have been reported in both model and exploited macroalgae. In addition, exo-metabolomic
 244 profiling in standardized *Ulva* cultures with a designed microbiome have shown growth phase-
 245 dependent biomarkers that might be relevant for aquaculture (Alsufyani *et al.*, 2017). Such
 246 analyses are assisted by an increasing number of sequenced macroalgal genomes. Currently 18
 247 public algal nuclear genomes have been sequenced, including four seaweeds. However, “-OMICS”
 248 studies at early developmental stages are hampered by a scarcity of tissue. While proteomics and
 249 metabolomics still require a significant biomass, transcriptomics can bypass this handicap through
 250 RNA amplification. Cell-specific expression patterns were thereby obtained using laser
 251 microdissection prior to RNA amplification on the model brown seaweed *Ectocarpus* (Saint-
 252 Marcoux *et al.*, 2015), and this technology is easily transferable to larger seaweeds.
 253 Finally, transgenesis will be a highly valuable tool to discover how molecular processes are
 254 regulated in seaweeds, and to interfere with these processes by knocking down/upregulating
 255 endogenous genes. So far, only four multicellular algae, namely *Ulva*, *Pyropia* (*Porphyra*), *Volvox*
 256 and *Gonium* are genetically transformable (Schiedlmeier *et al.*, 1994; Oertel *et al.*, 2015; Mikami,
 257 2014; Lerche & Hallmann, 2009), and *Ulva* is the only stably transformable seaweed (Oertel *et al.*,
 258 2015). These first successes must now be replicated in additional, diverse species, *via* investment
 259 of time and expertise.

260 Conclusion

261 A range of protocols are available to cultivate seaweeds, thanks to previous physiological studies
 262 carried out in an applied phycological context. Building on this key achievement, practices must be
 263 refined and developed with a more focused and on-demand approach. Indeed, demand from end-
 264 users is rising for new, high-commercial potential (mainly for food) seaweeds. However, because
 265 of their low production level, these seaweeds have not received high investment so far, and as a
 266 result, no standardised cultivation and preservation protocols exist. This second big step is much

267 more delicate, because of the greater number of species and of their reluctance to respond to the
268 simplest, classical protocols. The time has come, now that the first empirical studies have been
269 carried out, to engage the community in an in-depth study of the biological processes driving the
270 whole macroalgal life-cycle, from fertilization to the production of organisms. This must respond
271 to end-users' expectations of robustness against environmental constraints (e.g. climate, infection,
272 mechanical strain), biochemical composition and also natural and nature-friendly production
273 increasingly favoured by the consumers. This is even more necessary since, despite the benefit that
274 the development of cutting-edge technologies in animals and plants can bring to the sector, many of
275 these technologies need to be adapted to macroalgae because of their specific ecological niche
276 (highly saline) and their biology (in part due to their phylogenetic distance from better-known
277 organisms). Therefore, efforts must be intensified to fill the gaps in our fundamental knowledge of
278 macroalgal developmental mechanisms. We also believe that the scientific community of land plant
279 researchers will benefit from a deeper understanding of seaweed developmental biology.

280 **Acknowledgement**

281 This work is carried out in the frame of “Phycomorph” (<http://www.phycomorph.org/>), a network
282 funded by the COST Association (http://www.cost.eu/COST_Actions/fa/FA1406).

283 **Author contributions**

284 All authors contributed to the writing of the manuscript.

285 **References**

- 286 **Abreu M, Pereira R, Sassi J-F. 2014.** Marine algae and the global food industry. In: Pereira L, In:
 287 Neto J, eds. *Marine Algae*. CRC Press, 300–319.
- 288 **Alsufyani T, Weiss A, Wichard T. 2017.** Time course exo-metabolomic profiling in the green
 289 marine macroalga *Ulva* (Chlorophyta) for identification of growth phase-dependent biomarkers.
 290 *Marine Drugs*, **15**: 14.
- 291 **Arkema KK, Guannel G, Verutes G, Wood SA, Guerry A, Ruckelshaus M, Kareiva P, Lacayo**
 292 **M, Silver JM. 2013.** Coastal habitats shield people and property from sea-level rise and storms.
 293 *Nature Climate Change* **3**: 913–918.
- 294 **Arun A, Peters NT, Scornet D, Peters AF, Cock JM, Coelho SM. 2013.** Non-cell autonomous
 295 regulation of life cycle transitions in the model brown alga *Ectocarpus*. *New Phytologist* **197**: 503–
 296 510.
- 297 **Barrento S, Camus C, Sousa-Pinto I, Buschmann AH. 2016.** Germplasm banking of the giant
 298 kelp: Our biological insurance in a changing environment. *Algal Research-Biomass Biofuels and*
 299 *Bioproducts* **13**: 134–140.
- 300 **Bobadilla F, Rodriguez-Tirado C, Imarai M, Jose Galotto M, Andersson R. 2013.** Soluble
 301 beta-1,3/1,6-glucan in seaweed from the southern hemisphere and its immunomodulatory effect.
 302 *Carbohydrate Polymers* **92**: 241–248.
- 303 **Bogaert KA, Beeckman T, De Clerck O. 2017.** Two-step cell polarization in algal zygotes.
 304 *Nature Plants* **3**: 16221.
- 305 **Boland W. 1995.** The chemistry of gamete attraction: chemical structures, biosynthesis, and
 306 (a)biotic degradation of algal pheromones. *Proceedings of the National Academy of Sciences of the*
 307 *United States of America* **92**: 37–43.

- 308 **Bothwell JHF, Kisielewska J, Genner MJ, McAinsh MR, Brownlee C. 2008.** Ca²⁺ signals
 309 coordinate zygotic polarization and cell cycle progression in the brown alga *Fucus serratus*.
 310 *Development (Cambridge, England)* **135**: 2173–2181.
- 311 **Brownlee C, Bouget FY, Corellou F. 2001.** Choosing sides: establishment of polarity in zygotes
 312 of furoid algae. *Seminars in Cell & Developmental Biology* **12**: 345–351.
- 313 **Chapman AS, Stevant P, Larssen WE. 2015.** Food or fad? Challenges and opportunities for
 314 including seaweeds in a Nordic diet. *Botanica Marina* **58**: 423–433.
- 315 **Charrier B, Rolland E, Gupta V, Reddy CRK. 2015.** Production of genetically and
 316 developmentally modified seaweeds: exploiting the potential of artificial selection techniques.
 317 *Frontiers in Plant Science* **6**: 127.
- 318 **Coelho SM, Godfroy O, Arun A, Le Corguillé G, Peters AF, Cock JM. 2011.** OUROBOROS is
 319 a master regulator of the gametophyte to sporophyte life cycle transition in the brown alga
 320 *Ectocarpus*. *Proceedings of the National Academy of Sciences of the United States of America* **108**:
 321 11518–11523.
- 322 **Coelho SM, Peters AF, Charrier B, Roze D, Destombe C, Valero M, Cock JM. 2007.** Complex
 323 life cycles of multicellular eukaryotes: new approaches based on the use of model organisms. *Gene*
 324 **406**: 152–170.
- 325 **Corellou F, Brownlee C, Detivaud L, Kloareg B, Bouget FY. 2001.** Cell cycle in the *Fucus*
 326 zygote parallels a somatic cell cycle but displays a unique translational regulation of cyclin-
 327 dependent kinases. *The Plant Cell* **13**: 585–598.
- 328 **Cottier-Cook E, Nagabhatla N, Badis Y, Campbell ML, Chopin T, Dai W, Fang J, He P,**
 329 **Hewitt CL, Kim GH, et al. 2016.** Safeguarding the future of the global seaweed aquaculture
 330 industry. United Nations University (INWEH) and Scottish Association for Marine Science Policy
 331 Brief. ISBN 978-92-808-6080-1. 12pp.

- 332 **Cunningham EM, Guiry MD. 1989.** A Circadian Rhythm in the Long-Day Photoperiodic
 333 Induction of Erect Axis Development in the Marine Red Alga *Nemalion Helminthoides*^{1,2}.
 334 *Journal of Phycology* **25**: 705–712.
- 335 **Deniaud-Bouët E, Kervarec N, Michel G, Tonon T, Kloareg B, Hervé C. 2014.** Chemical and
 336 enzymatic fractionation of cell walls from Fucales: insights into the structure of the extracellular
 337 matrix of brown algae. *Annals of Botany* **114**: 1203–1216.
- 338 **Dittami SM, Barbeyron T, Boyen C, Cambefort J, Collet G, Delage L, Gobet A, Groisillier A,**
 339 **Leblanc C, Michel G, et al. 2014.** Genome and metabolic network of ‘Candidatus
 340 *Phaeomarinobacter ectocarpus* Ec32, a new candidate genus of Alphaproteobacteria frequently
 341 associated with brown algae. *Frontiers in Genetics* **5**.
- 342 **FAO. 2016.** Fisheries & Aquaculture - Fisheries and Aquaculture Fact Sheets.
- 343 **Fernand F, Israel A, Skjermo J, Wichard T, Timmermans KR, Golberg A. 2017.** Offshore
 344 macroalgae biomass for bioenergy production: Environmental aspects, technological achievements
 345 and challenges. *Renewable and Sustainable Energy Reviews* **75**: 35–45.
- 346 **García-Jiménez P, Brito-Romano O, Robaina RR. 2016.** Occurrence of jasmonates during
 347 cystocarp development in the red alga *Grateloupia imbricata*. *Journal of Phycology* **52**: 1085–
 348 1093.
- 349 **Goecke F, Labes A, Wiese J, Imhoff JF. 2010.** Chemical interactions between marine macroalgae
 350 and bacteria. *Marine Ecology Progress Series* **409**: 267–299.
- 351 **de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M,**
 352 **Crossman N, Ghermandi A, Hein L, et al. 2012.** Global estimates of the value of ecosystems and
 353 their services in monetary units. *Ecosystem Services* **1**: 50–61.
- 354 **Gupta V, Kumari P, Reddy CRK. 2015.** Development and characterization of somatic hybrids of
 355 *Ulva reticulata* Forsskal (x) *Monostroma oxyspermum* (Kütz.) Doty. *Frontiers in Plant Science* **6**:
 356 3.

- 357 **Gwo HH, Chen CS. 1999.** Evidence of fusion and artificially initialized parthenogenesis in
 358 isogametes of *Endarachne binghamiae* (Scytosiphonaceae, Phaeophyta) from Taiwan. *Journal of*
 359 *Applied Phycology*. **11**: 567–577.
- 360 **Han JW, Klochkova TA, Shim J, Nagasato C, Motomura T, Kim GH. 2014.** Identification of
 361 three proteins involved in fertilization and parthenogenetic development of a brown alga,
 362 *Scytosiphon lomentaria*. *Planta* **240**:1253–1267.
- 363 **He J, Chen JP. 2014.** A comprehensive review on biosorption of heavy metals by algal biomass:
 364 Materials, performances, chemistry, and modeling simulation tools. *Bioresource Technology* **160**:
 365 67–78.
- 366 **He P, Yarish C. 2006.** The developmental regulation of mass cultures of free-living conchocelis for
 367 commercial net seeding of *Porphyra leucosticta* from Northeast America. *Aquaculture* **257**: 373–
 368 381.
- 369 **Holdt SL, Edwards MD. 2014.** Cost-effective IMTA: a comparison of the production efficiencies
 370 of mussels and seaweed. *Journal of Applied Phycology* **26**: 933–945.
- 371 **Joubert Y, Fleurence J. 2008.** Simultaneous extraction of proteins and DNA by an enzymatic
 372 treatment of the cell wall of *Palmaria palmata* (Rhodophyta). *Journal of Applied Phycology* **20**:
 373 55–61.
- 374 **Kamiya M, West JA. 2008.** Origin of apomictic red algae: outcrossing studies of different strains
 375 in *Caloglossa monotracha* (Ceramiales, Rhodophyta). *Journal of Phycology* **44**: 977–984.
- 376 **Krause-Jensen D, Duarte CM. 2016.** Substantial role of macroalgae in marine carbon
 377 sequestration. *Nature Geoscience* **9**: 737–742.
- 378 **Krumhansl KA, Scheibling RE. 2012.** Detrital subsidy from subtidal kelp beds is altered by the
 379 invasive green alga *Codium fragile ssp fragile*. *Marine Ecology Progress Series* **456**: 73–85.
- 380 **Kumar M, Kuzhiumparambil U, Pernice M, Jiang Z, Ralph PJ. 2016.** Metabolomics: an
 381 emerging frontier of systems biology in marine macrophytes. *Algal Research-Biomass Biofuels*
 382 *and Bioproducts* **16**: 76–92.

- 383 **Lalrinsanga PL, Deshmukhe G, Chakraborty SK, Dwivedi A, Barman N, Kumar N. 2009.**
 384 Preliminary studies on cryopreservation of vegetative thalli of some economically important
 385 seaweeds of India. *Journal of Applied Aquaculture* **21**: 250–262.
- 386 **Largo DB, Fukami K, Nishijima T, Ohno M. 1995.** Laboratory-induced development of the ice-
 387 ice disease of the farmed red algae *Kappaphycus alvarezii* and *Eucheuma denticulatum*
 388 (Solieriaceae, Gigartinales, Rhodophyta). *Journal of Applied Phycology* **7**: 539–543.
- 389 **Lee YN, Nam KW. 2016.** Cryopreservation of gametophytic thalli of *Ulva prolifera* (Ulvales,
 390 Chlorophyta) from Korea. *Journal of Applied Phycology* **28**: 1207–1213.
- 391 **Lerche K, Hallmann A. 2009.** Stable nuclear transformation of *Gonium pectorale*. *BMC*
 392 *Biotechnology* **9**: 64.
- 393 **Li J, Pang S, Shan T, Liu F, Gao S. 2014.** Zoospore-derived monoecious gametophytes in
 394 *Undaria pinnatifida* (Phaeophyceae). *Chinese Journal of Oceanology and Limnology* **32**: 365–371.
- 395 **Li Y, Zhou C, Yan X, Zhang J, Xu J. 2016.** Simultaneous analysis of ten phytohormones in
 396 *Sargassum horneri* by high-performance liquid chromatography with electrospray ionization
 397 tandem mass spectrometry. *Journal of Separation Science* **39**: 1804–1813.
- 398 **Loureiro R, Gachon CMM, Rebours C. 2015.** Seaweed cultivation: potential and challenges of
 399 crop domestication at an unprecedented pace. *New Phytologist* **206**: 489–492.
- 400 **Luning K, Dring MJ. 1975.** Reproduction, growth and photosynthesis of gametophytes of
 401 *Laminaria saccharina* grown in blue and red-light. *Marine Biology* **29**: 195–200.
- 402 **Makkar HPS, Tran G, Heuzé V, Giger-Reverdin S, Lessire M, Lebas F, Ankers P. 2016.**
 403 Seaweeds for livestock diets: A review. *Animal Feed Science and Technology* **212**: 1–17.
- 404 **Matsuo Y, Imagawa H, Nishizawa M, Shizuri Y. 2005.** Isolation of an algal morphogenesis
 405 inducer from a marine bacterium. *Science (New York, N.Y.)* **307**: 1598.
- 406 **Mazarrasa I, Olsen YS, Mayol E, Marbà N, Duarte CM. 2013.** Rapid growth of seaweed
 407 biotechnology provides opportunities for developing nations. *Nature Biotechnology* **31**: 591–592.

- 408 **Mazarrasa I, Olsen YS, Mayol E, Marbà N, Duarte CM. 2014.** Global unbalance in seaweed
409 production, research effort and biotechnology markets. *Biotechnology Advances* **32**: 1028–1036.
- 410 **Mikami K. 2014.** A technical breakthrough close at hand: feasible approaches toward establishing
411 a gene-targeting genetic transformation system in seaweeds. *Frontiers in Plant Science* **5**: 498.
- 412 **Nakahara H. 1984.** Alternation of generations of some brown algae in unialgal and axenic
413 cultures. 北海道大學理學部海藻研究所歐文報告 = *Scientific papers of the Institute of*
414 *Algological Research, Faculty of Science, Hokkaido University* **7**: 77–194.
- 415 **Neveux N, Magnusson M, Mata L, Whelan A, de Nys R, Paul NA. 2016.** The treatment of
416 municipal wastewater by the macroalga *Oedogonium* sp. and its potential for the production of
417 biocrude. *Algal Research* **13**: 284–292.
- 418 **Oertel W, Wichard T, Weissgerber A. 2015.** Transformation of *Ulva Mutabilis* (chlorophyta) by
419 Vector Plasmids Integrating into the Genome. *Journal of Phycology* **51**: 963–979.
- 420 **Pang SJ, Lüning K. 2004.** Breaking seasonal limitation: year-round sporogenesis in the brown
421 alga *Laminaria saccharina* by blocking the transport of putative sporulation inhibitors.
422 *Aquaculture* **240**(1-4):531–541.
- 423 **Pang SJ, Lüning K. 2006.** Tank cultivation of the red alga *Palmaria palmata*: Year-round
424 induction of tetrasporangia, tetraspore release in darkness and mass cultivation of vegetative thalli.
425 *Aquaculture* **252**: 20–30.
- 426 **Parfrey LW, Lahr DJG, Knoll AH, Katz LA. 2011.** Estimating the timing of early eukaryotic
427 diversification with multigene molecular clocks. *Proceedings of the National Academy of Sciences*
428 *of the United States of America* **108**: 13624–13629.
- 429 **Popper S, Michel G, Herve C, Domozych DS, Willats WGT, Tuohy MG, Kloareg B, Stengel**
430 **DB. 2011.** Evolution and diversity of plant cell walls: from algae to flowering plants. In: Merchant
431 SS, In: Briggs WR, In: Ort D, eds. Annual Review of Plant Biology, Vol 62. Palo Alto: *Annual*
432 *Reviews*, 567–588.

- 433 **Qian W-G, Li N, Lin L-D, Xu T, Zhang X, Wang L-H, Zou H-X, Wu M-J, Yan X-F. 2016.**
 434 Parallel analysis of proteins in brown seaweed *Sargassum fusiforme* responding to hyposalinity
 435 stress. *Aquaculture* **465**: 189–197.
- 436 **Rebours C, Marinho-Soriano E, Zertuche-González JA, Hayashi L, Vásquez JA, Kradolfer P,**
 437 **Soriano G, Ugarte R, Abreu MH, Bay-Larsen I, et al. 2014.** Seaweeds: an opportunity for
 438 wealth and sustainable livelihood for coastal communities. *Journal of Applied Phycology* **26**:
 439 1939–1951.
- 440 **Reisewitz SE, Estes JA, Simenstad CA. 2006.** Indirect food web interactions: sea otters and kelp
 441 forest fishes in the Aleutian archipelago. *Oecologia* **146**: 623–631.
- 442 **Rorrer GL, Cheney DP. 2004.** Bioprocess engineering of cell and tissue cultures for marine
 443 seaweeds. *Aquacultural Engineering* **32**: 11–41.
- 444 **Saint-Marcoux D, Billoud B, Langdale JA, Charrier B. 2015.** Laser capture microdissection in
 445 *Ectocarpus siliculosus*: the pathway to cell-specific transcriptomics in brown algae. *Frontiers in*
 446 *Plant Science* **6**: 54.
- 447 **Schiedlmeier B, Schmitt R, Muller W, Kirk M, Gruber H, Mages W, Kirk D. 1994.** Nuclear
 448 Transformation of *Volvox carteri*. *Proceedings of the National Academy of Sciences of the United*
 449 *States of America* **91**: 5080–5084.
- 450 **Schmid C, Schroer N, Muller D. 1994.** Female gamete membrane-glycoproteins potentially
 451 involved in gamete recognition in *Ectocarpus siliculosus* (phaeophyceae). *Plant Science* **102**: 61–
 452 67.
- 453 **Seghetta M, Tørring D, Bruhn A, Thomsen M. 2016.** Bioextraction potential of seaweed in
 454 Denmark - An instrument for circular nutrient management. *The Science of the Total Environment*
 455 **563–564**: 513–529.
- 456 **Shan T, Pang S, Li J, Li X, Su L. 2015.** Construction of a high-density genetic map and mapping
 457 of a sex-linked locus for the brown alga *Undaria pinnatifida* (Phaeophyceae) based on large scale

marker development by specific length amplified fragment (SLAF) sequencing. *BMC Genomics* 16.

Shan TF, Pang SJ, Gao, SQ. 2013. Novel means for variety breeding and sporeling production in the brown seaweed *Undaria pinnatifida* (Phaeophyceae): Crossing female gametophytes from parthenosporophytes with male gametophyte clones. *Phycological Research* 61: 154–61

Spoerner M, Wichard T, Bachhuber T, Stratmann J, Oertel W. 2012. *Ulva mutabilis* (Chlorophyta) depends on a combination of two bacterial species excreting regulatory factors. *Journal of Phycology* 48: 1433–1447.

Stacey GN, Day JG. 2014. Putting cells to sleep for future science. *Nature Biotechnology* 32: 320–322.

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* 29: 436–459.

Tapia JE, González B, Goulitquer S, Potin P, Correa JA. 2016. Microbiota influences morphology and reproduction of the brown alga *Ectocarpus* sp. *Frontiers in Microbiology* 7.

Uji T, Hirata R, Fukuda S, Mizuta H, Saga N. 2014. A codon-optimized bacterial antibiotic gene used as selection marker for stable nuclear transformation in the marine red alga *Pyropia yezoensis*. *Marine Biotechnology (New York, N.Y.)* 16: 251–255.

Vesty EF, Kessler RW, Wichard T, Coates JC. 2015. Regulation of gametogenesis and zoosporogenesis in *Ulva linza* (Chlorophyta): comparison with *Ulva mutabilis* and potential for laboratory culture. *Frontiers in Plant Science* 6: 15.

Wang L, Mao Y, Kong F, Cao M, Sun P. 2015. Genome-wide expression profiles of *Pyropia haitanensis* in response to osmotic stress by using deep sequencing technology. *BMC Genomics* 16: 1012.

- 482 **Wichard T, Oertel W. 2010.** Gametogenesis and gamete release of *Ulva mutabilis* and *Ulva*
 483 *lactuca* (Chlorophyta): Regulatory effects and chemical characterization of the ‘swarming
 484 inhibitor’. *Journal of Phycology* **46**: 248–259.
- 485 **Zhou W, Sui Z, Wang J, Chang L. 2013.** An orthogonal design for optimization of growth
 486 conditions for all life history stages of *Gracilariopsis lemaneiformis* (Rhodophyta). *Aquaculture*
 487 **392**: 98–105.

488 **Box and Figure legends**

489 **Box 1: Life cycle stages in seaweeds and possible manipulations**

490 Seaweed life cycles comprise several (usually 4) multicellular phases, including vegetative and
 491 fertile sporophytes and vegetative and fertile gametophytes (grey boxes). On the left, grey arrows
 492 indicate the different natural alternatives that seaweeds can use to reproduce (either sexually or
 493 asexually). On the right, brown, red and green horizontal lines represent the 3 groups of seaweeds.
 494 Transition between two successive phases, and bypassing or maintenance of one phase (either by
 495 delaying the maturation of the organism or by asexual looping) are ways to exert a tight control on
 496 the life cycle. Straight arrows indicate controls over a given phase of the life cycle (maintenance,
 497 induction or inhibition). Dashed arrows indicate asexual looping. A few specific examples are
 498 represented by the numbers that follow. [1] vertical arrow: maintaining vegetative growth of the
 499 brown seaweed *Saccharina latissima* gametophytes under red light or by sub-culturing (grinding)
 500 filaments; horizontal arrow: induction of gametophyte fertility under blue light (Luning & Dring,
 501 1975). [2] sporulation maintenance by removal of the basal meristem of *S. latissima* (Pang &
 502 Lüning, 2004). [3] maintenance of the vegetative stage of the sporophyte: in *Porphyra conchocelis*
 503 by temperature, photoperiod and irradiance (He & Yarish, 2006); of the reproductive stage of the

511 sporophyte: in *Palmaria* tetrasporophytes by short daylength (Pang & Lüning, 2006). [4] control of
 512 the shift to the reproductive phase of the vegetatively propagated *Gracilariopsis* gametophyte by
 513 temperature optimisation (Zhou *et al.*, 2013). [5] identification of sporulation-inhibiting factors
 514 (Glycoprotein SP-1 and low molecular weight factor SP-2) from *Ulva* gametophytes and
 515 sporophytes (Wichard & Oertel, 2010; Vesty *et al.*, 2015). [6] parthenogenesis in brown algae
 516 (Nakahara, 1984) and red algae (*Undaria* female spore seeding; Shan *et al.*, 2013). [7] production
 517 of gametophytes from gametes of the *Ectocarpus siliculosus* mutant *ouroboros* (Coelho *et al.*,
 518 2011). [8] production of *Ulva* gametophytes from the germination of its own gametes when
 519 separated from another mating type (Wichard & Oertel, 2010). [9] germination of
 520 parthenosporophytes (instead of gametophytes in this strain) from *Ectocarpus* zoospores by an
 521 inhibiting factor produced by the parthenosporophyte (Arun *et al.*, 2013).

522 **Figure 1: Position of macroalgae in the scientific and societal landscapes.**

523 Macroalgae grow rapidly in a wide range of temperatures, using only sunlight, atmospheric carbon
 524 and naturally nutritious coastal waters. They are therefore valuable feedstock for the production of
 525 food, feed, biofuel, hydrocolloids, fertilisers, cosmetics, probiotics, biodegradable packaging
 526 through aquaculture and IMTA (see text for details). They provide curative ecological roles
 527 necessitated by human activities (waste-water treatments and seabed recolonisation). Ecology also
 528 benefits from a knowledge of macroalgal reproductive mechanisms *via* a better understanding of
 529 dispersion and persistence of both natural and exotic populations. This also contributes to the
 530 development of conservation protocols for threatened or susceptible populations. Because their life
 531 histories differ from land plants, macroalgae also inspire molecular evo-devo studies involving the
 532 whole green lineage.

533 **Figure 2: Importance of the microscopic early developmental stages in the life cycle of**
 534 **exploited seaweeds: Example of the kelp *Saccharina latissima*.**

535 Production of kelp (large brown macroalga) sporophyte juveniles takes place in hatcheries under
 536 controlled growth conditions. Cultures of microscopic male and female gametophytes are produced
 537 from spores of macroscopic, mature plants collected from the sea. Gametophyte cultures are grown
 538 to fertility under controlled temperature and light conditions (see Box 1 for details). Microscopic,
 539 fertile, recently fertilised gametophytes, or (in turn) juvenile sporophytes are spread onto
 540 cultivation support materials (ropes or 2D substrates), which are subsequently deployed into the
 541 sea. Photos kindly provided by Teis Boderskov (Aarhus University, Denmark) and Eric
 542 Tamigneaux (Merinov, Canada).

543 **Figure 3: Scope of beneficial outflow from basic research to seaweed aquaculture.**

544 Sexual reproduction (top right) gives rise to polarised embryos (left), which progressively grow
 545 and differentiate, giving tissues and organs with specific shape and cellular functions (e.g. blade,
 546 stipe, holdfast, reproductive organs). The study of the different steps of the life cycle (here
 547 simplified, with adult representing either the sporophyte or the gametophyte) at the basic level (in
 548 blue) can lead to the control and improvement of key processes in seaweed aquaculture (in green).
 549 In hatcheries, density of juveniles on the cultivation support material depends on both the
 550 fertilisation rate and the adhesive potential of the embryos. Fertilisation rate itself depends on the
 551 physical interactions between the two gametes (taxis, specific recognition and membrane fusion).
 552 Better knowledge of the cell cycle and characterisation of the pluripotent cells (zygotes, meristems)
 553 will both contribute to develop cryopreservation protocols. Metabolic patterning of seaweed organs
 554 and tissues, mediated by molecular, biochemical or cellular markers, will assist farmers in

555 monitoring seaweed growth and fitness both in hatcheries and in the field. All these processes are
556 under the control of abiotic and biotic factors (see text and Box 1 for references).

For Peer Review

Box 1

Box 1: Life cycle stages in seaweeds and possible manipulations

Seaweed life cycles comprise several (usually 4) multicellular phases, including vegetative and fertile sporophytes and vegetative and fertile gametophytes (grey boxes). On the left, grey arrows indicate the different natural alternatives that seaweeds can use to reproduce (either sexually or asexually). On the right, brown, red and green horizontal lines represent the 3 groups of seaweeds. Transition between two successive phases, and bypassing or maintenance of one phase (either by delaying the maturation of the organism or by asexual looping) are ways to exert a tight control on the life cycle. Straight arrows indicate controls over a given phase of the life cycle (maintenance, induction or inhibition). Dashed arrows indicate asexual looping. A few specific examples are represented by the numbers that follow. [1] vertical arrow: maintaining vegetative growth of the brown seaweed *Saccharina latissima* gametophytes under red light or by sub-culturing (grinding) filaments; horizontal arrow: induction of gametophyte fertility under blue light (Luning & Dring, 1975). [2] sporulation maintenance by removal of the basal meristem of *S. latissima* (Pang & Lüning, 2004). [3] maintenance of the vegetative stage of the sporophyte: in *Porphyra conchocelis* by temperature, photoperiod and irradiance (He & Yarish, 2006); of the reproductive stage of the sporophyte: in *Palmaria tetrasporophytes* by short daylength (Pang & Lüning, 2006). [4] control of the shift to the reproductive phase of the vegetatively propagated *Gracilariopsis* gametophyte by temperature optimisation (Zhou et al., 2013). [5] identification of sporulation-inhibiting factors (Glycoprotein SP-1 and low molecular weight factor SP-2) from *Ulva* gametophytes and sporophytes (Wichard & Oertel, 2010; Vesty et al., 2015). [6] parthenogenesis in brown algae (Nakahara, 1984) and red algae (*Undaria* female spore seeding; Shan et

al., 2013). [7] production of gametophytes from gametes of the *Ectocarpus siliculosus* mutant *ouroboros* (Coelho et al., 2011). [8] production of *Ulva* gametophytes from the germination of its own gametes when separated from another mating type (Wichard & Oertel, 2010). [9] germination of parthenosporophytes (instead of gametophytes in this strain) from *Ectocarpus* zoospores by an inhibiting factor produced by the parthenosporophyte (Arun et al., 2013).

For Peer Review

Figure 1: Position of macroalgae in the scientific and societal landscapes.

Macroalgae grow rapidly in a wide range of temperatures, using only sunlight, atmospheric carbon and naturally nutritious coastal waters. They are therefore valuable feedstock for the production of food, feed, biofuel, hydrocolloids, fertilisers, cosmetics, probiotics, biodegradable packaging through aquaculture and IMTA (see text for details). They provide curative ecological roles necessitated by human activities (waste-water treatments and seabed recolonisation). Ecology also benefits from a knowledge of macroalgal reproductive mechanisms via a better understanding of dispersion and persistence of both natural and exotic populations. This also contributes to the development of conservation protocols for threatened or susceptible populations. Because their life histories differ from land plants, macroalgae also inspire molecular evo-devo studies involving the whole green lineage.

Figure 2

Figure 2: Importance of the microscopic early developmental stages in the life cycle of exploited seaweeds: Example of the kelp *Saccharina latissima*.

Production of kelp (large brown macroalga) sporophyte juveniles takes place in hatcheries under controlled growth conditions. Cultures of microscopic male and female gametophytes are produced from spores of macroscopic, mature plants collected from the sea. Gametophyte cultures are grown to fertility under controlled temperature and light conditions (see Box 1 for details). Microscopic, fertile, recently fertilised gametophytes, or (in turn) juvenile sporophytes are spread onto cultivation support materials (ropes or 2D substrates), which are subsequently deployed into the sea. Photos kindly provided by Teis Boderskov (Aarhus University, Denmark) and Eric Tamigneaux (Merinov, Canada).

Figure 3

Figure 3: Scope of beneficial outflow from basic research to seaweed aquaculture.

Sexual reproduction (top right) gives rise to polarised embryos (left), which progressively grow and differentiate, giving tissues and organs with specific shape and cellular functions (e.g. blade, stipe, holdfast, reproductive organs). The study of the different steps of the life cycle (here simplified, with adult representing either the sporophyte or the gametophyte) at the basic level (in blue) can lead to the control and improvement of key processes in seaweed aquaculture (in green).

In hatcheries, density of juveniles on the cultivation support material depends on both the fertilisation rate and the adhesive potential of the embryos. Fertilisation rate itself depends on the physical interactions between the two gametes (taxis, specific recognition and membrane fusion). Better knowledge of the cell cycle and characterisation of the pluripotent cells (zygotes, meristems) will both contribute to develop cryopreservation protocols. Metabolic patterning of seaweed organs and tissues, mediated by molecular, biochemical or cellular markers, will assist farmers in monitoring seaweed growth and fitness both in hatcheries and in the field. All these processes are under the control of abiotic and biotic factors (see text and Box 1 for references).