Viewpoint

Furthering knowledge of seaweed growth and development to facilitate sustainable aquaculture

Summary

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

Ecological and societal position of macroalgae

Macroalgae are macroscopic aquatic organisms belonging to three distinct and distantly related eukaryotic lineages (commonly named green, red, and brown algae). Their unicellular ancestors diverged > 1.6 billion yr ago (Parfrey *et al.*, 2011), implying independent acquisitions of multicellularity, and leading to a bewildering diversity of life cycles, fertilization processes and morphogenetic strategies. At the ecological level, macroalgae fulfil important roles as key habitat-structuring agents and primary producers in coastal ecosystems. The goods and services seaweeds (marine macroalgae) support are varied (Fig. 1), and include elevated secondary production, nutrient cycling, energy capture and flow, and coastal defence (Steneck *et al.*, 2002). They can also significantly contribute to carbon sequestration at a level exceeding that of angiosperm marine coastal vegetation (up to 1.5 times as much as seagrass meadows, salt marshes and mangroves and up to 2% of the annual anthropogenic emission; Krause-Jensen & Duarte, 2016 and references therein). In addition, macroalgae support complex food webs in coastal zones and provide habitats and food for associated organisms, from apex predators to invertebrates (Reisewitz *et al.*, 2006). Macroalgal communities also enable transfer of biomass between ecosystems (Krumhansl & Scheibling, 2012), removal of dissolved nutrients from coastal waters and coastal protection from erosion (Arkema *et al.*, 2013). de Groot *et al.* (2012) estimated the value of coastal ecosystem services provided by macroalgae to be over 28 000 intl.\$ $ha^{-1} yr^{-1}$.

Seaweeds are also an alternative/additional source of food, feed, fuel, biomolecules and livelihood for humans. Over 80% of macroalgal production and harvesting is at present destined for human consumption directly (Abreu *et al.*, 2014) or as hydrocolloids (thickeners, gelling agents, etc.) (Rebours *et al.*, 2014). Macroalgae are also used as fertilizers and animal feed (Makkar *et al.*, 2016). In addition, the industrial sector uses seaweed biomass for nutraceuticals, cosmetics, and biotechnological and pharmaceutical applications, thus propelling the growth of seaweed biotechnology (Mazarrasa *et al.*, 2013). Currently, *c.* 28 million tonnes of seaweeds per year (wet weight) are produced and, as a proxy for the growth of the biotechnology market of seaweed-derived products, seaweed-related patent applications increased at a rate of 11% yr^{-1} since 1990 (Mazarrasa *et al.*, 2014).

While in Asia 99% of seaweed production is sourced from cultivation (accounting for 93% of the global production in 2013) (FAO, 2016), the dominant practice of non-Asian countries is still harvesting natural stocks. However, the availability of wild stocks under the current scenario of global change needs to be assessed, while management plans for seaweed exploitation must be adapted to the natural population dynamics of commercially important species. Increasing demands for high-quality seaweed biomass may therefore affect the long-term sustainability of seaweed exploitation. Seaweed cultivation is the alternative to cope with industry's demand for biomass, concomitantly protecting natural resources (Fig. 1). Unlike terrestrial crops, they do not compete for arable land, fertilizer and freshwater resources. Furthermore, the development of integrated multi-trophic aquaculture (IMTA: co-cultivation of seaweeds with fin/shell fishes) enables recapture of excessive inorganic nutrients released in coastal areas by fish farms, thereby improving their sustainability (Holdt & Edwards, 2014). Beyond aquaculture proper, seaweed cultivation could also function as a general instrument for circular resource management (Seghetta *et al.*, 2016), treatment of waste water produced by land-based farming and municipal treatment plants (Neveux *et al.*, 2016), heavy metal biosorption (He & Chen, 2014) and recolonization of artificial reefs (Fig. 1). As a response to this assessment, the European seaweed aquaculture sector has progressively

© 2017 The Authors
New Phytologist © 2017 New Phytologist Trust

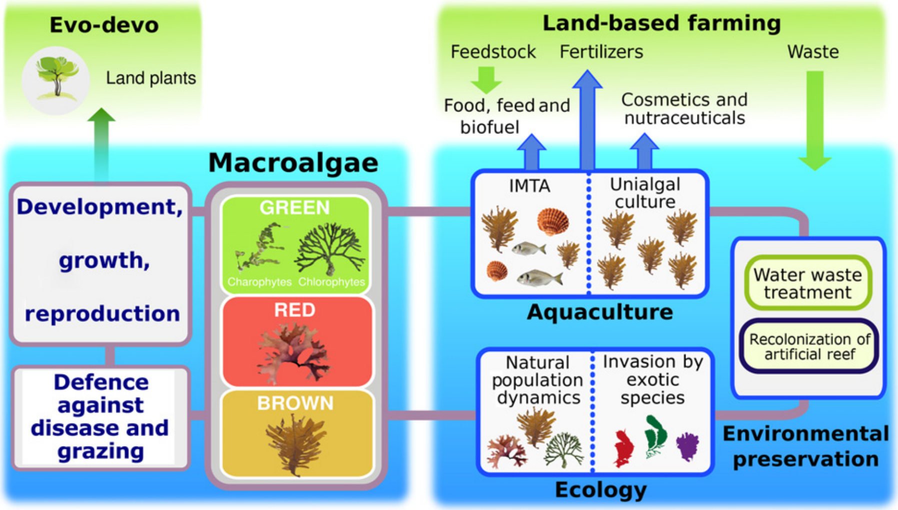


Fig. 1 Position of macroalgae in the scientific and societal landscapes. Macroalgae grow rapidly in a wide range of temperatures, using only sunlight, atmospheric carbon and naturally nutritious coastal waters. They are therefore valuable feedstock for the production of food, feed, biofuel, hydrocolloids, fertilizers, cosmetics, probiotics, and biodegradable packaging through aquaculture and integrated multi-trophic aquaculture (IMTA; see main text for details). They can play curative ecological roles in processes necessitated by human activities (e.g. waste-water treatments and seabed recolonization). 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 those of land plants, macroalgae also inspire molecular evo-devo studies involving the whole green lineage.

expanded, accounting for 12% of total European biomass production in 2013 (FAO, 2016). Further expansion calls for advances in seaweed production technology, which rely on a better knowledge of both the environmental and the intrinsic factors controlling the development of macroalgae.

How could developmental biology help resolve bottlenecks in seaweed aquaculture?

Mastering genetics through the control of the life cycle

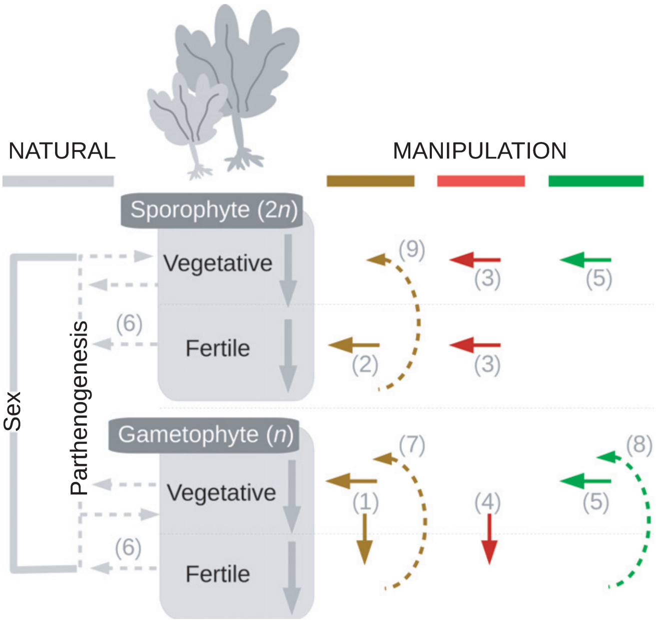
Most seaweeds have complex, biphasic life cycles, involving free-living haploid gametophyte and diploid sporophyte generations (Coelho *et al.*, 2007) (Box 1). Either phase of the life cycle can be exploited, depending on the seaweed species. The harvestable biomass of kelps consists of sporophytes up to several metres long (45 m in *Macrocystis*), while in nori (*Pyropia* and *Porphyra*), the life stage of interest is the haploid gametophyte. Other exploited seaweeds, for example *Gracilaria* and *Chondrus* (red algae), have isomorphic life cycles, with both sporophyte and gametophyte developing macroscopic exploitable thalli. Currently, clonal propagation (e.g. in the red alga *Kappaphycus*) and recourse to a limited number of parent genotypes (e.g. in kelp) account for the production of most commonly cultivated seaweeds. The resulting impoverishment of genetic diversity increases seaweed susceptibility to diseases and decreases their fitness within their cultivation environment (Loureiro *et al.*, 2015). For example, the continuous vegetative propagation of the carrageenophyte *Kappaphycus* in intensively cultivated areas has increased its vulnerability to diseases (e.g. bacterial mediated 'ice-ice' disease), thereby dramatically impacting the production in various countries (Largo *et al.*, 1995). This problem requires counteraction by the selection of new breeding strains, potentially through artificial hybrids (Gupta *et al.*, 2015), but more optimally through crossings, as somatic hybridization usually results in severe and unstable phenotypic alteration (Charrier *et al.*, 2015). However, while in some seaweeds the promotion of sexual reproduction still requires development (e.g. *Gracilariopsis*; Zhou *et al.*, 2013), the loss of the genetic patrimony resulting from cross-fertilization might be detrimental to maintaining specific and valuable genotypes resulting from decades of selection. Therefore, manipulating the different steps of the seaweed life cycles would allow a balance between the maintenance of given genotypes of interest and controlled breeding. Progress in basic research opens up possible paths to bypass steps of the life cycle, thereby allowing us to achieve this goal (Box 1).

Manipulating the sexual life cycle

Most cultivated seaweeds reproduce sexually (e.g. kelps and the red algae *Porphyra* spp.), placing both time and genetic constraints on seaweed farmers. Physiological studies have long been establishing protocols for maintaining seaweeds in a vegetative stage or shifting them to the next phase using specific temperature and light conditions, or even by tissue ablation. This allows year-round production of juveniles and increases the cultivated net biomass (Pang & Lüning, 2004). Several illustrations of these practices applied to exploited seaweeds are displayed in Box 1. Recent fundamental studies propose potential alternatives. Treatments with algal phytohormones could be used to control the vegetative-to-reproductive transition and speed up reproduction, as illustrated in the red alga *Grateloupia imbricata* upon addition of methyl jasmonate (García-Jiménez *et al.*, 2016).

© 2017 The Authors
New Phytologist © 2017 New Phytologist Trust

Box 1 Life-cycle stages in seaweeds and possible manipulations



Seaweed life cycles comprise several (usually four) 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 three 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 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 subculturing (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, for example in *Porphyra* conchocelis by temperature, photoperiod and irradiance (He & Yarish, 2006); maintenance 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 optimization (Zhou *et al.*, 2013). (5) Identification of sporulation-inhibiting factors (Glycoprotein SI-1 and low-molecular-weight factor SI-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).

Promoting parthenogenesis

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

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

© 2017 The Authors
New Phytologist © 2017 New Phytologist Trust

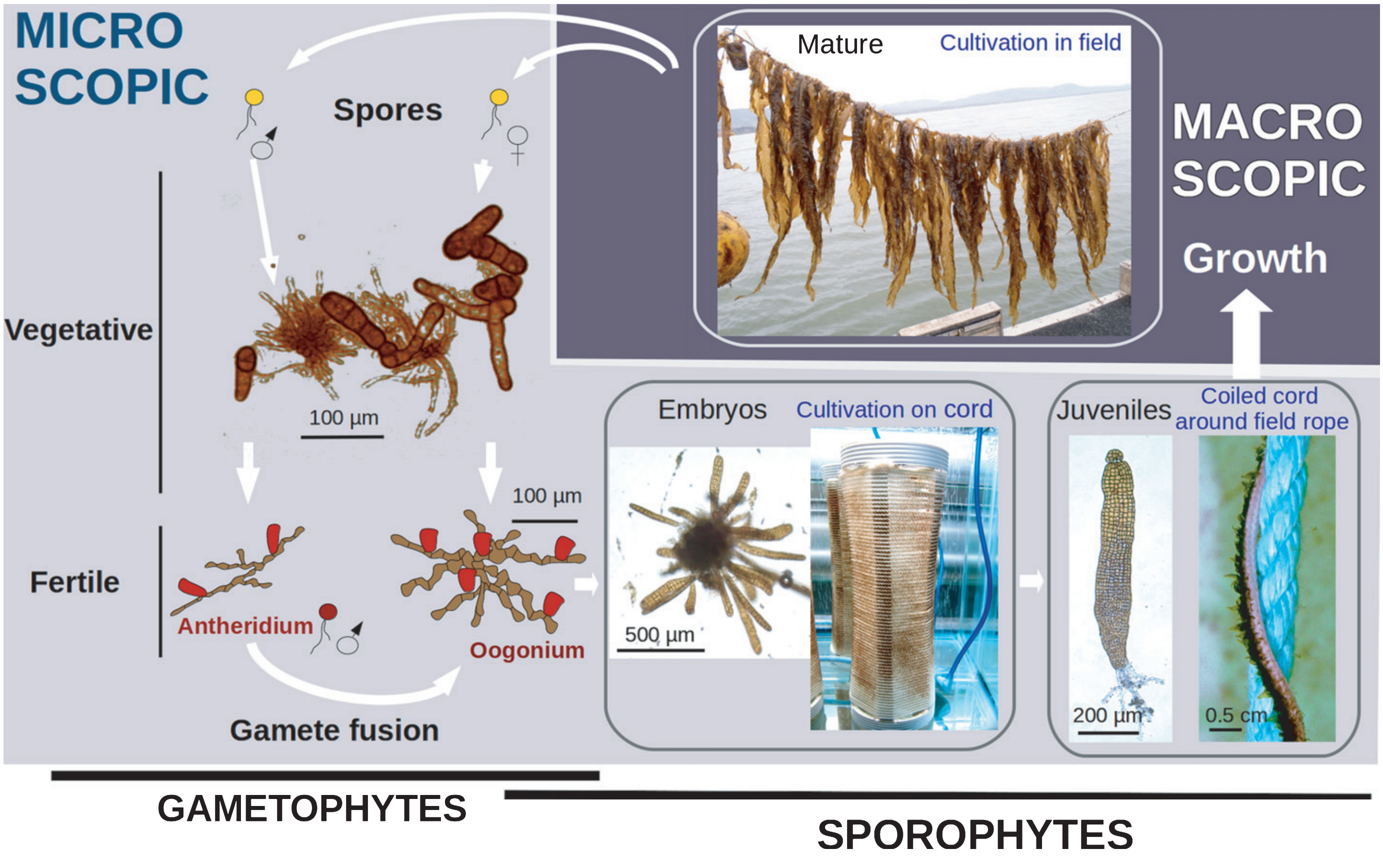


Fig. 2 Importance of the microscopic early developmental stages in the life cycle of exploited seaweeds: example of the kelp *Saccharina latissima*. Production of kelp (large brown macroalga) sporophyte juveniles takes place in hatcheries under controlled growth conditions. Cultures of microscopic male 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 fertilized gametophytes, or (in turn) juvenile sporophytes are spread onto cultivation support materials (ropes or 2D substrates), which are subsequently deployed into the sea. Photographs were kindly provided by Teis Boderskov (Aarhus University, Denmark) and Eric Tamigneaux (Merinov, Canada).

their genotypes, emphasizing the importance of a control over morphogenesis.

In parallel to these improvements for seaweeds cultivated offshore (Fernand *et al.*, 2017), standardized protocols should also be developed specifically for not yet cultivated, high-value seaweeds amenable to on-shore cultivation. These include 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 probably 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* and *Undaria*), together with the gametophyte in red seaweeds (*Gracilaria*, *Kappaphycus* and *Euchema*) and in some isomorphic green (*Ulva*) seaweeds. Optimizing fertilization success could help control the rate of production of seaweed embryos in hatcheries, which, when too high, impedes the quality of sporophyte juveniles (Figs 2, 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 concerning, for example, the periodicity of gamete release, attraction of gametes to the opposite sex or mating type, and cell–cell recognition (Fig. 3), stands in stark contrast to the wealth of eco-physiological and biochemical studies that predate the molecular era. As an illustration, in certain *Ulva* species, gametogenesis and subsequent gamete release can be artificially induced by

© 2017 The Authors
New Phytologist © 2017 New Phytologist Trust

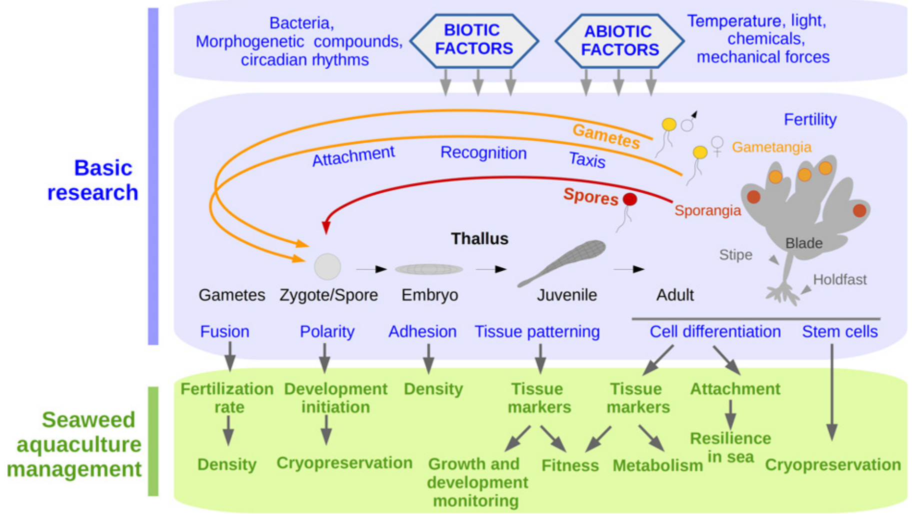


Fig. 3 Scope of beneficial outflow from basic research to seaweed aquaculture. Sexual reproduction (top right) gives rise to polarized embryos (left), which progressively grow and differentiate, producing tissues and organs with specific shape and cellular functions (e.g. blade, stipe, holdfast, and 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, the density of juveniles on the cultivation support material depends on both the fertilization rate and the adhesive potential of the embryos. The fertilization rate itself depends on the physical interactions between the two gametes (taxis, specific recognition and membrane fusion). Better knowledge of the cell cycle and characterization of the pluripotent cells (zygotes and meristems) will both contribute to the development of 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 main text and Box 1 for references).

removal of sporulation and swarming inhibitors (Vesty *et al.*, 2015 and references therein) but, so far, neither these inhibitors nor the signalling pathways inducing gametogenesis have been characterized. Similar cases could be made for pheromone signalling in brown seaweeds (Boland, 1995) and glycoprotein recognition between opposite-sex gametes (Schmid *et al.*, 1994).

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

Controlled growth and organogenesis factors: towards biomass production monitoring

Production of large seaweed biomass with specific features of industrial interest (polysaccharides, proteins and pigments) depends on both seaweed net growth and seaweed capacity to grow organs and tissues with specific structures and compositions. Indeed, the quantity and quality of key compounds vary within the algal body (β-glucan in *Durvillaea*: Bobadilla *et al.*, 2013; phytohormones in *Sargassum*: Li *et al.*, 2016), and cells with thicker walls, storage organelles and vacuoles might be more resistant to dehydration, chemical exposure, eutrophication, and pathogen attacks, and hence be of high interest. Unfortunately, macroalgal cell fate specification is one of the least understood areas of macroalgal biology. Undoubtedly, both endogenous (e.g. bacteria: Spoerner *et al.*, 2012; circadian rhythm: Cunningham & Guiry, 1989) and abiotic environmental factors (light, temperature and sea currents) are required (Fig. 3), but the intrinsic signalling pathways are largely unknown. To understand how to manipulate hatchery culture conditions to give juveniles the best start in life in tune with aquaculture demands, additional studies assessing the molecular impact of the surrounding physical and chemical environment (light, nutrients, salinity and water movement) are required. In some seaweeds, complex interactions with bacteria are a prerequisite for proper cell growth and differentiation into specific tissues (Goecke *et al.*, 2010). This has been well illustrated in green seaweeds (*Ulva* and *Monostroma*: Matsuo *et al.*, 2005; Spoerner *et al.*, 2012), as well as in brown algal species where bacteria might control their life cycle (Tapia *et al.*, 2016) and their morphology in waters with different salinities (Dittami *et al.*, 2014). It is tempting to hypothesize that controlling macroalgal development with bacteria will regulate the chemical composition of the macroalga and its value as a cash crop. This is mainly relevant for land-based aquaculture starting with a defined seed-stock (axenic germlings) and a synthetic microbiome, which could influence the production of primary and secondary metabolites. However, further work determining macroalgal–bacterial interactions throughout algal life cycles is necessary to discriminate between mutualistic, beneficial and pathogenic interactions.

Current technological requirements

Reliable, cost-effective and long-term maintenance of genetic resources is a major requirement to ensure the sustainability of the quality of the exploited traits (e.g. biomass yield, quality of extracted polysaccharides, and texture and taste of species for human consumption; Chapman *et al.*, 2015). Both subculturing of macroalgal explants and cryopreservation of macroalgal omnipotent cells are current techniques to vegetatively propagate macroalgae over time. However, subcultivation is time-consuming and reiteration of the protocol over years is a source of bacterial or fungal contamination. Long-term preservation (through refrigeration or liquid-nitrogen freezing) of commercially important seaweed explants has therefore received increasing attention and several protocols are now available. Techniques depend on the species (e.g. gametophytic filaments of *Macrocystis*: Barrento *et al.*, 2016; pieces of *Ulva* thalli: Lee & Nam, 2016; and apical meristems of *Gracilaria*: Lalrinsanga *et al.*, 2009) and a better knowledge of both the mitotic activities within the thallus and the underlying molecular mechanisms governing cell proliferation vs cell differentiation would accelerate the assessment of the regenerative potential of these seaweeds and the necessary development of adequate protocols (Stacey & Day, 2014) (Fig. 3). Basic research has revealed specificities in brown seaweeds, specifically in the *Fucus* embryo, where cell division is subject to distinct control mechanisms compared with other eukaryotes (Corellou *et al.*, 2001). As bacteria play a crucial role in many algal developmental processes (Goecke *et al.*, 2010), macroalgal preservation should also consider cryopreservation of algae with their natural microbiome rather than axenic explants. Therefore, development of seaweed biobanking procedures may be pivotal to meet future aquaculture demands.

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

In addition to the requirement for cell biology and genetic adjustments, '-omics' technology must be adapted to the level of analysis required to tackle developmental mechanisms taking place at the microscopic and early developmental stages (Figs 2, 3). Several transcriptomic (Wang *et al.*, 2015), proteomic (Qian *et al.*, 2016) and metabolomic (Kumar *et al.*, 2016 and references therein) studies have been reported in both model and exploited macroalgae. In addition, exo-metabolomic profiling in standardized *Ulva* cultures with a designed microbiome have shown growth phase-dependent biomarkers that might be relevant for aquaculture (Alsufyani *et al.*, 2017). Such analyses are assisted by an increasing number of sequenced macroalgal genomes. Currently, 18 public algal nuclear genomes have been sequenced, including four seaweeds. However, '-omics' studies at early developmental stages are hampered by a scarcity of tissue. While proteomics and metabolomics still require a significant biomass, transcriptomics can bypass this handicap through RNA amplification. Cell-specific expression patterns were thereby obtained using laser microdissection before RNA amplification in the model brown seaweed *Ectocarpus* (Saint-Marcoux *et al.*, 2015), and this technology is easily transferable to larger seaweeds.

Finally, transgenesis will be a highly valuable tool to discover how molecular processes are regulated in seaweeds, and to interfere with these processes by knocking down/up-regulating endogenous genes. So far, only four multicellular algae, namely *Ulva*, *Pyropia* (*Porphyra*), *Volvox* and *Gonium*, are genetically transformable (Schiedlmeier *et al.*, 1994; Lerche & Hallmann, 2009; Mikami, 2014; Oertel *et al.*, 2015), and *Ulva* is the only stably transformable seaweed (Oertel *et al.*, 2015). These first successes must now be replicated in additional, diverse species, via the investment of time and expertise.

Conclusions

A range of protocols are available to cultivate seaweeds, thanks to previous physiological studies carried out in an applied phycological context. Building on this key achievement, practices must be refined and developed with a more focused and on-demand approach. Indeed, demand from end-users is rising for new, high-commercial potential (mainly for food) seaweeds. However, because of their low production level, these seaweeds have not received high investment so far and, as a result, no standardized cultivation and preservation protocols exist. This second big step is much more problematic, because of the greater number of species involved and their reluctance to respond to the simplest, classical protocols. The time has come, now that the first empirical studies have been carried out, to engage the community in an in-depth study of the biological processes driving the whole macroalgal life cycle, from fertilization to the production of organisms. This must respond to end-users' expectations of robustness against environmental constraints (e.g. climate, infection and mechanical strain), biochemical composition and also natural and nature-friendly production increasingly favoured by the consumers. This is even more necessary as, despite the benefit that the development of cutting-edge technologies in animals and plants can bring to the sector, many of these technologies need to be adapted to macroalgae because of their specific ecological niche (highly saline) and their biology (in part because of their phylogenetic distance from better known organisms). Therefore, efforts must be intensified to fill the gaps in our fundamental knowledge of macroalgal developmental mechanisms. We also believe that the scientific community of land plant researchers will benefit from a deeper understanding of seaweed developmental biology.

© 2017 The Authors
New Phytologist © 2017 New Phytologist Trust

Acknowledgements

This work was carried out in the framework of 'Phycomorph' (http://www.phycomorph.org/), a network funded by the COST Association (http://www.cost.eu/COST_Actions/fa/FA1406).

Author contributions

All authors contributed to the writing of the manuscript.

Bénédicte Charrier[1]*, Maria Helena Abreu[2], Rita Araujo[3], Annette Bruhn[4], Juliet C. Coates[5], Olivier De Clerck[6], Christos Katsaros[7], Rafael R. Robaina[8] and Thomas Wichard[9]

[1]Morphogenesis of Macroalgae, UMR8227, CNRS-UPMC, Station Biologique, Roscoff 29680, France;
[2]Travessa Alexandre da Conceição, ALGAplus Lda, Íllhavo 3830-196, Portugal;
[3]Water and Marine Resources Unit, Joint Research Centre – Directorate for Sustainable Resources, European Commission, via E. Fermi, Ispra (VA) 2749-21027, Italy;
[4]Department of BioScience, Aarhus University, Vejlsøvej 25, Silkeborg 8600, Denmark;
[5]School of Biosciences, University of Birmingham, Birmingham B15 2TT, UK;
[6]Department of Biology, Ghent University, Krijgslaan 281 S8, Ghent 9000, Belgium;
[7]Department of Biology, Morphogenesis of Macroalgae, National and Kapodistrian University of Athens, Athens 157 84, Greece;
[8]Facultad de Ciencias del Mar, Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria 35017, Spain;
[9]Institute for Inorganic and Analytical Chemistry, Friedrich Schiller University Jena, Lessingstr. 8, Jena 07743, Germany
(*Author for correspondence: tel +33 2 98 29 56 53; email benedicte.charrier@sb-roscoff.fr)

References

Abreu M, Pereira R, Sassi J-F. 2014. Marine algae and the global food industry. In: Pereira L, Neto J, eds. *Marine algae, biodiversity, taxonomy, environmental assessment, and biotechnology.* Boca Raton, FL, USA: CRC Press, 300–319.

Alsufyani T, Weiss A, Wichard T. 2017. Time course exo-metabolomic profiling in the green marine macroalga *Ulva* (Chlorophyta) for identification of growth phase-dependent biomarkers. *Marine Drugs* **15**: 14.

Arkema KK, Guannel G, Verutes G, Wood SA, Guerry A, Ruckelshaus M, Kareiva P, Lacayo M, Silver JM. 2013. Coastal habitats shield people and property from sea-level rise and storms. *Nature Climate Change* **3**: 913–918.

Arun A, Peters NT, Scornet D, Peters AF, Cock JM, Coelho SM. 2013. Non-cell autonomous regulation of life cycle transitions in the model brown alga *Ectocarpus. New Phytologist* **197**: 503–510.

Barrento S, Camus C, Sousa-Pinto I, Buschmann AH. 2016. Germplasm banking of the giant kelp: our biological insurance in a changing environment. *Algal Research-Biomass Biofuels and Bioproducts* **13**: 134–140.

Bobadilla F, Rodriguez-Tirado C, Imarai M, Jose Galotto M, Andersson R. 2013. Soluble β-1,3/1,6-glucan in seaweed from the southern hemisphere and its immunomodulatory effect. *Carbohydrate Polymers* **92**: 241–248.

Bogaert KA, Beeckman T, De Clerck O. 2017. Two-step cell polarization in algal zygotes. *Nature Plants* **3**: 16221.

Boland W. 1995. The chemistry of gamete attraction: chemical structures, biosynthesis, and (a)biotic degradation of algal pheromones. *Proceedings of the National Academy of Sciences, USA* **92**: 37–43.

Bothwell JHF, Kisielewska J, Genner MJ, McAinsh MR, Brownlee C. 2008. Ca^{2+} signals coordinate zygotic polarization and cell cycle progression in the brown alga *Fucus serratus. Development (Cambridge, England)* **135**: 2173–2181.

Brownlee C, Bouget FY, Corellou F. 2001. Choosing sides: establishment of polarity in zygotes of fucoid algae. *Seminars in Cell & Developmental Biology* **12**: 345–351.

Chapman AS, Stevant P, Larssen WE. 2015. Food or fad? Challenges and opportunities for including seaweeds in a Nordic diet. *Botanica Marina* **58**: 423–433.

Charrier B, Rolland E, Gupta V, Reddy CRK. 2015. Production of genetically and developmentally modified seaweeds: exploiting the potential of artificial selection techniques. *Frontiers in Plant Science* **6**: 127.

Coelho SM, Godfroy O, Arun A, Le Corguillé G, Peters AF, Cock JM. 2011. *OUROBOROS* is a master regulator of the gametophyte to sporophyte life cycle transition in the brown alga *Ectocarpus. Proceedings of the National Academy of Sciences, USA* **108**: 11518–11523.

Coelho SM, Peters AF, Charrier B, Roze D, Destombe C, Valero M, Cock JM. 2007. Complex life cycles of multicellular eukaryotes: new approaches based on the use of model organisms. *Gene* **406**: 152–170.

Corellou F, Brownlee C, Detivaud L, Kloareg B, Bouget FY. 2001. Cell cycle in the *Fucus* zygote parallels a somatic cell cycle but displays a unique translational regulation of cyclin-dependent kinases. *The Plant Cell* **13**: 585–598.

Cottier-Cook E, Nagabhatla N, Badis Y, Campbell ML, Chopin T, Dai W, Fang J, He P, Hewitt CL, Kim GH *et al.* 2016. *Safeguarding the future of the global seaweed aquaculture industry.* United Nations University (INWEH) and Scottish Association for Marine Science Policy Brief. ISBN 978-92-808-6080-1.

Cunningham EM, Guiry MD. 1989. A circadian rhythm in the long-day photoperiodic induction of erect axis development in the marine red alga *Nemalion helminthoides. Journal of Phycology* **25**: 705–712.

Deniaud-Bouët E, Kervarec N, Michel G, Tonon T, Kloareg B, Hervé C. 2014. Chemical and enzymatic fractionation of cell walls from Fucales: insights into the structure of the extracellular matrix of brown algae. *Annals of Botany* **114**: 1203–1216.

Dittami SM, Barbeyron T, Boyen C, Cambefort J, Collet G, Delage L, Gobet A, Groisillier A, Leblanc C, Michel G *et al.* 2014. Genome and metabolic network of 'Candidatus *Phaeomarinobacter ectocarpi*' Ec32, a new candidate genus of Alphaproteobacteria frequently associated with brown algae. *Frontiers in Genetics* **5**: 241.

FAO. 2016. *Fisheries & aquaculture – fisheries and aquaculture fact sheets.* [WWW document] URL http://www.fao.org/fishery/factsheets/en [accessed 2 August 2017].

Fernand F, Israel A, Skjermo J, Wichard T, Timmermans KR, Golberg A. 2017. Offshore macroalgae biomass for bioenergy production: environmental aspects, technological achievements and challenges. *Renewable and Sustainable Energy Reviews* **75**: 35–45.

García-Jiménez P, Brito-Romano O, Robaina RR. 2016. Occurrence of jasmonates during cystocarp development in the red alga *Grateloupia imbricata. Journal of Phycology* **52**: 1085–1093.

Goecke F, Labes A, Wiese J, Imhoff JF. 2010. Chemical interactions between marine macroalgae and bacteria. *Marine Ecology Progress Series* **409**: 267–299.

de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L *et al.* 2012. Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services* **1**: 50–61.

Gupta V, Kumari P, Reddy CRK. 2015. Development and characterization of somatic hybrids of *Ulva reticulata* Forsskal (×) *Monostroma oxyspermum* (Kutz.) Doty. *Frontiers in Plant Science* **6**: 3.

Gwo HH, Chen CS. 1999. Evidence of fusion and artificially initialized parthenogenesis in isogametes of *Endarachne binghamiae* (Scytosiphonaceae, Phaeophyta) from Taiwan. *Journal of Applied Phycology* **11**: 567–577.

Han JW, Klochkova TA, Shim J, Nagasato C, Motomura T, Kim GH. 2014. Identification of three proteins involved in fertilization and parthenogenetic development of a brown alga, *Scytosiphon lomentaria. Planta* **240**: 1253–1267.

He J, Chen JP. 2014. A comprehensive review on biosorption of heavy metals by algal biomass: materials, performances, chemistry, and modeling simulation tools. *Bioresource Technology* **160**: 67–78.

© 2017 The Authors
New Phytologist © 2017 New Phytologist Trust

He P, Yarish C. 2006. The developmental regulation of mass cultures of free-living conchocelis for commercial net seeding of *Porphyra leucosticta* from Northeast America. *Aquaculture* **257**: 373–381.

Holdt SL, Edwards MD. 2014. Cost-effective IMTA: a comparison of the production efficiencies of mussels and seaweed. *Journal of Applied Phycology* **26**: 933–945.

Joubert Y, Fleurence J. 2008. Simultaneous extraction of proteins and DNA by an enzymatic treatment of the cell wall of *Palmaria palmata* (Rhodophyta). *Journal of Applied Phycology* **20**: 55–61.

Kamiya M, West JA. 2008. Origin of apomictic red algae: outcrossing studies of different strains in *Caloglossa monotricha* (Ceramiales, Rhodophyta). *Journal of Phycology* **44**: 977–984.

Krause-Jensen D, Duarte CM. 2016. Substantial role of macroalgae in marine carbon sequestration. *Nature Geoscience* **9**: 737–742.

Krumhansl KA, Scheibling RE. 2012. Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile ssp fragile. Marine Ecology Progress Series* **456**: 73–85.

Kumar M, Kuzhiumparambil U, Pernice M, Jiang Z, Ralph PJ. 2016. Metabolomics: an emerging frontier of systems biology in marine macrophytes. *Algal Research-Biomass Biofuels and Bioproducts* **16**: 76–92.

Lalrinsanga PL, Deshmukhe G, Chakraborty SK, Dwivedi A, Barman N, Kumar N. 2009. Preliminary studies on cryopreservation of vegetative thalli of some economically important seaweeds of India. *Journal of Applied Aquaculture* **21**: 250–262.

Largo DB, Fukami K, Nishijima T, Ohno M. 1995. Laboratory-induced development of the ice-ice disease of the farmed red algae *Kappaphycus alvarezii* and *Eucheuma denticulatum* (Solieriaceae, Gigartinales, Rhodophyta). *Journal of Applied Phycology* **7**: 539–543.

Lee YN, Nam KW. 2016. Cryopreservation of gametophytic thalli of *Ulva prolifera* (Ulvales, Chlorophyta) from Korea. *Journal of Applied Phycology* **28**: 1207–1213.

Lerche K, Hallmann A. 2009. Stable nuclear transformation of *Gonium pectorale. BMC Biotechnology* **9**: 64.

Li J, Pang S, Shan T, Liu F, Gao S. 2014. Zoospore-derived monoecious gametophytes i*n Undaria pinnatifida* (Phaeophyceae). *Chinese Journal of Oceanology and Limnology* **32**: 365–371.

Li Y, Zhou C, Yan X, Zhang J, Xu J. 2016. Simultaneous analysis of ten phytohormones in *Sargassum horneri* by high-performance liquid chromatography with electrospray ionization tandem mass spectrometry. *Journal of Separation Science* **39**: 1804–1813.

Loureiro R, Gachon CMM, Rebours C. 2015. Seaweed cultivation: potential and challenges of crop domestication at an unprecedented pace. *New Phytologist* **206**: 489–492.

Luning K, Dring MJ. 1975. Reproduction, growth and photosynthesis of gametophytes of *Laminaria saccharina* grown in blue and red-light. *Marine Biology* **29**: 195–200.

Makkar HPS, Tran G, Heuzé V, Giger-Reverdin S, Lessire M, Lebas F, Ankers P. 2016. Seaweeds for livestock diets: a review. *Animal Feed Science and Technology* **212**: 1–17.

Matsuo Y, Imagawa H, Nishizawa M, Shizuri Y. 2005. Isolation of an algal morphogenesis inducer from a marine bacterium. *Science* **307**: 1598.

Mazarrasa I, Olsen YS, Mayol E, Marbà N, Duarte CM. 2013. Rapid growth of seaweed biotechnology provides opportunities for developing nations. *Nature Biotechnology* **31**: 591–592.

Mazarrasa I, Olsen YS, Mayol E, Marbà N, Duarte CM. 2014. Global unbalance in seaweed production, research effort and biotechnology markets. *Biotechnology Advances* **32**: 1028–1036.

Mikami K. 2014. A technical breakthrough close at hand: feasible approaches toward establishing a gene-targeting genetic transformation system in seaweeds. *Frontiers in Plant Science* **5**: 498.

Nakahara H. 1984. Alternation of generations of some brown algae in unialgal and axenic cultures. *Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido University* **7**: 77–194.

Neveux N, Magnusson M, Mata L, Whelan A, de Nys R, Paul NA. 2016. The treatment of municipal wastewater by the macroalga *Oedogonium sp.* and its potential for the production of biocrude. *Algal Research* **13**: 284–292.

Oertel W, Wichard T, Weissgerber A. 2015. Transformation of *Ulva Mutabilis* (chlorophyta) by Vector Plasmids Integrating into the Genome. *Journal of Phycology* **51**: 963–979.

Pang SJ, Lüning K. 2004. Breaking seasonal limitation: year-round sporogenesis in the brown alga *Laminaria saccharina* by blocking the transport of putative sporulation inhibitors. *Aquaculture* **240**: 531–541.

Pang SJ, Lüning K. 2006. Tank cultivation of the red alga *Palmaria palmata*: year-round induction of tetrasporangia, tetraspore release in darkness and mass cultivation of vegetative thalli. *Aquaculture* **252**: 20–30.

Parfrey LW, Lahr DJG, Knoll AH, Katz LA. 2011. Estimating the timing of early eukaryotic diversification with multigene molecular clocks. *Proceedings of the National Academy of Sciences, USA* **108**: 13624–13629.

Popper S, Michel G, Hervé C, Domozych DS, Willats WGT, Tuohy MG, Kloareg B, Stengel DB. 2011. Evolution and diversity of plant cell walls: from algae to flowering plants. In: Merchant SS, Briggs WR, Ort D, eds. *Annual review of plant biology, vol. 62.* Palo Alto, CA, USA: Annual Reviews, 567–588.

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. Parallel analysis of proteins in brown seaweed *Sargassum fusiforme* responding to hyposalinity stress. *Aquaculture* **465**: 189–197.

Rebours C, Marinho-Soriano E, Zertuche-González JA, Hayashi L, Vásquez JA, Kradolfer P, Soriano G, Ugarte R, Abreu MH, Bay-Larsen I *et al.* 2014. Seaweeds: an opportunity for wealth and sustainable livelihood for coastal communities. *Journal of Applied Phycology* **26**: 1939–1951.

Reisewitz SE, Estes JA, Simenstad CA. 2006. Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. *Oecologia* **146**: 623–631.

Rorrer GL, Cheney DP. 2004. Bioprocess engineering of cell and tissue cultures for marine seaweeds. *Aquacultural Engineering* **32**: 11–41.

Saint-Marcoux D, Billoud B, Langdale JA, Charrier B. 2015. Laser capture microdissection in *Ectocarpus siliculosus*: the pathway to cell-specific transcriptomics in brown algae. *Frontiers in Plant Science* **6**: 54.

Schiedlmeier B, Schmitt R, Muller W, Kirk M, Gruber H, Mages W, Kirk D. 1994. Nuclear Transformation of *Volvox carteri. Proceedings of the National Academy of Sciences, USA* **91**: 5080–5084.

Schmid C, Schroer N, Muller D. 1994. Female gamete membrane-glycoproteins potentially involved in gamete recognition in *Ectocarpus siliculosus* (phaeophyceae). *Plant Science* **102**: 61–67.

Seghetta M, Tørring D, Bruhn A, Thomsen M. 2016. Bioextraction potential of seaweed in Denmark – an instrument for circular nutrient management. *The Science of the Total Environment* **563–564**: 513–529.

Shan T, Pang S, Li J, Li X, Su L. 2015. Construction of a high-density genetic map and mapping 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**: 902.

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**: 154–161.

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**: 197.

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, NY, USA)* **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.

© 2017 The Authors
New Phytologist © 2017 New Phytologist Trust

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.

Wichard T, Oertel W. 2010. Gametogenesis and gamete release of *Ulva mutabilis* and *Ulva lactuca* (Chlorophyta): regulatory effects and chemical characterization of the 'swarming inhibitor'. *Journal of Phycology* **46**: 248–259.

Zhou W, Sui Z, Wang J, Chang L. 2013. An orthogonal design for optimization of growth conditions for all life history stages of *Gracilariopsis lemaneiformis* (Rhodophyta). *Aquaculture* **392**: 98–105.

Key words: development, life cycle, macroalgae, morphogenesis, reproduction, seaweeds.

About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Trust, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <26 days. There are **no page or colour charges** and a PDF version will be provided for each article.
- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.
- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)
- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**

© 2017 The Authors
New Phytologist © 2017 New Phytologist Trust