Understanding “green” multicellularity: do seaweeds hold the key?

Juliet C. Coates, Umm-E Aiman, Bénédicte Charrier

To cite this version:

Juliet C. Coates, Umm-E Aiman, Bénédicte Charrier. Understanding “green” multicellularity: do seaweeds hold the key?. Frontiers in Plant Science, Frontiers, 2015, 5, pp.UNSP 737. 10.3389/fpls.2014.00737. hal-01223891

HAL Id: hal-01223891
https://hal.sorbonne-universite.fr/hal-01223891
Submitted on 3 Nov 2015

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L’archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d’enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution 4.0 International License
Understanding “green” multicellularity: do seaweeds hold the key?

Juliet C. Coates¹*, Umm-E-Aiman¹ and Bénédicte Charrier²,³

¹ School of Biosciences, University of Birmingham, Birmingham, UK
² Integrative Biology of Marine Models, CNRS, Station Biologique, Roscoff, France
³ Integrative Biology of Marine Models, Sorbonne Universités, Université Pierre et Marie Curie Univ., Station Biologique, Roscoff, France

*Correspondence: j.c.coates@bham.ac.uk

INTRODUCTION
Living organisms are unicellular, composed of a single cell, or multicellular, where a group of up to ~10^12 cells function co-operatively (Kaiser, 2001). All multicellular organisms evolved from single-celled ancestors; every individual organism arises from a unicell and reproduces by forming unicells. Multicellularity enables competitive advantages, and may have shaped our oxygen-rich atmosphere (Grosberg and Strathmann, 1998; Kaiser, 2001; Schirrmieister et al., 2013). Multicellularity has evolved multiple times: animals, plants, algae, amoebae, fungi, and bacteria are or can all be multicellular (King, 2004; Grosberg and Strathmann, 2007; Rokas, 2008; Claessen et al., 2014). Multicellularity can be clonal (arising from division of a single cell) or aggregative (aggregation of genetically diverse cells), with clonal multicellularity considered evolutionarily more stable (Grosberg and Strathmann, 1998). The molecular mechanisms by which organisms become multicellular are not well understood. In this article, we outline eukaryotic multicellular evolution, and discuss how to increase our future understanding.

EVOLUTION OF UNICELLULAR–MULTICELLULAR TRANSITIONS: A GENETIC TOOLKIT FOR MULTICELLULARITY?
The most well-studied group of multicellular organisms are animals, where multicellularity likely arose once, giving rise to today’s diversity of complex forms. Organisms in animal sister lineages, the aquatic “prostil” choanoflagellates and filasterceans (forming holozoans collectively, with animals), can be unicellular or multicellular. Comparison of unicellular holozoan and animal genomes suggests that part of the “toolkit” of genes required to orchestrate multicellular development (genes for cell adhesion, cell–cell signaling and certain transcription factors) was already present in unicellular ancestors of both holozoans and animals (Abedin and King, 2008; King et al., 2008; Sebe-Pedros et al., 2011; Fairclough et al., 2013; Suga et al., 2013), although “metazoan-specific innovations” also exist (Suga et al., 2013).

Data from algae extends this “common toolkit” hypothesis to other kingdoms. The Chlamydomonas (unicellular) and Volvox (simple multicellular) genomes are remarkably similar (Merchant et al., 2007; Prochnik et al., 2010), with very few species-specific genes, and expansion of Volvox extracellular matrix (ECM) gene families (Prochnik et al., 2010). Much is now understood about the evolutionary steps to multicellularity in Volvocine algae (Herron et al., 2009), but the underlying molecular–genetic mechanisms are unknown.

The genome sequence of Ectocarpus, a multicellular brown alga, reveals no obvious trends of specific gene loss/gain in independent multicellular lineages (Cock et al., 2010). Ectocarpus contains possible integrin domains, which are important for animal development and also present in unicellular Holozoa (Cock et al., 2010). Ectocarpus also highlights the independent evolution of large receptor-kinase protein families as a step to drive complex multicellular evolution from a eukaryotic ancestor (Cock et al., 2010), as also suggested in plants (Shiu and Bleecker, 2001) and holozoans (Hunter and Plowman, 1997; Suga et al., 2014). Multicellular fungi possess unique non-receptor kinases (Stajich et al., 2010). Thus, transitions to multicellularity most likely largely require co-option of pre-existing genes, via changes in expression or regulation.

UNDERSTANDING UNICELLULAR–MULTICELLULAR LIFE-CYCLE TRANSITION MECHANISMS
All multicellular organisms possess a unicellular life-cycle stage, undergoing a unicellular–multicellular transition in every generation. In the most complex organisms (animals and terrestrial plants), these transitions are challenging to characterize experimentally, as the unicells (gametes, zygotes) are hidden deep within host tissues (e.g., Figure 1B). However, there are eukaryotes of varying complexity that offer tractable systems to define molecular changes underpinning unicellular–multicellular transitions, enabling new opportunities for characterization and comparison.

MODES OF MULTICELLULARITY ON THE UNIKONT BRANCH
Animals, Holozoa, fungi, and amoebae (collectively, Unikonts) are a key branch of the tree of life (Figure 1A). Multicellularity has arisen many times in Unikonts, but
FIGURE 1 | Transitions between unicellular and multicellular states in plants, algae, and their relatives. (A) Simplified tree of life showing the Unikont and plant/algal lineages and their evolutionary relationships, including divergence times in millions or billions of years ago (mya or bya, respectively). Animals, choanoflagellates, filastereans, and ichthyosporeans are collectively known as holozoans (purple boxes). Plants and green algae (green boxes) together with red algae (red box) form the Archaeplastida, while brown algae are part of a separate lineage evolving from a common eukaryotic ancestor 1.6 billion years ago. (B) Highly simplified flowering plant life cycle showing unicellular-multicellular transitions (orange arrow) and multicellular-unicellular transitions (blue arrows). The multicellular seed (orange) houses the unicellular diploid zygote (brown) surrounded by multicellular endosperm tissue (yellow). The zygote develops into a multicellular embryo within the seed, which then germinates to form the multicellular diploid adult sporophyte plant. Within the sporophyte flower, meiosis occurs to produce single-celled haploid gametes (female ovules and male pollen) in the multicellular diploid ovaries and anthers, respectively. The unicellular megaspores develop into a multicellular (seven-celled) haploid megagametophyte, completely surrounded by maternal multicellular tissue, prior to fertilization of one megagametophyte nucleus to form a zygote buried within the maternal- and developing seed-tissue. The microspores within the anther form a pollen grain with two cells that degenerate when the pollen germinates, allowing transfer of nuclei to the megagametophyte. Although the mature pollen grain (haploid gametophyte) is an accessible unicell it does not germinate to form a multicellular structure by itself, but only after fertilization has occurred. (C) Simplified life cycle of an early-evolving spore-bearing land plant, such as a moss (Bryophyte), showing unicellular-multicellular transitions (orange arrow), and multicellular-unicellular transitions (blue arrows). A haploid spore (brown) germinates to form a haploid multicellular filament, which eventually produces haploid multicellular leafy structures (gametophytes). Gametophytes produce haploid sperm or eggs, which fuse to form a unicellular diploid zygote, which divides by mitosis to form a multicellular diploid sporophyte. The sporophyte matures and then divides by meiosis to form haploid spores, which are released from the capsule. (D) Simplified life cycle of a macroalga such as Ulva (green seaweed) showing unicellular-multicellular transitions (orange arrows) and multicellular-unicellular transitions (blue arrows). Multicellular blade (thallus) tissue, a haploid gametophyte or a diploid sporophyte, arises from haploid spores and a diploid zygote, respectively. Gametes from two different mating types (+ and −) are required for fusion and zygote formation to occur. Sporophyte and gametophyte blades are essentially morphologically identical, as are gametes of different mating types. Isolated gametes in culture are capable of undergoing a parthenogenetic life cycle. Representative images of Ulva linza sporophyte thalli and spores in culture are shown (courtesy of Eleanor Vesty). Life cycles for red and brown algae are similar, but often more complex, with non-isomorphic multicellular stages and/or gametophyte or sporophyte reduced in size.
there is no correlation between an organism’s relatedness to animals and its mode of multicellularity. Several Holozoa have recently-identified multicellular life-cycle stages (Fairclough et al., 2010; Dayel et al., 2011; Sebe-Pedros et al., 2013; Suga and Ruiz-Trillo, 2013), with the ichthysoporean Creolimax fragrantissima forming a colony via a multinucleate syncitium (Suga and Ruiz-Trillo, 2013). The choanoflagellate Sulpingoeca rosetta has clonal multicellularity, like animals (Fairclough et al., 2010), with two distinct multicellular morphologies, chains and rosettes (Dayel et al., 2011). Cytokinesis genes, cell–cell adhesion genes and receptor tyrosine kinases were all upregulated in rosettes (Fairclough et al., 2013), while a C-type lectin gene is required for rosette formation (Levin et al., 2014). The Filasterian Capsasp a owczarzaki assumes aggregative multicellularity, with deposition of ECM (Sebe-Pedros et al., 2013). C. owczarzaki upregulates integrin-mediated adhesion and signaling genes in aggregates compared to unicellular stages (Sebe-Pedros et al., 2013), strengthening the idea that multicellularity requires changes in gene regulation.

Reverse transitions from multicellularity likely occurred in Unikonts: fungi may have evolved as filamentous organisms >1 billion years ago (Butterfield, 2005), although many extant yeast species are entirely unicellular. Multicellularity can be selected for in the lab in the normally unicellular baker’s yeast Saccharomyces cerevisiae (Ratcliff et al., 2012): this is clonal multicellularity, like in choanoflagellates and animals. Multicellular social amoebae diverged from Metazoa ~1.2 billion years ago (Figure 1A). The best-known example, Dictyostelium, forms aggregates from motile cells (Coates and Harwood, 2001; Schaap, 2011). Notably, the protist Fonticula alba, in the sister group to fungi, also shows aggregative multicellularity (Brown et al., 2009). Unicellular–multicellular transcriptional changes are conserved over large evolutionary distances: Dictyostelium discoideum and Dictyostelium purpureum diverged ~400 MYA but share similar morphologies and incredibly similar global gene expression profiles during their unicellular–multicellular transitions (Parikh et al., 2010).

MULTICELLULARITY AND ENVIRONMENTAL SENSING

Unicellular–multicellular changes play key roles in the adaptation of some microorganisms to the environment. Selection pressures driving transitions to multicellularity include nutrient stress, predation and competition. Social amoebae aggregate in response to starvation, forming a fruiting body containing stress-resistant spores (Schaap, 2011). Some strains of S. cerevisiae form filaments in response to nitrogen starvation (Liu et al., 1996). Some green microalgae (including Desmodesmus and Scenedesmus) transition between unicellular and multicellular states, similarly to choanoflagellates (Lürling, 2003). These algae form multicellular structures due to nutrient-limitation (Trainor and Shubert, 1974; Siver and Trainor, 1981) competitor algae (Lef laive et al., 2008), animal predators (Hessen and Van Donk, 1993; Lampert et al., 1994; Lürling and Van Donk, 1996; Kampe et al., 2007) or toxins (Lürling, 2003).

Becoming multicellular to escape predators can have a physiological cost via a reduction in growth rate. The benefit of multicellularity as a defense mechanism depends on the population dynamics of co-occurring species and the environmental conditions determining the prey’s growth rate: in the absence of a predator and under nutrient-replete competitive conditions multicellularity can have an adverse effect on the organism’s fitness (Yokota and Sterner, 2011). Multicellularity can also affect green organisms’ productivity: in Desmodesmus armatus, light-acclimation occurred in two-celled colonies, whereas maximum photosynthetic rates occurred in four-celled colonies (Matusiak-Mikulin et al., 2006). As microagal multicellular morphs and unicells occupy different spaces in the water, unicellular–multicellular transitions can have far-reaching effects on the whole ecosystem (Lürling, 2003).

One emerging paradigm is that signals from eukaryotic-associated bacteria may drive multicellular complexity. C. owczarzaki can form aggregates under axenic conditions (Sebe-Pedros et al., 2013) and filamentous colonies in S. rosetta occur without bacteria (Dayel et al., 2011), but S. rosetta rosette colony formation is induced only in the presence of it’s bacterial prey species (Dayel et al., 2011), which releases a specific sphingolipid signal that induces rosette formation (Alegado et al., 2012), perhaps enabling S. rosetta to feed more efficiently. Signals from microorganisms also profoundly affect the development of green seaweeds and land plants (Parniske, 2000; Matsuo et al., 2005; Marshall et al., 2006; Spoerner et al., 2012), although both can form multicellular structures in axenic conditions.

“GREEN” MULTICELLULARITY: INDEPENDENT ACQUISITIONS

Acquisition of multicellularity underpinned the key transition of plants to land, but the mechanism(s) by which this occurred are unknown. Land plants evolved from algae (Figure 1A); algae have evolved multicellularity many times independently of land plants. In particular, the Chlorophyte algae include many “simple” multicellular species alongside morphologically complex green seaweeds (Niklas, 2014). Genomic information to define mechanisms underpinning “green” unicellular–multicellular transitions is lacking compared to the holozoan–animal comparative studies.

As with animals, it seems that the genetic toolkit for green multicellularity was present in unicellular ancestors (Chlamydomonas/ Volvox genomes were discussed in Section Evolution of Unicellular–Multicellular Transitions: A Genetic Toolkit for Multicellularity?). Colonial “morphs” can be induced, or selected for, in usually unicellular microalgae e.g., Chlamydomonas (Lürling and Beekman, 2006; Ratcliff et al., 2013) and Chlorella (Boraas et al., 1998). Formation of the Chlamydomonas diploid zygote requires homologs of transcription factors involved in land plant meristem specification, implying that plant multicellular body plans may have evolved from algal sexual developmental mechanisms (Lee et al., 2008). In Scenedesmus, multicellularity correlated with reactive oxygen species production and activation of a kinase (Lef laive et al., 2008); redox state may also have been a driver of animal multicellularity (Blackstone, 2000).

It is technically difficult to study the unicellular–multicellular transition in most land plants at the molecular or
genetic level. Embryos/gametes exist only transiently in the flowering plant life cycle, and are surrounded by multicellular tissues (Figure 1B). Early-branching spore-bearing plants such as mosses and ferns are more experimentally tractable models for studying unicellular–multicellular transitions, as a unicell, the spore, can be isolated (and stored) prior to germination into multicellular structures (Figure 1C).

We believe that seaweeds are the best group of organisms in which to define the molecular changes involved in unicellular–multicellular transitions, as every seaweed has a unique life cycle that alternates between unicellular and multicellular stages, involving at least two separate unicellular–multicellular transitions: germination of spores into gametophytes, and germination of gametes and/or zygotes into sporophytes (Figure 1D). Thus, seaweeds represent exciting new systems in which unicellular–multicellular transitions can be studied with relative ease.

SEaweeds as Key Systems to Understand unicellular–Multicellular Transitions: Understanding seaweed multicellularity will have economic importance

The emerging model systems Ulva (a green seaweed) and Ectocarpus (a brown seaweed) offer new ways to define the molecular basis of unicellular–multicellular transitions in complex systems. Relatively large numbers of Ulva unicells (spores or gametes) can be induced and isolated, far more easily than the spores of land plants, from more than one Ulva species (Richard and Oertel, 2010; Vesty et al., 2015). It is this propensity for multicellular tissues to form unicells (which give rise to new multicellular structures) that leads to Ulva forming nuisance blooms: thus it is key to understand the basic biology of these processes. Ulva can now be grown in axenic laboratory-based culture, including via parthenogenesis (Richard and Oertel, 2010; Spoerner et al., 2012), enabling a step-change in the methods we can use to understand seaweed biology and development. Ectocarpus has well-developed forward genetics, including a series of mutants (Le Bail et al., 2011; Cock et al., 2014), some of which are specifically altered in the spatial organization of the multicellular body [forming callus instead of polarized filaments; gri mutants (Le Bail et al., 2010)], or impaired maintenance of cell–cell adhesion: bib mutants (Charrier et al., in review).

Many green, red and brown seaweeds are of profound economic importance, both positively as sources of food, fuel and useful chemicals, and negatively as biofoulers (Callow and Callow, 2011) or invasive species that are damaging to marine ecosystems (Smetacek and Zingone, 2013). Until now, seaweeds have been a neglected group of organisms for large-scale gene discovery, thus understanding seaweed growth and development lags behind our equivalent knowledge in land plants. Genome sequences are available for the red seaweeds (and food crops) Pyropia and Chondrus (Collen et al., 2013; Nakamura et al., 2013), and for Ectocarpus (Cock et al., 2010) with an Ulva genome-sequencing project underway. Chondrus is also an emerging macroalgal model system, taking ~2 years to complete its life cycle in the lab. Thus, the time is right to instigate a step-change in the understanding of seaweed biology, including the regulation of its unicellular–multicellular transitions. This will enable new knowledge to apply to seaweed culture (for food and fuel) and control (of blooms and biofouling).

Wider Perspectives on Understanding seaweed multicellularity

Current data suggests that the genetic toolkit underpinning unicellular–multicellular transitions was present in unicellular ancestors, in both Unikonts and “green” organisms. Whether the toolkit is conserved between animals and plants is unknown. Using new “green” systems such as spore-plants, microalgae and seaweeds to define the molecular changes underpinning unicellular–multicellular transitions will shed new light on this question, and will also enable new understanding of how multicellular land plants evolved. Combined with the application of new basic biological knowledge to economically and environmentally important seaweed species, we are entering a new era of plant- and algal biology.

Acknowledgments

This work was supported by a Royal Society–Leverhulme Trust Senior Research Fellowship 2013–14 to Juliet C. Coates and a Commonwealth Scholarship to Umm-E-Aiman.

References

Abedin, M., and King, N. (2008). The premetazoan ancestry of cadherins. Science 319, 946–948. doi: 10.1126/science.1151084

Alegado, R. A., Brown, L. W., Cao, S., Deremenjian, R. K., Zuzzow, R., Fairclough, S. R., et al. (2012). A bacterial sulfonolipid triggers multicellular development in the closest living relatives of animals. Elife 1:e00013. doi: 10.7554/eLife.00013

Blackstone, N. W. (2000). Redox control and the evolution of multicellularity. Bioessays 22, 947–953. doi: 10.1002/1521-1878(200011)22:10<947::AID-BIES10>3.0.CO;2-W

Boraas, M. E., Seale, D. B., and Bozhorn, J. E. (1998). Phagotrophy by a flagellate selects for colonial prey: a possible origin of multicellularity. Evol. Ecol. 12, 153–164. doi: 10.1023/A:1006527528063

Brown, M. W., Spiegel, F. W., and Silberman, J. D. (2009). Phylogeny of the “forgotten” cellular slime mold, Fonticula alba, reveals a key evolutionary branch within Opisthokonta. Mol. Biol. Evol. 26, 2699–2709. doi: 10.1093/molbev/msp185

Butterfield, N. I. (2005). Probable protorozoic fungi. Paleobiology 31, 165–182. doi: 10.1666/0094-8373(2005)031<0165:PFOPF>2.0.CO;2

Callow, J. A., and Callow, M. E. (2011). Trends in the development of environmentally friendly fouling-resistant marine coatings. Nat. Commun. 2, 244. doi: 10.1038/ncomms1251

Claessen, D., Rozen, D. E., Kuipers, O. P., Sogaard-Andersen, L., and Van Wezel, G. P. (2014). Bacterial solutions to multicellularity: a tale of biofilms, filaments and fruiting bodies. Nat. Rev. Microbiol. 12, 115–124. doi: 10.1038/nrmicro3178

Coates, J. C., and Harwood, A. J. (2001). Gametophyte to sporophyte: the independent evolution of multicellularity in brown algae. Nature 416, 617–621. doi: 10.1038/35057530

Cock, J. M., Stemek, L., Rouze, P., Scornet, D., Allen, A. E., Amoutzias, G., et al. (2010). The Ectocarpus genome and the independent evolution of multicellularity in brown algae. Nature 465, 617–621. doi: 10.1038/nature09016

Colmen, J., Porcel, B., Carre, W., Ball, S. G., Chaparro, C., Tonon, T., et al. (2013). Genomic structure and metabolic features in the red seaweed Chondrus crispus shed light on evolution of the Archaeplastida. Prot. Natl. Acad. Sci. U.S.A. 110, 5247–5252. doi: 10.1073/pnas.1221591110

Dayel, M. I., Alegado, R. A., Fairclough, S. R., Levin, T. C., Nichols, S. A., McDonald, K., et al. (2011). Cell differentiation and morphogenesis in the colony-forming choanoflagellate Salpingoeca rosetta. Dev. Biol. 357, 73–82. doi: 10.1016/j.ydbio.2011.06.003
Fairclough, S. R., Chen, Z., Kramer, E., Zeng, Q., Young, S., Robertson, H. M., et al. (2013). Premetazoan genome evolution and the regulation of cell differentiation in the choanoflagellate Salpingoeca rosetta. Genome Biol. 14:R15. doi: 10.1186/gb-2013-14-2-r15

Fairclough, S. R., Dayel, M. I., and King, N. (2010). Multicellular development in a choanoflagellate. Curr. Biol. 20, R875–R876. doi: 10.1016/j.cub.2010.09.014

Grosberg, R. K., and Strathmann, R. R. (1998). One

Grosberg, R. K., and Strathmann, R. R. (2007). The pro-

Hunter, T., and Plowman, G. D. (1997). The pro-

Kaiser, D. (2001). Building a multicellular organ-

Herron, M. D., Hackett, J. D., Aylward, F. O., Lampert, W., Rothhaupt, K. O., and Von Elert, E. (2003). A unicellular stage in multicellular life histories. Curr. Biol. 13, 112–116. doi: 10.1016/S0169-5347(03)0133-x

Grosberg, R. K., and Strathmann, R. R. (2007). The evolution of multicellularity: a minor major evolution? AARES 38, 621–654. doi: 10.1146/annurev.ecolsys.36.102403.114735

Herron, M. D., Hackett, J. D., Aylward, F. O., and Michod, R. E. (2009). Triassic origin and the evolution of multicellular volvocine algae. Proc. Natl. Acad. Sci. U.S.A. 106, 3254–3258. doi: 10.1073/pnas.0811205106

Hessens, D. O. and Van Donk, E. (1995). Morphological changes in Scenedesmus induced by substances released from Daphnia. Arch. Hydrobiol. 127, 129–140.

Hunter, T., and Plowman, G. D. (1997). The protein kinases of budding yeast: six score and more. Trends Biochem. Sci. 22, 18–22.

Kaiser, D. (2001). Building a multicellular organ-

Premetazoan genome evolution and the regula-

The evolution of multicellularity: a minor major evolution? AARES 38, 621–654. doi: 10.1146/annurev.ecolsys.36.102403.114735

Liu, H., Styles, C. A., and Fink, G. R. (1996). Auxin metabolism and function in the multi-

McGinnis, S. and Stearns, K. (2001). Ectocarpus siliculosus (Chlorophyta) depends on a combination

Lee, J. H., Lin, H., Joo, S., and Goodenough, U. (2008). Early sexual origins of homeoprotein

Lutze, H., Greaney, A. J., Wetzel, L., and King, N. (2014). The rosetteless gene controls development in the choanoflagellate S. rosetta. Elife 3:e04070. doi: 10.7554/elife.04070

Liu, H., Styles, C. A., and Fink, G. R. (1996). Auxin metabolism and function in the multi-

Macnab, S., Achat, N., and Charrier, B. (2011). ETOILE regulates develop-

Lee, J. H., Lin, H., Joo, S., and Goodenough, U. (2008). Early sexual origins of homeoprotein

Matsu, Y., Imagawa, H., Nishizawa, M., and Shizuri, Y. (2005). Isolation of an algal morphogenesis inducer from a marine bacterium. Science 307, 1598. doi: 10.1126/science.1105486

Matsuki-Mikulín, K., Tukaj, C., and Tukaj, Z. (2006). Relationships between growth, develop-

Kong, N. (2004). The unicellular ancestry of ani-

King, N., Westbrook, M. I., Young, S. L., Kuo, A., Abedin, M., Chapman, J., et al. (2008). The genome of the choanoflagellate Monosiga brevi-

Lampert, W., Rothaupt, K. O., and Von Elert, E. (1994). Chemical induction of colony formation in a green alga (Scenedesmus acutus) by grazers (Daphnia). Limnol. Oceanogr. 39, 1543–1550. doi: 10.4319/lo.1994.39.7.1543

Le Bail, A., Billoud, B., Kowalczyk, N., Kowalczyk, M., Gicquel, M., Le Panse, S., et al. (2010). Auxin metabolism and function in the multicellular brown alga Ectocarpus siliculosus. Plant Physiol. 153, 128–144. doi: 10.1104/pp.109.149708

Le Bail, A., Billoud, B., Le Panse, S., Chenivesse, S., and Charrier, B. (2011). ETOHE regulates develop-

Liu, H., Styles, C. A., and Fink, G. R. (1996). Auxin metabolism and function in the multi-

Macnab, S., Achat, N., and Charrier, B. (2011). ETOILE regulates develop-

Lee, J. H., Lin, H., Joo, S., and Goodenough, U. (2008). Early sexual origins of homeoprotein

Leclaire, J., Lacroix, G., Nicaise, Y., and Ten-Hage, L. (2008). Colony induction and growth inhibition in Desmodesmus quadridispina (Chlorococcales) by allelochemicals released from the filamentous alga Uromonas confervicolum (Ullothricales). Environ. Microb. 10, 1536–1546. doi: 11.1111/j.1462-9902.2008.01569.x

Leclaire, J., Lacroix, G., Nicaise, Y., and Ten-Hage, L. (2008). Colony induction and growth inhibition in Desmodesmus quadridispina (Chlorococcales) by allelochemicals released from the filamentous alga Uromonas confervicolum (Ullothricales). Environ. Microb. 10, 1536–1546. doi: 11.1111/j.1462-9902.2008.01569.x

Leclaire, J., Lacroix, G., Nicaise, Y., and Ten-Hage, L. (2008). Colony induction and growth inhibition in Desmodesmus quadridispina (Chlorococcales) by allelochemicals released from the filamentous alga Uromonas confervicolum (Ullothricales). Environ. Microb. 10, 1536–1546. doi: 11.1111/j.1462-9902.2008.01569.x

Leclaire, J., Lacroix, G., Nicaise, Y., and Ten-Hage, L. (2008). Colony induction and growth inhibition in Desmodesmus quadridispina (Chlorococcales) by allelochemicals released from the filamentous alga Uromonas confervicolum (Ullothricales). Environ. Microb. 10, 1536–1546. doi: 11.1111/j.1462-9902.2008.01569.x

Lee, J. H., Lin, H., Joo, S., and Goodenough, U. (2008). Early sexual origins of homeoprotein

Liu, H., Styles, C. A., and Fink, G. R. (1996). Auxin metabolism and function in the multi-

Macnab, S., Achat, N., and Charrier, B. (2011). ETOILE regulates develop-

Macnab, S., Achat, N., and Charrier, B. (2011). ETOILE regulates develop-

Lee, J. H., Lin, H., Joo, S., and Goodenough, U. (2008). Early sexual origins of homeoprotein

Lee, J. H., Lin, H., Joo, S., and Goodenough, U. (2008). Early sexual origins of homeoprotein

Lee, J. H., Lin, H., Joo, S., and Goodenough, U. (2008). Early sexual origins of homeoprotein
Suga, H., Chen, Z., de Mendoza, A., Sebe-Pedros, A., Brown, M. W., Kramer, E., et al. (2013). The Capsaspora genome reveals a complex unicellular prehistory of animals. *Nat. Commun.* 4, 2325. doi: 10.1038/ncomms3325

Suga, H., and Ruiz-Trillo, I. (2013). Development of ichthyosporeans sheds light on the origin of metazoan multicellularity. *Dev. Biol.* 377, 284–292. doi: 10.1016/j.ydbio.2013.01.009

Suga, H., Torruella, G., Burger, G., Brown, M. W., and Ruiz-Trillo, I. (2014). Earliest Holozoan expansion of phosphotyrosine signaling. *Mol. Biol. Evol.* 31, 517–528. doi: 10.1093/molbev/msu241

Trainor, F. R., and Shubert, L. E. (1974). *Scenedesmus* morphogenesis. Colony control in dilute media. *J. Phycol.* 10, 28–30.

Vesty, E. F., Kessler, R. W., Wichard, T., and Coates, J. C. (2015). Regulation of gametogenesis and zoosporogenesis in *Ulva linza* (Chlorophyta): comparison with *U. mutabilis* and potential for laboratory culture. *Front. Plant Sci.* 6:15. doi: 10.3389/fpls.2015.00015

Wichard, T., and Oertel, W. (2010). Gametogenesis and gamete release of *Ulva mutabilis* and *U. latuca* (Chlorophyta): regulatory effects and chemical characterization of the “Swarming Inhibitor.” *J. Phycol.* 46, 248–259. doi: 10.1111/j.1529-8817.2010.00816.x

Yokota, K., and Sterner, R. W. (2011). Trade-offs limiting the evolution of coloniality: ecological displacement rates used to measure small costs. *Proc. Biol. Sci.* 278, 458–463. doi: 10.1098/rspb.2010.1459

**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.