Emerging Model Organism

Ectocarpus: A Model Organism for the Brown Algae

Susana M. Coelho,^{1,2,4} Delphine Scornet,^{1,2} Sylvie Rousvoal,^{1,2} Nick T. Peters,^{1,2}
Laurence Dartevelle,^{1,2} Akira F. Peters,^{2,3} and J. Mark Cock^{1,2}

¹UPMC Université Paris 06, The Marine Plants and Biomolecules Laboratory, UMR 7139, Station Biologique de Roscoff, BP74, 29682 Roscoff Cedex, France

²CNRS, UMR 7139, Laboratoire International Associé Dispersal and Adaptation in Marine Species, Station Biologique de Roscoff, BP74, 29682 Roscoff Cedex, France

³Bezhin Rosko, 29250 Santec, France

The brown algae are an interesting group of organisms from several points of view. They are the dominant organisms in many coastal ecosystems, where they often form large, underwater forests. They also have an unusual evolutionary history, being members of the stramenopiles, which are very distantly related to well-studied animal and green plant models. As a consequence of this history, brown algae have evolved many novel features, for example in terms of their cell biology and metabolic pathways. They are also one of only a small number of eukaryotic groups to have independently evolved complex multicellularity. Despite these interesting features, the brown algae have remained a relatively poorly studied group. This situation has started to change over the last few years, however, with the emergence of the filamentous brown alga *Ectocarpus* as a model system that is amenable to the genomic and genetic approaches that have proved to be so powerful in more classical model organisms such as *Drosophila* and *Arabidopsis*.

BACKGROUND

Ectocarpus siliculosus is a small filamentous brown alga. Seaweeds of the genus *Ectocarpus* are found worldwide along temperate coastlines, where they grow on rocky substrates or epiphytically on other algae and seagrass. Research on *E. siliculosus* has a long history (Charrier et al. 2008), and this was one of the reasons that led to this species being selected ~7 yr ago as a genetic and genomic model organism for the brown algae (Peters et al. 2004). Other important arguments for selecting *Ectocarpus* included its small size, the fact that the entire life cycle can be completed relatively rapidly (3 mo) in the laboratory (Müller et al. 1998), its high fertility, and the ease with which genetic crosses can be performed (Peters et al. 2004, 2008).

The brown algae are members of the stramenopiles (or heterokonts), together with organisms such as diatoms and oomycetes. The stramenopiles diverged from other major eukaryotic groups such as the opisthokonts (animals and fungi) and the archaeplastida (which includes land plants) over a billion years ago. One consequence of this unusual phylogenetic history is that brown algae show many novel features with regard to their metabolism and cell biology, making them prime targets for explorative research. The brown algae are also important because they are one of only a small number of eukaryotic groups that have evolved complex multicellularity (Cock et al. 2010). However, another consequence of the large phylogenetic distance that separates stramenopiles from

⁴Correspondence: coelho@sb-roscoff.fr

intensely studied groups such as animals, fungi, and green plants is that model organisms developed for these latter groups are of limited relevance to brown algal biology. Given this context, the emergence of *Ectocarpus* as a model organism is expected to have a considerable impact on brown algal research.

SOURCES AND HUSBANDRY

Ectocarpus strain collections are maintained at the Culture Collection of Algae and Protozoa (CCAP), Scottish Association for Marine Science, Oban, Scotland (<http://www.ccap.ac.uk/>), the Macroalgal Culture Collection at Kobe University (<http://www.research.kobe-u.ac.jp/rcis-ku-macc/>), and at the Station Biologique in Roscoff, France (<http://www3.sb-roscoff.fr/>). These three institutions currently hold, in triplicate, 328 *Ectocarpus* strains from a broad range of geographical locations and ecological niches. Sampling campaigns have been performed recently around the coast of Britain, along the Channel coast in France, along the Pacific coasts of Peru and Chile, and in Korea, resulting in another collection of ~1500 strains, which is maintained at the Station Biologique in Roscoff. These strain collections are being exploited to study the biodiversity and ecology of *Ectocarpus* in the field and also as a source of genetic diversity for laboratory-based studies.

In addition to the field-isolated strains, laboratory-based projects are also generating important biological material. For example, a segregating population was created for the construction of a genetic map (Heesch et al. 2010) and an ongoing TILLING (Targeting Induced Local Lesions in Genomes) project necessitates the maintenance of a large number of mutant lines. Altogether, >3000 genetically distinct, laboratory-generated strains are being maintained in Roscoff.

The *Ectocarpus* strain collection is organized as a centralized resource and a barcode system is being developed to identify and handle individual strains within the collection. Strains are maintained in duplicate as unialgal cultures free of eukaryotic contaminants in growth chambers or incubators in 5–10 mL of medium at low light intensity ($1\text{--}3\ \mu\text{mol photons m}^{-2}\text{ s}^{-1}$) and low temperature (5–15°C). The medium in these long-term storage cultures is renewed once a year. Data on geographical origin, morphology, and other relevant features are maintained in a retrievable database that is being linked to the barcode storing system.

The culture collections have been of key importance for the establishment of *Ectocarpus* as a model organism. The collections are widely exploited, not only by members of the *Ectocarpus* Genome Consortium, but also by a broader community of scientists. The collections also serve as a basis for exchanges between laboratory- and field-based research programs. Standard procedures for growing *Ectocarpus* in the laboratory are described in *How to Cultivate Ectocarpus* (Coelho et al. 2012a).

RELATED SPECIES

The genus *Ectocarpus* currently contains three species, *E. siliculosus*, *E. fasciculatus*, and *E. crouaniorum* (Peters et al. 2010b). However, there is accumulating evidence that these three taxa do not adequately describe the species diversity within the genus and additional species are likely to be defined in the future (Peters et al. 2010a). Phylogenetic analysis indicates that the Ectocarpales emerged relatively recently within the brown algae and that they are a sister group to the order Laminariales, which includes most of the large kelp species (Silberfeld et al. 2010). Brown algae belonging to other families within the Ectocarpales differ from *Ectocarpus* in terms of their physiology, cytology, life histories, and ecology and may be suitable for comparative studies in the near future.

USE OF ECTOCARPUS AS A MODEL SYSTEM

Research on *Ectocarpus* began in the 19th century with a description of species and investigation of their taxonomic positions (Dillwyn 1809). Subsequent studies were aimed at investigating the life

cycle and the ultrastructure of the organism at different stages of the life cycle (Müller 1972). Additional work included identification of the sexual pheromone and its role in gamete recognition (Boland et al. 1995) and characterization of the *Ectocarpus* virus EsV-1 (Delaroque et al. 2001). The following sections describe recent work performed using *Ectocarpus* as a model organism. Additional emerging topics, not discussed here, include sex determination, gamete recognition, and parthenogenesis.

The *Ectocarpus* Life Cycle

Ectocarpus has a haploid–diploid life cycle, involving alternation between two multicellular generations, the sporophyte and the gametophyte. Diploid sporophytes produce haploid meiospores in unilocular sporangia. Following release, the meiospores germinate to give the haploid gametophyte generation. Gametophytes are dioecious, producing either male or female gametes, which fuse to produce the diploid zygotes that reinitiate the sporophyte generation. There are several possible variations on this basic life cycle; in particular, gametes that do not find a gamete of the opposite sex with which they are able to fuse to form a zygote can develop parthenogenetically to produce sporophytes. It has long been something of a mystery as to how these partheno-sporophytes, which are derived from a haploid cell, are able to produce meiospores (which are normally produced by a reductive meiotic division). Recent work has shown that partheno-sporophytes solve this problem in two different ways (Bothwell et al. 2010). Either there is an endoreduplication event very early during development resulting in a diploid individual, or the algae remain haploid and the meiospores are produced via a nonreductive apomeiotic division in the developing unilocular sporangium.

Both generations of the *Ectocarpus* life cycle develop from single cells released into the medium by the parent(s). Moreover, the two generations show clear morphological differences, and yet are sufficiently similar to allow the isolation of mutants that lead to the conversion of one generation into the other. These features, and the fact that life cycle generation is not determined by ploidy (e.g., see the section on haploid partheno-sporophytes above), make *Ectocarpus* a particularly interesting model to study the genetic regulation of life cycle progression (Coelho et al. 2007). Interestingly, the two *Ectocarpus* generations show radically different patterns of initial cell division, development starting with a symmetric division in the sporophyte, to produce a basal filament, but with an asymmetric division in the gametophyte, leading to the production of a rhizoid and an upright filament (Peters et al. 2008). This difference has facilitated screens for life cycle mutants. For example, the *immediate upright* (*imm*) mutant shows partial conversion of the sporophyte generation into the gametophyte generation (Peters et al. 2008). *imm* mutant sporophytes retain sporophyte reproductive characteristics, producing spores and not gametes, but they have several developmental features typical of the gametophyte, including an asymmetric initial cell division that leads to the production of a rhizoid and an upright filament. More recently, a second mutant has been isolated, which shows complete conversion of the sporophyte generation into a gametophyte (Coelho et al. 2011). This mutant has been named *ouroboros* after the symbol for the cycle of life. Current work is aimed at identifying the loci corresponding to the *imm* and *oro* mutations.

Morphogenesis

Analysis of the early development of the *Ectocarpus* sporophyte using a morphometric approach showed that the pattern of development is highly variable, both in terms of cell differentiation and branching of the filament (Le Bail et al. 2008). However, this variability appears to occur within a certain level of biological constraint, resulting in organisms with similar final architectures. This has allowed early development to be modeled using a stochastic automaton (Billoud et al. 2008). The variability in the pattern of early development in *Ectocarpus* contrasts with the highly ordered development of other model organisms such as *Fucus* or *Arabidopsis*. A recent study has shown that a mutation at the *ETOILE* locus results in a modified pattern of early development, mutant algae initiating branching more rapidly than wild-type individuals (Le Bail et al. 2011).

Responses to Biotic and Abiotic Stresses

Coastal ecosystems are relatively aggressive environments and *Ectocarpus* is not only prone to infection by a wide range of pathogens, including viruses, oomycetes, chytrids, hyphochytrids, and parasites related to the Plasmodiophorea (Müller et al. 1998, 1999; Maier et al. 2000; Gachon et al. 2009), but is also subject to considerable abiotic stress because of continuous variations in temperature, salinity, and light intensity. Microarray analysis has indicated that there is extensive reprogramming of the *Ectocarpus* transcriptome, even in response to relatively mild stresses, with transcripts for a large proportion of the expressed genes showing changes in abundance (Dittami et al. 2009). Moreover, many of the genes that show regulatory changes in response to stress are of unknown function, suggesting that novel mechanisms of stress resistance remain to be discovered in this species.

Metabolism

Many brown algae are able to accumulate high concentrations of iodide from seawater. Seaweeds of the order Laminariales are thought to use apoplastic iodine as an antioxidant, and the emission of iodine by this system may have a significant impact on atmospheric chemistry (Küpper et al. 2008). Analysis of the *Ectocarpus* genome identified not only enzymes that may be involved in this system, but also a number of dehalogenases and haloalkane dehalogenases (Cock et al. 2010). These latter enzymes may help *Ectocarpus* grow epiphytically on other brown algae by defending it against halogenated molecules produced by these hosts as defense molecules.

The carbon storage system of brown algae is unusual, involving the accumulation of reserves of mannitol and the β -1,3-glucan laminarin rather than α -1,4-glucans such as starch or glycogen. Recent analysis of the evolutionary origins of these storage systems (Michel et al. 2010b), using data from the *Ectocarpus* genome sequence, has brought into question the idea of a common origin for stramenopile and alveolate plastids, proposed under the “chromalveolate hypothesis” (Cavalier-Smith 1999). The study by Michel et al. (2010b) proposes that, whereas the alveolate lineage was probably able to acquire starch metabolism from its endosymbiont by modifying its existing glycogen pathway, the stramenopile lineage did not have this option because it had already lost the glycogen metabolic pathway. The existence of starch in one lineage but not the other therefore suggests two independent endosymbiotic events. The mannitol pathway was probably acquired later by the brown algal lineage via a horizontal transfer event from actinobacteria, along with another key metabolic pathway in brown algae, alginate biosynthesis (Michel et al. 2010a).

Ecology

We have only limited knowledge about the ecology of *Ectocarpus* (Charrier et al. 2008) and there are many open questions in this domain. In ecophysiological experiments, different strains (which we now know belong to different species) survived temperatures of up to 23°C for arctic strains but up to 33°C for subtropical strains, and growth temperature optima were correlated with the conditions with which each strain was confronted in the field. When the responses to temperature of the two generations were different, the gametophyte was the less tolerant generation (Bolton 1983). The same tendency (large variability among different strains, and higher tolerance of the sporophyte) was found for salt tolerance (Thomas and Kirst 1991a,b). The production of reproductive organs by sporophytes of Mediterranean strains of *Ectocarpus* was shown to be regulated by temperature, with meiospore-containing unilocular sporangia being produced at lower temperatures and mitospore-containing plurilocular sporangia being produced at higher temperatures (Müller 1963). Recent phenological observations on *E. crouaniorum* from Brittany (Peters et al. 2010b) may provide an explanation for some of the differences between the generations; in this species, the epilithic sporophytes are small and found all year round, often as microscopic forms, whereas the gametophytes are ephemeral, occurring only in spring. The sporophyte generation might therefore be expected to be adapted to cope with more extreme physical conditions. There are no phenological data for both generations of other species of *Ectocarpus*.

The different species of *Ectocarpus* may be found in different zones on the shore. In megatidal Brittany, *E. crouaniorum* occurs in the upper intertidal zone, whereas *E. siliculosus* and *E. fasciculatus* are found in the mid-intertidal and the subtidal zones, respectively (Peters et al. 2010b). *Ectocarpus* is more often found epiphytic on marine macrophytes than epilithic, but little has been published about the host ranges of the different species and their interactions with basiphytes. *E. fasciculatus* occurs regularly as an endophyte in the blades of *Laminaria digitata* (Russell 1983a,b), but it is not known how it is able to overcome the host's defense. *Ectocarpus* is normally fixed to a substratum, but it may be detached and can survive as a floating thallus. Morphological changes have been shown to occur when *Ectocarpus* grows without being attached to a substrate, possibly as a result of lost polarity (Russell 1967a,b). Thalli of *Ectocarpus* harbor a diverse biota of small, sessile, or motile animals (e.g., crustaceans and nematodes) and protists (e.g., ciliates and benthic diatoms). The interactions with these organisms, some of which may feed on the *Ectocarpus* thallus or on released reproductive cells, have not been studied so far.

GENETICS, GENOMICS, AND ASSOCIATED RESOURCES

Following the selection of *Ectocarpus* as a model, considerable effort was invested in the development of genomic and genetic tools for this organism. The most important of these was the assembly and analysis of the complete 214 Mbp genome sequence (Cock et al. 2010). For access to the *Ectocarpus* genome sequence, see <http://bioinformatics.psb.ugent.be/webtools/bogas/>. Additional tools that have been developed for *Ectocarpus* include RNA-seq data, a large expressed sequence tag (EST) collection, whole-genome tiling arrays, deep sequencing of small RNAs, EST-based expression microarrays (Dittami et al. 2009), a genetic map (Heesch et al. 2010), stramenopile-adapted bioinformatic tools (Gschloessl et al. 2008), and proteomic (Ritter et al. 2010) and metabolomic methodologies. Genetic tools have also been developed, including protocols for ultraviolet and chemical mutagenesis, phenotypic screening methods, genetic crosses, methods for handling large populations, a large number of genetic markers, and defined strains for genetic mapping (Heesch et al. 2010). For a step-by-step protocol on how to carry out genetic crosses, see **Genetic Crosses between *Ectocarpus* Strains** (Coelho et al. 2012b).

ACKNOWLEDGMENTS

Work was supported by Centre National de la Recherche Scientifique, Université Pierre et Marie Curie, Groupement d'Intérêt Scientifique Génomique Marine, the Interreg program France (Channel)-England (project Marinexus), and Agence Nationale de la Recherche (Project Bi-cycle). N.P. was supported by IRES NSF Grant Number OISE-0652093.

REFERENCES

- Billoud B, Le Bail A, Charrier B. 2008. A stochastic 1D nearest-neighbour automaton models the early development of the brown alga *Ectocarpus siliculosus*. *Func Plant Biol* 35: 1014–1024.
- Boland W, Pohnert G, Maier I. 1995. Biosynthesis of algae pheromones. 4. Pericyclic-reaction in nature—spontaneous cope rearrangement inactivates algae pheromones. *Angew Chem* 34: 1602–1604.
- Bolton JJ. 1983. Ecocline variation in *Ectocarpus siliculosus* (Phaeophyceae) with respect to temperature growth optima and survival limits. *Mar Biol* 73: 131–138.
- Bothwell JH, Marie D, Peters AF, Cock JM, Coelho SM. 2010. Role of endoreduplication and apomeiosis during parthenogenetic reproduction in the model brown alga *Ectocarpus*. *New Phytol* 188: 111–121.
- Cavalier-Smith T. 1999. Principles of protein and lipid targeting in secondary symbiogenesis: Euglenoid, dinoflagellate, and sporozoan plastid origins and the eukaryote family tree. *J Eukaryot Microbiol* 46: 347–366.
- Charrier B, Coelho SM, Le Bail A, Tonon T, Michel G, Potin P, Kloareg B, Boyen C, Peters AF, Cock JM. 2008. Development and physiology of the brown alga *Ectocarpus siliculosus*: Two centuries of research. *New Phytol* 177: 319–332.
- Cock JM, Sterck L, Rouzé P, Scornet D, Allen AE, Amoutzias G, Anthouard V, Artiguenave F, Aury JM, Badger JH, et al. 2010. The *Ectocarpus* genome and the independent evolution of multicellularity in brown algae. *Nature* 465: 617–621.
- 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.
- 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*. *Proc Natl Acad Sci* 108: 11518–11523.

- Coelho SM, Scornet D, Rousvoal S, Peters N, Darteville L, Peters AF, Cock JM. 2012a. How to cultivate *Ectocarpus*. *Cold Spring Harb Protoc* doi: 10.1101/pdb.prot067934.
- Coelho SM, Scornet D, Rousvoal S, Peters N, Darteville L, Peters AF, Cock JM. 2012b. Genetic crosses between *Ectocarpus* strains. *Cold Spring Harb Protoc* doi: 10.1101/pdb.prot067942.
- Delaroque N, Müller DG, Bothe G, Pohl T, Knippers R, Boland W. 2001. The complete DNA sequence of the *Ectocarpus siliculosus* Virus EsV-1 genome. *Virology* 287: 112–132.
- Dillwyn LW. 1809. In *British Confervae or Colored Figures and Descriptions of the British Plants Referred by Botanists to the Genus Conferva* pp. 1–87; plates 69 and 100–109; W. Phillips, London, UK.
- Dittami S, Scornet D, Petit J, Ségurens B, Da Silva C, Corre E, Dondrup M, Glatting K, König R, Sterck L, et al. 2009. Global expression analysis of the brown alga *Ectocarpus siliculosus* (Phaeophyceae) reveals large-scale reprogramming of the transcriptome in response to abiotic stress. *Genome Biol* 10: R66.
- Gachon CMM, Strittmatter M, Müller DG, Kleinteich J, Küpper FC. 2009. Detection of differential host susceptibility to the marine oomycete pathogen *Eurychasma dicksonii* by real-time PCR: Not all algae are equal. *Appl Environ Microbiol* 75: 322–328.
- Gschloessl B, Guermeur Y, Cock J. 2008. HECTAR: A method to predict subcellular targeting in heterokonts. *BMC Bioinformatics* 9: 393.
- Heesch S, Cho GY, Peters AF, Le Corguillé G, Falentin C, Boutet G, Coëdel S, Jubin C, Samson G, Corre E, et al. 2010. A sequence-tagged genetic map for the brown alga *Ectocarpus siliculosus* provides large-scale assembly of the genome sequence. *New Phytol* 188: 42–51.
- Küpper FC, Carpenter LJ, McFiggans GB, Palmer CJ, Waite TJ, Boneberg EM, Woitsch S, Weiller M, Abela R, Grolimund D, et al. 2008. Iodide accumulation provides kelp with an inorganic antioxidant impacting atmospheric chemistry. *Proc Natl Acad Sci* 105: 6954–6958.
- Le Bail A, Billoud B, Maisonneuve C, Peters AF, Cock JM, Charrier B. 2008. Early development pattern of the brown alga *Ectocarpus siliculosus* (Ectocarpales, Phaeophyceae) sporophyte. *J Phycol* 44: 1269–1281.
- Le Bail A, Billoud B, Le Panse S, Chenivresse S, Charrier B. 2011. ETOILE regulates developmental patterning in the filamentous brown alga *Ectocarpus siliculosus*. *Plant Cell* doi: 10.1105/tpc.110.081919.
- Maier I, Parodi E, Westermeier R, Müller DG. 2000. *Maullinia ectocarpii* gen et sp nov (Plasmodiophorea), an intracellular parasite in *Ectocarpus siliculosus* (Ectocarpales, Phaeophyceae) and other filamentous brown algae. *Protist* 151: 225–238.
- Michel G, Tonon T, Scornet D, Cock JM, Kloareg B. 2010a. The cell wall polysaccharide metabolism of the brown alga *Ectocarpus siliculosus*: Insights into the evolution of extracellular matrix polysaccharides in eukaryotes. *New Phytol* 188: 82–97.
- Michel G, Tonon T, Scornet D, Cock JM, Kloareg B. 2010b. Central and storage carbon metabolism of the brown alga *Ectocarpus siliculosus*: Insights into the origin and evolution of storage carbohydrates in eukaryotes. *New Phytol* 188: 67–81.
- Müller DG. 1963. Die Temperaturabhängigkeit der Sporangienbildung bei *Ectocarpus siliculosus* von verschiedenen Standorten. *Pubbl staz zool Napoli* 33: 310–314.
- Müller DG. 1972. Studies on reproduction in *Ectocarpus siliculosus*. *Soc Bot France Mémoires*; 87–98.
- Müller D, Kapp M, Knippers R. 1998. Viruses in marine brown algae. *Adv Virus Res* 50: 49–67.
- Müller DG, Küpper FC, Küpper H. 1999. Infection experiments reveal broad host ranges of *Eurychasma dicksonii* (Oomycota) and *Chytridium polysiphoniae* (Chytridiomycota), two eukaryotic parasites in marine brown algae (Phaeophyceae). *Phycol Res* 47: 217–223.
- Peters AF, Marie D, Scornet D, Kloareg B, Cock JM. 2004. Proposal of *Ectocarpus siliculosus* (Ectocarpales, Phaeophyceae) as a model organism for brown algal genetics and genomics. *J Phycol* 40: 1079–1088.
- Peters AF, Scornet D, Ratn M, Charrier B, Monnier A, Merrien Y, Corre E, Coelho SM, Cock JM. 2008. Life-cycle-generation-specific developmental processes are modified in the immediate upright mutant of the brown alga *Ectocarpus siliculosus*. *Development* 135: 1503–1512.
- Peters AF, Mann AD, Córdova CA, Brodie J, Correa JA, Schroeder DC, Cock JM. 2010a. Genetic diversity of *Ectocarpus* (Ectocarpales, Phaeophyceae) in Peru and northern Chile, the area of origin of the genome-sequenced strain. *New Phytol* 188: 30–41.
- Peters AF, van Wijk SJ, Cho GY, Scornet D, Hanyuda T, Kawai H, Schroeder DC, Cock JM, Boo SM. 2010b. Reinstatement of *Ectocarpus crouaniorum* Thuret in Le Jolis as a third common species of *Ectocarpus* (Ectocarpales, Phaeophyceae) in western Europe, and its phenology at Roscoff, Brittany. *Phycol Res* 58: 157–170.
- Ritter A, Ubertini M, Romac S, Gaillard F, Delage L, Mann A, Cock JM, Tonon T, Correa JA, Potin P. 2010. Copper stress proteomics highlights local adaptation of two strains of the model brown alga *Ectocarpus siliculosus*. *Proteomics* 10: 2074–2088.
- Russell G. 1967a. The ecology of some free-living Ectocarpaceae. *Helgol Wiss Meeresunters* 15: 155–162.
- Russell G. 1967b. The genus *Ectocarpus* in Britain. II. The free-living forms. *J Mar Biol Assoc UK* 47: 233–250.
- Russell G. 1983a. Formation of an ectocarpoid epiflora on blades of *Laminaria digitata*. *Mar Ecol Progr Series* 11: 181–187.
- Russell G. 1983b. Parallel growth patterns in algal epiphytes and *Laminaria* blades. *Mar Ecol Progr Series* 13: 303–304.
- Silberfeld T, Leigh JW, Verbruggen H, Cruaud C, de Reviers B, Rousseau F. 2010. A multi-locus time-calibrated phylogeny of the brown algae (Heterokonta, Ochrophyta, Phaeophyceae): Investigating the evolutionary nature of the “brown algal crown radiation”. *Mol Phylogenet Evol* 56: 659–674.
- Thomas DN, Kirst GO. 1991a. Differences in osmoacclimation between sporophytes and gametophytes of the brown alga *Ectocarpus siliculosus*. *Physiol Plant* 83: 281–289.
- Thomas DN, Kirst GO. 1991b. Salt tolerance of *Ectocarpus siliculosus* (Dillw.) Lyngb: Comparison of gametophytes, sporophytes and isolates of different geographic origin. *Bot Acta* 104: 26–36.

Cold Spring Harbor Protocols

***Ectocarpus*: A Model Organism for the Brown Algae**

Susana M. Coelho, Delphine Scornet, Sylvie Rousvoal, Nick T. Peters, Laurence Darteville, Akira F. Peters and J. Mark Cock

Cold Spring Harb Protoc; doi: 10.1101/pdb.emo065821

Email Alerting Service

Receive free email alerts when new articles cite this article - [click here](#).

Subject Categories

Browse articles on similar topics from *Cold Spring Harbor Protocols*.

[Bioinformatics/Genomics, general](#) (192 articles)
[Developmental Biology](#) (728 articles)
[Emerging Model Organisms](#) (321 articles)
[Evolution](#) (92 articles)
[Evolutionary Development \(Evo-Devo\)](#) (97 articles)
[Genetics, general](#) (374 articles)

To subscribe to *Cold Spring Harbor Protocols* go to:
<http://cshprotocols.cshlp.org/subscriptions>