Discipline Courses-I
Semester-I
Paper: Phycology and Microbiology
Unit-X
Lesson: Ectocarpales and Fucales
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Ectocarpales

It is the least specialized and most primitive group of Phaeophyceae where majority of the plants are annuals. The plant body exhibits great range of morphological diversity. The body plan is **heterotrichous** with various advances exhibited by the erect portion. The group has simple filamentous types as in *Ectocarpus siliculosus* as well as relatively elaborate forms with compact filaments whose intercalary growth may be diffuse or restricted to distinct meristematic zones with many colourless and multicellular hairs showing basal meristem.

Reproduction is **isogamous** as in *E. siliculosus* to **anisogamous** as in *E. secundus*. Life cycle which essentially is **diplo-haplontic**, in early forms is **isomorphic** as in *Ectocarpus* sp. and in relatively advanced forms like *Colpomania sinuosa*, it is **heteromorphic** alternating between erect and filamentous prostrate thalli (Toste et al 2003). The haploid gametophyte produces biflagellate gametes in plurilocular gametangia and the diploid sporophyte produces haploid meiospores or meiozoospores in unilocular sporangia and asexual diploid zoospores in **plurilocular** sporangia.

Ectocarpus sp

Habit and habitat

It is of worldwide distribution preferring temperate waters. It grows attached to rocks and stones but may occur as an **epiphyte** attached to other algae and plants. *E. fasiculatus* occurs as an **endophyte** in the blades of *Laminaria digitata* (Russell 1983). *Ectocarpus* is normally fixed to the substratum but it may be detached, surviving as a floating thallus. Here it perhaps loses its polarity (Russell 1967). According to Cock et al (2010), two enzymes---dehalogenases and haloalkane dehalogenases may help *Ectocarpus* grow epiphytically on other algae by defending it against halogenated molecules produced by the hosts as defense mechanisms.

Morphology and construction

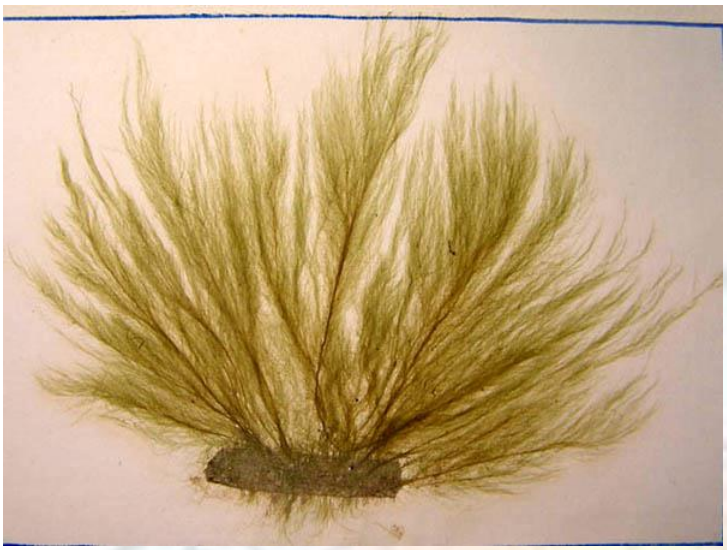

Figure *Ectocarpus* thallus is simple feather like and is attached to the substratum or the host by a small holdfast.

Source:

http://cfb.unh.edu/phycokey/Choices/Fucophyceae/ECTOCARPUS/Ectocarpus_05_600x450_sp.jpg

The members are macroscopic, multicellular, and heterotrichous in construction. The lower parts of the filaments are variously aggregated to form a more or less solid, creeping portion which covers the substratum and acts as a prostrate rhizoid-like portion. This prostrate system gives rise to a number of upright branches uniseriate in construction that form an erect system.

There is no special apical cell and the growth occurs by the division of an intermediate group of cells in the filament, which forms a meristematic zone, growth therefore is of intercalary type. Cells of the filaments are shortly cylindrical to regular containing single nucleus and irregularly- shaped chromatophores with pyrenoids. Rest of the cell contents are typical of the brown algae.

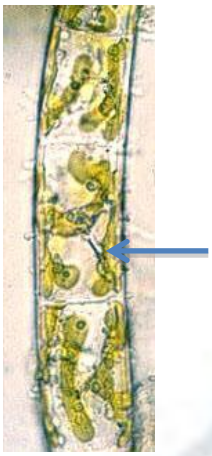

Figure: *Ectocarpus* is characterized by the presence of irregularly shaped chromatophores with pyrenoids(arrow)

Source:http://www.horta.uac.pt/species/Algae/Ectocarpus_siliculosus/Ectocarpus_siliculosus_b.jpg

Reproduction

Asexual reproduction occurs by flagellate zoospores produced in unilocular and plurilocular sporangia but always on the sporophyte.

Figure: A section of the *Ectocarpus* thallus with plurilocular and unilocular sporangia

Source:**http://starcentral.mbl.edu/msr/rawdata/viewable/ectocarpus_conifervoides_1271319570_g_543w.jpg**

Regarding sexual reproduction, most of the species are dioecious while some are monoecious where + and – gametangia occur on the same thallus.

There are two characteristic reproductive structures, the unilocular and the plurilocular sporangia.

Figure : *Ectocarpus* thallus with plurilocular sporangium.

Source:http://cfb.unh.edu/phycokey/Choices/Fucophyceae/ECTOCARPUS/Ectocarpus_04_600x483_kobe-u.ac.jp.jpg
http://cfb.unh.edu/phycokey/Choices/Fucophyceae/ECTOCARPUS/Ectocarpus_01_500x511_branch_sheath_rock.jpg

The unilocular sporangium produced on a diploid sporophyte (also referred to as meiosporangium) is a single large globular or pear-shaped cell which becomes densely filled with protoplasm.

Figure: Unilocular sporangia

Source: http://www.jochemnet.de/fiu/bot4404/Br_Ectocarpus_Uniloculi.jpg

The nucleus divides first meiotically and then mitotically without the cell wall formation. Around each nucleus small amount of cytoplasm gets collected and nuclei get transformed into pear-shaped, biflagellate zoospores or meiozoospores which are liberated through a small pore in the apical region. They swim for sometime settling down to give rise to a

haploid plant --- the gametophyte. This haploid plant represents the gametophytic stage of the alga (which produces only one type of spore producing structures, the gametangia).

The sporophyte also produces plurilocular sporangia either on same plant that bears unilocular sporangia or on different plant. These plurilocular sporangia on diploid filament produce asexual zoospores that germinate to produce diploid filaments like parents.

Sexual plants or gametophytes in most cases are dioecious, bearing plurilocular sporangia which are generally regarded as gametangia. The plurilocular gametangia are either sessile on a branch or at the end of a short row of sterile cells. The protoplasmic contents divide by transverse and longitudinal walls into a large number (upto 660 in *E. siliculosus*) of cells, each of which produces biflagellate motile gamete, similar in structure to the products of unilocular sporangia but with a difference that these structures on liberation fuse in pairs to form zygote. The zygote later gives rise to a diploid plant, the sporophyte.

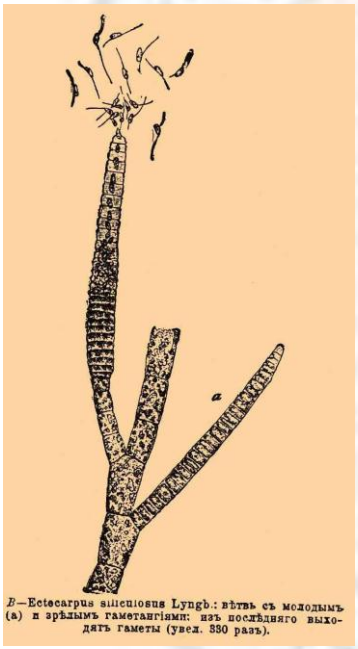

Figure: *Ectocarpus*- Liberation of zoospores

Source: http://content62.eol.org/content/2012/06/15/22/71058_orig.jpg

Thus the sporophytic phase bears two types of sporangia, the unilocular and the plurilocular. The unilocular sporangia are meant for regeneration of the gametophyte or the monoploid plant and the plurilocular for asexual reproduction (diploid to diploid). The production of reproductive organs by sporophyte was shown to be regulated by temperature with meiospore-containing unilocular sporangia being produced at lower temperature and mitospore-containing plurilocular sporangia being produced at higher temperature (Müller 1963).

What is interesting about *E. siliculosus* is that morphologically it is isogamous but functionally oogamous. The 'female' gamete is +vely thigmotactic. This means if the gamete touches the surface it settles down and attaches itself to the surface. It then secretes within 30 minutes of release 'ectocarpene', a chemical that diffuses into the surrounding waters (Müller 1969). Another recently discovered chemical secreted by the female gamete is preectocarpene (Pohnert and Boland 2002). The male gamete has a +ve **chemotaxis** and it swims towards the source of ectocarpene. The male gametes respond in 4 ways (Maier 1995; Maier and Calenberg 1994). They display a preference to remain close to solid surfaces (a **thigmotactic** response), which increases the presence of pheromones. It also results in decreasing the swimming speed of the male gametes (an **orthokinetic** response) and increases their rate of turning (a **klinokinetic** response) as pheromone concentration increases. Müller (1979) termed this behaviour as chemo-**thigmo-klinokinesis.** The male gametes are naked biflagellate cells of 6-12 µm length. The male gametes become attached to the female with the tip of the anterior flagellum and rotate the female. The gametes are pulled forward by the flagellum which bears tripartite tubular hairs. The short posterior directed flagellum is smooth with a steering function (Müller and Falk 1973). Though many male gametes make an effort to fuse, only one succeeds in the act and others leave. The posterior ends of two gametes then fuse to form a diploid zygote which grows to give rise to a new plant.

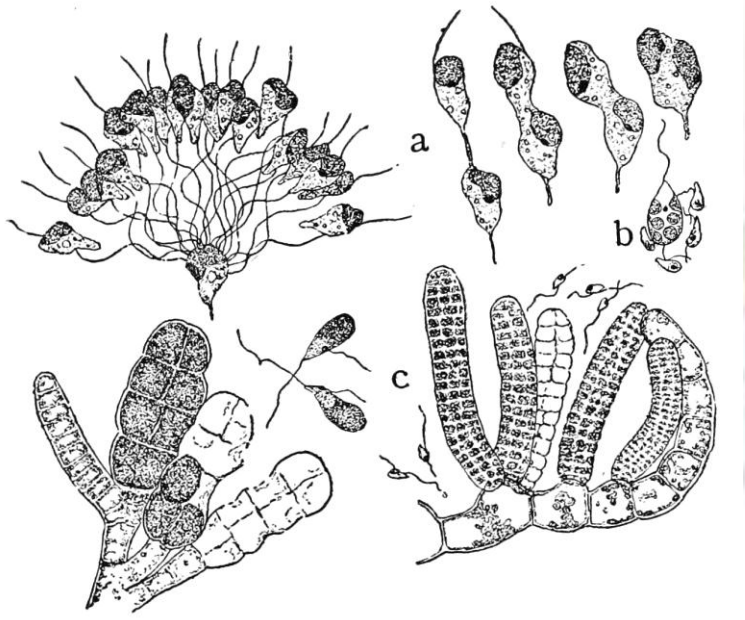

Figure: Sexual reproduction in *Ectocarpus* a. clump formation between one female and many male gametes. b. the two gametes fuse and form the zygote. c. liberation of the zoospores

Source: http://content61.eol.org/content/2012/06/15/22/02777_orig.jpg

Life cycle

Ectocarpus has a haploid-diploid life cycle involving alternation between two multicellular generations: the sporophyte and the gametophyte. The haploid and diploid plants are morphologically indistinguishable making it an isomorphic type of life cycle.

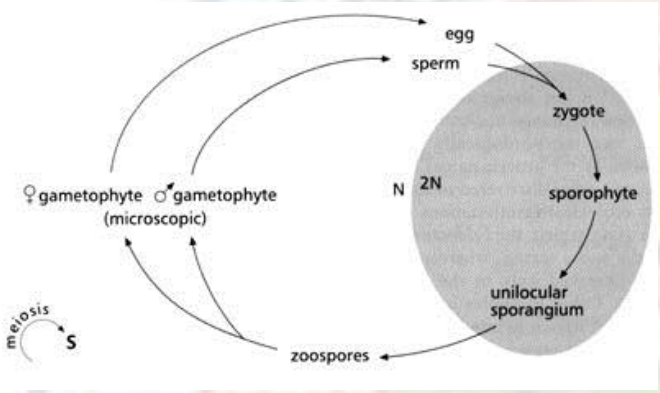

Figure: *Ectocarpus* life cycle

Source: http://www.jochemnet.de/fiu/bot4404/Br_Laminaria_lifecycle.jpg

Do u know?

Gametes which do not find a mate can develop **parthenogenetically** into a sporophyte. These partheno-sporophytes (Bothwell et al 2010) through endoduplication event early during development form diploid individuals or they remain haploid and meiospores are produced via **non reductive apomeiotic** division in the developing unilocular sporangium. Gametophytes become new sporophytes and alternation of generation is bypassed.

The algal genetics group in Roscoff (France) proposed *E.siliculosus* as a model organism for the application of genetics and genomic approaches to brown algae (Peters et al 2004). A detailed multigene study has provided information of algal phylogeny. The Ectocarpales are considered as the ancestral group for all other brown algae, a sister group to the Laminariales and are thought to have changed least since the origin of Phaeophyceae. The ancestral Ectocarpalean algal group with isomorphic **diplohaplontic** life cycle is suggested to have creeping filaments with apical growth and erect filaments with intercalary growth. All other orders of brown algae are thought to have been derived from the ancestral

Ectocarpales where the simple filamentous Ectocarpalean morphology represents a secondarily derived simplification (Schaechter 2011).

Fucales

Fucales, the largest order of Pheaophyceae, is a morphologically diverse group (Rousseau and De Reviers 1999). Fucales worldwide in distribution , are represented by quite different taxa in different parts of the globe. To exampify, *Fucus* attains greatest development in cold waters of Northern hemisphere whereas in tropical waters *Sargassum* predominates; *Cystophora* is common in Australia and *Durvillaea* is widespread in the subantarctic regions especially southern New Zealand and Chile. *Pelvetia canaliculata* is said to be upper shore alga because it 'shuns water' (Schonbeck and Norton1979). It is well adapted to an existence of alternating submersion in seawater and exposure to air and is more maritime than marine. Whatever their preferences, the members are found exclusively in marine habitats; in the intertidal and up into the spray zone.

Although most of the members are lithophytes, and remain attached to rocks through holdfast (in some members like *Turbinaria conoides* holdfast is much more elaborate with finger-like extensions known as haptera which provide stronger anchorage to the alga), unattached forms that propagate vegetatively are also known e.g. *Sargassum natans* which occurs in North Atlantic Ocean as huge floating masses is known to form Sargasso Sea. It is the only seaweed which reproduces sexually while afloat. Some species like *Fucus cottonii* are commonly found in well drained muddy/ sandy areas at the uppermost extent of tidal influence in salt marshes. They lack holdfasts, remain entangled amongst salt marsh vascular plants and are called ecads (see Wallace et al 2004). *F.radicans* grows in brackish environments.

Fucales are characterized by the following features:

- The plants are perennial with first year showing vegetative growth and reproduction occurring during the second year. Once reproductive maturity is reached, a regular seasonal periodicity in vegetative growth and reproduction occurs throughout the life of the alga.
- Growth occurs by apical cell (3 sided in Sargassaceae and 4 sided in Fucaceae) giving rise to a parenchymatous thallus.
- Reproductive structures (gametangia) are always present in more or less flask-shaped **conceptacles** which may be scattered but more frequently are limited to the inflated tips of special branches, the receptacles. Meiosis occurs during gametogenesis.

- Reproduction is oogamous with large non- motile egg and a small motile sperm. The fertilization is external.
- In several fucoids, the reproductive periodicity is correlated with lunar or tidal cycles (see Pearson and Serrao 2006).
- Life cycle is animal-like with gametes the only haploid phase.
- The members exhibit a diplontic life history.

Fucus sp

Habit and habitat

Fucus commonly known as bladder wrack or rockweed is frequently seen in northern temperate waters forming broad, dense canopies in the mid intertidal zone. *Fucus* spp are dominant members of the intertidal and shallow subtidal communities along North Atlantic and North Pacific Coasts (Lüning 1990) and the canopies are important to other algae for providing protection from desiccation.

Morphology and Anatomy

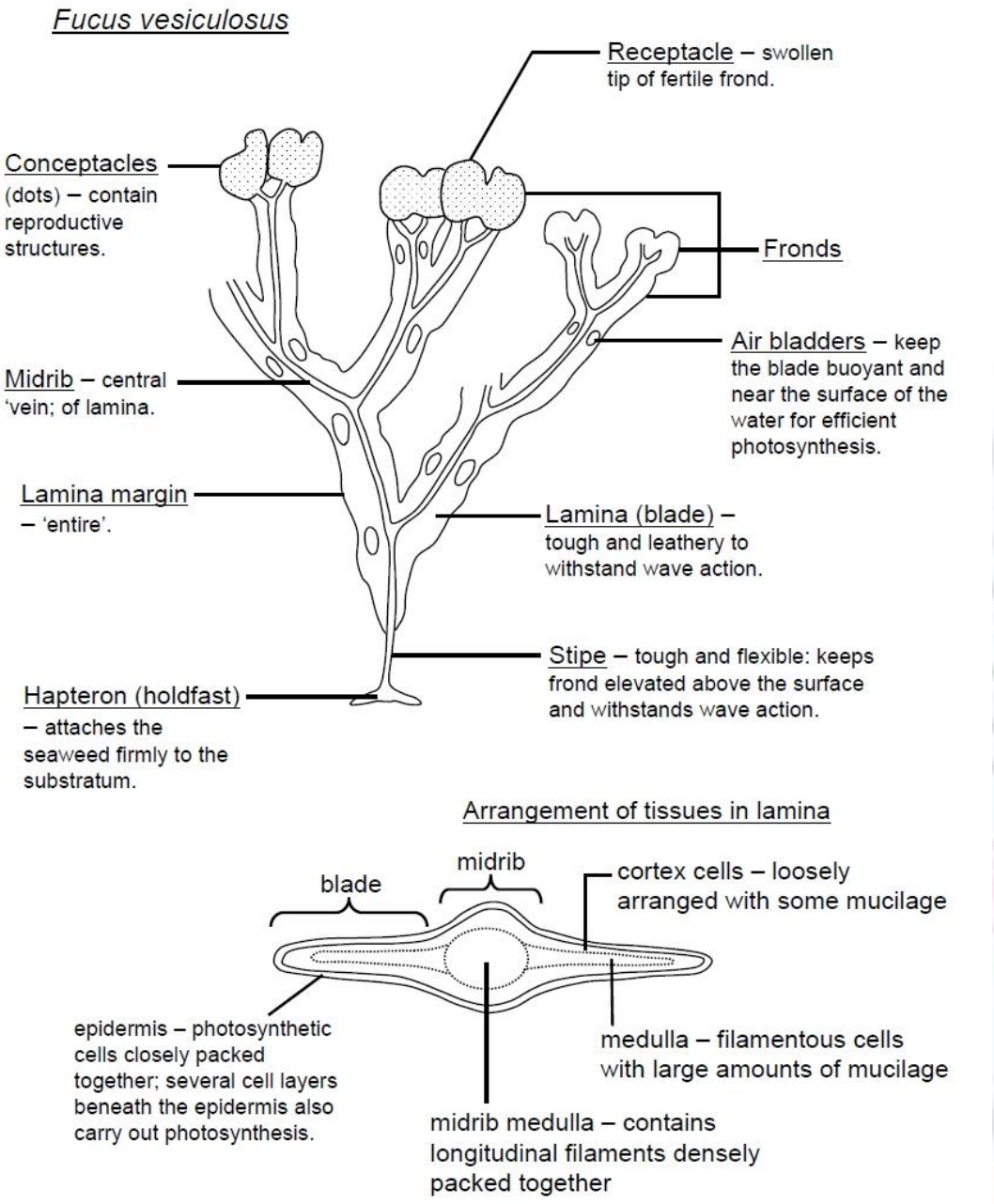

Figure: Morphology of the *Fucus* plant body.

Source: http://cronodon.com/images/Seaweeds_structure.jpg

The thallus is well differentiated into holdfast, stipe, blades and floats. Perennial thallus is anchored firmly on the substratum with an irregular or disc shaped holdfast. Towards the end of the growth period when the thallus dies, the plant regenerates from the holdfast. The holdfast gives rise to a stipe which ultimately leads to dichotomously branched blades which are flattened, with a distinct thick midrib on either side of which are wings. Gas filled

air vesicles or **pneumatocysts** are present in pairs on either side of the midrib which is also known to bear **cryptostomata**, the sterile cavaties bearing phaeophycean hairs .

Figure: *Fucus vesiculosus*, commonly known as bladder wrack because of the prominent air bladders or pneumatocysts.

Source: http://upload.wikimedia.org/wikipedia/commons/8/80/Bladder_Wrack_%28Fucus_vesiculosus%29_-_geograph.org.uk_-_224125.jpg

For more images visit: http://www.arkive.org/bladder-wrack/fucus-vesiculosus/photos.html

The tip of the thallus is invaginated with apical cell deep seated in the groove filled with mucilage. The apical cell cuts off derivatives which differentiate into outer **meristoderm**, middle cortex and inner medulla. Cortex forms the second tissue which acts as the storage zone and the medulla which is the innermost zone, has a mechanical function. Cortical and medullary cells give rise to long thick walled tubular cells which grow into the mucilage of the medulla and penetrate it growing downwards in it. Such cells are called hyphae and are so prominent at maturity that medulla seems a solid mass of thick walled hyphae (Godwin and Godwin 1945).

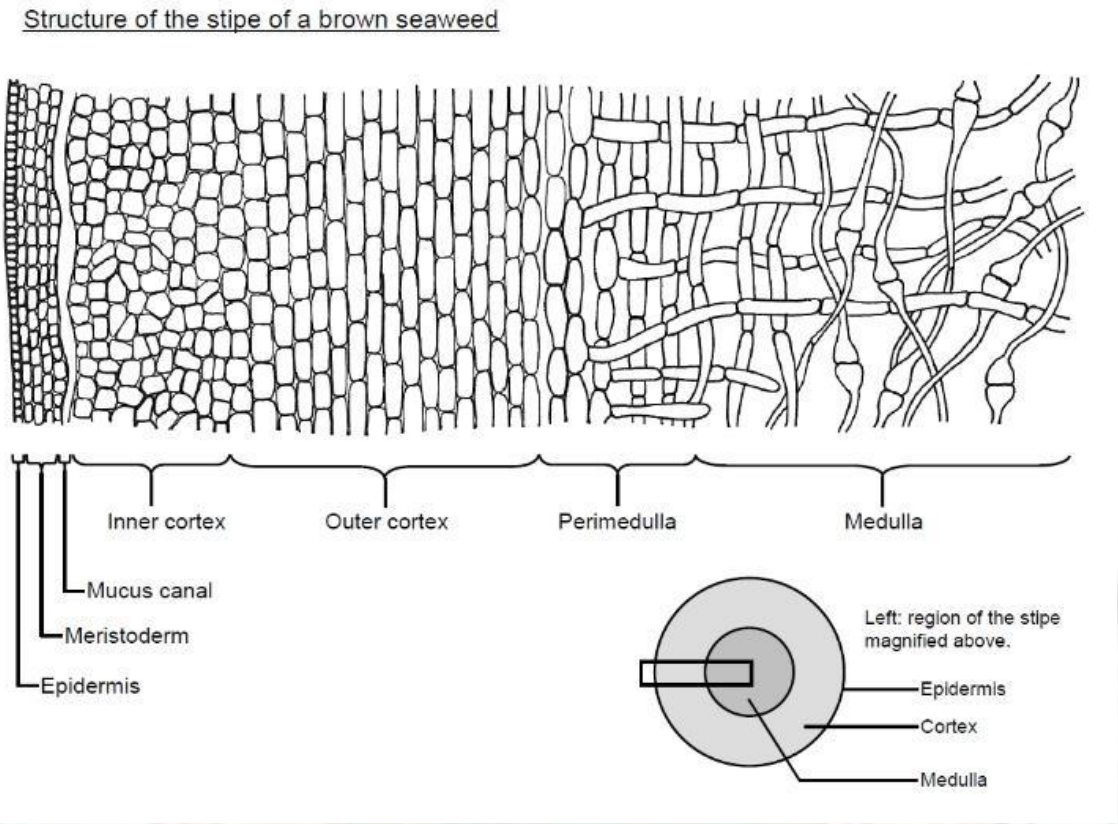

Figure: Section of the thallus through the stipe of *Fucus*

Source: http://cronodon.com/sitebuilder/images/Seaweeds_histology-738x531.jpg

The mature thallus is built from two sources---by the primary meristem and by the meristematic activity of the meristoderm. The primary meristematic zone lying in the apical groove extends beneath and around the sides of the apical cell and is called promeristem. The second meristem arises from the anticlinal and periclinal divisions in the meristoderm. *Fucus* shows an extraordinary method of increasing the thickness and strength of the midrib and stipe. It is referred to a method which involves cell growth from places other than the apical growing region and can be called as secondary growth (Godwin and Godwin 1945). The meristoderm besides having meristematic activity is also known to possess a large number of **physodes**. These phenol-containing vacuoles help the alga against intense sunlight and UV radiation. They are also involved in acting as a block in **polysermy** and are known to play an important role as herbivore deterrant (Schoenwaelder 2002). .

Reproduction

Fucus has the potential of asexual reproduction via the formation of adventive embryos on the rhizoids (Mc Lachlan and Chen 1972). It can also regenerate new apical meristems and distinct apical cells from wound healing tissue (Fulcher and Mc Cully 1969).

Sexual reproduction in *Fucus* is a highly complex and a co-ordinated seasonal phenomenon. In all cases towards the onset of sexual reproduction, the tips of mature ultimate fronds become swollen with mucilage and develop into receptacles that are covered with tiny pores or ostiole, each pore connecting to a chamber called a conceptacle .

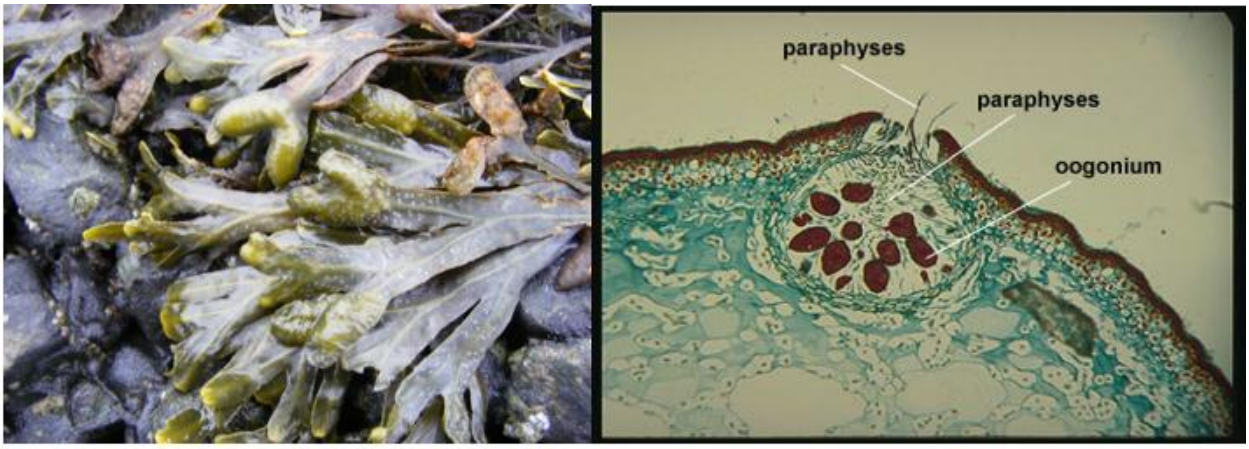

Figure: A. Thallus at the time of reproduction. Also seen are dot like structures the released oogonia **B.** V.S. of the receptacle showing female conceptacles bearing oogonia near the floor while the opening or the ostiole is lined by periphyses. Also seen are the dot-like structures, the released oogonia.

Source:A.http://upload.wikimedia.org/wikipedia/commons/0/0a/Fucus_vesicolosus_DSCF2551.JPG

B. http://www2.puc.edu/Faculty/Gilbert_Muth/phot0075.jpg

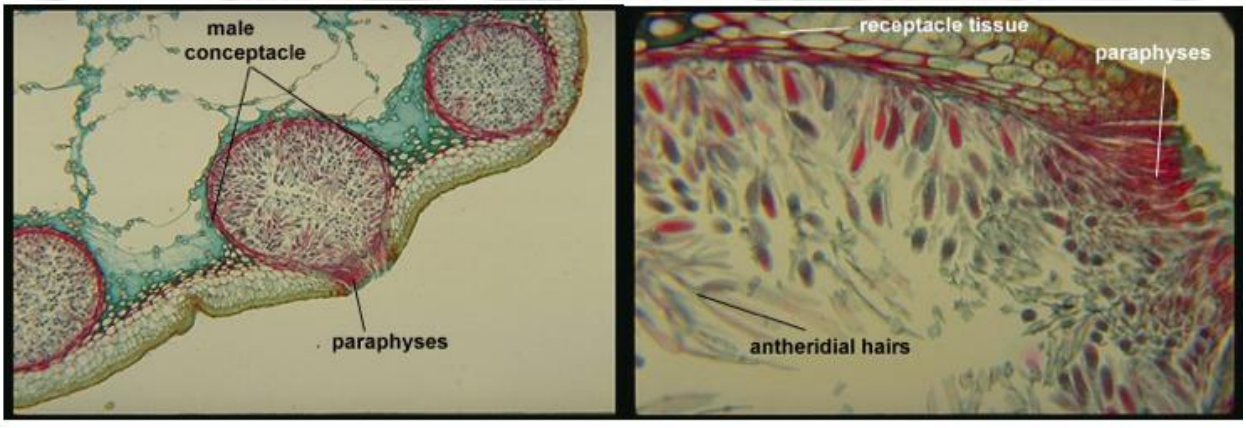

Figure: Section through the male conceptacle and magnified view of the antheridia

Source: http://www2.puc.edu/Faculty/Gilbert_Muth/phot0070.jpg

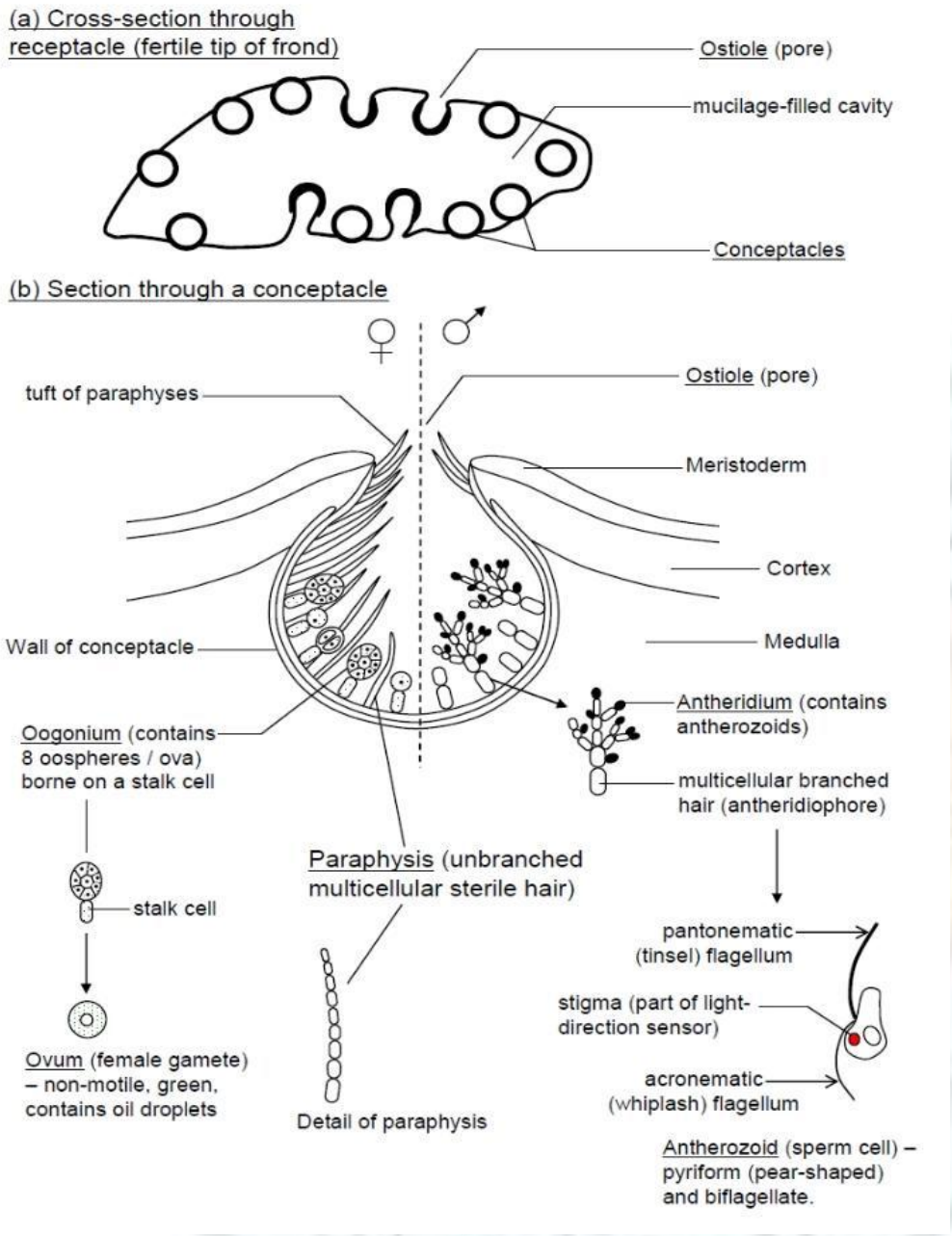

Figure: Portion of a male conceptacle enlarged to show antheridia.

Source: http://cronodon.com/sitebuilder/images/Seaweed_receptacle-732x932.jpg

The conceptacle is similar to cryptostomata in shape but is fertile and bears gametangia and a few sterile hairs. The distribution and function of these hairs is more specialized; the hairs near the ostiole are the **periphyses** and rest are the **paraphyses**. The periphyses help in lubricating the exit point of the conceptacle and facilitate in gamete expulsion (Kaur and Vijayaraghavan1993). At maturity, the conceptacles become swollen accommodating the

developing gametangia. This gives receptacles a warty appearance. The onset of receptacle formation occurs in late autumn in response to short days (Bird and Mc Lachlan 1976).

The reproduction is of oogamous type. In *Fucus vesiculosus* and *F. serratus* both the sexes---the antheridia and the oogonia are formed on separate plants and the species are dioecious. In *F. spiralis* however both the sexes occur on the same plant; condition being monoecious. In some of these monoecious species both sexes occur in the same conceptacle (i.e. the conceptacle itself is bisexual). In such cases the distribution of antheridia and oogonia is never intermixed. The antheridia are formed towards the opening, the ostiole and the sides of the conceptacle while the oogonia appear on the floor of the conceptacle or in other monoecious thalli, the conceptacles may themselves be unisexual, the receptacle itself being bisexual.

Mechanism of reproduction

The female gametangium or the oogonium remains embedded in the wall of the conceptacle with the help of a short stalk cell. The mature oogonium has three wall layers: the outer-exochiton, middle--- mesochiton and inner--- endochiton. The nucleus undergoes a meiotic division followed by one mitotic division giving rise to 8 haploid eggs. When the eggs are mature and ready to be shed, the exochiton ruptures and the eight eggs wrapped in the two wall layers are extruded out of the ostiole. At the same time a great deal of mucilage is also produced by the periphyses. The ostiole receives the secretions from the periphyses, the sterile hairs present near the opening making the exit of 'egg sac' easy. Even the paraphyses are involed in secretions. Once released out, the mesochiton and the endochiton also get dissolved and the eggs are set free for the reunion with spermatozoids.

The male gametangia, the antheridia are more in number and are found on the branched colourless hairs found all over in unisexual conceptacles or near the ostiole and sides in the bisexual conceptacle. Each antheridium has a two layered wall and the nucleus undergoes one meiotic and four mitotic divisions resulting in 64 nuclei. Each nucleus gets incorporated in a biflagellate spermatozoid. When the spermatozoids are mature, the outer layer of the wall ruptures and the spermatozoid packets are released through the ostiole. Once released, the inner layer of the wall also gets dissolved and the spermatozoids are set free in the water.

Gamete release which occurs in winter and early spring in *Fucus* is synchronous and is in response to the multiple environmental cues of light, dark, lunar and tidal cycles. In the tidal pools the release occurs at low tide whereas in intertidal members it is at high tides.

High release and settlement occurs exclusively under calm conditions, while turbulent waters discourage the release.

Fertilization

The intertidal fucoids face problems of gamete dispersal, gamete union and propagule recruitment. There is an obligate need to avoid gamete dilution for externally fertilizing species. Dilution may affect species depending on mating types eg selfing species may be less affected by gamete dilution. *F. spiralis*, a monoecious species (selfing species) has a greater egg dispersal radius; egg release and inbreeding occurring both when emersed and immersed. In *F. vesiculosus*, a dioecious species (outbreeding species), specific adaptation for timing egg release is seen. The egg release in such species is tied to periods when thalli are emersed in exposed habitats to avoid rapid gamete dilution that require outcrossing for fertilization (Ladah et al.2008). Moreover in such species, the gamete release (oogonium and antheridial) is also a co-ordinated event.

The chemical attractant **fucoserratene** is secreted by the eggs. This chemical signal is perceived by the spermatozoids that swim towards the egg and surround it. With the combined efforts of many spermatozoids, the egg is made to rotate till one spermatozoid gets entry and others are rejected. After a few hours of formation, the zygote adheres to the substratum. The first division in the zygote is unequal and gives rise to a larger thallus progenitor cell (TPC) and a smaller rhizoid progenitor cell (RPC). The RPC divides predominantly in one plane initially forming branching filaments of early holdfast whilst the TPC divides into all planes and forms germlings from which the whole plant is derived. The life cycle is therefore, diplontic.

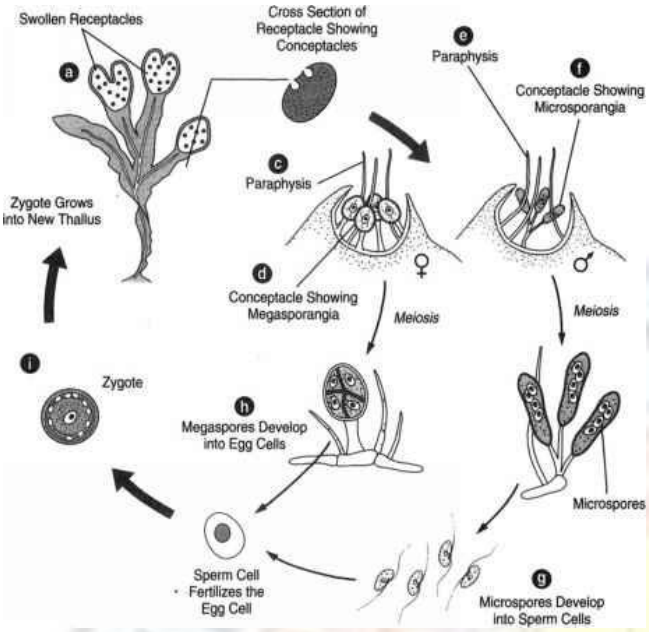

Figure: Life cycle of *Fucus* with gametic meiosis.

Source:http://www.78steps.com/green-algae/images/3297_103_123-brown-algae-reproduction.jpg

Summary

The order Ectocarpales containing the genus *Ectocarpus* is traditionally considered to be the most primitive in the Phaeophyceae because of the uniseriate thallus construction and more or less isomorphic alternation of generation. On the other hand Fucales, is the largest and the most advanced group of Phaeophyceae. Whereas the reproductive structures of Ectocarpales are contained in the simple sporangia and all are motile, the reproductive structures in Fucales are contained in conceptacles which are extremely complex in structure and function. Sexual reproduction is oogamous with small motile male gamete and large non-motile egg.

Exercise/ Practice

Short Questions

1. Write an explanatory note on types of sporangia found in *Ectocarpus*.
2. What are pheromones? What role do they play in reproduction?
3. With the help of neat diagram explain the structure of a bisexual conceptacle.
4. Fucoids are an extremely advance group of algae. Comment.

Glossary

Heterotrichous-In certain algae, a body that is divided into both prostrate and erect parts.

Isogamy reproduction resulting from union of two gametes identical in size and structure, as in protozoa.isog´amous

Anisogamous -A union between two gametes that differ in size or form.

Diplo-haplontic -A multicellular gametophyte, which is haploid with *n* chromosomes, alternates with a multicellular sporophyte, which is diploid with 2*n* chromosomes, made up of *n* pairs

Isomorphic- Having a similar structure or appearance but being of different ancestry (that is not related genetically.

Heteromorphic- dissimilar in shape, structure, or magnitude.

Plurilocular-Having several cells or loculi, specifically plurilocular, many-celled sporangia, each cell containing a single spore, as in many algae.

Epiphyte - a plant that grows upon another plant (such as a tree) non-parasitically or sometimes upon some other object derives its moisture and nutrients from the air and rain and sometimes from debris accumulating around it.

Endophyte-a fungus, or occasionally an alga or other organism, that lives within a plant

Chemotaxis- The characteristic movement or orientation of an organism or cell along a chemical concentration gradient either toward or away from the chemical stimulus.

Thigmotaxis- movement of an organism toward or away from any object that provides a mechanical stimulus.

Parthenogenesis- is a form of asexual reproduction in which growth and development of embryos occur without fertilization.

Klinokinesis- movement that is induced by stimulation and that involves essentially random alteration of direction

Conceptacle- One of many specialized hollow chambers containing reproductive structures that appear as dark, dotlike bodies on the surface of receptacles in certain algae and fungi.

Meristoderm-The outer meristematic layer of the thallus of certain brown algae (Phaeophyta). The cells of the meristoderm divide to increase the width of the thallus.

Physodes -any of various vesicular intracellular inclusions (phlorotanins) of brown algae that are of uncertain constitution and function.

Polyspermy-If more than one sperm penetrates an egg a situation called polyspermy, an abnormal embryo results, which would not survive.

Periphysis- a hair-like projection inside the ostiole of a conceptacle, perithecium or pycnidia**..**

Paraphysis- One of the erect sterile filaments often occurring among the reproductive organs of certain fungi, algae, and mosses.

Fucoserratene- Constituents of marine brown algae comprising 1,3,5-octatriene, 1,3,5-octatriene**.**

Suggested Readings

Bird N.L. and McLachlan J. 1976. Control of formation of receptacles in *Fucus distichus* L. subsp. *distichus* (Phaeophyceae, Fucales). Phycologia Vol. 15: 79-84.

Bothwell J.H., Marie D., Peters A.F., Cock J.M., and Coelho S.M. 2010. Role of endoreduplication and apomeiosis during parthenogenetic reproduction in the model brown alga *Ectocarpus*. New Phytol. 188: 111–121.

Cock J.M., Sterck L., Rouzé P., Scornet D., Allen A.E., Amoutzias G., Anthouard V., Artiguenave F., Aury J.M., and Badger J.H. 2010. The *Ectocarpus* genome and the independent evolution of multicellularity in brown algae. Nature 465: 617–621.

Fulcher R.G. and Mc Cully M.E. 1969. Histological studies on the genus Fucus.IV. Regeneration and adventive embryony. Can. J. Bot. 47:1643-1649.

Godwin H. and Godwin H. 1945. Plant biology: An Outline of the Principles Underlying Plant Activity. University Press Cambridge.

Kaur I. and Vijayaraghavan M.R. 1993. Histogenesis and conceptacle organization in *Sargassum vulgare* C. Agardh (Fucales, Phaeophyta). Japanese Journal of Phycology 41: 247-252

Ladah L.B., Fedderson F., Pearson G.A.; and Serrao E.A. 2008. Egg release and settlement patterns of dioecious and hermaphroditic fucoid algae during the tidal cycle. Marine Bio logy 155: 583.

Lüning K. 1990. Seaweeds—Their Environment, Biogeography and Ecophysiology. John Wiley & Sons, Inc., New York.

Maier I, and Calenberg M. 1994. Effect of extracellular Ca^{2+} and Ca^{2+}-antagonists on the movement and chemoorientation of male gametes of *Ectocarpus siliculosus* (phaeophyceae). Bot. Acta. 107:451–460.

Mc Lachlan J. and Chen L.C.M. 1972. Formation of of adventives embryos from rhizoidal filaments in sporelings of four species of *Fucus* (Phaeophyceae). Can. J. Bot. 50:1814-1844.

Müller D.G. 1963. Die Temperaturabhängigkeit der Sporangienbildung bei *Ectocarpus siliculosus* von verschiedenen Standorten. Pubbl staz zool Napoli 33: 310–314.

Müller D.G. 1995. Brown Algal Pheromones. In : Progress in Phycological research (F.E Round and DG Chapman Eds.) Vol 11:sz6r51-102, Biopress Ltd. Bristol.

Müller D.G. and Falk H. 1973. Flagellar structure of the gametes of *Ectocarpus siliculosus* (Phaeophyta) as revealed by negative staining. Arch. Mikrobiol. 91:313-22.

Müller D.G.1979. Genetic affinity of *Ectocarpus siliculosus* (Dillwyn) Lyngbye. from the Mediterranean, North Atlantic and Australia. Phycologia 18:312-18.

Pearson G. A. and Serr~ao, E. A. 2006. Revisiting synchronous gamete release by fucoid algae in the intertidal zone: fertilization success and beyond? Integr. Comp. Biol. 46:587–97.

Peters A.F., Marie D., Scornet D., Kloareg B.,and Cock J.M. 2004. Proposal of *Ectocarpus siliculosus* (Ectocarpales, Phaeophyceae) as a model organism for brown algal genetics and genomics. J Phycol. 40: 1079–1088.

Pohnert G. and Boland W. 2002. The oxylipin chemistry of attraction and defense in brown algae and diatoms. Natural Products Reports 19:108-122.

Rousseau F. and De Reviers B. 1999. Phylogenetic relationships within the Fucales (Phaeophyceae) based on combined partial SSU+LSU rDNA sequence data. European J Phycology Vol34 pp 53-64.

Russell G. 1967. The genus *Ectocarpus* in Britain. II. The free-living forms. J. Mar. Biol. Assoc. UK. 47: 233–250.

Russell G. 1983. Formation of an ectocarpoid epiflora on blades of *Laminaria digitata*. Mar. Ecol. Prog. Ser. Vol. 11: 181-187.

Schaechter M. 2011. Eukaryotic Microbes Academic Press.

Schoenwaelder M.E.A. 2002. The occurrence and cellular significance of physodes in brown algae. Phycologia 41:125-139.

Schonbeck M.W. and Norton T.A. 1979. Drought hardening in the upper shore seaweeds *Fucus spiralis* and *Pelvetia canaliculata*. Journal of Ecology. 67:687-696.

Toste M.F., Parente M.I., Neto A.I. and Fletcher R.L. 2003. Life history of *Colpomenia sinuosa* (Scytosiphonaceae, Phaeophyceae) in the Azores. J. Phycol. 39: 1268-1274

Wallace I., Klein A.S. and Mathieson A.C. 2004. Determining the affinities of salt marsh fucoids using microsatellite markers: evidence of hybridization and introgression between two species of *Fucus* (Phaeophyta) in a Maine estuary. J. Phycol. 40:1015-27.