

Biological Interactions during the Life History of Seaweed -A Microscopic Review-

Ichiro Mine*

Graduate School of Kuroshio Science, Kochi University
(2-5-1, Akebono, Kochi 780-8520, Japan)

Abstract

Seaweed is important for human beings as food. From an ecological viewpoint, it also occupies a substantial position as the primary producer in the marine food chain and as a nursery for many marine animals. Fundamental biological features are in great diversity in seaweed. The composition of photosynthetic pigments is distinct among three major groups of seaweed; green, brown and red algae. There is also a wide range of life history patterns including the isomorphic and heteromorphic alternation of haploid gametophyte/diploid sporophyte found in all groups of seaweed.

In order to understand how seaweed vegetation is constructed, it is important to know how the algae live in the seashore environment, coexisting with a variety of other organisms. In this talk, I present interesting examples of research concerning the biological interactions occurring at the cell-to-cell level in three consecutive stages of the life history of seaweed: (1) spore attachment and germination, (2) vegetative growth and morphogenesis, and (3) sexual reproduction. Topics include several earlier and recent studies, for example, the inhibition of spore attachment by medium conditioned with parent thallus, trace morphogenetic substance inducing single-layer, blade-like thallus in the green alga *Monostroma*, and physiological mechanisms that support the sexual recognition of gametes during fertilization in the external environment.

Introduction

Seaweed, or benthic marine algae, differs from the plant known as “sea grass” which belongs to a group of higher flowering plants (monocots), and contains many groups of algae but it is usually distinguished from unicellular algae or phytoplanktons. Seaweed is divided into three major groups, green algae, brown algae and red algae. These names originated from the color of their bodies and the difference in the body color is caused by the difference of the composition of photosynthetic pigments. It is distributed in only coastal regions of the sea because it is a benthic organism and lives by photosynthesis. In principle, algae require a water environment, so they can live up as far as the splash zone in the seashore and down to about 30 m deep in the sea, where they can get enough light for photosynthesis (Fig. 1).

Seaweed is ecologically important as a primary producer in the marine ecosystem. It is well known that nearly half of the primary production on the earth is synthesized in the ocean according to the amount of chlorophyll distribution. Because seaweed lives only along the

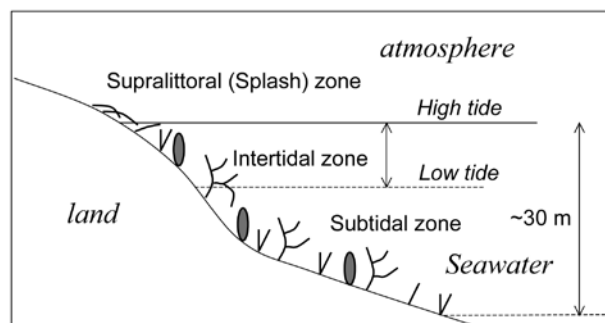


Fig. 1. Distribution of seaweeds along seashore

edge (seashore) of the ocean, amount of the primary production might not be so significant, but the efficiency is quite remarkable. It sometimes reaches more than 1.5-kg carbon per square meter (Mann, 1973). This value is comparable to the production in the tropical rain forest. In addition, seaweed also serves as the place where other marine organisms grow during their early development. Actually, seaweed beds are sometimes referred to as the nursery of marine animals.

Seaweed is also economically important, especially as food. For example, compared to what is caught from

*Corresponding author: e-mail mine@cc.kochi-u.ac.jp

nature, we Japanese cultivate a large amount of seaweed, which sums to nearly 30% of total fishery cultivation products. The especially the striking production is of *Porphyra* or Nori (about 100 billion yen according to statistics by the Fisheries Agency, Japan, 2005), and we eat it very often in daily life.

Basic biological studies have revealed that seaweed shows many life history patterns and there are a variety of interactions between individual seaweeds and other organisms and the environment during its life history. In this review, I firstly introduce the variation of life histories in seaweed and then show a number of selected studies concerning the interactions among organisms occurring in the stages of the life history of seaweed in order to provide information useful in studying the coastal vegetation of seaweed.

1. Variation of life histories in seaweed

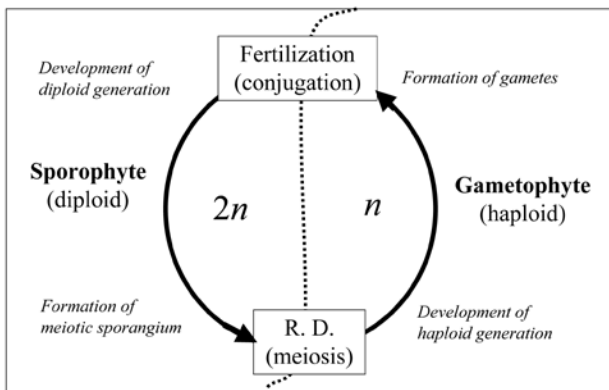


Fig. 2. Basic pattern of life history

Figure 2 shows the basic pattern of life history of eukaryotes except for animals. In the life history, the haploid gametophyte and diploid sporophyte alternate to each other through fertilization and reduction division. In animals, the products of reduction division, egg and sperm, fertilize to form the diploid generation directly without development of haploid cells. Therefore, their life history lacks haploid generation. In contrast, other groups of eukaryotic organisms, e.g., plants, fungi and algae, principally show life histories that alternate diploid and haploid generations. Moreover, in the terrestrial plants such as seed plants, ferns and mosses, life history patterns are fundamentally common within each group. For example, the main body of mosses is haploid and the diploid generation develops from the fertilized egg to only a small body, parasitic to the female haploid generation. Ferns also represent “heteromorphic” alternation of sporophyte and gametophyte generations but the haploid generation, usually called prothallium, is much smaller

than the diploid generation in the main body of ferns.

In seaweed, the life history patterns are further diverse compared to other groups of organisms. Here, I will show the examples of three representative life history patterns from the three major groups of seaweed as follows:

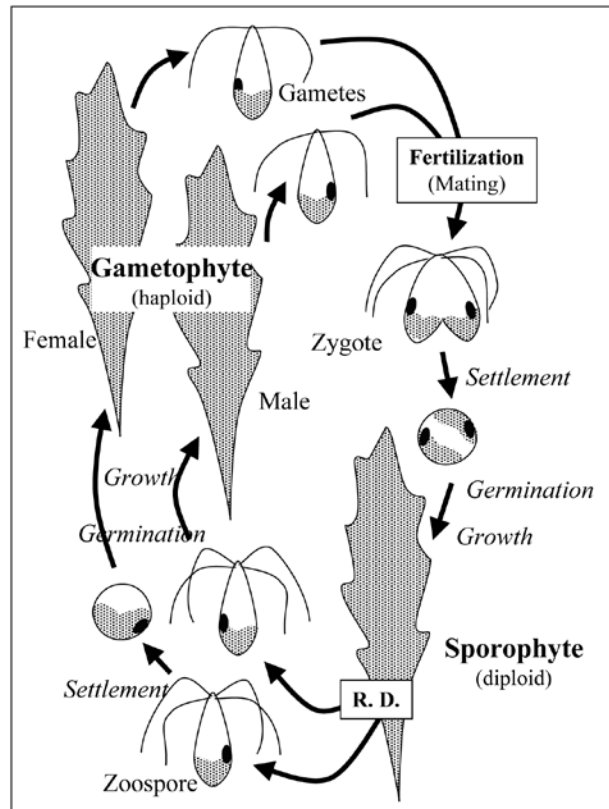


Fig. 3. Isomorphic life history of the green alga *Enteromorpha*

In the green alga *Enteromorpha*, (Fig. 3), the alternation of generations is “isomorphic” and the sporophyte and female and male gametophytes are not distinguishable from each other by external morphology. The fertilization, or conjugation, is carried out by actively motile, female and male gametes with two flagella. Kelp, the brown alga *Laminaria* (Fig. 4), exhibits heteromorphic alternation between macroscopic diploid sporophyte and female and male, microscopic haploid gametophytes. The fertilization occurs between non-motile egg and motile sperm that are produced by the microscopic gametophytes.

In contrast, the macroscopic thalli of the red alga *Porphyra* are the haploid gametophyte (Fig. 5). The zygote develops diploid spores that grow into microscopic diploid sporophytes. In addition, there are no motile cells with flagella in the life history of red algae. Thus all of the three basic patterns: alternation of isomorphic generations, alternation of macroscopic sporophyte

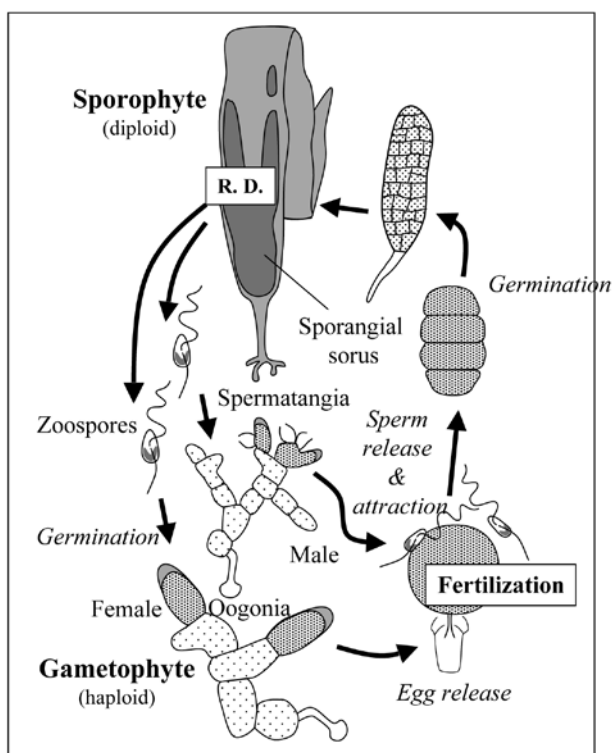


Fig. 4. Heteromorphic life history of the brown alga *Laminaria*. "Sporophyte > Gametophyte" type

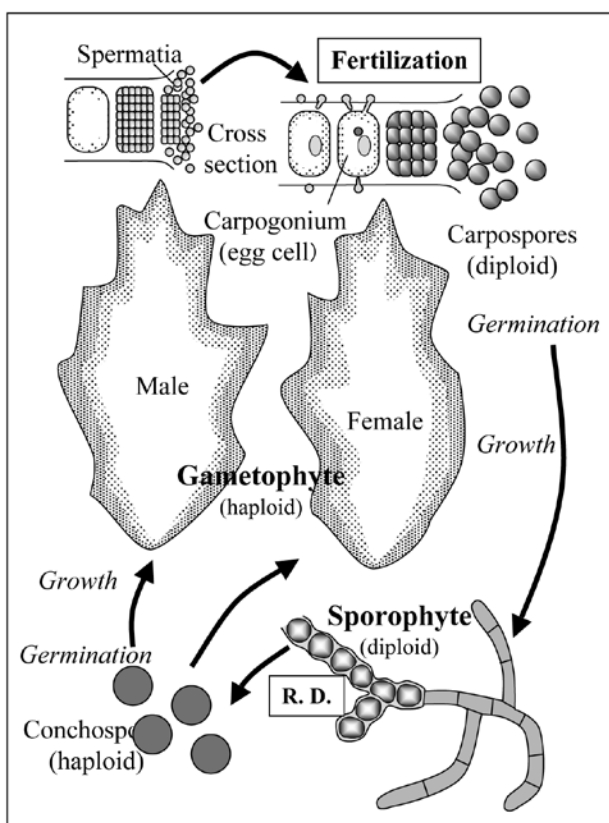


Fig. 5. Heteromorphic life history of the red alga *Porphyra*. "Gametophyte > Sporophyte" type

and microscopic gametophyte, and alternation of macroscopic gametophyte and microscopic sporophyte, exist in seaweed. Actually, all of these patterns occur in each of the three major groups; green algae, brown algae and red algae.

2. Biological interactions in the vegetative phase

A number of studies have revealed that various kinds of interactions occur among the algae and also between seaweed and other organisms during the stages of vegetative development of seaweed. The life of seaweed begins with the attachment and germination of spores. In general, the differentiation of the algal body is not so obvious as in terrestrial plants, but usually organs that function as a holdfast are developed early. For example, a rhizoid is differentiated from the upright thallus as in this slide. Sometimes the rhizoid develops into a complicated structure and produces adhesive substances to hold the algal body on the rock, even in strong water movement in the seashore (Fletcher and Callow 1992).

In the red alga *Palmaria* sp. an interesting biological interaction has been observed in spore attachment (Mine and Tatewaki, unpublished). Spores of the alga are liberated from mature sporophyte into seawater and upon their settlement on a suitable substratum, they firmly attach to and largely expand on the substratum before the first cell division in germination (Fig. 6a, b). The spores were experimentally collected by incubating a parent plant in the synthetic medium ASP12, and the parent plant was then removed. The spores were left in the medium conditioned with the parent plant and further subjected to spore-settlement experiments.

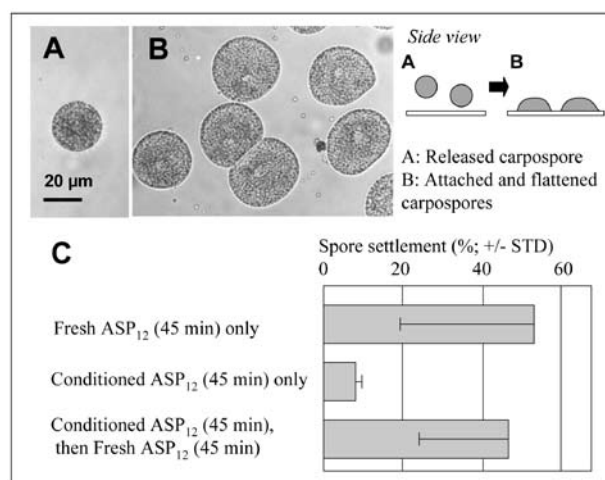


Fig. 6. Spore settlement in the red alga *Palmaria* sp. and inhibition of spore attachment by conditioned medium

After re-suspension of spores in the fresh medium, spores readily attached and settled on the glass substratum, but spores re-suspended in the conditioned medium again did not settle well (Fig. 6c). If the unattached spores were transferred to the fresh medium, they readily attached and began germination at once. These results indicate that the parent plant may produce and secrete some substances that inhibit the attachment of its own spores. Although there are no data from the field experiments, this may have some ecological significance because such inhibition may result in wider distribution of spores and control of the growth of epiphytes.

After the settlement and germination of spores, the thallus of the seaweed is formed by vegetative growth. There are several examples of plant growth substances, or hormones, such as auxins, that control the vegetative growth of higher, terrestrial plants. It may be possible that such plant growth hormones are also involved in seaweed growth. But as investigated so far, the results are controversial and no general conclusion is obtained (e.g., Buggeln, 1976; Lin and Stekoll, 2007).

On the other hand, there is one example of growth hormone originally discovered in seaweed. The marine red alga *Griffithsia* is in the form of branching filaments composed of giant multinuclear cells that attain a few millimeters in size. When one of the intercalary cells is injured leaving an empty cell wall cylinder, a wound-healing reaction occurs. In the reaction, repair shoot cells are cut from the upper and lower neighboring cells, the repair cells elongate by tip growth until they fuse with each other, and then the newly formed cell replaces the dead cell. Waaland and her colleagues found that some substance secreted by the alga is required for the elongation of the repair shoot cells (Waaland and Watson, 1980). The extracts contained a glycoprotein of certain molecular mass that exhibited an activity inducing the tip growth of the shoot cells.

In terms of the regulation of morphogenesis, an important finding was made using the green alga *Monostroma*. As implied by the name, the blade-like thallus is composed of a single layer of regularly arranged vegetative cells. About 25 years ago, Tatewaki and colleagues reported that a species of *Monostroma* grows into an irregular mass of cells when it is cultured axenically using an artificial, synthetic medium, and the monostromatic thallus morphology was recovered when the cell mass was cultured with bacteria or other seaweed (Tatewaki *et al.*, 1983).

This indicates that the thallus morphogenesis of *Monostroma* is induced by the exogenous substance that is produced by co-existing organisms. A number of

researchers have explored this morphogenetic substance from various marine organisms, but were not successful mainly because the amount of the substance was quite small. Finally, in 2005, Matsuo and his colleagues extracted the substance from the epiphytic marine bacterium living on the surface of a green alga, determined its chemical structure, and named it Thallusin (Matsuo *et al.*, 2005). They confirmed that the substance has the morphogenetic activity by a bioassay at a very low concentration. In addition, thallusin also induces the morphogenesis and germination of other blade-like green algae, such as *Ulva* and *Enteromorpha*. This substance may play multiple important roles in biological interactions during the vegetative development in the life history of green algae.

3. Sexual reproduction

The goal of life history is reproduction of the next generation. There are many environmental factors that control the reproductive development of seaweed, for example, temperature and light. Since the aqueous environment is shared with a number of co-existing organisms such as animals, plants, fungi, algae and microorganisms, there should be particular mechanisms that ensure the success of mating between gametes produced by the gametophytes of the same seaweed species during sexual reproduction. Actually, seaweed has developed a variety of such mechanisms that enable the female and male gametes to recognize each other in the external aqueous environment. Several selected studies on the sexual reproduction of the three major groups of seaweed are presented in the last section of this review.

As I mentioned above, sexual reproduction occurs between flagellate motile gametes in green algae. Although no studies are available for seaweed, these gametes may recognize each other by the specific aggregation between flagella of different mating types through fibrous agglutinins on the flagellar surfaces as revealed in the unicellular *Chlamydomonas* (Goodenough, 1991). The gametes of green algae exhibit an alternation of phototactic behavior that may influence the success of their sexual reproduction (Fig. 7). In many species of green seaweed, both female and male gametes show positive phototaxis (Togashi *et al.*, 1999). This may cause the co-localization of both gametes near the surface of seawater, improving the possibility of their encounter. On the other hand, the zygotes usually become negatively phototactic, enabling them to swim towards the bottom of the seashore where they can find the substratum to be settled.

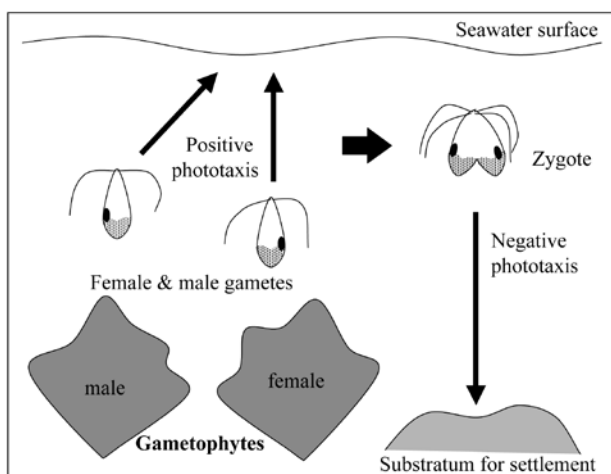


Fig. 7. Alternation of phototaxis during fertilization in green algae

The motile cells of green algae sense the light by a special cell structure called as “eyespot”. In green algae, the eyespot is on the side of the cell in both gametes. But the site of gamete fusion is opposite for female and male gametes (Miyamura *et al.*, 2003). This results in the side-by-side arrangement of the two eyespots in the same side of the zygote so that the zygote can perceive the light in the same way as the gametes do.

The brown algal gametes, at least the male ones, are also motile by means of flagella. It is known that the male gametes are attracted toward female gametes after settlement of the female. It is also known that the mass of the brown algal female gametes has a characteristic smell. Müller and co-workers collected the pungent substance from living female gametes of a number of brown algae using an air pump and an air filter made of activated charcoal. They collected more than ten small hydrocarbons with different structures according to taxa, and indicated that these substances act as sexual pheromones in brown algal fertilization by bioassay (Maier and Müller 1986). However, the number of brown algal pheromones so far discovered (less than 20) is much smaller than the number of the taxa of brown algae, therefore, the sexual attraction of male gametes can not be species-specific. Actually, the taxonomically close species use a common substance as sexual pheromone as seen in this crossing experiment. This indicates that sexual attraction by pheromone is effective in the early stages of fertilization until gamete attachment but incompatibility in sexual reproduction between different species may occur in later stages, such as gamete fusion or subsequent development of the zygote in brown algae (Schmid, 1993).

In red algae, the egg cell known as carpogonium is formed on the female gametophyte. As mentioned

earlier, red algae do not produce flagellated motile cells, and the male gametes are also not motile and are known as spermatia. After release from the male gametophyte, they must find the carpogonium of the same species in the seashore environment, while being transported passively by the movement of seawater. There are some mechanisms or devices that may enhance the encounter of gametes. For example, carpogonium usually has a long protrusion of the cell, called as trichogyne, to effectively catch the mass of spermatia (Hawkes, 1990).

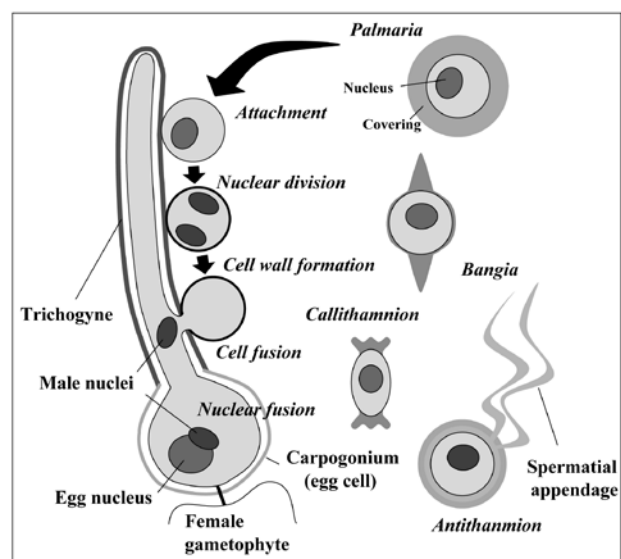


Fig. 8. Various structures of spermatium surface and fertilization process in red algae

Spermatia develop their extracellular coverings in various forms according to species. Some of them have appendages extending outward (Fig. 8). Labeling with a certain lectin conjugated with a fluorochrome resulted in strong fluorescence on two appendages and cell surface in the red alga *Antithamnion*. The appendages are flexible and their length is much greater than the original cell size (Kim and Fritz 1993, Mine *et al.*, 2003). After experimentally mixing the spermatia with female gametophytes bearing carpogonium, spermatia attached to the

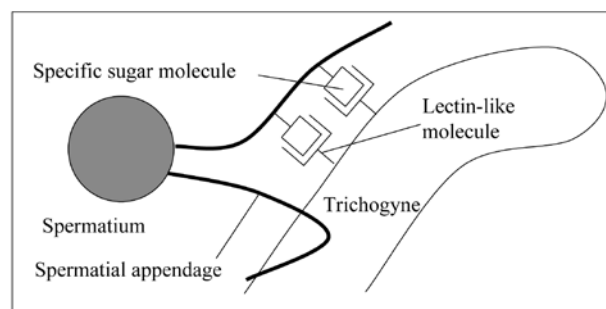


Fig. 9. Spermatium attachment to trichogyne via its appendages

trichogyne via their appendages entangling around the trichogyne. Inhibitory experiments of fertilization of this alga have shown that a specific lectin-sugar binding is involved in the attachment between spermatium and trichogyne (Fig. 9).

Perspectives

In this review, I have shown that there are a number of interesting examples of biological interaction occurring in the life history of seaweed. These data may represent the fact that the vegetation of seaweed is influenced by the external environment and other organisms co-existing in the seashore. In the opposite direction, it is also possible that the algal vegetation may influence the seashore environment. For example, bare-ground is one of major current problems in marine ecosystems, where the seashore environment is considerably ruined. In such bare-ground, some kind of seaweed is among the dominant organisms in addition to numerous sea urchins. And, the recovery from bare-ground is indicated by the growth of other species of seaweed readily edible by animals.

Recently, a genome project of a brown alga has started. Interestingly, this project is motivated by the biological significance in the regulation of life history patterns. Including such up-to-date research, further research from the viewpoint of basic biology will provide useful information for our understandings about the construction of seaweed vegetation and, moreover, the infrastructure of the marine ecosystem.

A modified transcript of the invited lecture presented by the author in the “Symposium of Kuroshio Current - related Studies” (December 5, 2007 at Institute of Marine Science, National Sun Yat-sen University, Kaohsiung, Taiwan)

References

- Buggeln, R. G. 1976. Auxin, an endogenous regulator of growth in algae? *Journal of Phycology* 12, 355-358.
- Fletcher, R. L. and Callow, M. E. 1992. The settlement, attachment and establishment of marine algal spores. *Br. phycol. J.* 27, 303-329.
- Goodenough, U. W. 1991. *Chlamydomonas* Mating Interactions. In “Microbial Cell-Cell Interactions” ed. by Dworkin, M., pp. 71-112, American Society of Microbiology.
- Hawkes, M. W. 1990. Reproductive strategies. In “Biology of the Red Algae” ed. by Cole, K. M. and Sheath, R. G., pp. 455-476, Cambridge University Press.
- Kim, G. H. and Fritz, L. 1993. Gamete recognition during fertilization in a red alga, *Antithamnion nipponicum*. *Protoplasma* 174, 69-73.
- Lin, R. and Stekoll, M. S. 2007. Effects of plant growth substances on the conchocelis phase of alaskan *Porphyra* (Bangiales, Rhodophyta) species in conjunction with environmental variables. *J. Phycol.* 43, 1094-1103.
- Maier, I. and Müller, D. G. 1986. Sexual pheromones in algae. *Biol. Bull.* 170, 145-175.
- Mann, K. H. (1973) Seaweeds: Their Productivity and Strategy for Growth: The role of large marine algae in coastal productivity is far more important than has been suspected. *Science* 182, 975-981.
- Matsuo, Y., Imagawa, H., Nishizawa, M. and Shizuri, Y. 2005. Isolation of an algal morphogenesis inducer from a marine bacterium. *Science* 307, 1598.
- Mine, I., Kubouchi, Y. and Okuda, K. 2003. Fine structure of spermatial surface in the red alga *Antithamnion nipponicum* (Rhodophyta). *Phycol. Res.* 51, 109-117.
- Miyamura, S., Hori, T. and Nagumo, T. 2003. Eyespot behavior during the fertilization of gametes in *Ulva arasakii* Chihara (Ulvoephyceae, Chlorophyta). *Phycol. Res.* 51, 143-146.
- 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.
- Schmid, C. E. 1993. Cell-cell-recognition during fertilization in *Ectocarpus siliculosus* (Phaeophyceae). *Hydrobiologia* 260/261, 437-443.
- Tatewaki, M., Provasoli, L. and Pintner, I. J. 1983. Morphogenesis of *Monostroma oxyspermum* (Kütz.) Doty (Chlorophyceae) in axenic culture, especially in bialgal culture. *J. Phycol.* 19, 409-416.
- Togashi, T., Motomura, T. and Ichimura, T. 1999. Gametic behavior in a marine green alga, *Monostroma angicava*: An effect of phototaxis on mating efficiency. *Sexual Plant Reprod.* 12, 158-163.
- Waaland S. D. and Watson, B. A. 1980. Isolation of a cell-fusion hormone from *Griffithsia pacifica* Kylin, a red alga. *Planta* 149, 493-497.