

Chapter 1

AN INTRODUCTION TO THE ECOLOGICAL SIGNIFICANCE OF SEAWEEDS ON COASTAL ECOSYSTEMS

S. Satheesh, A. A. Siddik,*

M. A. Ba-Akdah and A. A. Al-Sofyani

Department of Marine Biology, Faculty of Marine Sciences,
King Abdulaziz University, Jeddah, Saudi Arabia

ABSTRACT

Seaweeds (macroalgae) play a key role in coastal ecosystems by providing space for marine microorganisms and higher organisms, as a nursery ground for fishes and maintain the overall biodiversity structure. Seaweeds are also considered as major primary producers in the reef ecosystems and form an important part of trophic structure. For environmental monitoring programme, seaweeds are used as good bioindicators to assess the pollutant level in marine waters. Besides, many seaweed species have phytochemicals and attain economic significance. This chapter describes the ecological significance of seaweed communities in coastal ecosystems and discusses the need for conservation of seaweed beds.

*Corresponding Author E-mail: ssathianeson@kau.edu.sa, satheesh_s2005@yahoo.co.in

Keywords: seaweeds, ecosystem engineer, bioindicator, bioactive metabolites, coastal ecosystems

INTRODUCTION

Seaweeds or macroalgae are the abundant space occupiers and primary producers in the marine ecosystems with great ecological and economic significance (Egan et al. 2013; Ba-akdah et al. 2005). Seaweeds grow abundantly along the coastline, particularly on rocky shore regions. Generally, they are abundant in the intertidal region due to the availability of the substratum (Figure 1).

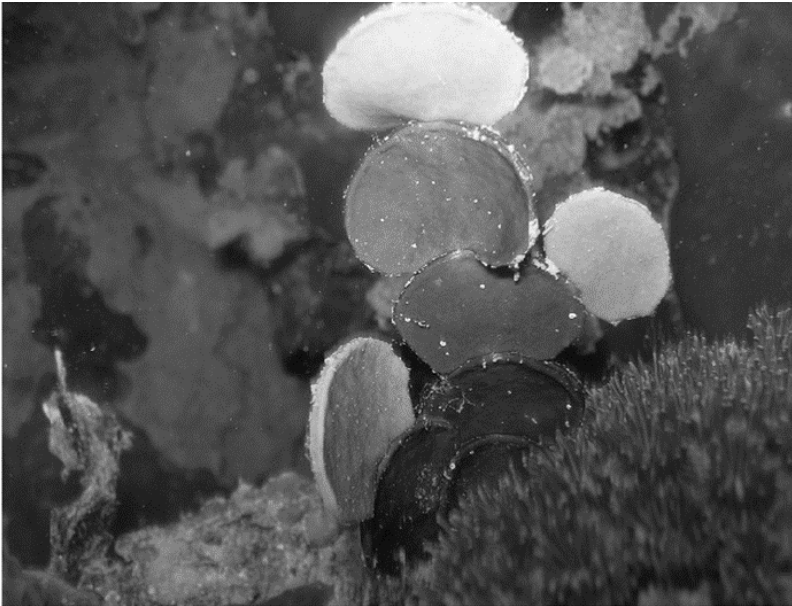
Seaweeds are classified into three main groups based on the presence of photosynthetic pigments, storage of food products and fine structure of the cells (Dhargalkar and Kavlekar, 2004). The broad seaweed groups are Chlorophyceae (green algae), Phaeophyceae (brown algae) and Rhodophyceae (red algae). The green algae contain photosynthetic pigments such as chlorophyll *a*, *b* and carotenoids. In brown algae, the photosynthetic pigments include chlorophyll *a*, *c* and fucoxanthin. The carotenoid fucoxanthin and others give yellow to deep brown colour to the brown algae (Dhargalkar and Kavlekar, 2004). The red seaweeds have chlorophyll *a*, phycobilins and carotenoids as photosynthetic pigments. The colouration of red seaweeds is due to the presence of phycobilins which include red coloured phycoerythrin and blue coloured phycocyanin (Dhargalkar and Kavlekar, 2004).

There are considerable variations among the species which are classified under these three groups, particularly on ecological and physiological aspects (Toth and Pavia, 2007). For example, brown seaweeds are normally larger in size and some are commonly called as kelp (McHugh, 2003). Kelps (large seaweeds of the order Laminariales) are abundant throughout the temperate seas (Steneck et al. 2002) and provide an extensive ecosystem for many marine communities. Kelp forests usually support high primary productivity and enhanced secondary productivity in coastal ecosystems (Smale et al. 2013). Red and green macroalgae are small in size with the size ranging from a few centimeters to a meter (McHugh, 2003). Macroalgae lack specialized tissues such as root system and vascular structures which are present in plants (Graham and Wilcox, 1999). It has been estimated that about 200 species of seaweeds are exploited for valuable economically important products such as aging, agars, carrageenans and food products (Zemke-White and Ohno, 1999).

Seaweed production along the coastal regions of the world, particularly in Asian countries increases in the recent past due to the economic significance.



A



B

Figure 1. Distribution of seaweeds on coastal ecosystems. A) Growth of *Ulva* on a rocky shore B) *Halimeda* on a reef.

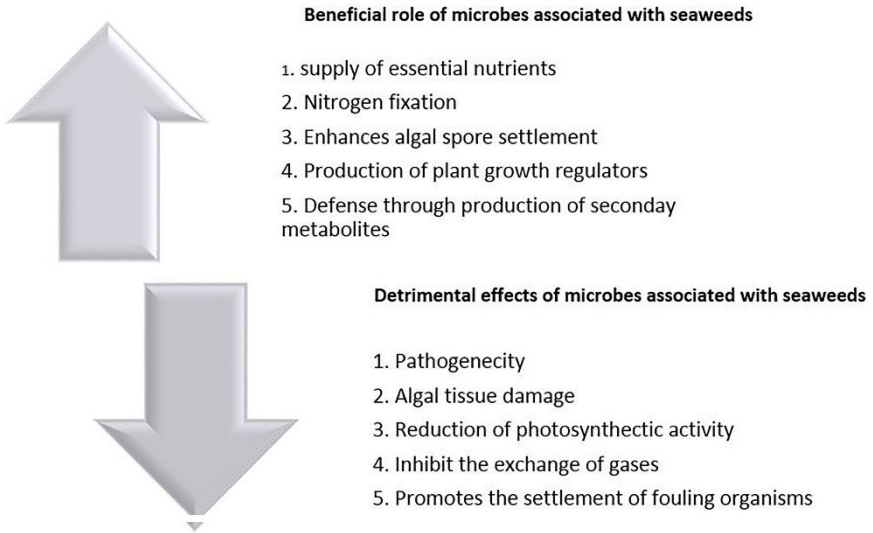


Figure 2. Possible advantages and disadvantages of microbes associated with seaweeds in coastal ecosystems.

MACROALGAE-MICROBE ASSOCIATION

All the living and non-living surfaces in the marine waters are colonized by the microbial population from the surrounding environment. The surface of marine invertebrates and macroalgae is also no exception as they are colonized by microorganisms (Egan et al. 2013; Satheesh et al. 2016). Seaweeds provide a microhabitat for many microorganisms with densities varied between 10^2 to 10^7 cells cm^{-2} depending on macroalgal species, sampling season and region (Armstrong et al. 2000; Bengtsson et al. 2010). The macroalga-microbe relationship is attributed for many purposes (Figure 2). The associated microorganisms, particularly the bacterial community provide protection and maintain the health of host alga (Egan et al. 2013). Many studies have indicated that bacterial communities associated with macroalgae are necessary for the normal morphological development of algal host (Matsuo et al. 2003; Singh et al. 2011). In addition, microbial communities also supply essential nutrients, mainly fixed nitrogen to the macroalgal host (Philips and Zeman, 1990). It has been noted that the nitrogen fixation activity of associated bacteria significantly influences the growth of seaweeds particularly red and

green seaweeds (Chisholm et al. 1996; Singh et al. 2011; Singh and Reddy, 2014).

Research studies also indicated that bacterial communities associated with macroalgae enhance the settlement of zoospores in many algal species (Dillon et al. 1989; Joint et al. 2000; Shin, 2008). Another important role of microorganisms associated with the macroalgae is the production of plant growth regulators (Sing and Reddy, 2014). These plant growth regulators may affect the growth of the macroalgae as evidenced from previous studies (Spoerner et al. 2012). On the other hand, the microbial communities associated with seaweeds produce biologically active compounds (mainly for antifouling) and these compounds ensure the protection of the host (Goecke et al. 2010; Satheesh et al. 2016). However, some studies also revealed the negative aspect of microbes associated with macroalgae. For instance, the microbial films on macroalgae may reduce the incident light, inhibit the exchange of gases and hinder photosynthesis (Wahl, 1989; 2008). Also, the microbial communities associated with the algal surface may be a source of disease-causing pathogen to the host (Largo et al. 1995). While microbe-macroalga association provides an opportunity to explore some useful compounds, the functional role of this association in coastal ecosystem processes needs to be studied in detail.

SEAWEEDS AS A HABITAT FOR INVERTEBRATES

Seaweeds are reported to provide nutrition and shelter to diverse groups of invertebrates (Wikstrom and Kautsky, 2004; Cacabelos et al. 2010; Ba-akdah et al. 2015). Most importantly, the macroalgae increase the amount of space for attachment of sessile organisms; provide protection from environmental conditions such as wave action, desiccation and heat (Viejo, 1999). Studies from various coastal regions suggest that the invertebrates associated with the seaweeds are taxonomically and morphologically diverse, and exhibit a wide range of trophic habits. For example, these associated organisms may consist of filter feeders (Caine, 1977), detritus feeders (Zimmerman et al., 1979), predators which eat other epifauna (Roland, 1978) and herbivores which eat epiphytic algae or the host plant (Brawley and Feil, 1987; Duffey, 1990; Viejo, 1999).

Marine invertebrates such as polychaetes, amphipods, isopods and gastropods are commonly observed on the surface of seaweeds and these organisms may form an important food source for juvenile fishes, which are

also abundant in seaweed habitats (Bray and Ebeling, 1975; Jones, 1988). In general, by acting as refugia for marine invertebrates, seaweeds contribute largely to the maintenance of biodiversity and coastal ecosystem functioning. For example, diversity and abundance of organisms are high in those coastal habitats which possess vegetation than unvegetated regions (Steneck et al. 2002).

SEAWEEDS AS A BIOINDICATOR FOR ENVIRONMENTAL MONITORING

The coastal environments throughout the world are experiencing constant exposure to pollutants from anthropogenic sources. Many marine sessile organisms are considered as bioindicators for environmental quality assessment of the marine waters. A bioindicator is an organism which gives overall information on the presence or absence of a pollutant and the concentration. Seaweeds can be used as good indicators to monitor the environmental changes due to anthropogenic and natural stressors because of their sessile mode of life (attached to a substratum) and abundance in most of the rocky coastal regions of the world (Philips, 1980). Several previous investigations revealed the effectiveness of seaweeds as bioindicators of heavy metal pollution in the marine environment (Villares et al. 2001; Chaudhuri et al. 2007; Juanes et al. 2008) as they have the ability to accumulate the metals (Haroon et al. 1995). The thallus of the seaweeds absorbs the nutrients and other materials from the surrounding environment. Hence, the toxic elements present in the water will also get accumulated in seaweeds.

ROLE OF SEAWEEDS IN NUTRIENT RECYCLING IN COASTAL ECOSYSTEMS

The seaweeds are a source of nutrient recycling and act as a base for food chains in oligotrophic coastal waters (Blanche 1992). This is due to the fact that seaweeds have photosynthetic activities in which they absorb carbon dioxide and release oxygen. According to Ryther (1963), global benthic macroalgae production was estimated at about 10% of phytoplankton. Seaweeds support other biosystems such as reefs, seagrass meadows, and mangroves by exporting good amount of particulate organic matters carried

out by currents and tides (Hurd et al. 2014). Further, seaweeds are reported to be involved in the biogeochemical cycling of nutrients, particularly, nitrogen and phosphorus (Atkinson and Smith, 1983; Lapointe et al. 1992). Seaweeds also play an important role in maintaining water quality by removing the nutrients and organic materials, particularly in the eutrophicated regions (Okuda, 2008).

MACROALGAL CHEMICAL DEFENSE AGAINST PREDATORS

The majority of the seaweeds produce secondary metabolites (Amsler 2008), also known as allelochemicals as a defense mechanism against herbivores. These compounds are toxic to microorganisms (Culioli et al. 2008) and invertebrates (Davis et al. 2005). The production of these biologically active compounds is due to the competition and predation (Hay 1996). Competition mainly occurs between macroalgal communities owing to the availability of limited space for growth and distribution. Macroalgae are constantly subjected to attack from various herbivores that feed on algae (Rothausler et al. 2005). Marine herbivores also play important roles in structuring and functioning of coastal ecosystems (McCarty and Sotka, 2013). For example, the distribution of macroalgal communities of coastal ecosystems mainly depends on the defense mechanism of the algae (Van Alstyne, 1989, Hay 1997). Many studies have demonstrated the ability of macroalgal compounds for preventing fouling and grazing by herbivores (Paul et al. 2001; Amsler and Fairhead, 2005; Pansch et al. 2009; Thabard et al. 2011). Macroalgae that exposed to higher herbivory and predation are reported to produce more biologically active compounds. This view is supported by the ability of the seaweeds to induce chemical defenses in response to the attack of herbivores (Flothe et al. 2014). The secondary metabolites produced by the seaweeds in response to competition and predation had biotechnological applications as they could be used as a potential lead for the development of biopharmaceuticals, nutraceuticals, and antifouling compounds.

THREATS TO SEAWEED BIODIVERSITY

Coastal ecosystems are considered as the most vulnerable environment to anthropogenic and climate change induced impacts. Mainly, human activities along the coastal region have increased in recent times that produced deleterious effects on the marine biota (McIntyre, 1977). Seaweed beds along with other coastal systems provide important services to the ecosystem and any change in these systems will affect the human societies (Harley et al. 2012). Seaweeds are under threat in developing countries, where they are being disturbed by a variety of human activities. Mainly, changes in the coastal regions due to reclamation or construction activities resulted in serious deleterious effects on seaweed habitats (Okuda, 2008). Also, changes in global temperature and ocean acidification process are causing major shifts in biological systems (Harley et al. 2012). Seaweed growth, recruitment, survival, and reproduction are influenced by different environmental parameters such as temperature, salinity and nutrient concentration (Luning and Neushul, 1978; Lobban and Harrison, 1997; Steen 2004). Increasing concern about the destruction of seaweed beds and changes to the habitats warrant observational and experimental studies on macroalgal communities for better management of natural marine systems.

CONCLUSION

Seaweeds are an important ecosystem engineer which provides space for many marine organisms and structuring the coastal biodiversity. The functional role of seaweeds in coastal ecosystems is multifold from nutrient recycling to harbour micro- and macro-organisms. While, seaweeds exploited for many commercial purposes, including biologically active materials, a holistic approach is needed for conservation of this precious coastal system. Aquaculture of economically important seaweeds is progressing mainly for the food market and biofuel production (Neori, 2009; Borines et al. 2011; Egan et al. 2013). In addition, secondary metabolites produced by the seaweeds could be utilized as a potential source for pharmacological compounds and antifouling compounds. The ecological and economic significance of seaweeds emphasize the need for adequate conservation and management strategies.

REFERENCES

- Amsler, C.D. and Fairhead, V.A. 2005. "Defensive and sensory chemical ecology of brown algae." *Adv. Bot. Res.* 43:1-91.
- Amsler, C.D. (Ed.), 2008. *Algal chemical ecology*. London: Springer. 313. <http://dx.doi.org/10.1007/978-3-540-74181-7>.
- Armstrong, E., Rogerson, A., and Leftley, J.W. 2000. "The abundance of heterotrophic protists associated with intertidal seaweeds." *Estuar. Coast. Shelf Sci.* 50: 415-424.
- Atkinson, M. J and Smith, S. V. 1983. "C:N:P ratios of benthic marine plants." *Limnol. Oceanogr.* 28(3): 568-574.
- Ba-akdah, M.A., Satheesh S., Al-sofyani, A.A. 2015. "Habitat preference and seasonal variability of epifaunal assemblages associated with macroalgal beds on the Central Red Sea coast, Saudi Arabia." *J. Mar. Biol. Assoc. UK*, 1-11. doi:10.1017/S0025315415001678.
- Bengtsson, M., Sjøtun, K., and Øvreås, L. 2010. "Seasonal dynamics of bacterial biofilms on the kelp *Laminaria hyperborea*." *Aquat. Microb. Ecol.* 60:71-83.
- Blanche, K.R. 1992. "Preliminary observations on the distribution and abundance of seaweed flies (Diptera: Coelopidae) on beaches in the Gosford district of New South Wales, Australia." *Aust. J. Ecol.* 17: 27-34.
- Borines, M.G., McHenry, M.P., and de Leon, R.L. 2011. "Integrated macroalgae production for sustainable bioethanol, aquaculture and agriculture in Pacific island nations." *Biofuels, Bioprod. Biorefin.* 5: 599-608.
- Brawley, S. H., and Fei, X.G. 1987. "Studies of mesoherbivory in aquaria and in an unbarricaded marine culture farm on the Chinese coast." *J. Phycol.* 23:614-623.
- Bray, R.N., and Ebeling, A.W. 1975. "Food, activity, and habitat of three 'picker-type' microcarnivorous fishes in the kelp forests off Santa Barbara, California." *Fish Bulletin* 73:815-829.
- Cacabelos, E., Olabarria, C., Incera, M., Jesu's, S. and Troncoso, J.S. 2010. "Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae." *Estuar. Coast. Shelf Sci.* 89:43-52.
- Caine, E.A. 1977. "Feeding mechanisms and possible resource partitioning of the Caprellidae (Crustacea: Amphipoda) from Puget Sound, US." *Mar. Biol.* 42:331-336.

- Chaudhuri, A., Mitra, M., Havrilla, C., Waguespack, Y and Schwarz, J. 2007. "Heavy metal biomonitoring by seaweeds on the Delmarva Peninsula, east coast of the US." *Bot. Mar.* 50: 151-158.
- Chisholm, J.R.M., Dauga, C., Ageron, E., Grimont, P.A.D., and Jaubert, J.M. 1996. "Roots in mixotrophic algae." *Nature* 381: 565.
- Christopher, D. G. Harley, Kathryn, M., Anderson, Kyle W. Demes, Jennifer P. Jorve, Rebecca L. Kordas, Theraesa A. Coyle. 2012. "Effects of climate change on global seaweed communities." *J. Phycol.* 48(5):1064-1078.
- Culioli, G, Ortalo-Magne, A, Valls, R, Hellio, C, Clare, A.S, Piovetti, L. 2008. "Antifouling activity of meroditerpenoids from the marine brown alga *Halidryssiliquosa*." *J. Nat. Prod.* 71:1121-1126.
- Dan, A. Smale, Michael, T. Burrows, Pippa Moore, Nessa O'Connor, and Stephen, Hawkins, J. 2013. "Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective." *Ecol. Evol.* 3(11): 4016-4038.
- Davis, AR., Benkendorff, K and Ward, DW. 2005. "Responses of common SE Australian herbivores to three suspected invasive Caulerpa spp." *Mar. Biol.* 146(5):859-868. doi:http://dx.doi.org/10.1007/s00227-004-1499-z.
- Dhargalkar, V.K., and Kavlekar, D. 2004. *Seaweeds - a field manual*. Edited by X.N. Verlecar, Vijaykumar Rathod. Goa: National Institute of Oceanography.
- Dillon, P.S., Maki, J.S., and Mitchell, R. 1989. "Adhesion of *Enteromorpha* aswarmers to microbial films." *Microb. Ecol.* 17: 39-47.
- Duffy, J.M. 1990. "Amphipods on seaweeds: partners or pests?" *Oecologia* 83:267-276.
- Egan, S., Harder, T., Burke, C., Steinberg, P., Kjelleberg, S., and Thomas, T. 2013. "The seaweed holobiont: understanding seaweed-bacteria interactions." *FEMS Microbiol. Rev.* 37:462-476.
- FAO. 2002. "Prospects for seaweed production in developing countries in Corporate document depository." Fisheries and aquaculture department, FAO.
- Flothe, C.R., John, U., and Molis, M. 2014. "Comparing the Relative Importance of Water-Borne Cues and Direct Grazing for the Induction of Defenses in the Brown Seaweed *Fucusvesiculosus*." *Plos One* 9(10): 109-247.
- Goecke, F., Labes, A., Wiese, J., and Imhoff, J. 2010. "Chemical interactions between marine macroalgae and bacteria." *Mar. Ecol. Prog. Ser.* 409:267-300.

- Graham, L., and Wilcox, L. 1999. *Algae*. Prentice-Hall, Upper Saddle River, NJ.
- Gunilla, B. Toth, and Henrik, Pavia. 2007. "Induced herbivore resistance in seaweeds: a meta-analysis." *J. Ecol.* 95:425-434.
- Haroon, A.A., Szaniawska, A., and Surosz, W. 1995. "Changes in heavy metal accumulation in *Enteromorpha* spp. from the Gulf of Gda'nsk." *Oceanologia* 37 (1): 99-110.
- Hay, M.E. 1996. "Marine chemical ecology: what is known and what is next?" *J. Exp. Mar. Biol. Ecol.* 200:103-139.
- Hay, M.E. 1997. "The ecology and evolution of seaweed-herbivore interactions on coral reefs." *Coral Reefs* 16:S67-S76.
- Hurd, C.L., Harrison, P.J., Bischof, K., Guam, C.S.L. 2014. *Seaweed Ecology and Physiology*, 2nd edition. Cambridge University Press.
- Joint, I., Callow, M.E., Callow, J.A., and Clarke, K.R., 2000. "The attachment of *Enteromorpha* zoospores to a bacterial biofilm assemblage." *Biofouling* 16: 151-158.
- Jones, G.P. 1988. "Ecology of rocky reef fish of north-eastern New Zealand a review." *New Zeal. J. Mar. Fresh* 22:445-462.
- Juanes, J.A. Guinda, X., Puente, A., and Revilla, J.A. 2008. "Macroalgae, a suitable indicator of the ecological status of coastal rocky communities in the NE Atlantic." *Ecolindic* 8:351-359.
- Lapointe, B. E., Littler, M. M., and Littler, D.S. 1992. "Nutrient availability to marine macroalgae in siliciclastic versus carbonate-rich coastal waters." *Estuaries* 15: 75-82.
- Largo, D.B, Fukami, K., and Nishi-jima, T. 1995. "Occasional pathogenic bacteria promoting ice-ice disease in the carrageenan-producing red algae *Kappaphycus Alvarezii* and *Eucheumadentic-ulatum* (Solieriaceae, Gigartinales, Rhodophyta)." *J. Appl. Phycol.* 7, 545-554.
- Lobban, C.S., and Harrison, P.J. 1997. *Seaweed Ecology and Physiology*. New York: Cambridge University Press.
- Lu'ning, K. and Neushul, M. 1978. "Light and temperature demands for growth and reproduction of Laminarian gametophytes in southern and central California." *Mar. Biol.* 45:297-309.
- Matsuo, Y. Suzuki, M., Kasai, H., Shizuri, Y., and Harayama, S. 2003. "Isolation and phylogenetic characterization of bacteria capable of inducing differentiation in the green alga *Monostroma oxyspermum*." *Environ. Microbiol.* 5: 25-35.

- McCarty, A.T. and Sotka, E.E. 2013. "Geographic variation in feeding preference of a generalist herbivore: the importance of seaweed chemical defenses." *Oecologia* 172:1071-1083 doi: 10.1007/s00442-012-2559-6.
- McHugh, D.J. 2003. *A guide to the seaweed industry*. FAO Fisheries Technical Paper 441:105.
- McIntyre, A. D. 1977. *Sandy foreshores*. In *The Coastline*. (Ed. R. S. K. Barnes) Wiley: Chichester.
- Neori, A. 2009. "Essential role of seaweed cultivation in integrated multi-trophic aquaculture farms for global expansion of mariculture: an analysis." *Nineteenth International Seaweed Symposium* 2:117-120. Borowitzka MA, Critchley, AT, Kraan S, Peters A, Sjøtun, K and Notoya, M, eds. Netherlands: Springer.
- Okuda, K. 2008. "Coastal Environment and Seaweed-bed Ecology in Japan." *Kuroshio Science* 2-1: 15-20.
- Pansch, C., Cerda, O., Lenz, M., Wahl, M., and Thiel, M. 2009. "Consequences of light reduction for anti-herbivore defense and bioactivity against mussels in four seaweed species from northern-central Chile." *Mar. Ecol. Prog. Ser.* 381: 83-97.
- Paul, V.J., Cruz-Rivera, E., and Thacker, R.W. 2001. "Chemical mediation of macroalgal-herbivore interactions: ecological and evolutionary perspectives." *Marine Chemical Ecology* edited by J.B. McClintock and B.J. Baker, 227-265. New York: CRC Press.
- Philips, D.J.H. 1980. *Quantitative aquatic biological indicators* 488. Barking: Applied Science Publishers.
- Philips, E., and Zeman, C. 1990. "Photosynthesis, growth and nitrogen fixation by epiphytic forms of filamentous cyanobacteria from pelagic Sargassum." *Bull. Mar. Sci.* 47:613-621.
- Roland, W. 1978. "Feeding behaviour of the kelp clingfish *Rimicolamuscum* residing on the kelp *Macrocystis integrifolia*." *Can. J. Zool.* 56:711-712.
- Rothausler, E., Macaya, E.C., Molis, M., Wahl, M., and Thiel, M. 2005. "Laboratory experiments examining inducible defense show variable responses of temperate brown and red macroalgae." *Rev. Chil. Hist. Nat.* 78: 603-614.
- Ryther, J. H. 1963. *Geographic variations in productivity*. In: Hill, M.N. (Ed.), New York: The Sea. John Wiley and Sons. 347-380.
- Satheesh, S., Ba-akdah, M.A., and Al-Sofyani, A.A. 2016. "Natural antifouling compound production by microbes associated with marine macroorganisms- A review." *Electron J. Biotechnol.* 21:26-35.

- Shin, H.W. 2008. "Rapid attachment of spores of the fouling alga *Ulvafasciata* on biofilms." *J. Environ. Biol.* 29: 613-619.
- Singh, R.P., and Reddy, C.R.K., 2014. "Seaweed-microbial interactions: key functions of seaweed-associated bacteria." *FEMS Microbiol. Ecol.* 88:213-230.
- Singh, R., Mantri, V., Reddy, C., and Jha, B. 2011. "Isolation of seaweed-associated bacteria and their morphogenesis inducing capability in axenic cultures of the green alga *Ulvafasciata*." *Aquat. Biol.* 12: 13-21.
- Spoerner, M., Wichard, T., Bachhuber, T., Stratmann, J., and Oertel, W. 2012. "Growth and thallus morphogenesis of *Ulva mutabilis* (Chlorophyta) depends on a combination of two bacterial species excreting regulatory factors." *J. Phycol.* 48:1433-1447.
- Steen, H. 2004. "Effects of reduced salinity on reproduction and germling development in *Sargassum muticum* (Phaeophyceae, Fucales)." *Eur. J. Phycol.* 39:293-299.
- Steneck, R.S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M. and Estes, J. A. 2002. "Kelp forest ecosystems: biodiversity, stability, resilience and future." *Environ. Conserv.* 29:436-459.
- Thabard, M., Gros, O., Hellio, C., and Mare'chal, J.H. 2011. "*Sargassum polyceratum* (Phaeophyceae, Fucaceae) surface molecule activity towards fouling organisms and embryonic development of benthic species." *Bot. Mar.* 54: 147-157.
- Van Alstyne, K.L. 1989. "Adventitious branching as a herbivore-induced defense in the intertidal brown alga *Fucus distichus*." *Mar. Ecol. Prog. Ser.* 56:169-176.
- Viejo, R.M. 1999. "Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain." *Aquat. Bot.* 64:131-149.
- Villares, R., X. Puente, and Carballeira. A. 2001. "*Ulva* and *Enteromorpha* as indicators of heavy metal pollution." *Hydrobiologia* 462: 221-232.
- Wahl, M. 1989. "Marine epibiosis I. Fouling and antifouling: some basic aspects." *Mar. Ecol. Prog. Ser.* 58:175-189.
- Wahl, M. 2008. "Ecological lever and interface ecology: Epibiosis modulates the interactions between host and environment." *Biofouling* 24:427-438.
- Wikstrom, S.A., and Kautsky, L. 2004. "Invasion of a habitat-forming seaweed: effects on associated biota." *Biol. Invasions* 6:141-150.

- Zemke-White, W.L., Ohno, M. 1999. "World seaweed utilization: An end of the century summary." *J. Appl. Phycol.* 11:369-76.
- Zimmerman, R., Gibson R., and Harrington J. 1979. "Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community." *Mar. Biol.* 54:41-47.