CHAPTER 2

LITERATURE REVIEW

CHAPTER 2

LITERATURE REVIEW

2.1 *Sargassum* C. Agardh

"*Sargassum*" is derived from a Spanish word for seaweed, *Sargasso*, and used by navigators to describe floating algae. *Sargassum* is one the of seven genera in the family Sargassaceae (Kuetzing), and the largest genus in the order Fucales. The genus is divided into five subgenera, namely, *Phyllotrichia, Schizophycus*, *Bactrophycus, Arthrophycus* and *Sargassum* (=Eusargassum) in the Agardhian system. Wormersley (1954) has united the subgenera *Schizophycus* with *Phyllotrichia,* supported by Yoshida (1983) and Tseng (1995). Tseng (1995), Yoshida (1995) and Phillips (1995) gave detailed reviews on the taxonomy of *Sargassum*; the history from C. A Agardh who established the genus *Sargassum* in 1820 until the current status of *Sargassum,* the key to subgenera and the morphological differences between the subdivisions of the genus.

Sargassaceae is characterized by specialized branch systems, a single egg per oogonium and thallus with a three sided apical cell (Bold & Wynne 1978; Womersley 1987; Lee 1989). The branching in this family is always monopodial (Fritsch 1945; Lee 1989) and species can be distinguished by the lateral branch systems. The lateral branch systems bear one or two leaf-like structures at their base. Vesicles and receptacles will be found in the remainder of the branch.

Species of *Sargassum* exhibit the most complex morphology among Fucales. Figure 1 shows a high degree of morphological differentiation of *Sargassum*. *Sargassum* plants consist of holdfast (discoid, conical, scutellate or fibrous), stem (erect or repent), branch (terete, triquetrous or flat; either smooth or with spines), leaves (simple, furcated; entire, serrate or double serrate; either with retroflex, horizontal or vertical insertion), vesicles (round apex, apiculate, crowned; stalk terete, compressed or leafy; phyllocyst), receptacle (simple, branched; either smooth or with spines) and cryptostomata which are found on the leaves.

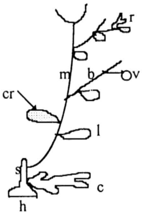

Figure 1. Drawing of a *Sargassum* plant.
b = secondary branch; c = cauline leaf; cr = cryptostomata; h = holdfast; l = leaf; m = main branch; r = receptacle; s = stem; v = vesicles.

There are two methods of reproduction for *Sargassum*. Some species are capable of vegetative regeneration by fragmentation, for example *S. natans* (L.) Meyen (Vashishta 1973; Bold & Wynne 1978) and *S. fluitans* Borg. (Bold & Wynne 1978). The usual reproduction method is sexual and is oogamous.

Sargassum shows a typical cyclosporian life cycle as in *Fucus*. Figure 2 shows a graphic representation of the life cycle and the explanations are cited from Vashishta (1973).

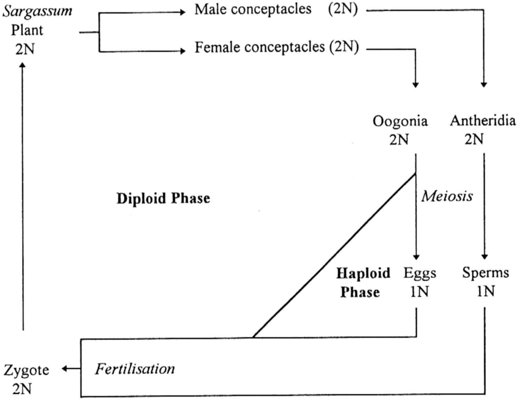

Figure 2. Graphic representation of the *Sargassum* life cycle.
(Source : Vashishta 1973)

The life cycle consists of only a single morphological organised individual, the sporophyte, which is bushy in habit. The diploid sex organs (antheridia and oogonia) are lodged in flask-shaped depressions of the diploid thallus, the conceptacles, which are confined to the receptacles. The thalli may be monoecious or dioecious but the conceptacles are always unisexual. The original single nucleus within the antheridium undergoes meiosis, and the four haploid nuclei undergo a series of mitotic divisions, resulting in 64 haploid nuclei which are incorporated into 64 small biflagellate sperms. The first two nuclear division of the oogonium constitute meiosis, then these four haploid nuclei undergo a mitotic division to produce a total of eight haploid nuclei per oogonium. Seven nuclei degenerate in the cytoplasm of the functional egg and the other one nuclei enlarges to become the functional haploid female nucleus. Diploid zygote is formed by the fusing of the haploid male and female gametes. The zygote germinates without undergoing any resting period and forms the diploid thallus. The sexual or gametophyte generation in the life cycle has been completely suppressed resulting in a morphologically unorganised gametophyte plant. The gametophyte is reduced to gametes. Thus, *Sargassum* exhibits no alternation of morphologically organised generations. However, a cytological alternation of generation is present, from the diploid condition to haploid at the time of gamete formation (meiosis) and back to the diploid condition in zygote formation (fertilisation).

Russel and Fielding (1981) define 'life-form' as comprising the characteristics such as the thallus form, longevity, growth habit and reproductive system in the life-history of a seaweed. Mathieson and Penniman (1986) categorized the life form of *Sargassum* into three types :

1. Annuals :

   Seasonal thalli living less than one year and passing adverse season[s] in a resting or juvenile stage or being completely absent from the community.

   Non-seasonal thalli persisting less than one year, but populations present year-round as overlapping generations.

2. Perennials :

   Major portion of thallus present year round and persisting for more than one year.

3. Pseudoperennials :

   Most plants of the population passing adverse season[s] in a reduced perennating form.

Most species of *Sargassum* are pseudoperennials (Tsuda 1972; Fletcher & Fletcher 1975; De Wreede 1976; Prince & O'Neal 1979; Prince 1980; Ang 1985). Ang and Trono (1987) studied eight species of *Sargassum* in Philippines : *S. baccularia* (Mertens) C. Agardh, *S. cinctum* J. Agardh, *S. crassifolium* J Agardh, *S. ilicifolium* (Turner) C. Agardh, *S. notarisii* Zanardini, *S. oligocystum* Montagne, *S. paniculatum* J. Agardh and

S. siliquosum J. Agardh. The authors found that all these species except *S. crassifolium*, *S. notarisii* and *S. oligocystum* are pseudoperennial, i.e., lateral branches die back at the end of the reproductive period and new laterals arise from the basal holdfast and primary axis in the following growing season. Some species have been described as annuals (Tsuda 1972; Umezaki 1984), for example *S. siliquosum* J. Agardh (Largo *et al.* 1994). Trono (1992) reported that growth of *Sargassum* species in the Philippines is seasonal with both perennial and annual species. Some species are perennial, like, *S. cymosum* C. Agardh in Brazil (De Paula & De Oliveira 1982), *S. polyceratium* Montagne in Curacao, Netherlands Antilles (De Ruyter Van Steveninck & Breeman 1987) and *S. polycystum* C. Agardh (Largo *et al.* 1994), where primary laterals are continually produced and shed during the year.

2.2 Distribution of *Sargassum*

Phillips (1995) gave a comprehensive review on the distribution of the subgenera and species of *Sargassum* (Phaeophyta) in the Pacific basin. The author reviewed the current taxonomy status of *Sargassum* as well as the biogeography of the subgenera and genus in the Pacific basin, emphasizing on diversity and endemism.

Subgenus *Phyllotricha* consists of 16 species distributed worldwide, with 15 restricted to the Pacific basin (ten in Australia and New Zealand, one in New Caledonia and two in Phillipines) and one in the Atlantic basin. Subgenus *Arthrophycus* has seven species distributed in Australia (five species), New Zealand (one species), and Philippines (one species). The subgenus *Phyllotrichia* and *Arthrophycus* are mainly distributed in the southern area of Australia (Womersley 1987). *Bactrophycus* has 22 species in Eastern Asia, nine in Philippines and one in Northeastern Pacific. *Bactrophycus,* one of the five subgenera of *Sargassum* is an ecologically important group, known only in the eastern Asiatic region (Tseng *et al.* 1985). Most of the species found in the temperate regions of Japan coast are included in the subgenus *Bactrophycus* (Yoshida 1983). Subgenus *Sargassum* is the most widely distributed and prolific in the tropical (above 25°C) and subtropical (summer temperatures 20 - 25°C) regions of Pacific basin with the highest concentration in New Caledonia, southern Japan and China, Malaysia and Singapore and, Philippines. This subgenus has only a few species recorded in southern Australia (Womersley 1987).

A few studies on the distribution and ecology of marine algae have been reported in Peninsular Malaysia (Sivalingam 1977, 1978; Arumugam 1981; Crane 1981; Phang 1984, 1986, 1988, 1995) and Sabah (Khew 1978). Only Subgus *Sargassum* has been found in Malaysia. There are total 23 species of *Sargassum* recorded in Malaysia. Table 1 is the list of *Sargassum* species and sites recorded in Malaysia by various authors (Khew 1978; Crane 1981; Phang 1984, 1995; Ahmad & Hindun 1991; Phang & Wee 1991; Ahmad & Go 1994; Ahmad 1995).

2.3 Phenological Studies

Phenology is defined by Lieth (1974) as "the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species".

According to Phillips (1990), phenological responses imply responses of plants to environmental factors at a site; a phenomenon of the interaction of the structural and functional components of the plants with the environment. Differences in the presence and absence of phenological events or in timing of these events for a species over a latitudinal or ecological gradient reflects differences in the adaptational responses or perhaps ecotypic structure of the species. Phenological observations include the time of appearance of the reproductive organs, seasonal variation in growth, biomass and development of plants.

Table 1. List of Malaysian *Sargassum* (Fucales, Sargassaceae) species.

Species	Site
S. baccularia (Mertens) C. Agardh	Cape Rachado, Port Dickson
S. binderi (Sonder) J. Agardh	West coast, Peninsular Malaysia
S. cinereum J. Agardh	Sabah
S. cristaefolium J. Agardh	West coast, Peninsular Malaysia
S. duplicatum J. Agardh	Tioman Island and Sabah
S. filipendula C. Agardh	Sabah
S. fluitans (Borgesen) Borgesen	Tioman Island
S. granuliferum C. Agardh	West coast, Peninsular Malaysia
S. grevillei J. Agardh	Penang
S. hornschuchii Agardh	Sabah
S. ilicifolium (Turner) C. Agardh	West coast, Peninsular Malaysia
S. muticum (Yendo) Fensholt	Tioman Island
S. myriocystum J. Agardh	Tioman Island
S. oligocystum Montagne	Cape Rachado
S. polycystum C Agardh	West coast, Peninsular Malaysia
S. sandei Reinbold	West coast, Peninsular Malaysia
S. siliquosum J. Agardh	West coast, Peninsular Malaysia
S. spathulaefolium J. Agardh	West coast, Peninsular Malaysia
S. tenerrimum J. Agardh	Sabah
S. ?torvum J. Agardh	Tioman Island
S. virgatum (Mertens) Agardh	West coast, Peninsular Malaysia
S. vulgare C. Agardh	Sabah
S. wightii Greville	West coast, Peninsular Malaysia

(Compiled from : Khew 1978; Crane 1981; Phang 1984, 1995; Ahmad & Hindun 1991; Phang & Wee 1991; Ahmad & Go 1994; Ahmad 1995.)

The literature on tropical algal (*Sargassum*) ecology and phenology was scarce in the 1970's, expanding only in 1980's and 1990's. De Wreede (1976) summarized the seasonality of *Sargassum* species as recorded in the literature from 1900's to 1970's. The author pointed out that these studies did not measure the standing crop but estimated it visually except in the work done by Doty (1971). For example, the work done by Tsuda (1972) estimated the percentage of cover and Misra (1966) estimated the standing crop. Realizing the inadequate phenological data on seaweeds, changes were made in the studies from 1980's onwards. Studies have shifted from estimation of standing crop visually to the measurement of the specific plant in general. For example, detail phenological studies on three *Sargassum* species (*S. johnstonii* Setchell & Gardner, *S. herporhizum* Setchell & Gardner and *S. sinicola* Setchell & Gardner var. *camouii* (Dawson) Norris & Yensen) in the northern Gulf of California by McCourt (1983, 1984) and two *Sargassum* species (*S. siliquosum* J. Agardh and *S. paniculatum* J. Agardh) in the reef flat of Balibago, Philippines by Ang (1982, 1985). Schiel and Choat (1980) and Schiel (1985) reported on the effect of *Sargassum* plant density on growth rate, survival and reproduction.

Literature dealing with seasonality of abundance and phenology of tropical and subtropical *Sargassum* species from 1970 onwards included reviews from India (Chauhan & Krishnamurthy 1971; Raju & Venugopal 1971; Thomas & Subbaramaiah 1991), Guam (Tsuda 1972), Hawaii (De Wreede 1976), Florida (Prince & O'Neal 1979; Kilar & Hanisak 1989), California (McCourt 1984; Espinoza & Rodriguez 1987), Philippines (Ang 1982, 1985; Ang & Trono 1987; Ohno *et al.* 1987; Trono & Lluisma 1990; Largo & Ohno 1992; Largo *et al.* 1994, Ohno *et al.* 1995) and Tanzania (Shunula 1988). The phenology of *Sargassum* reported varies with species and locations, but revealed seasonal cycles in growth, abundance and reproduction. The distinct seasonal growth cycles are influenced by the environmental factors (Luning & Tom-Dieck 1989; Luning 1993; Lobban & Harrison 1994). It was shown that the local physico-chemical conditions influenced the seasonal changes in algal population in the tropical regions where marked seasonal changes in temperature are absent. The influence of environmental factors on the phenology of seaweeds will be discussed in Section 2.4.

2.3.1 Thallus Length

Thallus length is usually based on the measurement of the longest branch of the plant. Most *Sargassum* plants have an average length of less than 100 cm (Ohno *et al.* 1995). The range of thallus length varies with species; for example, the range of thallus length for *S. polycystum* is 17-78 cm, while *S. binderi* is 16-18 cm (Ohno *et al.* 1987).

The range of the thallus length varies with location as reported by Ohno *et al.* (1995). The range of thallus length for *Sargassum* species was observed to vary in different parts of Philippines; Luzon Island (2-60 cm), Central Visayas (12-80 cm) and Palawan and Tamboanga (20-110 cm).

Thallus length varies with fertile and nonfertile plants. McCourt (1985) recorded that the fertile stipes of three *Sargassum* species involved in the studies were either equal in length or significantly ($p < 0.05$, Mann-Whitney tests) longer than nonfertile stipes.

S. polyceratium plants growing in an intertidal population have a higher number of primary laterals, larger plant size, more and longer main axes per holdfast as compared to the population in deep-water (De Ruyter Van Steveninck & Breeman 1987).

Table 2 shows the location, time and maximum length values for *Sargassum* species reported by various authors from different parts of the world.

2.3.2 Size Classes

Individuals at various stages of development in a *Sargassum* population have branches in various length classes. Therefore, size-class structure analysis will give a clear picture of whether there is continuous recruitment, size reduction, or other changes in the population. For example, more than 35% of the primary lateral branches of *Sargassum* sp. were up to 50 cm on the coast of Luzon, Philippines and this indicated that new primary branches were initiating while old branches were undergoing decay (Ohno *et al.* 1995).

Table 2. Mean maximum length (± sd) or maximum size of *Sargassum* species.

Location	Species	Mean maximum length(±sd) (cm)	Maximum size (cm)	Month	References
India	*S. swartzii*	-	80	December	Chauhan & Krishnamurthy 1971
Guam	*S. polycystum*	-	30	-	Tsuda 1972
Southern Japan	*S. horneri*		400-500	-	Ohno 1984
Philippines	*S. siliquosum*	126.7±38.3	-	September	Ang 1985
	S. paniculatum	88.7±23.9	-	November	
Curacao, Netherlands Antilles	*S. polyceratium*	12.3±7.3	31	-	De Ruyter van Steveninck & Breeman 1987
Tanzania	*S. aquifolium*	-	36	May 1983	Shunula 1988
		-	35	March 1984	
	S. asperifolium	-	40	May 1983	
		-	45	March 1984	
India	*S. wightii*	-	64	December	Thomas & Subbaramaiah 1991
Philippines	*S. siliquosum*	74.61±26.02	-	December	Largo & Ohno 1992
	S. myriocystum	65.71±17.96	-	December	
Korea	*S. thunbergii*	6.33±1.89	-	June 1990	Koh *et al.* 1993
Magnetic Island, Queensland, Australia	*S. fissifolium*		57	March 1992	Martin-Smith 1993
	S. linearifolium		61	September 1991	
	S. oligocystum		77	March 1992	
	S. tenerrimum		80	January 1992	
Philippines	*S. polycystum*	26.71	-	-	Largo *et al.* 1994
	S. siliquosum	54.53	-	-	

Table 3 shows the differences in length classes for various locations in Philippines (Ohno *et al.* 1995).

Table 3. Length classes for *Sargassum* species in Philippines reported by Ohno *et al* (1995).

Location	Length classes (cm)	% Frequency
Central Visayas	50 or less	> 80
Mactan Island (Cebu)	100	5
Palawan Island & Zamboanga	50	40
(Southern Philippines)	100	25

Prince and O'Neal (1979) reported that 21-37% of the *Sargassum pteropleuron* Grunow population was greater than 50 cm from October to December in Florida, and mostly did not exceed 20 cm by the end of the winter die-back.

The natural population of many seaweeds which are perennials often consists of different age classes (Loban & Harrison 1994). Harrison *et al.* (1986) noted that the uptake rate of nutrient (nitrate and ammonium) by *Laminaria groenlandica* decreases while its age increases; the uptake rate (per gram of dry weight) for first year plants was three times greater than second and third year plants.

2.3.3 Reproduction

Although seawater temperature influences growth and reproduction in seaweeds (details in Section 2.4.1), the latter may be species specific. Studies conducted by Breeman *et al.* (1988 in Luning & Tom-Dieck 1989) showed that even a small temperature change may cause severe influence on the completion of a life cycle for seaweeds. The male and female gametophytes of *Bonnemaisonia hamifera* Hariot exhibit a different temperature range for sexual maturation where the males start to mature at lower temperature than females and finish reproduction before the females begin. The onset of reproduction usually occurred after the plants attained maximum growth (Chauhan & Krishnamurthy 1971; Raju & Venugopal 1971; Tsuda, 1972; De Wreede 1976; Ang 1984; Largo & Ohno 1992).

Species of *Sargassum* allocate biomass differentially to different modes of reproduction. As shown by McCourt (1985), the allocation of biomass to sexual reproduction (receptacles) tissue and vegetative (holdfast) tissue differed absolutely and relatively in three *Sargassum* species that form the bulk of the intertidal algal canopy in northern Gulf of California. Deysher and Norton (1982) showed that the intertidal benthic *Sargassum* can reproduce either vegetatively through lateral encroachment of basal holdfasts or sexually through the shedding of fertile, receptacle-bearing branches that may float and disperse propagules in a great distance.

Norton (1977) noted that vegetative branches grow five times faster than branches bearing sexual structures (receptacles).

The fertility of many species tends to be seasonal in temperate region. Whereas many algae show two reproductive periods of maximal fertility in warm-temperate regions. The first in spring and the second during autumn. Sideman and Mathieson (1983) recorded two reproductive periods (spring and fall) for *Fucus distichus* in New England. Many species in cold temperate regions are fertile in summer and early autumn. In many cases, the reproductive structures develop at the end of vegetative growth period for example, *Fucus spiralis* in New England (Niemeck & Mathieson 1976).

Table 4 indicates that the onset of reproduction and maturation occurs at different times of the year for different *Sargassum* species.

2.3.4 Growth Rate

Growth rate is defined by Brinkhius (1985) as a measure of the velocity of growth, or an index relating the multiplication of organic mass to time. Underestimation of growth rate might occur in repeated measurements of the thalli length to calculate growth rate, due to losses from grazing and blade erosion.

Table 4. Summary of fertile periods in *Sargassum* species.

Location	Species	Fertile Period	References
India	*S. wightii*	October - December	Umamaheswara Rao 1969
India	*S. plagiophyllum*	July onward	Raju & Venugopal 1971
Guam	*S. polycystum*	February	Tsuda 1972,1974
	S. duplicatum	June	
Japan	*S. confusum* *S. hemiphyllum* *S. horneri* *S. micracanthum* *S. muticum* *S. patens* *S. thunbergii* *S. tortile*	April & June	Okuda *et al.* 1984
Philippines	*S. siliquosum*	October	Ang 1985
	S. baccularia	March - April	
	S. paniculatum	Late November	
Philippines	*S. cinctum* *S. crassifolium* *S. ilicifolium* *S. notarisii* *S. oligocystum* *S. paniculatum* *S. siliquosum*	Most probably in late August - December	Ang & Trono 1987
Tanzania	*S. aquifolium*	May - September	Shunula 1988
	S. asperifolium	February - June	
Philippines	*S. siliquosum*	Produce receptacles in August. Fully mature in November.	Largo & Ohno 1992
	S. myriocystum *(=S. polycystum)*	Produce receptacles in September. Fully mature in March	
Australia	*S. fissifolium* *S. oligocystum* *S. tenerrimum*	February - May	Martin-Smith 1993
	S. linearifolium	September - January	
Philippines	*S. siliquosum*	September - December	Largo *et al.* 1994
	S. polycystum	March - May	

Prince and O'Neal (1979) reported that maximum growth rate of *S. pteropleuron* in Florida occurred in late summer with a mean rate of 0.63 cm day^{-1} (1976) and 0.71 cm day^{-1} (1977), and the maximum growth rate generally did not exceed 2.5 cm day^{-1}.

Ang (1985) reported the fastest growth for *S. siliquosum* plants and plantlets of *S. siliquosum* in Philippines to be 16.5±8.2 mm day^{-1} from July to August and 1.1±0.8 mm day^{-1} in April, respectively. Growth rate of *S. paniculatum* was higher from June to October with a range of 3.8 to 5.2 mm day^{-1} compared to 1.8 to 3.3 mm day^{-1} from February to June (Ang 1985).

Schiel (1985) reported that the growth rates of *S. sinclairii* Hook. & Harv. in northern New Zealand became higher rather than lower in the higher density of the plants. On the other hand, density dependency was not observed in *S. thubergii* (Mertens ex Roth) Kuntze by Koh et al (1993) in Korea. However, the authors feel that the size dependent effect on growth rate must be considered.

Culture studies of growth rate in the laboratory had been carried out with *S. muticum*. Hales and Fletcher (1989) found maximum growth of the germlings (*S. muticum*) during the first two weeks of culture occurred at

25°C (0.21 mm day^{-1}) while growth at 30°C averaged approximately 0.09 mm day^{-1}. Growth rate of 0.28 mm day^{-1} was obtained at 44μEm^{-2}s^{-1} after two weeks' culture. The mean germling growth rate was approximately 0.03 mm day^{-1} at 6.8 ‰, and 0.36 mm day^{-1} at full seawater salinity. Maximum receptacle growth (approximately 0.16 mm day^{-1}) occurred in cultures maintained at 23.8‰ (Hales & Fletcher 1990).

Environmental factors like solar radiation, water temperature, nutrient concentration and water movement play an important role in controlling the growth rate of seaweed populations (details in Section 2.4). The extremes of environmental factors resulted in the diminished growth of the plants especially in the intertidal area.

2.3.5 Standing Crop

Standing crop is measured by the above-ground biomass (usually as dry weight per unit area) which estimates the above ground production only. Biomass methods are insensitive to losses due to fragmentation, herbivory, and secretion or leaching of organics (Anon 1989) but they are best used for long term comparisons (several months to a year).

Standing crop of *Sargassum* varies at different locations. The subtidal population of *S. siliquosum* has longer thalli and greater biomass production as compared to the intertidal population of *S. polycystum* (Largo *et al.* 1994). Similar pattern was found in Cape Rachado, Port Dickson, Malaysia by Phang (1995), where biomass near to the shore was lower than near the reef edge.

Ohno *et al.* (1995) recorded different biomass range of *Sargassum* species in various parts of Philippines. In Luzon area, the standing crop of *Sargassum* species had a range of 0.3 (< 50% cover) to 12 (100% cover) kg wet wt m^{-2}, and in Central Visayas area, the range was from 0.3 (< 50% cover) to 10 (100% cover) kg wet wt m^{-2}.

Table 5 gives the standing crop of *Sargassum* species recorded in the literature from different authors. Generally, the standing crop of *Sargassum* in warm waters is smaller than that of more temperate waters (Ohno 1984). The effect of environmental factors will be discussed in Section 2.4.

Table 5. Standing crop of *Sargassum* species recorded in the literature.

Location	Species	Mean Standing Crop (kg m^{-2})		References
		wet wt	dry wt	
Japan	*Sargassum* species	2 - 6		Umezaki 1971, Taniguchi & Ohkuba 1975, Ohno 1984 in Ohno *et al.* 1995
Japan	*S. thunbergii*	4.25		Umezaki 1974 in Ohno *et al.* 1987
Hawaii (Kapapa transect)	*S. oligocystum*		0.25	De Wreede 1976
Coast of Curacao, Netherlands Antilles	*Sargassum* bed		0.44	Wanders 1976
Balibago Batagas (Luzon Is.), Philippines	*Sargassum*		0.4	Ang 1984
Hawaii	*S. polyphyllum*	0.8262	0.1877	Glenn *et al.* 1990
	S. echinocarpum	0.1285	0.0228	
	S. obtusifolium	0.0007	0.0015	
Philippines	*S. crassifolium*		0.647	Trono & Lluisma 1990
	S. polycystum		0.447	
	S. cristaefolium		0.430	
	S. oligocystum		0.282	
India	*S. wightii*		2.4	Thomas & Subbaramaiah 1991
Korea	*S. thunbergii*		0.011-0.039	Koh *et al.* 1993
Magnetic Island, Australia	*S. fissifolium*	*0.1866		Martin-Smith 1993
	S.linearifolium	*0.1565		
	S. oligocystum	*0.2917		
	S. tenerrimum	*0.2303		
Liloan, Cebu, Philippines	*S. siliquosum*	6.61		Largo *et al.* 1994
	S. polycystum	3.07		

* = Maximum weight

2.4 Environmental Parameters

Environmental factors such as light, temperature, salinity, pH, irradiance, nutrients, water movement/waves, desiccation and rainfall have marked influence on the seasonality of algae (McQuid 1985; Luning & Tom-Dieck 1989; Luning 1990; Lobban & Harrison 1994).

2.4.1 Temperature

Temperature has long been recognised as an important factor affecting the growth, biomass and reproduction of *Sargassum* besides playing an important role in the patterns of geographical distribution for this genus (Misra 1966; Luning 1990).

The optimal temperatures for growth are different for species from different geographical areas (Luning 1990). For example, the optimal temperatures for polar species, cold temperate species, warm temperate species, and warm temperate to tropical species are 0-10°C, 10-15°C, 10-20°C and 15-30°C, respectively.

Although the tropics has been regarded as "thermally uniform" (McCourt 1984), a recent research by Glenn *et al.* (1990) on *S. pollyphyllum* J. Agardh showed that even a small seasonal temperature variation is important in controlling algal standing crop and productivity. The author concluded that the tropical seaweeds can be controlled by temperature as the temperate species, and most *Sargassum* species have maximum and minimum abundance related to temperature.

Hanisak and Samuel (1987) found that the *S. natans* from the Sargasso Sea which has an optimum growth temperature of 18-30°C, has lost the ability to grow at the temperature of 12°C, which favours the growth of benthic *Sargassum* species from Florida. High growth rate of *S. muticum* at high temperature enables this species to invade the warm waters (Norton 1977). Experiments tested the growth of *Sargassum* embryos under four temperature levels (20, 24, 28 and 32°C) by De Wreede (1976). This study concluded that growth was the best at or near 24°C and poorest at 32°C. The author also observed that *S. oligocystum* Montagne, S. *obtusifolium* J. Agardh and *S. polyphyllum* J. Agardh, had longer thalli at the lower temperature of 22°C to 25°C. Prince and O'Neal (1979) recorded that growth of *S. filipendula* C. Agardh in culture was optimal at 25°C, inhibited at 30°C and death occurred within 5 days at 35°C. Largo and Ohno (1992) observed that *Sargassum* in Philippines developed longer primary lateral branches when water temperature was at 27°C.

Reproduction is influenced by temperature (De Wreede 1976; McCourt 1984; Luning 1990; Lobban & Harrison 1994). Luning (1990) gave a few examples for species showing a close dependance on temperature for reproduction from different biogeographical climates. Studies showed that a drop in the water temperature might have triggered the onset of reproduction of *Sargassum* species in Hawaii (De Wreede 1976) and Florida (Prince O'Neal 1979).

According to De Wreede (1976) and McCourt (1984), tropical and subtropical *Sargassum* species attained maximum abundance, growth and fertility in cooler months of the year. This observation is in contrast to temperate species which tend to do so in warmer months (Fletcher & Fletcher 1975). This statement is not generally valid as there are exceptions to the hypothesis (Tsuda 1972; Ang 1985; De Ruyter Van Steveninck & Breeman 1987). Table 6 gives a summary of the occurrence of peak thallus length, biomass and growth of *Sargassum* species from different geographical areas reported in literature, either in the warmer or cooler months of the year.

Table 6. Seasonality of *Sargassum* reported in literature.

References	Locations	Peak abundance / length / growth / fertility	
		Warmer Months	Cooler Months
Misra 1966	India		*Sargassum* species grew abundantly during winter, very poor in summer.
Chauhan & Krishnamurthy 1971	India		*S. swartzii* attained maximum growth rate in October - November; abundant in October - January.

Table 6. Seasonality of *Sargassum* reported in literature [Continued].

References	Locations	Peak abundance / length /	growth / fertility
		Warmer Months	Cooler Months
Raju & Venugopal 1971	South India	*S. plagiophyllum* attained highest height in July-August (warmer months).	
Tsuda 1972	Guam	*S. duplicatum* (=*S. cristaefolium*) peaked in size and abundance in June (warmer months). *S. polycystum* didn't show any distinct seasonality.	
Umezaki 1974 in Ohno *et al* 1987	Japan	*S. thunbergii* peaked in length and weight and increased in growth in summer at 27-29°C.	
Fletcher & Fletcher 1975 Kane & Chamberlain 1979	British Isles	*S. muticum* reached peak size in summer.	
De Wreede 1976	Hawaii	Maximum growth rate in warmer months.	Thallus height and fertility of *Sargassum* species peaked in the cooler months (November - March).
Prince & O'Neal 1979	Florida	*S. pteropleuron* attained maximum growth rate during the warmer months.	Plants became senescent during the cooler water temperature of the winter.
Ngan & Price 1980	Townsville region, Queensland, Australia	*S. oligocystum* showed active growth during summer.	
McCourt 1984	Gulf of California	*S. johnstonii*, *S. herporhizum* and *S. sinicola* var *camouii* were shortest in summer.	The plants peaked in size and fertility in the spring in between periods of seasonal extremes (February - April) as temperature began to rise.
Ang 1985	Philippines	*S. siliquosum* and *S. paniculatum* attained maximum growth and higher growth rate in warmer months.	The plants were shortest in cooler months.

Table 6. Seasonality of *Sargassum* reported in literature [Continued].

References	Locations	Peak abundance / length /	growth / fertility
		Warmer Months	Cooler Months
De Ruyter Van Steveninck & Breeman 1987	Curacao, Netherlands Antilles	*S. polyceratium* attained maximum biomass, growth rates, plant size and proportion of fertile plants in late summer - early autumn when water temperatures were also highest..	Minimum in biomass, growth rates, plant size and proportion of fertile plants in winter when water temperatures decreased or at lowest.
Espinoza & Rodriguez 1987	California, Mexico		*S. sinicola* peaked in thallus length and reproduction when water was cooler.
Shunula 1988	Pange Island, Zanzibar, Tanzania		*S. aquifolium* and *S. asperifolium* peaked in growth and fertility between May - September 1983 and February - June 1984, during low water and air temperature.
Kilar & Hanisak 1989	Florida	*S. polyceratium* had minimum growth in mid-summer.	Maximum growth from mid-fall to mid-winter.
Largo *et al.* 1994	Central Visayas, Philippines		*S. polycystum* and *S. siliquosum* had a peak growth in December coincided with months of lower temperature.
Thomas & Subbaramaiah 1991	India		*S. wightii* peaked in growth and reproduction in winter months (October - December), and growth rate (August - October)
Largo & Ohno 1992	Cebu, Central Philippines		*S. myriocystum* and *S. siliquosum* attained maximum length in December. Active growth occurred during the colder months.

Table 6. Seasonality of *Sargassum* reported in literature [Continued].

References	Locations	Peak abundance / length /	growth / fertility
		Warmer Months	Cooler Months
Martin-Smith 1993	Magnetic Island, Queensland, Australia	*S. tenerrimum*, *S. fissifolium* and *S. oligocystum* showed biomass and length peaks in summer (December - February) followed by a late summer peak in reproduction (March - May).	*S. linearifolium* had earlier peaks in both size (June - September) and reproduction (September - January).
Schaffelke *et al.* 1997	Central Great Barrier Reef, Australia	Maximum growth rates of *S. baccularia* occurred in summer, followed by a peak fertility.	Negative growth rates in autumn/winter.

2.4.2 Salinity

"Salinity" is defined as grams of salts per kilogram of solution. Generally, the salinity of the open-ocean surface water is 34‰ to 37 ‰. The value is lower off the coast in areas with great rainfall and higher in subtropical area with high rates of evaporation and low rainfall (Groen 1980 in Lobban & Harrison 1994).

There are two types of species based on the response to salinity; "euryhaline species" which can tolerate a wide range of salinities and "stenohaline species" which only tolerant to a narrow range of salinities (Druehl 1981). The dependence of growth rate on salinity follows an optimum curve (Druehl 1981). The width of the optimum curve and the steepness of growth decline in a particular species, at higher or lower salinity values, depends on whether the species has a more euryhaline or stenohaline character.

Sargassum seasonality was influenced by the seasonal variation in salinity (De Wreede 1976). De Wreede (1976) conducted an extensive culture study of *Sargassum* embryos, *S. obtusifolium*, *S. oligocystum* (=*S. echinocarpum* J. Agardh) and S. *polyphyllum* under five salinity regimes (from 15 to 35 parts per thousand salt) in a growth chamber. The experiment showed that an optimum growth occurred most frequently at 30‰ and 35‰; and occurred more often at 35‰ than 30‰. Contrary to the above finding, significant negative correlation was found between the biomass of *S. wightii* and salinity in India by Thomas and Subbaramaiah in 1991. In culture, germlings (*S. muticum*) survived at salinities down to 20‰ and vegetative branches down to 9‰; the rate of growth for both was much reduced (Norton 1977). The interacting effect of temperature and salinity is important. At higher temperature and lower salinities, grow is usually less. The interaction effect for embryos of *S. echinocarpum* and *S. obtusifolium* is highly significant indicating that the young stages perform better in cooler and higher salinity waters (De Wreede 1978).

A decrease in the number of algal species can be caused by a reduction in the salinity (Nygren 1975). Tsuda (1972 in Glenn *et al.* 1990) related that the disappearance of *S. duplicatum* from the reef flats in Guam was due to the diluted salinity after the rainy season. Intertidal seaweeds will be affected by the extreme salinity changes because of evaporation or rain/runoff (Lobban & Harrison 1994). In contrast, maximum growth at lower salinities occurs in estuarine red algae, *Bostrychia radicans* and *Caloglossa leprieurii* (Yarish *et al.* 1979; Yarish & Edward 1982). Also the two major orders of brown algae, Fucales and Laminariales, have members which can grow at salinities as low as 2 - 4‰ (Surif & Raven 1989). The chemical composition of fucoids is influenced by low salinity. Contents of mannitol, ash and chloride declined as reported in the field (Munda 1967 in Lobban & Harrison 1994) and laboratory (Munda & Kremer 1977 in Lobban & Harrison 1994).

Tolerance range of salinity is different for various species as the range of natural marine and brackish water is from 10 ‰ to 70 ‰, and the most common range is from 25‰ to 35‰. For example, *S. filipendula* can tolerate a wide range of 4.9‰ to 36‰ (Earle 1969), *S. cristaefolium* (=*S. duplicatum*) and *S. granuliferum* have a much narrower range from 33‰ to 36‰ (Tsuda 1972), and field populations of *S muticum* have been found within 70 to 100% normal seawater salinity (Hales & Fletcher 1989).

2.4.3 pH

The alkalinity of seawater is higher and more stable if compared with fresh water. The inorganic-carbon properties of seawater are different from those in air and fresh water. Plants in water can use a similar concentration of CO_2 as in air, but with a lower diffusion rate of 10^4 times than in air. Photosynthetic rates achieved its maximum at atmospheric equilibrium (pH 8.2 to 8.4) and declined at higher pH approaching zero between pH 9.5 to 10.5 in natural seawater (Sand-Jensen & Gordon 1984). For example, the optimum pH for photosynthesis in *Amphiroa* species lies between 6.5 and 7.5 (Lobban & Harrison 1994).

CO_2 in water is part of the carbonate buffer system (figure 3) and inorganic carbon is potentially available as bicarbonate (HCO_3^-). pH, salinity and temperature influence the relative proportion of the forms of inorganic carbon. For example, in seawater of pH 8 and salinity 35%0, about 90% of the inorganic carbon occurs as HCO_3^-. Oceanic seawater has a high and constant HCO_3^- concentration (about 2.0 mM) and a lower CO_2 concentration than fresh water (about 0.14 mM at atmospheric equilibrium of 15°C) (Sand-Jensen & Gordon 1984).

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \overset{pK' = 6.0}{\leftrightarrow} HCO_3^- + H^+ \overset{pK' = 9.1}{\leftrightarrow} CO_3^{2-} + H^+ \leftrightarrow HCO_3^- \leftrightarrow CO_2 + OH^-$$

Figure 3. The carbonate equilibrium.
(Source : Lobban & Harrison 1994)

A diverse group of marine algae representing six macroalgae from the reds (*Ceramium rubrum* and *Polysiphonia violaceae*), brown (*Fucus vesiculosus*) and greens (*Chaetomorpha linum, Ulva lactuca* and *Enteromorpha* sp.) were able to use HCO_3^- for photosynthesis with high affinity (Sand-Jensen & Gordon 1984). Uptake of bicarbonate was shown in fucoids (Fucales) and kelps (Laminariales) (Surif & Raven 1989).

Cooper and Pasha (1935 in Misra 1966) reported some physiological aspects (osmotic pressure and pH) of Indian marine algae (*S. bacciferum, Dictyota atomaria* and *Padina tetrastomatica*). The authors concluded that "the pH value of cell-sap of all algal species of Chlorophyceae, Phaeophyceae and Rhodophyceae is remarkably uniform, fluctuating between 6.6 and 7.0; and the pH value of the sea-water is about 8.0-8.31." Thomas and Subbaramaiah (1991) reported that biomass and growth of *S. wightii* in India was also influenced by pH.

2.4.4 Nutrients

Nutrient availability is an important factor which regulates the biology, growth and productivity of seaweeds (DeBoer 1981). In some cases, nutrient availability may control the biochemical content, reproduction, development, morphology and distribution of seaweeds. Availability of inorganic nutrients has been implicated as the most important factor limiting seaweed productivity in subtropical and tropical regions.

Nitrogen is the most important element that frequently limits algal growth in the sea, and nitrate and ammonium are the important ions for seaweed growth. Phosphorous occurs in seawater mainly as orthophosphate (HPO_4^{2-}) (Luning 1990). Nitrogen and phosphorous uptake rates are lower in coarse species with low surface-volume ratios than in filamentous species or species with numerous hairs. Phosphorous and nitrogen normally occur at such low concentrations in seawater that they often become the limiting nutrient factors (DeBoer 1981; Lobban *et al.* 1985). In many instances, however, periods of rapid growth occur during times when the external nutrient concentrations are relatively low.

The uptake of nitrate in some macroalgae are inhibited by as much as 50% in the presence of ammonium (DeBoer 1981), and inhibition occurs in mature plants and not in germlings (Lobban & Harrison 1994). Nutrient uptake abilities vary for different stages of a species; between early life-history stages and mature thalli. For example, the ammonium and nitrate-uptake rates for *Fucus distichus* germlings were eight and thirty times, respectively higher than those for the mature thalli (Thomas et al. 1985 in Lobban & Harrison 1994).

Lobban and Harrison (1994) observed that marked seasonal fluctuations in nutrient availability (especially nitrogen) affect growth rates (Lobban & Harrison 1994). *S. sinicola* from two study sites (El Cajete and Las Pascas in the southern Gulf of Caliofornia, Mexico) reached greater lengths in 1985 when nitrate concentrations and temperature were minimal. On the other hand, in 1984 when nitrate concentration was greater, the annual maximum length for *S. sinicola* has the lowest value of the three-year study. These observations suggest that *S. sinicola* in the southern Gulf of California is not nitrate-limited (Espinoza & Rodriguez 1987). Different results were reported for *S. pteropleuron* from southern Florida which reached annual maximum growth rate when nitrate concentration and water temperature were high (Prince & O'Neal 1979).

Growth-enrichment studies by Lapointe (1986 in Lobban & Harrison 1994) utilizing *in situ* cage cultures and a shipboard flowing-seawater culture system were conducted in the summer with whole-plant populations of pelagic *Sargassum natans* and *S. fluitans* in the western

Sargasso Sea. Phosphorous enrichment doubled the growth and photosynthetic rates of the two *Sargassum* species in comparison with those being nitrogen enriched and non-enriched.

The onset of sexual or asexual reproduction in microalgae has frequently been attributed to nutrient availability. Similar relationships occur in seaweeds although the occurrence are not as well documented. Mohsen *et al.* (1974 in Lobban & Harrison 1994) reported that conditions of N depletion enhance gamete formation in *Ulva fasciata*, whereas higher N concentrations favour vegetative growth and asexual reproduction.

Wallentinus (1984) compared the nitrate, ammonium and phosphate uptake abilities of 17 macroalgae in relation to their morphology. The author found higher uptake rates in short-lived, filamentous, delicately branched or monostromatic forms (eg. *Cladophora glomerata, Enteromorpha procera*, etc.) that had high surface area : volume (SA:V) ratio as compared to late-successional, long-lived coarse species with low SA:V ratio (eg. *Fucus vesiculosus, Phyllophora truncata*, etc.)

2.4.5 Wave

Wave action played a role in determining the growth, morphological and standing crop of *Sargassum* species. As reported by De Wreede (1976), *S. pollyphyllum* and *S. oligocystum* attained maximum standing crop during the period when storm waves are most common in Hawaii. De Paula and De Oliveira (1982) observed that *S. cymosum* plants that were exposed to wave action in Rocky intertidal shore, Sao Paulo, Brazil, were smaller and shorter. De Ruyter Van Steveninck and Breeman (1987) reported that high turnover rates resulting in relatively small size of the intertidal *S. polyceratium* plants, were caused by the wave exposure and desiccation. In the Philippines, exposure to waves during the monsoon period (August/September to November) reduced the plant growth by mechanical tearing of the thalli and reduced water transparency due to the suspension of the bottom sediments (Largo *et al.* 1994).

2.4.6 Desiccation

The term "desiccation" is equivalent to "dehydration". The daytime low tide during hot weather accelerates evaporation and is detrimental to the seaweeds. For example, daytime lower low tides in October and November in southern California often coincide with dry offshore winds, further exacerbating evaporation stress and leading to algal die-off (Gunhill 1980b, 1985 in Lobban & Harrison 1994).

The effect of desiccation on the intertidal seaweeds is partly a salinity stress because the concentration of salt in the water increases as water evaporates, and water is lost from the marine plants as soon as they are emerged. The higher up on the shore the plants grow, the longer time they are exposed to the desiccation. These plants are generally more drought-resistant than those nearer to the low water. As shown by the work of Hurd and Dring (1991), the degree of tolerance to desiccation (measured by how quickly species recovered their maximal phosphate-uptake rate after losing 50% of their water through desiccation) increased with increasing shore height of the fucoid algae. Schonbeck and Norton (1979) reported that some fucoids have an ability to "harden" to drought condition as their duration of exposure gradually increases.