STUDIES ON SPORULATION IN SOME COMMERCIALLY IMPORTANT MARINE ALGAE OF MANDAPAM COAST

Thesis submitted

in partial fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY IN MARICULTURE

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DECLARATION

I hereby declare that this thesis entitled **"Studies on sporulation in some commercially important marine algae of Mandapam coast"** is based on my own research work and it has not previously formed the basis for the award of any degree, diploma, associateship, fellowship or other similar titles or recognition.

Kochi - 14
23.10.2000

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CERTIFICATE

Certified that the thesis entitled **"Studies on sporulation in some commercially important marine algae of Mandapam coast"** is a bonafide record of the work carried out by **Ms. Soniya Sukumaran** under my guidance and supervision at the Central Marine Fisheries Research Institute during the tenure of her Ph.D. (Mariculture) Programme (1996 - 1999) and no part thereof has been presented for the award of any other degree, diploma or any other similar titles or recognition.

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A C K N O W L E D G E M E N T

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CONTENTS

Introduction

INTRODUCTION

Marine algae are macroscopic plants constituting an important marine living renewable resource. They are used as human food, livestock feed and fertilizer for land plants in many parts of the world besides having the prime importance of being the only source for the production of agar, carrageenan and alginates. These phytochemicals are extensively used in various industries such as food, confectionery, textile, pharmaceutical, cosmetics, dairy, liquor, canning, paint, varnish, paper etc. mostly as gelling, stabilising and thickening agents and have an estimated billion dollar global market (Zilinskas and Lundin, 1993). A summary of sources, chemical composition, properties and important applications of these phytochemicals given by Nambisan (1998) is presented in Table 1.

The commercial exploitation of seaweeds is going on since 1966 and the export of economically important seaweeds such as *Gelidiella, Gracilaria* and *Sargassum* was banned by the Govt. of India in 1975 as agar and algin industries were started in India by 1970. In recent years many industries producing these phytochemicals have come up in India but as yet the production do not meet the demand. The annual demands of raw materials by Indian seaweed based industries are 2000 tonnes and 12,000 tonnes (dry weight) of agarophytes and alginophytes respectively. Annually, about 60 tonnes of agar and 500 tonnes of alginates are produced. In India carrageenan is not yet produced. However its demand is nearly 200 tonnes per year. Since the indigenous production of agar and alginates is unable to meet the increasing demand, India is importing about 10-12 tonnes of pharmaceutical grade agar, 35 tonnes of alginates and 140 tonnes of carrageenan costing foreign exchange of about Rs.10 crores (Zaidi *et al.*, 1999) This is mainly due to the paucity of raw materials particularly agar yielding seaweeds.

Table - 1

Sources, chemical composition, properties and applications of phytochemicals

Phytochemical	Raw Material	Chemical composition	Important properties	Selected applications
Agar: (mixtures of agarose and agaropectin)	*Gelidium* *Gracilaria* *Gelidiella* *Pterocladia* *Gracilariopsis*	**Agarose** = alternating 1,4 linked **α**-D galactose and 3,6 anhydro **α**-L-galactose backbone (agarobiose) substituted with varying percentages of methoxyl ester sulfate and ketal pyruvate groups **Agaropectin** = alternating D-galactose and L-galactose units. D-galactose can be substituted by D-galactose-4-sulphate, by 4,6-0 (1 carboxyl ethylidene)-D-galactose in certain terminal chain positions or even by D-galactose 2,6-disulphate, while part of L-galactose can be replaced by 3,6 anhydro-L-galactose	**Agarose** • Gel aqueous solutions at low concentrations • Form ion dependent thermoreversible gels • Controllable electroendosinosis (EEO) • Minimal non-specific protein reactivity • Significant degree of hysteresis **Agar** • Gel aqueous solutions at low concentration • Form thermoreversible gels • Relatively inset • Significant degree of hystersis • Retain moisture • Resist hydrolysis by terrestrial microorganisms	Matrices for • Electrophoresis • Immunoassays • Microbial and cell culture • Chromatography • Immobilized Systems • Baking icings • Jelly candies • Canned meats • Dental impression media • Laxatives • Microbial culture matrix • Raw material for agarose
Algin / Alginates	*Undaria* *Macrocystis* *Laminaria* *Sargassum* *Turbinaria*	1,4 - linked **α**-L-guluronic acid and ß-D-mannuronic acid subunits in GG, MM and MG domains	• Ammonium and alkali metal salts are soluble in water, whereas free alginic acid and alkaline earth and group II salts are insoluble and can form gels • Bind water • Thicken aqueous systems • Suspend solids	• Frozen foods to maintain structure on thawing • Baking icings • Salad dressings • Tabletting agent • Dental impression media • Textile sizing • Matrics for immobilized systems

Phytochemical	Raw Material	Chemical composition	Important properties	Selected applications
Carrageenan		Kappa and iota Alternating 1.3-linked α-D-galactose and 1,4 linked 3.6-anhydro-ß-D- galactose backbone (carrabioses) substituted with varying percentages of ester sulfate	• Bind moisture • Stabilize emulsions • Control flow and texture properties of food systems • High protein reactivity-strong interactions with milk proteins	• Frozen dessert stabilizers • Chocolate milk stabilisers • Texturizers for low-fat foods • Low calorie jellies • Toothpaste binders • Air fresheners • Personal care products • Pet foods
Kappa	*Euchema (cottonii)* *Kappaphycus (alvarezii)* *Gigartina (radula)*	4-sulfated on the galactose subunits (~25% ester sulfate)	• Form strong rigid gels with potassium and calcium ions • Exhibit synergy with locust bean and konjac gums.	
Iota	*Euchema (spinosum)*	4-Sulfated on the galactose Subunits and 2-sulfated on the 3,6-anhydrozalactose subunits (~32% ester sulfate)	• Form elastic aqueous gels with calcium ions • Exhibit synergy with locust bean gum and starch • Suspend particulates	
Lambda	*Chondrus (crispus)* *Gigartina (radula)*	Alternating 2-sulfated 1.3-linked α-D-galactose and 2.6-disulfate 1.4-linked ß-D galactose backbone (minimal 3.6-anhydro-ß-D-galactose) (~ 35% ester sulfate)	• Non gelling aqueous system viscosifier	

Now, *Gelidiella acerosa, Gracilaria edulis, G. crassa, G. foliifera, Sargassum* spp., *Turbinaria* spp. and *Cystoseira trinodis* exploited mostly from the natural seaweed beds of Tamil Nadu coast are used as raw materials for the production of agar and alginates by Indian seaweed industries. Data collected by the Central Marine Fisheries Research Institute on the seaweed landings (dry wt. in tonnes) from Tamil nadu coast during the period 1978-1999 showed that the quantity of *Gelidiella acerosa* landed varied from 102 to 541, *Gracilaria edulis* from 105 to 982, *G. crassa* from 2 to 96, G. *foliifera* from 3 to 110, *Sargassum* spp. from 491 to 5000, *Turbinaria* spp. from 122 to 1281 and *Cystoseira trinodis* from 61 to 94 (Ramalingam *et al.,* 2000). In the collections of *Sargassum* and *Turbinaria* species, the major constituents were *Sargassum wightii* and *Turbinaria conoides*. *Gelidiella acerosa* is used for manufacture of bacteriological grade agar and *Gracilaria* spp. for food grade agar. Whenever there is scarcity for *Gracilaria edulis*, other species like *G. crassa* and *G. foliifera* are exploited from Mandapam area of south Tamil Nadu coast.

Gracilaria constitutes one of the most economically important species the world over because of its fast growth rate, adaptation to culture conditions and yield of good quality food grade agar. *Gracilaria crassa* is commercially exploited since 1983 from Gulf of Mannar islands and Mandapam coast. *Gracilaria crassa* grows attached to pebbles and stones in shallow areas and small quantity is harvested by handpicking. The cost of *Gracilaria crassa* is Rs.4000/- per tonne (dry wt.). The agar yield in the laboratory method is 23% on dry at basis with a gel strength of 140 g/cm^2.

Species of *Sargassum* are the major constituent of the seaweeds harvested for commercial use since 1966 and form about 70% of the total seaweeds harvested. *S. wightii* is the most dominant species. The cost of dried *Sargassum* is Rs.3000/- per tonne (dry wt.). *Sargassum wightii* yields 32% of alginic acid on dry wt. basis in the laboratory method. Species of *Turbinaria* are collected since 1975 along Mandapam and Rameswaram coast and Gulf of Mannar islands. The cost of dried *Turbinaria* is Rs.4000 per tonne. It yields 18% alginic acid on dry wt. basis in the laboratory method. *Hypnea valentiae* yields 25-30% carrageenan on dry wt. basis in the laboratory method.

The increasing demand of raw materials for the Indian seaweed industries has led to competition among the harvesters resulting in ecologically and economically unsound harvesting and management practices. This has led to a decrease in the natural stock of seaweeds. Hence seaweed cultivation is the only solution to solve this problem. For example, the Japanese and Korean *Porphyra* industries, the Chinese *Laminaria* industry and the Philippines *Eucheuma* industry are now mainly based on the cultured seaweeds.

Basically there are two methods in cultivation of seaweeds: one by means of vegetative propagation using fragments obtained from mother plants and the other by means of reproductive propagation using swarmers (gametes and zoospores), oospores, tetraspores, carpospores and monospores. There are merits and demerits in spore culture and fragment

culture methods. The number of fragments that can be obtained for propagation depends on size and maturity of the plants. In contrast to vegetative fragments, the number of spores produced by an alga is enormous and by suitable culture techniques most of the spores could be made viable and grown into adult plants. It would be also possible to multiply the plants to a very great extent.

Some work in the direction of culturing the spores of economically important seaweeds was carried out in the recent past years. Information is available on the settlement and development of germlings of different species of marine algae in the laboratory and their transplantation to the sea for further growth to harvestable size plants. From all these studies it is evident that by proper care under controlled conditions of the laboratory, a high rate of survival of germlings could be achieved and transplantation of germlings to the sea could be done successfully for large scale cultivation of seaweeds. The rhythmic liberation of spores also indicates the possibility of successfully raising the germlings in a nursery and further culture. Knowledge on the factors influencing spore release is very useful for conservation and management of natural stock of seaweeds. A better understanding of algal spore ecology will be helpful in basic ecological studies and for taking up large scale production of seaweeds by spores method. In India, seaweeds are used mainly for manufacture of agar and algin and hence, attempts are being made to cultivate the agar, carrageenan and algin yielding seaweeds.

In this context, an attempt has been made in the present investigation to study the suitable environmental conditions required for the liberation of maximum quantity of spores in some of the commercially important seaweeds of Mandapam coast. Two species of red algae, *Gracilaria crassa* and *Hypnea valentiae* and two species of brown algae, *Sargassum wightii* and *Turbinaria conoides* growing in Mandapam area were selected for the study considering their economic value. The work was carried out for a period of over two years from October 1997 to December 1999 and detailed information was collected on the fruiting behaviour and spore producing capacities of these four algae. Experiments were conducted under laboratory conditions to study the seasonal variations in the shedding of carpospores and tetraspores and periodicities in the daily liberation of these two types of spores in *Gracilaria crassa* for a period of one year from April, 1998 to March, 1999. Effect of important environmental factors such as exposure to air (desiccation), salinity, temperature, light and photoperiod on spore output in these four algae were studied in detail. The shape and size of spores produced by these plants were also studied. Hydrological and environmental parameters from a collection locality were also recorded.

Review of Literature

REVIEW OF LITERATURE

Investigations have been made on different aspects such as taxonomy, ecology, biology, physiology, biochemicals and utilisation in the members of Gigartinales (Rhodophyta) and Fucales (Phaeophyta) occurring in many parts of the world for the last five decades because of their commercial value as sources of agar, carrageenan and alginate. Studies were made on the fruiting behaviour, sporulation, spore germination and spore culture in different species of *Gracilaria* (Jones, 1959, Hoyle, 1975; Penniman, 1977; Hoyle, 1978, Friedlander and Dawes, 1984 and Luhan, 1996), *Hypnea* (Mshigeni, 1976 a; 1976 b, 1976 c and 1978), *Sargassum* (Tahara, 1909; Prince, 1974; Fletcher and Fletcher, 1975; De Wreede, 1976; Smith, 1976; Norton, 1977 and 1981; Fletcher, 1980; Okuda, 1981; Ang, 1985; Shunula, 1988; Hales and Fletcher, 1989), and *Turbinaria* (Blomquist, 1945) growing in other parts of the world.

In India, some important and commonly occurring members of Gigartinales and Fucales have received more attention. Among Gigartinales much work was done on the distribution, ecology, biology, chemical constituents, culture and commercial utilization of *Gracilaria* spp. (Ahmed, 1966; Oza and Krishnamurthy, 1967 and 1968; Krishnamurthy *et al.,* 1969; Mohan Joseph and Krishnamurthy, 1977; Umamaheswara Rao, 1972 a; 1972 b; 1973; 1975 and 1976; Rama Rao and Thomas, 1974; Oza, 1975; 1976; 1978 and 1979; Thomas and Krishnamurthy, 1976; Thomas, 1977; Subba Rangaiah *et al.,* 1975, Rama Rao, 1977 a; Chennubhotla *et al.,* 1978a; 1979 and 1986; Subba Rangaiah, 1978; 1983 a and 1984; Kaliaperumal *et al.,* 1986; Oza *et al.,* 1989; Mal and Subbaramaiah, 1990 a and 1990 b and

Kaladharan *et al.,* 1996), *Hypnea musciformis* and *Hypnea valentiae* (Rama Rao, 1970; 1972; 1974; 1977 a; 1977 b; 1978; 1979; 1982 and 1992; Rama Rao and Krishnamurthy, 1968, and 1978; Subba Rangaiah, 1978; 1983b and 1988; Rama Rao and Subbaramaiah, 1986; Solimabi *et al.,* 1980; Rama Rao *et al.,* 1985; Subba Rangaiah and Umamaheswara Rao, 1983 and Rengasamy and Ilanchelian, 1988). Among members of Fucales, certain species of *Sargassum* (Krishna Pillai, 1957; Chauhan and Krishnamurthy, 1967 and 1971; Srinivasan, 1966; Umamaheswara Rao, 1969a and 1969b; Chauhan, 1972; Umamaheswara Rao and Kaliaperumal, 1976; Kalimuthu, 1980; Chennubhotla *et al.,* 1982; Alankara Rao *et al.,* 1988, Inderdeep Kaur and Vijayaraghavan, 1992 and Appa Rao, 1998) and *Turbinaria* (Shah and Vaidya, 1965; Umamaheswara Rao and Kalimuthu, 1972; Kaliaperumal and Umamaheswara Rao, 1975; Kaliaperumal and Kalimuthu, 1976; Kaliaperumal *et al.,* 1977; Chennubhotla *et al.,* 1978b and Sokhi and Vijayaraghavan, 1986) were investigated in detail. In this chapter the literature pertinent to the present study on fruiting behaviour and sporulation has been reviewed.

FRUITING BEHAVIOUR

In the literature, variations have been observed on the phenology of different genera and species of Gigartinales and Fucales depending upon the environmental conditions in different latitudes. Fritsch (1945) reported that abundance of sexual plants were more than the asexual plants in Gigartinales. Jones (1959) reported that fertile plants were found

throughout the year in *Gracilaria verrucosa* with seasonal variation in their abundance. Accordingly cystocarpic plants of *Gracilaria verrucosa* were most abundant in autumn and early winter while tetrasporic plants were most abundant in July. In *Gracilaria corticata* collected from Mahabalipuram, tetrasporic and cystocarpic plants were not recorded (Srinivasan, 1946). Ahmed (1966) reported tetrasporic plants in *Gracilaria verrucosa* in April and cystocarpic plants in December - June with a peak in January - February. Male plants were not recorded in the population. In the same plant growing in different geographical areas, fertile plants were found for few months only (Oza and Krishnamurthy, 1968). In *Gracilaria corticata* along the Mandapam coast, tetrasporic plants were present during March-April and September-December while cystocarpic plants were present during September-December (Umamaheswara Rao, 1975).

Plants with reproductive structures occurred in *Gracilaria edulis* and *Gracilaria foliifera* along Rameswaram coast in all months of the year. In *Gracilaria edulis* vegetative or sterile plants were predominant throughout the period of study. Antheridial and cystocarpic plants were seen only in the month of January and only very few plants were observed. Tetrasporophytes occurred in all months except in October or November. In *Gracilaria foliifera* tetrasporic plants were seen from January to September and cystocarpic plants from February to March and July to December (Umamaheswara Rao, 1973). In *Gracilariopsis sjoestedtii*, definite fruiting periodicity was observed. Plants bearing reproductive structures were seen during the maximum biomass period from November to March. Cystocarpic

plants were more abundant than tetrasporophytes during the fruiting season and no male gametophytes were found (Umamaheswara Rao, 1973). The tetrasporic plants of *Gracilaria edulis* in the Gulf of Mannar were predominant over vegetative plants throughout the year. Cystocarpic plants were much lesser in number than both the tetrasporic and vegetative plants whereas spermatangial plants were still fewer and restricted to few months only. Peak abundance of tetrasporic plants (82%) was in May and September (84%). Cystocarpic plants were encountered in all months except in May and July. A maximum of 16% of cystocarpic plants were found both in the months of February and October (Rama Rao and Thomas, 1974).

Gracilaria verrucosa from British Columbia (Whyte *et al.,* 1981) and some population of *Gracilaria tikvahiae* in the martitime province of Canada (Bird *et al.,* 1977) had a preponderance of tetrasporic plants. In contrast, the attached population of *Gracilaria tikvahiae* from Barrachois Harbour, Nova Scotia had equivalent numbers of the three phases (Bird, 1976). Plants of *Gracilaria corticata* were found during August - December forming an intertidal population of this species at the infralittoral fringe at Mandapam Camp, Gulf of Mannar which also comprised of cystocarpic plants. By the end of January the population disappeared from the intertidal zone (Mohan Joseph and Krishnamurthy, 1977). Maximum occurrence of tetrasporic thalli in *Gracilaria foliifera* in New Hampshire was in June and July (Penniman, 1977). Observations on wild populations of *Gracilaria bursapastoris* and *Gracilaria coronopifolia* showed that the proportion of tetrasporic individuals in the population of these two

Gracilaria species dominated the combined male and female gametophytic stages. There were significantly more males than female thalli in the *G.coronopifolia* population whereas the gametophytes of *G. bursapastoris* occurred in the expected 1:1 ratio. Tetrasporic thalli of *G. coronopifolia* evinced a biphasic seasonal pattern with high proportions in winter and summer. *G. bursapastoris* showed a low proportion of tetrasporic plants in winter cystocarpic thalli were not abundant in *G. bursapastoris* in late winter and summer and in *G. coronopifolia* in winter and spring (Hoyle, 1978).

Oza (1979 and 1984) reported that in *Gracilaria corticata*, tetrasporic plants were present throughout the year while the sexual plants occurred seasonally on the coast of Veraval. Cystocarpic plants were present from September to December and maximum tetrasporic plants were seen in April and August. In Manila Bay, although fertile thalli of *Gracilaria verrucosa* were observed almost throughout the year, there appeared to be significant differences in the ratio of the populations of tetrasporpohytes, cystocarpic and spermatangial thalli. Monthly samples showed the preponderance of cystocarpic plants and the low occurrence of the male thalli (Trono and Rhodora Azanza Corrales, 1979). In *Gracilaria corticata* along Visakhapatnam coast, reproductive plants were observed throughout the year more abundantly than vegetative plants. Of the total plants examined about 77% were in fruiting condition, of which 17% were of cystocarpic, 16% of antheridial and 45% of tetrasporic plants. There were no significant changes in the abundance of sexual and asexual generations during

different months. Peak for both tetrasporic and cystocarpic plants was during November - December (Subba Rangaiah, 1983a). Populations of *Gracilaria textorii* occurred in three months only from December to February. There were no vegetative plants and all plants were found in fruiting condition. The frequency of sexual plants was high. In the populations observed for three growth seasons, 51.33 to 57.33% of cystocarpic plants, 12.67 to 14.50% of male plants and 30 to 34.17% of tetrasporophytes were recorded (Subba Rangaiah, 1984)

Tetrasporic plants of *Gracilaria corticata, Gelidiella acerosa, Gracilaria edulis* and *Hypnea musciformis* were observed in all months of the year along the Mandapam coast. Carposporophytes of *Gracilaria corticata* and *Gracilaria edulis* were seen continuously throughout the year, while in *Hypnea musciformis* they were found only in some months at Pudumadam. But at Kilakkarai, cystocarpic plants were observed almost throughout the year. Cystocarpic plants were not found in the population of *Gelidiella acerosa* (Shoba, 1985).

The tetrasporic plants of *Gracilariopsis sjoestedtii* were found during December to March and June, whereas cystocarpic plants were seen during December to March and June to August. In *Gracilaria foliifera*, the tetrasporic plants were seen from March to June and February and cystocarpic plants from March to June. In both plants, no male plants were recorded. In *Gracilaria foliifera* there were no vegetative plants and the samples consisted of tetrasporic and cystocarpic plants. Tetrasporophytes

were more abundant than carposporophytes. In the population of *G. sjoestedtii* occurring at Pamban, 77.2% of plants were in fruiting condition. Cystocarpic plants were predominant over tetrasporic and vegetative plants. In *G. sjoestedtii* growing at Kilakkarai, 96% of plants were in fruiting condition. Tetrasporophytes were more in number than cystocarpic and vegetative plants (Chennubhotla *et al.,* 1986).

Tetrasporic plants were abundant almost throughout the year and are predominant in the population over cystocarpic plants in *Gracilaria arcuata var. arcuata* and G. *corticata* var. *corticata*. Vegetative plants occurred only for 2 months in *Gracilaria arcuata* var. *arcuata* and they were absent in *G. corticata* var. *cylindrica*. Male plants were not found in both species during the entire period of investigation. In these two species, reproductive structures occurred without any seasonal changes. There were 35% to 92.2% of tetrasporic plants and 7.1% to 65% of cystocarpic plants in *G. arcuata* var. *arcuata*. The tetrasporic plants varied from 66% to 96.1% and the cystocarpic plants varied from 3.9% to 34% in *Gracilaria corticata* var. *cylindrica* (Kaliaperumal *et al.,* 1986).

In *Gracilaria tikvahiae*, the plants were vegetative throughout most of the two years study period. However, discrete maxima of tetrasporic and spermatangial plants occurred during June - July while cystocarpic plants were maximal during July - August (Penniman *et al.,* 1986).

Reproductive individuals of *Gracilaria edulis* and *Gracilaria foliifera* in Indonesia were recorded throughout the sampling periods with only small differences in the pattern of their occurrence. A greater abundance of sporophytes than gametophytes was found in September in *Gracilaria edulis* and *G. foliifera* in July (Atmadja, 1988). In *Gracilaria verrucosa* from the coast of Beyt Island, Gujarat, tetrasporic and cystocarpic phases were found almost throughout the year. Mixed plants with tetrasporangia and cystocarps were also recorded. Peak tetrasporic phase (78%) was observed during February. Cystocarpic phase of *G. verrucosa* occurred throughout the year except in monsoon (July / August). Two peaks were observed one in May and the other in January. Tetrasporic and cystocarpic plants were seen during January - June and September - December (Oza *et al.*, 1989).

The carposporophytes and tetrasporophytes of *Gigartina canaliculata* showed no significant seasonal differences and representatives of both phases were found in all months (Pacheco Ruiz and Aguilar Rosas, 1984). In *Gracilaria pacifica* at Baja California, Mexico, tetrasporic plants were more abundant in summer and less in winter. Cystocarpic plants were absent in one population whereas in another population vegetative and cystocarpic plants were dominant with maximum plants in spring and summer and tetrasporic plants were more abundant in summer and less in winter-spring (Aguilar Rosas *et al.*, 1993). Plant fertility in *Gracilaria heteroclada* collected from Jaro, Philippines was seasonal with the highest percentage of carposporophytes and tetrasporophytes during January (48%) and May (64%) respectively (Luhan, 1996). Study on the seasonal variation

of the reproductive thalli of the agarophyte *Gracilaria blodgetii* showed that majority (43.87%) of plants from the natural population were tetrasporic plants, 32.04% of plants were female while the remaining 24.14% consisted of sterile plants (Gerung *et al.,* 1997). In coastal Mediterranean lagoon along South France, fertile thalli in *Gracilaria bursapastoris* occurred throughout the year but population fertility was maximum in spring. *G. gracilis* showed a shorter fertility period in winter (Marinho Soriano *et al.,* 1998).

Isaac and Hewitt (1953) conducted detailed studies on *Hypnea spicifera* and reported that tetrasporic and sexual plants occurred at all seasons. Sexual plants always constituted a very small portion of the population. The studies conducted by Conover (1964) on the reproduction of benthic marine algae in the Texas lagoons revealed that in *Hypnea musciformis* sexual plants were restricted to one season only. The studies conducted by Mshigeni (1976 b) in *Hypnea cervicornis*, *H. cordacea* and *H. nidifica* show that among the fertile plants, tetrasporophytes were most predominant throughout the year followed by cystocarpic and spermatangial plants. In *H. nidifica* only tetrasporic and vegetative plants were found throughout the study period and sexual plants were not seen.

The reproductive capacity of the two species of *Hypnea*, especially *Hypnea musciformis* at Veraval, west coast of India was studied over different seasons by Rama Rao (1977 b). The tetrasporophytes in *Hypnea musciformis* occurred throughout the year with no distinct peak, while cystocarpic plants occurred for 11 months at Pamban and for 7 months at

Krusadai Island. Maximum frequency of tetrasporic and cystocarpic plants of *H. valentiae* at Pamban and Krusadai Island occurred in February and June / July respectively. Male plants were not observed both in *Hypnea musciformis* and *H. valentiae*. At Visakhapatnam coast, the tetrasporophytes were abundant throughout the year with two half-yearly peaks in *Hypnea valentiae* and carposporophytes occurred for 3-4 months. From the yearly means, it is evident that 86.49% of fruiting plants were observed (Subba Rangaiah, 1978; Subba Rangaiah and Umamaheswara Rao, 1983). Tetrasporic plants of *Hypnea musciformis* were observed in all months of the year along Mandapam coast. Carposporophytes of *Hypnea musciformis* were found only in some months at Pudumadam. But at Kilakkarai the cystocarpic plants were observed almost throughout the year (Shoba, 1985).

In some brown algae fruiting was seen for a short period of 3-7 months (Umamaheswara Rao, 1969 b; Umamaheswara Rao and Kalimuthu, 1972; Umamaheswara Rao and Kaliaperumal, 1976). De Wreede. (1976) reviewed the studies on tropical *Sargassum* and found that 12 out of 15 species including *Sargassum oligocystum* and *S. tenerrimum* showed seasonal peak in fertility between November and March. In *Sargassum wightii*, the fruiting plants occurred around Mandapam during the maximum growth period extending from October to December or January (Umamaheswara Rao and Kaliaperumal, 1976). In contrast, Ang (1985) reported seasonal peaks in reproduction between July and November in *Sargassum siliquosum* and *S. paniculatum* growing at Philippines. In

Sargassum aquifolium and *S. asperifolium* in Zanzibar, Tanzania, reproduction was more pronounced during best growing season between January and July (Shunula, 1988). In *Sargassum muticum*, reproduction occurred in summer and dormancy began in autumn and *Cystoseira nodicaulus* reproduced almost throughout the year and began dormancy at the end of autumn and winter (Arenas *et al.,* 1995). On the north coast of Spain, *Sargassum muticum* was fertile between spring and summer. Maturation occurred gradually from April to September. Senescence occurred simultaneously with full maturity increasing from June to September (Arenas and Fernandez, 1998).

Turbinaria ornata had a prolonged fruiting period of 8-10 months and the number of fruiting plants varied from month to month which closely agreed with the growth cycle of this alga (Umamaheswara Rao and Kalimuthu, 1972). In *Turbinaria decurrens,* plants with receptacles occurred for 11 months from August to June with large number of fruiting plants during the peak growth period, December - February (Kaliaperumal and Umamaheswara Rao, 1975; Kaliaperumal and Kalimuthu, 1976). The abundance of fertile plants varied seasonally in *Sargassum* and *Turbinaria* species with maximum number or 100% during peak growth periods.

In *Turbinaria conoides*, plants with reproductive structures "Receptacles" occurred for five months between October to February and maximum number of reproductive plants were noticed in the month of January. The fruiting cycle of this alginophyte started in the month of October and ended in the month of February (Chennubhotla *et al.,* 1978 b). The fucoid algae

Fucus vesiculosus var. *spiralis* showed a broader reproductive periodicity than *Ascophyllum nodosum* being maximal during March - June and minimal during winter (Knight and Parke, 1950; Mathieson *et al.*, 1976; Perkins, 1974). *Fucus distichus* ssp. *endentatus* and *F. distichus* ssp. *evanescens* had maximum reproductive plants in spring and early autumn (Sideman and Mathieson, 1983; South and Hooper, 1980).

SPORE OUTPUT

Though some information is available on the seasonal spore shedding of red algae, many members of Gigartinales have not been studied. Studies on this aspect in Fucales are also very limited. Corresponding with the fruiting behaviour, different species showed marked variations in spore shedding and spore discharge was observed for a short period or throughout the year. The seasonal variation in the liberation of spores in different algae studied so far has been reviewed here with special emphasis on Indian species studied in this specific area.

Suto (1950 a and 1950 b) estimated the spore output from the fronds of *Gelidium*. It varied from 10^4 to 10^5 spores/g wt./day and the spore shedding was found mainly for one day. Jones (1959) reported that maximum production of mature viable tetraspores in *Gracilaria verrucosa* was in July. Except for a period in spring, viable carpospores can be obtained at all times. Maximum production of carpospores apparently occurred in August - September. Boney (1960 a) estimated the number of spores released per gram fresh weight per hour in eight species of red algae

and observed maximum number of 10, 512 tetraspores / g fr.wt. / day in *Ceramium ciliatum* and a minimum of 120 tetraspores in *Polysiphonia nigrescens* and concluded that the species which tend to make a shorter annual appearance on the shore have a greater spore output than the species with more protracted reproductive periods. While working on the spore output of *Antithamnion plumula,* Boney (1960b) estimated about 50% of the spores on the first day, only 20% on second day and gradual decrease in the subsequent days. In the case of *Gracilaria millardetii,* Krishnamurthy (1967 b) reported a maximum of 68,520 tetraspores / plant and the maximum carpospore output was 42,782 carpospores/plant.

In *Sargassum swartzii*, maximum liberation of 5,53,331 oospores/plant was recorded by Chauhan and Krishnamurthy (1967). Oza and Krishnamurthy (1968) found that in *Gracilaria verrucosa* a single mature cystocarpic plant produced upto 19,700 carpospores per day in December, the season of maximum spore shedding. In *Cystoseira indica*, spore shedding was observed in the months of May and November. Occasional spore formation and liberation were however observed between June and September. Maximum spore output of 5,11,251 oospores/plant was found in November, when plants on attaining maturity began to liberate oogonia. Both the number of conceptacles and the spore output per receptacle increased in December, but since the number of receptacles per plant declined due to shedding of some fruiting branches, the spore output per plant was low when compared to that in November (Mairh and Krishnamurthy, 1968).

In *Gracilaria verrucosa* about 200 to 2000 carpospores can be obtained from a single cystocarp (Kim, 1970). Subbaramaiah (1970) reported that *Ulva fasciata* produced a maximum of 1,15,34,400 swarmers / plant. *Dictyota dichotoma* and *Centroceras clavulatum* also produced spores throughout the year (Umamaheswara Rao and Sreeramulu, 1970). In *Monostroma nitidum*, the maximum liberation occurred usually during the period of mid neap tide. Such periodic phenomena were observed regularly during the period ranging from early February to early June every year and the time interval between successive periods was about 14 days from the date when gamete liberation ceased. The formation and liberation of gametes in *M. nitidum* in the natural habitat took place periodically in strict correspondence with the lunar rhythm (Ohno, 1972).

Sreenivasa Rao (1971 and 1974) studied seasonal variation in tetraspore output in *Gelidiella acerosa* growing in the tide pools at Veraval. In *Gelidiella acerosa* two spore shedding seasons were observed in a year from April to May and from October to November, each shedding season lasting for 25 to 30 days. Maximum number of tetraspores recorded was 20,000 tetraspores / plant. In *Gracilaria verrucosa*, spore maturation was observed only at certain periods of the year. The cystocarpic plants had a peak reproductive activity in the month of December and this activity declined in the months of March to May, probably due to adverse temperature conditions in these months (Ogata *et al.*, 1972). In the case of

Gelidium robustum, both the tetrasporic and carposporic plants showed a clean rhythmic activity and in every case the carposporic plants released a greater number of spores. Moreover, the period of activity of the carposporic plants was longer sometimes being twice or three times as long as that of tetrasporic plants. A maximum of 2,99,072 carpospores and 27,453 tetraspores were liberated per month from each thallus of about 12.5 to 15 cm length. In Baja California, *Gelidium robustum* had peak spore production during August and September. The total number of spores released gradually decreased towards January and February, coinciding with winter (Guzman del Pro *et al.*, 1972). In *Saccorhiza dermatodea,* individual sporangia were found to contain 128 zoospores (Norton, 1972). Neushul *et al.* (1972) estimated 3,50,000 spores / mm^2 of sporangia area on each side of sporophyll in *Macrocystis pyrifera*.

The spore shedding in *Gracilaria edulis* growing at Rameswaram was reported by Rama Rao and Thomas (1974). The total spore output per plant showed peak values in July and August with gradual decrease by January. The higher values of spore output were seen again in February - March, while in April - May there was no spore liberation. Maximum carpospore output was 6,49,873 spores / plant in August and lowest spore output was 6,919 spores / plant in January. The tetraspore output in *Gelidiella acerosa* from Pudumadam was recorded by Umamaheswara Rao (1974). Liberation of tetraspores was seen during the entire fruiting season with peak output

in May - June and November - December. Within the two peak periods of spore production, the tetraspore output varied from about 5,000 to 10,000/g fr.wt. of the plant. Kaliaperumal and Umamaheswara Rao (1975) reported a maximum spore shedding of 28,196 oospores / plant in *Turbinaria decurrens*. During the fruiting season, peak output of spores was observed in November. Umamaheswara Rao (1976) found tetraspore and carpospore shedding in all months of the year in *Gracilaria corticata* growing at Mandapam with maximum output in March - April and again between September and December. Seasonally tetraspore production varied between 26,500 and 1,44,000 spores / g fr.wt. / day and carpospore production from 1,183 to 2,374 spores / cystocarp / day.

In *Sargassum wightii* the spore shedding period commenced from November and ended by January with a peak output of oospores in December. *S. wightii* had a maximum liberation of 3,70,272 oospores / plant (Umamaheswara Rao and Kaliaperumal, 1976). Kaliaperumal *et al.* (1977) reported that *Turbinaria ornata* had a maximum spore output of 33,810 oospores / plant. In *Gracilaria corticata* growing at Mandapam camp, the peak season for sporulation in cystocarpic plants was during October - November. From August the activity increased gradually, reached the peak in November and dropped suddenly in December. The total number of carpospores liberated ranged from 2,260 to 8,66,700 spores / plant or 239 to 53,200 carpospores / g fr.wt. (Mohan Joseph and Krishnamurthy, 1977). The

estimates of oospore output given by Chennubhotla *et al.* (1978 b) for *Turbinaria conoides* ranged from 56 to 11,312 oospores / plant and no periodicity was observed in the liberation of spores.

Oza (1979) conducted laboratory experiments with *Gracilaria corticata* occurring at Veraval coast. Two peak periods of sporulation were observed. In February, the total number of carpospores shed was 947. In July a total of 2,35,000 spores were shed. Studies on the seasonal rhythm in the shedding of tetraspores and carpospores in *Hypnea valentiae* from Mandapam coast were carried out by Rama Rao (1979). Maximum number of 3,14,000 tetraspores / plant and 7,01,000 carpospores / plant were observed in February and October respectively. Kaliaperumal and Umamaheswara Rao (1982) observed clear cut seasonal periodicity in the liberation of tetraspores from *Gelidiopsis variabilis* of Visakhapatnam coast with peak shedding from July to September. The spore output in different months of the year varied from 20 to 2,60,940 spores / g fr.wt. / day.

Subba Rangaiah (1983 a) reported the shedding of tetraspores and carpospores from *Gracilaria corticata* of Visakhapatnam coast in all months of the year and the peak liberation of tetraspores was found during the period from December to February and again from August to October. The tetraspore shedding in *G. corticata* varied from a minimum of 13,705 to a maximum of 3,33,300 spores / g fr.wt. / day whereas the carpospores varied

from 300 to 3,100 spores / cystocarp / day. Peak production of carpospores was noted during January - February and in August. In *Hypnea valentiae* growing at the same locality, Subba Rangaiah and Umamaheswara Rao (1983) observed the tetraspore shedding throughout the year with maximum liberation in January to February / March and August to September. The carpospore shedding was seen from November to February and again in June. The tetraspore shedding in this alga ranged from 1,63,200 to 8,49,140 spores / g fr.wt. / day and the carpospore liberation varied from 280 to 1,954 carpospores / cystocarp / day.

Subba Rangaiah (1984) reported tetraspore and carpospore shedding in *Gracilaria textorii* from December to February. The tetraspore output during the period of the growth ranged from 8,50,390 to 12,30,380 spores/ g fr.wt. / day whereas the carpospores were seen at a minimum of 1,127 and a maximum of 2,646 spores / cystocarp / day. In *Ulva fasciata*, profuse liberation of spores was observed near full moon and new moon days and spore liberation was comparatively more near full moon days than new moon days. Spore production started when moon passed equator and ended when it attained the last quarter position. Plants from exposed habitats produced more swarmers than those from submerged habitats. Further, plants collected during morning periods produced more spores than those collected during noon or afternoon periods (Oza *et al.*, 1985).

The tetraspore output ranged from 5,774 to 3,89,793 spores / g fr.wt. in *Gelidiella acerosa* collected from Pudumadam. In *Gelidiella acerosa*, spore liberation occurred in all months of the year. Though there was no regular trend in spore output, maximum shedding of tetraspores was observed in the first year of the study in the month of July and in the second year from April to September with a low value in July. The tetraspore and carpospore shedding in *Gracilaria corticata* was found in all months of the year and regular changes were not observed either in the output of tetraspores or carpospores. The tetraspore output varied from 8,181 to 92,277 and carpospores from 8,086 to 4,87,178 spores / g fr.wt. / day. In *Gracilaria edulis*, the tetraspore output varied from 2,135 to 1,09,565 and carpospores from 28,652 to 3,27,833 spores / g fr.wt. / day. Marked seasonal changes were not seen in the liberation of both tetraspores and carpospores. Tetraspore output varied from 2,662 to 5,04,953 spores / g fr.wt. / day and carpospore output ranged from 16,112 to 6,46,385 and from 2,814 to 2,83,745 spores / g fr.wt. / day in *Hypnea musciformis* collected from Pudumadam and Kilakkarai respectively (Shoba, 1985).

In *Gracilariopsis sjoestedtii*, Subba Rangaiah (1985 a) observed the shedding of tetraspores and carpospores in all the seven months of its occurrence in the field. No seasonal variation was observed in this alga. The tetraspore shedding varied from a minimum of 3,20,500 and a maximum of 5,72,156 spores / g fr.wt. / day. The carpospores ranged from 3,867 to 6,807

spores / cystocarp / day. In *Pterocladia heteroplatos* and *Gelidium pusillum* (Kaliaperumal and Umamaheswara Rao, 1985 and 1986), the tetraspore output ranged from 1,427 to 7,94,055 and 1,149 to 10,78,505 spores/g fr.wt./ day and the carpospore output from 39,996 to 1,67,040 and 1,176 to 6,99,943 spores/g fr.wt./day respectively. Maximum number of tetraspores was liberated from *Gelidium pusillum* between April and August and low values in October and December. In *Gracilaria foliifera*, maximum quantity of spores was liberated in March. The quantity of tetraspores liberated during different months ranged from 500 to 11,508 and carpospores from 1,015 to 26,368 spores / g fr.wt. In *Gracilariopsis sjoestedtii* growing at Pamban, peak output of spores occurred in February. The number of tetraspores varied from 1,197 to 3,15,636 and carpospores from 2,700 to 1,42,672 spores / g fr.wt. In *Gracilariopsis sjoestedtii* growing at Kilakkarai, maximum production of spores was observed in January. The tetraspore output ranged from 52 to 3,27,791 and carpospore output from 14 to 2,52,151 spores / g fr.wt. (Chennubhotla *et al.,* 1986).

The spore producing capacity of *Gracilaria arcuata* var. *arcuata* and *Gracilaria corticata* var. *cylindrica* was low. Peak shedding of spores occurred during the maximum growth period in *G. arcuata* var. *arcuata*, while seasonal variations were not observed in the discharge of spores in *Gracilaria corticata* var. *cylindrica*. Monthly output of tetraspores and carpospores varied from 43 to 28,291 and from 10 to 40,055 spores / g fr.wt.

in *Gracilaria arcuata* var. *arcuata* and *G. corticata* var. *cylindrica* respectively (Kaliaperumal *et al.*, 1986). Naidu (1987) observed the swarmer shedding in *Ulva fasciata* and *Enteromorpha compressa* in all months of the year with maximum shedding corresponding to the two peak growth periods of the alga, one in February and the other in August. In *Ulva fasciata* the swarmer output varied from 6,15,730 to 19,16,120 swarmers / g fr.wt. / day, whereas in *Enteromorpha compressa* the swarmer output ranged from a minimum of 8,31,550 to a maximum of 24,14,800 swarmers / g fr.wt. / day. In *Fucus spiralis*, peak fertility occurred in September when a mean fecundity of 284.6 x egg m^{-2} was estimated (Robertson, 1987).

Umamaheswara Rao (1987) reported tetraspore and carpospore shedding in *Grateloupia filicina* from November to March. Tetraspore output along the growth cycle ranged from 50,000 to 4,00,000 spores / g fr.wt. / day. Spore output was high in November and decreased in the other months of the growth season indicating that the spore shedding capacity was more in small and rapidly growing plants. *Gracilaria asiatica* growing along the coast of China released a maximum quantity of tetraspores averaging 1,72,089 spores / g plant and 2,267 / spores / cm frond respectively during the best maturation period (Li Xiuliang and Li Meizhan, 1988). The optimal temperature period for carpospore release in the same alga was from the end of June to early July when each gram of female gametophyte with cystocarps could release 52,187 - 86,250 carpospores (Li

Xiuliang and Li Meizhan, 1989). In *Chondrus crispus* from the Gulf of Maine, tetrasporic plants released a maximum of 36,000 to 48,000 spore / sorus in May - June and a smaller maximum of 29,000 to 31,000 spores / sorus in December - January. Discharge of tetraspores was greater in the summer than in autumn-winter. Cystocarpic plants showed their maximum discharge during summer (48,000 spores / sorus). Subsequently a decrease was seen during autumn-winter with the lowest discharge (20,000 spores/ sorus) during April when the lowest number of reproductive plants occurred (Mathieson, 1989).

Narasimha Rao (1989 a and 1989 b) studied the spore producing capacities of three seasonally occurring algae of the Visakhapatnam coast. In this study, the plurispore production of *Ectocarpus mitchellae* and monospore output of *Bangiopsis subsimplex* varied between 1.2 and 2.4 millions/g fr.wt./day. The peak shedding of all types of spores in *Porphyra vietnamensis, Bangiopsis subsimplex* and *Ectocarpus mitchellae* was found during the maximum growth period i.e. between January and March. In *Porphyra vietnamensis*, the maximum monospores / g fr.wt. / day was 8,20,000 and minimum was 1,40,000. Maximum carpospores / g fr. wt. / day was 9,00,000 for the same plant (Narasimha Rao, 1989 a). In the carrageenophyte *Gigartina canaliculata*, these were no significant seasonal differences between the numbers of spores released by carposporophytes and tetrasporophytes. The alga released a maximum of 27,34,000 and a

minimum of 3,11,000 spores / plant for carposporophytes and a maximum of 20,50,000 and a minimum of 2,08,000 spores / plant for tetrasporophytes (Pacheco Ruiz *et al.,* 1989).

Giffordia mitchellae produced 6,93,478 to 13,29,278 plurispores / plant / day during the fruiting period which extended from November to May. *Rosenvingea nhatrangensis* and *Padina tetrastromatica* produced 9,70,000 to 16,00,000 plurispores / plant / day and 22,070 to 81,965 tetraspores / plant / day respectively. *Sargassum ilicifolium* produced 94 to 5,225 oospores / plant / day from October to April, whereas *Sargassum vulgare* produced 136 to 31,284 oospores / plant / day from October to March. *S. wightii* produced 15,642 to 52,896 oospores / plant / day during its fruiting period which extended from November to January. *Turbinaria deccurens* produced 8 to 1,616 oospores / plant / day from the fruiting plants which were present during the whole year (Umamaheswara Rao, 1990). Spore production was relatively higher in seasonal red and brown algae like *Grateloupia filicina, Gracilaria textorii, Ectocarpus mitchellae* and *Rosenvingea nhatrangensis*. This unusual production of reproductive elements may probably increase their chances of survival during the unfavourable period of the year (Umamaheswara Rao, 1990).

Banumathi and Subbaramaiah (1990) reported that in *Gelidiella acerosa* the liberation of spores per stichidium varied as follows: monospores 62 to 70, bispores 533 to 1000, tetraspores 26 to 36 and polyspores 15 to 19, total spores 647 to 1123. Peak spore shedding of 50,000 spores / g / day

occurred generally in March. The carpospore shedding capacity of *Gracilaria edulis* varied between 1696 and 6715 spores / cystocarp / day and 72,928 to 5,90,920 spores / g plant / day. In this study spore shedding was noted both in April and May with a maximum in April. The tetraspore shedding capacity of *Gracilaria edulis* varied from 44 to 6,439 spores / g plant / day (Mal and Subbaramaiah, 1990 b).

Shedding of tetraspores in the red algae *Bostrychia tenella* and *Caloglossa leprieurii* was observed throughout the year but with seasonal differences in their output. Carpospores were liberated from October to May when the material was available. Maximum shedding of carpospores and tetraspores was observed in December and January and the minimum number of tetraspores in August and carpospores in May (Narasimha Rao and Umamaheswara Rao, 1991). The carpospore output in *Gracilaria crassa* was seasonal, moderate and attained a maximum of 40 / g / day or 13 / cystocarp / day in June and a minimum of 12 / g / day or 4 / cystocarp / day in August (Shyam Sunder *et al.,* 1991). The egg release in five members of Fucales in Tsuyazaki, Japan was studied by Nanba and Okuda (1992). *Sargassum macrocarpum* released eggs in summer, *S. autumnale* and *S. siliquastrum* in spring. In *Myagropis myagroides* some plants released eggs from late winter but many plants released eggs from late winter to mid-spring.

Martin-Smith (1993) reported that *Sargassum tenerrimum, S. fissifolium* and *S. oligocystum* showed a late summer reproduction peak (March - May), while *S. linearifolium* had an earlier peak in reproduction (September - January). The tetraspore release per sorus was highest (150-250 spores / sorus / day) in winter in *Gelidium robustum* (Melo and Neushul, 1993). Maximum plurispore liberation was seen in December and minimum in May in *Rosenvingea nhatrangensis* (Narasimha Rao, 1995). In *Gelidium sesquipedale,* no clear seasonal pattern of reproduction was found. Tetraspore production was high in March 1990 with 10.4 x 10^6 spores / m^2 whereas the carpospore peak was lower, 4.9 x 10^5 spores / m^2 in July (Santos and Duarte, 1996).

Among the three members of Ceramiales studied by Sudhakar (1992) and Sudhakar and Subba Rangaiah (1993 and 1997 a), spore sheddings was observed in all months of the year in tetrasporophytes and carposporophytes of *Wrangelia argus* and *Centroceras clavulatum*. In the case of *Polysiphonia platycarpa*, the tetraspore and carpospore sheddings was during the short period of its occurrence in the field. The tetraspore and carpospore sheddings were maximum in two periods in both *Wrangelia argus* and *Centroceras clavulatum,* one between January - February / March and the other between July - August / September. Both types of spores liberated on first day and second day showed the same period of peak shedding in two periods. Tetraspore production varied from 3,928 to 1,91,940 spores / g

fr.wt. / day in *Wrangelia argus*. The carpospore output during the period of study ranged from 523 to 39,706 carpospores / g fr.wt./day. The tetraspore shedding in *Centroceras clavulatum* varied from 16,338 to 1,89,949 spores/ g fr.wt. / day and carpospores from 6,081 to 84,731 spores / g fr.wt. / day. In *Polysiphonia platycarpa*, tetraspore and carpospore sheddings were observed during 6 months from December to May. The tetraspore output varied from 43,513 to 1,78,697 spores / g fr.wt. / day and carpospores from 16,580 to 86,994 spores / g fr.wt. / day.

The tetraspore shedding varied from 4,240 to 5,28,461 spores / g fr.wt. / day in *Amphiroa fragilissima* on first day and from 4,318 to 2,31,538 spores / g fr.wt. / day on second day, whereas the carpospore output varied from 6,962 to 3,61,686 spores / g fr.wt. / day on the first day and from 1,861 to 1,27,692 spores / g fr.wt. / day on second day. The tetraspore shedding in *Jania rubens* varied from 84 to 1,597 spores / g fr.wt. / day on first day and from 47 to 928 spores / g fr.wt. / day on second day whereas, the carpospore shedding varied from 36 to 1,170 spores / g fr.wt. / day on first day and from 95 to 1,110 spores / g fr.wt. / day on second day. In *Grateloupia lithophila*, the tetraspore shedding varied from 17,090 to 8,60,435 spores / g fr.wt. / day on first day and from 7,415 to 7,53, 549 spores / g fr.wt. / day on second day. The carpospore shedding during the period of the study varied from 5,450 to 11,64,258 spores / g fr.wt. / day on first day and from 4,790 to 3,65,806 spores / g fr.wt. / day on second day. The tetraspore and

carpospore shedding were seen in all months of the year with two peak shedding periods coinciding with the two peak periods of growth, one between January - February and the other between June - July (Vanilla Kumari, 1997; Subba Rangaiah and Vanilla Kumari, 1999). In *Asparagopsis delilei* collected from three islands, maximum number of 11,917 carpospores/g fr.wt. in Putty Island in November; 5,032 carpospores / g fr.wt. in Valai Island in October and 22,300 carpospore / g fr. wt. in Krusadai Island were recorded. The minimum numbers for this alga from these islands were 390, 56 and 193 carpospores / g fr.wt. respectively (Vasuki *et al.,* 1999).

DIURNAL PERIODICITY

Periodicity in the daily liberation of spores was reported in some species of Gelidiales (Suto, 1950 a; Katada *et al.,* 1953; Umamaheswara Rao, 1974; Umamaheswara Rao and Kaliaperumal, 1987), Gigartinales (Matsui, 1969; Umamaheswara Rao, 1976; Umamaheswara Rao and Subba Rangaiah, 1981; Subba Rangaiah and Umamaheswara Rao, 1983; Subba Rangaiah, 1983 a; 1984 and 1985 a), Ulotrichales (Naidu, 1987), Bangiales (Narasimha Rao and Subba Rangaiah, 1991), Ceramiales (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1993; 1997 a and 1997 b), Fucales (Umamaheswara Rao, 1990; Subba Rangaiah, 1992; Appa Rao, 1998), Cryptonemiales (Vanilla Kumari, 1997) and other red algal species (Dring, 1974; Ngan and Price, 1983; Subba Rangaiah, 1986).

Suto (1950 a and 1950 b) found peak shedding of spores daily in the afternoon in *Gelidium amansii*. The mechanism of spore liberation in *Gelidium amansii* was later studied in detail by Katada *et al.* (1953) and Katada (1955). The shedding time of carpospores was always 3-4 hours earlier than that of tetraspores. The shedding of spores in *G. amansii* was seen daily in the afternoon. Fukuhara (1957) conducted experiments on the shedding of spores of *Iridophycus cornucopiae*. In this study, definite diurnal periodicity in the shedding of spores was not recognised and differences were not found in the time of shedding between carpospores and tetraspores. Biological rhythms in plants were recognised for many centuries and it was consistently demonstrated that rhythmic behaviour of many kinds exhibited in the natural environment continued under even constant conditions in the laboratory at least for a short period of time (Sweeney, 1963).

Matsui (1969) observed the release of tetraspores and carpospores from evening to mid-night in *Gloiopeltis tenax* and in the early morning hours in *Gloiopeltis furcata*. In *Gelidiella acerosa* growing in the tide pools at Gujarat coast (Sreenivasa Rao, 1971), the periodicity of tetraspores varied with the time of collection of plants. Shedding was related to the time of exposure and also to the combined effects of flooding of the tide pool. A definite periodicity was observed by Umamaheswara Rao (1974) in *Gelidiella acerosa* growing at Pudumadam and maximum tetraspore output was observed in the afternoon between 14.00-18.00 hours.

In *Turbinaria decurrens* periodic liberation of oospores was not found (Kaliaperumal and Umamaheswara Rao, 1975), The results of the study on Hawaiian species of *Hypnea* i.e. *H. cervicornis, H. cordacea* and *H. nidifica* showed that in these species spore production did not show any regular periodic rhythm (Mshigeni, 1976 b). In *Gracilaria corticata* (Umamaheswara Rao, 1976), peak spore output was observed during night time from 22.00-06.00 hours and both tetraspores and carpospores showed the same rhythm without any differences in the time of shedding. Subba Rangaiah (1978) observed maximum shedding of carpospore in *Hypnea valentiae* 4 hours earlier (10 PM to 2 AM) than peak tetraspore output (2AM - 6AM). A definite diurnal periodicity in the shedding of carpospores in *Hypnea valentiae* was reported by Rama Rao (1979).

Ngan and Price (1983) collected data on the diurnal periodicity of carpospore and tetraspore discharge in 14 red algae growing in the vicinity of Townsville region, Queensland, Australia under a variety of laboratory conditions. Experiments were conducted at hourly or bi-hourly intervals over periods of 24 hours or in some case 48 hours. Maximum shedding of tetraspores in *Gelidiopsis variabilis, Gelidium corneum, G. pusillum, Heterosiphonia wurdemanni, H. multiceps, Bostrychia radicans, B. tenella, Grateloupia divaricata, Hypnea pannosa, H. valentiae, Tolypiocladia glomerulata* and *Caloglossa bombayensis* occurred during morning hours i.e. 05.00 - 09.00. The tetraspores of *Acrocystis nana, Laurencia perforata, Leveillea jungermannioides* showed maximum liberation during afternoon hours i.e. (13.00-16.00 hours). The carpospores and tetraspores of *Coelothrix*

indica, Bostrychia binderi, Catenella nipae, Polysiphonia coacta, Gracilaria rhodotricha, Hypnea cervicornis, Sarconema filiforme, Solieria mollis and *S. robusta* showed maximum shedding during morning hours 05.00-09.00.

The maximum shedding of carpospores and tetraspores of *Laurencia papillossa, L. succisa, Acanthophora muscoides* and *A. spicifera* was in the afternoon i.e. 13.00 - 16.00 hours. The carpospores of *Ceramium fastigiatum, Chondrococcus hornemanni, Gelidium crinale, Gracilaria textorii* and *G. verrucosa* showed maximum shedding in the morning from 05.00 to 09.00 hours. Subba Rangaiah (1983 a) reported the peak shedding of carpospores and tetraspores from *Gracilaria corticata* of Visakhapatnam coast during early morning hours between 02.00 and 06.00 in all the months of the year. In *Gracilariopsis sjoestedtii* (Subba Rangaiah, 1985 a), peak liberation of tetraspores and carpospores was observed during early morning hours i.e. 02.00 to 06.00. In contrast to these observations, day time peak was seen in *Gracilaria textorii.* In this species, the peak shedding of tetraspores and carpospores was observed between 14.00 and 18.00 hours (Subba Rangaiah, 1984).

Peak shedding of tetraspores in *Aglaothamnion cordatum* and carpospores in *Hypnea valentiae* occurred between 22.00 and 02.00 hours (Subba Rangaiah, 1985 b; Umamaheswara Rao and Subba Rangaiah, 1981). Diurnal periodicity in the liberation of tetraspores with a prominent peak between 2PM and 6PM was observed in *Gelidiella acerosa* and a definite peak at one time of the day in the shedding of tetraspores and carpospores

was not seen in *Gracilaria corticata, G. edulis* and *Hypnea musciformis* and maximum liberation of spores occurred in these three species from 10PM to 2PM (Shoba, 1985). In *Gracilaria arcuata var. arcuata* and *G. corticata var. cylindrica*, there was no definite rhythm in diurnal output of tetraspores and carpospores (Kaliaperumal *et al.,* 1986). Naidu (1987) observed peak shedding of swarmers between 06.00 and 10.00 hours in *Ulva fasciata* and *Enteromorpha compressa* in all months of the year. Diurnal periodicity existed in the liberation of tetraspores and carpospores of *Grateloupia filicina*. Peak liberation of tetraspores and carpospores was seen in this alga in the early morning hours from 2AM to 6AM. The quantity of spores liberated was very low between 6PM and 2AM and from 6AM to 6PM (Umamaheswara Rao, 1987).

Umamaheswara Rao and Kaliaperumal (1987) studied the diurnal periodicity of spore shedding in *Gelidium pusillum, Gelidiopsis variabilis* and *Pterocladia heteroplatos* and found peak shedding of tetraspores and carpospores during 18.00 to 22.00 hours in *Gelidium pusillum* and tetraspores between 06.00 and 10.00 hours in *Gelidiopsis variabilis.* However, the daily spore output was irregular in *Pterocladia heteroplatos* without any seasonal fluctuations in the daily liberation of spores. Diurnal periodicity of carpospore shedding of *Gracilaria edulis* was studied by Mal and Subbaramaiah (1990 b) and reported the occurrence of a diurnal rhythm with a peak shedding time varying from 19.00 to 01.00 hours. In *Sargassum ilicifolium* and *Sargassum vulgare,* the maximum number of oospore production was observed in the night time i.e. between 02.00 and

06.00 hours, while in the case of *Padina tetrastromatica* day time peak shedding of tetraspores was observed between 06.00 and 10.00 hours (Umamaheswara Rao, 1990).

Regular diurnal periodicity in spore shedding was found with peak output of spores between 1.30 and 2.30 PM in *Gelidiella acerosa*. Shedding of spores was absent or minimum during night and morning hours (Banumathi and Subbaramaiah, 1990). Narasimha Rao and Subba Rangaiah (1991) recorded diurnal periodicity in the liberation of reproductive elements in *Ectocarpus mitchellae, Bangiopsis subsimplex* and *Porphyra vietnamensis* and observed peak shedding of swarmers / spores during noon time between 10.00 and 14.00 hours in all the three red algae. Maximum shedding of tetraspores and carpospores occurred between 02.00 and 06.00 hours in *Centroceras clavulatum* (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1993). In *Wrangelia argus,* an evening peak between 14.00 and 18.00 hours was found (Sudhakar and Subba Rangaiah, 1993). The highest daily release of eggs in *Fucus vesiculosus* was typically found from 18.00 to 22.00 hours (Andersson *et al.*, 1994). In *Rosenvingea nhatrangensis*, the daily peak shedding occurred between 2AM to 6AM (Narasimha Rao, 1995). The spore shedding in *Padina tetrastromatica* showed a diurnal periodicity with a peak output of spores between 06.00 and 10.00 hours in all eight months of its occurrence in a year at Visakhapatnam coast without any shifts in peak shedding (Appa Rao, 1995). In *Amphiroa fragilissima* and *Jania rubens*, the tetraspore and carpospore shedding showed maximum liberation during morning hours between 06.00 and 10.00 throughout the

year. The peak period of shedding of tetraspores and carpospores in a day was found between 10.00 and 14.00 hours in *Grateloupia lithophila* (Vanilla Kumari, 1997). The shedding of carpospores in *Asparagopsis delilei* was found to be high between 06.00 - 10.00 hours in August. There was 4 hours delay in the peak shedding of spores from October to January and peak discharge was observed between 10.00 and 14.00 hours (Vasuki *et al.*, 1999).

EFFECT OF ENVIRONMENTAL FACTORS ON SPORE SHEDDING

Spore liberation is an important aspect in the life-history of marine algae (Suto, 1950b) and any effect on it will lead to the depletion of natural population. Environmental factors are known to affect sporulation in different manner depending on the genus and species. Effects of environmental factors like desiccation, salinity, light and temperature on spore shedding and diurnal periodicity in the liberation of spores have been studied by some workers.

Exposure to air and desiccation

As early as 1910, Baker (1910) demonstrated that *Ascophyllum nodosum* required exposure to air to expel its gametes. The gametes are also more actively released in fresh water than salt water. Since the exposure and desiccation of the plants caused by tidal action influence the spore production (Suto, 1950b), experiments were conducted by some workers to study its effects. Katada (1955) observed no effect of desiccation

on the shedding of spores in *Gelidium amansii*. On the other hand, Matsui (1969) reported significant effect in *Gloiopeltis* species. In G. *tenax*, a large number of spores were liberated immediately after reimmersion of the fronds exposed for 2-6 hours and majority of the spores liberated even 10 hours before the peak of daily liberation. In *Gloiopeltis furcata*, reimmersion of the fronds around the peak daily liberation caused a great deal of spores to be liberated immediately after reimmersion and the exposure affected the time of subsequent liberation. In *Gelidiella acerosa* (Sreenivasa Rao, 1971) similar effect was not observed in the tetrasporic fronds exposed to air in shade. The number of tetraspores shed decreased in frond exposed for 1-2 hours and there was no spore output in fronds exposed from 4 to 12 hours Chamberlain and Evans (1973) suggested that the mucilage surrounding *Ceramium* spores actively imbibed water, perhaps creating internal pressure and facilitating spore expulsion. In *Gracilaria corticata* (Umamaheswara Rao, 1976), tetraspore output decreased markedly in fronds exposed for 1 hour and spore shedding was not found in fronds exposed for a period of 2 to 6 hours.

Discharge of viable gametes can be induced prematurely by mild over night desiccation in *Sargassum muticum* (Fletcher and Fletcher, 1975). Ripe gametes were obviously retained until an appropriate stimulus was offered. In the experiments conducted by Subba Rangaiah (1978), the tetrasporic thalli of *Gracilaria corticata*, *G. textorii*, *Gracilariopsis sjoestedtii* and *Hypnea valentiae* were exposed upto 105 minutes to air in the room and upto 90 minutes outside in the sun with 15 minutes intervals. The

tetraspore output decreased in all plants with increase in the duration of exposure of fronds and maximum output was seen under continuously submerged condition. It was apparent that the release of spores/gametes in seaweeds was often induced by desiccating and then rehydrating fertile thalli (Zechman and Mathieson, 1985). The tetraspore output in *Dictyota dichotoma* decreased very rapidly with increase in duration of exposure of the fronds to air and total inhibition of spores was found in the fronds exposed for 120 minutes (Umamaheswara Rao and Reddy, 1982). In *Gelidium pusillum, Pterocladia heteroplatos* and *Gelidiopsis variabilis* (Umamaheswara Rao and Kaliaperumal, 1983), desiccation often decreased the spore release and maximum output was obtained under submerged condition. In *Aglaothamnion cordatum* also a rapid decrease in the tetraspore shedding was seen after 45 minutes of exposure of the fronds to air and no spore shedding was observed after 1 hour (Subba Rangaiah, 1985b).

Shoba (1985) reported that in *Gracilaria edulis, G. corticata* and *Hypnea musciformis*, spore output declined with increase in the duration of exposure of fruiting thalli in shade and maximum number of spores were liberated from the plants mostly under submerged condition. In the data collected by Subba Rangaiah (1986) on monospore shedding from *Porphyra vietnamensis,* spore output was seen even when the plants were exposed to air for four hours. In some species growing in the lower intertidal region such as *Gracilaria corticata, G. textorii* and *Gracilariopsis sjoestedtii* (Umamaheswara Rao and Subba Rangaiah, 1986), *Wrangelia argus,*

Centroceras clavulatum and *Polysiphonia platycarpa* (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1997 a), desiccation led to decrease in spore output and maximum shedding was obtained under submerged condition. In *Ulva fasciata* and *Enteromorpha compressa* (Naidu, 1987), maximum swarmer shedding was seen in submerged condition and marked variation in the number of swarmers shed was not observed in these two Chlorophyceae members upto 4 hours of exposure. After 4 hours of exposure, the swarmer shedding declined rapidly and even after 24 hours of exposure of the fronds swarmer output was seen in *Ulva fasciata* and *Enteromorpha compressa*.

In *Gracilaria verrucosa* and *Iridaea ciliata*, maximum spore shedding occurred after the desiccation (Infante and Candia, 1988). Plurispore output decreased while increasing the duration of exposure to air in *Rosenvingea nhatrangensis* (Narasimha Rao, 1989 a and 1989 c). Maximum spore output was obtained at submerged condition and there was no spore output at 90 minutes of exposure. In *Dictyota dichotoma, Padina tetrastromatica, Sargassum vulgare* and *Sargassum ilicifolium* also, the tetraspore and oospore release decreased as the period of exposure increased (Umamaheswara Rao and Reddy, 1982 and Umamaheswara Rao, 1990) Plants of *Bangiopsis subsimplex* and *Porphyra vietnamensis* tolerated upto 6 hours of aerial exposure but exposure of *Ectocarpus mitchellae* to air rapidly reduced plurispore discharge. In this brown alga, maximum output of plurispores was observed during submergence and there was no spore output in plants exposed to air for 80 minutes. In the two algae, *Bangiopsis*

subsimplex and *Porphyra vietnamensis,* although peak output of spores also occurred from submerged plants, there was no sudden decrease in the quantity of spores released and monospores and/or carpospores of *Bangiopsis subsimplex* and *Porphyra vietnamensis* were liberated from plants exposed to air for periods of upto 6 hours. However, spore output from these two algae decreased rapidly between 3 and 6 hours of exposure and spore shedding was not observed in plants exposed for period greater than 7 hours (Narasimha Rao and Subba Rangaiah, 1991). Dehydration was not found to influence the pattern of egg release in *Fucus vesiculosus* (Andersson *et al.,* 1994).

In *Padina tetrastromatica,* spore shedding decreased with increase in the duration of exposure of fronds to air and maximum quantity of spores was obtained under submerged conditions, (Appa Rao, 1995). In *Asparagopsis delilei* (Ganesan and Subba Rao, 1997), the carpospore liberation was maximum in submerged condition. The plants desiccated for 0 and 30 minutes showed greater spore liberation, while decrease in spore output was observed in plants desiccated for 60,90 and 120 minutes. Daily rhythm in spore liberation showed that peak output of carpospores was observed on second day itself in both control condition and 30 minutes exposure and drastically decreased from third day onwards. Further the shedding extended upto 14 days in control condition and only for 8 days upto 30 minutes exposure. In *Jania rubens, Amphiroa fragilissima* and *Grateloupia lithophila*, spore shedding decreased with increase in the duration of exposure to air and maximum quantity of both types of spores

was obtained under submerged condition (Vanillakumari, 1997). Spore output in the desiccation experiments with *Padina boergesenii* (Ganesan *et.al.*, 1999) showed that in plants exposed to air during daytime, maximum liberation was observed in control (submerged) condition and declined rapidly upto 90 minutes exposure and complete inhibition was seen at 120 minutes exposure. During night time exposure, spore release increased gradually with increasing the time of exposure and maximum liberation was observed during 90 minutes exposure. In thallus exposed to sun, spore liberation was maximum at 10 minutes exposure and decreased during 15 and 20 minutes exposure.

Salinity

Studies made by Baker (1910) and West (1972) showed that reduced salinity (i.e. freshwater) is an important factor causing propagule discharge in *Ascophyllum nodosum* and *Audouniella purpurea*. The shedding of monospores decreased in dilute seawater than in normal seawater in the experiments conducted with conchocelis phase of *Porphyra tenera* by Yamasaki *et. al.* (1957). In *Enteromorpha intestinalis*, there was no liberation of zoospores at salinity less than 10‰ (Christie and Evans, 1962). Matsui (1969) studied the effect of different salinities on the liberation of spores in *Gloiopeltis tenax* and *G. furcata*. Significant influence was not observed in salinities ranging from 17‰ to 52‰. In salinities below 12‰ and above 60‰ liberation of spores was delayed and the number of spores liberated decreased in these two species of *Gloiopeltis*. There was a

tendency for spore liberation to be accelerated at 35‰. White and Boney (1969) observed spore production in salinities ranging from 35‰ to 39‰ in *Achrochaetium endophyticum*.

Salinity is an important environmental factor that affects the distribution of marine algal species and thus reflects not only the preferred or tolerant range of salinity of the species but also its ability to withstand changes with time (Burns and Mathieson, 1972; Bird *et al.*, 1979; Yarish and Edwards, 1982; Friedlander and Dawes, 1984; Bird and McLachlan, 1986). Normal production of zoospore or gametes was found in *Ulva fasciata* by Mohsen *et al.*, (1972) in the salinity range between 20 and 35‰. Higher salinities from 35‰ to 45‰ enhanced both the formation of swarmers and their discharge. In experiments conducted with *Gracilaria corticata* (Subba Rangaiah *et al.*, 1975), *Gracilaria textorii, Gracilariopsis sjoestedtii* and *Hypnea valentiae* (Umamaheswara Rao and Subba Rangaiah, 1986), *Ulva fasciata* and *Enteromorpha compressa* (Naidu, 1987), *Ectocarpus mitchellae* and *Bangiopsis subsimplex* (Narasimha Rao, 1989 a and 1989 b), *Wrangelia argus, Centroceras clavulatum* and *Polysiphonia platycarpa* (Sudhakar 1992; Sudhakar and Subba Rangaiah, 1997 a), maximum shedding of spores was found between 20 and 40‰. In *Dictyota dichotoma, Padina tetrastromatica, Sargassum vulgare* and *S. ilicifolium,* maximum shedding of tetraspores and oospores was found at 30‰ (Umamaheswara Rao and Reddy, 1982; Umamaheswara Rao, 1990).

In the case of *Gelidium pusillum, Pterocladia heteroplatos* and *Gelidiopsis variabilis* (Umamaheswara Rao and Kaliaperumal, 1983), tetraspore shedding was found to be maximum between 30‰ and 40‰. Peak spore output was seen at 30‰ salinity in *Gracilaria corticata, Gracilaria edulis* and *Hypnea musciformis* and at 40‰ in *Gelidiella acerosa*. The optimum range for peak shedding of spores in all the three algae was 30-40‰ salinity (Shoba, 1985). In *Aglaothamnion cordatum,* salinities between 30-40‰ were found to be favourable for the maximum shedding of tetraspores (Subba Rangaiah, 1985 b). Maximum shedding of monospores was seen in *Porphyra vietnamensis* at 20-30‰ (Subba Rangaiah, 1986).

In *Rosenvingea nhatrangensis* (Narasimha Rao, 1989 c), maximum plurispore shedding was seen at 30‰ and there was no sporulation at 0-10‰. Spore output decreased from 30‰ salinity onwards and was minimum at 50‰ salinity. Narasimha Rao and Subba Rangaiah (1991) reported the effect of salinity on spore liberation in *Bangiopsis subsimplex, Porphyra vietnamensis* and *Ectocarpus mitchellae*. In these three algae, spore release was not observed at 10‰ salinity. In *E. mitchellae* maximum number of plurispores was obtained at 30‰ salinity. There was no liberation at 60‰ salinity. In the other two species, maximum output of monospores and / or carpospores was obtained at 40‰ salinity. Spore output decreased above 50‰ although even at 60‰ salinity some spore shedding was noticed in these two red algae. Maximum number of spores was liberated in the red algae *Bostrychia tenella* and *Caloglossa leprieurii* when plants were submerged at 20‰ salinity (Narasimha Rao and Umamaheswara Rao, 1991).

The spore shedding in *Padina tetrastromatica* also varied in different salinities and peak liberation of spores was observed at 35‰ salinity (Appa Rao, 1995). Maximum number of tetraspores was released at 30‰ salinity while no tetraspores were formed at 25‰ salinity in *Gracilariopsis bailinae* (Rabanal *et al.,* 1997). In *Asparagopsis delilei*, the carpospore output was maximum at 40‰ salinity and minimum at 60‰ salinity and decreasing trend was observed below 20‰ and above 40‰ and lowest number of spores were released at 60‰ (Ganesan and Subba Rao, 1997). The tetraspore and carpospore shedding in *Jania rubens, Grateloupia lithophila* and *Amphiroa fragilissima* varied in different salinities tested and the optimum range observed for peak liberation of tetraspores and carpospores was 30‰ in all three algae (Vanilla Kumari, 1997). In *Padina boergesenii,* tetraspore liberation was seen within the range of 0 and 40‰. Spore liberation increased gradually from 5‰ salinity onwards and peak discharge was seen at 35‰. At 40‰ salinity sporulation again decreased (Ganesan *et al.,* 1999).

Temperature

Gametogenesis requires low to medium temperatures in several algal groups. A well known temperature response in this respect is the induction of fertility of Laminarian gametophytes by low temperature (Schreiber, 1930). Suto (1950 a and 1950 b) emphasized the importance of temperature on the shedding of tetraspores and carpospores in *Gelidium amansii*. The shedding season started in *Gelidium* when the seawater temperature rose to 20°C for tetraspores and 24°C for carpospores. There was an optimum

temperature range for shedding of spores and abnormal temperature delayed or hastened shedding by about 20 days. Katada *et. al.* (1953) and Katada (1955) studied the influence of water temperature on the shedding of spores of *Gelidium amansii*. The shedding time of tetraspores and carpospores was not restricted to the afternoon of a given day but varied in relation to changes in the seawater temperature. Peak shedding of spores was found between 12.00 and 14.00 hours during the period from June to September and after 14 hours in October and November. The time of shedding became earlier when the water temperature was less than 25°C. The diurnal periodicity was not affected by seasonal changes in seawater temperature in *Iridophycus cornucopiae* (Fukuhara, 1957).

The liberation of zoospores in *Enteromorpha intestinalis* during the period before spring tides was appreciably greater if the plants were kept at 20°C rather than at 4°C (Christie and Evans, 1962). *Ectocarpus siliculosus* formed unilocular zoidangia only at temperatures below 13°C whereby gametophytes were formed and the sexual phase of the life history was initiated (Muller, 1962 and 1967). Kurogi and Akiyama (1966) examined the effect of water temperature on the liberation of monospores in 6 species of *Porphyra* viz. *P. tenera, P. kuniedai, P. yezoensis, P. angusta, P. suborbiculata* and *P. pseudolinearis*. Monospores were liberated between 10° and 25°C in *P. tenera, P. yezoensis* and *P. angusta* and liberation was less or not seen in *P. kuniedai, P. suborbiculata* and *P. pseudolinearis* at these temperature ranges. Kurogi *et. al.* (1967) noticed differences in the optimum temperature of monospore liberation between the conchocelis of

the autumn and spring plants of *Porphyra umbilicalis*, although experiments from these plants were not carried out at the same time. Abundant monospores were liberated at 5°, 10° and 15°C in autumn plants, at 1°C in dioecious spring plants and 1° and 5°C in monoecious spring plants. Spore shedding was not accelerated by changing the water temperature in *Gloiopeltis tenax* and *G. furcata* (Matsui, 1969). Chen *et al.*, (1970) reported maximum discharge of conchospores in *Porphyra* at 3-7°C. Spore formation and release were delayed by decreasing temperature in *Bangia fuscopurpurea*, whereas higher temperatures favoured earlier spore formation and release (Sommerfeld and Nichols, 1973).

Spore production varied at 5 different temperatures ranging from 15°C to 35°C in *Hypnea valentiae* with peak spore output at 30°C. Since spore shedding was affected adversely below 20°C and above 30°C, the temperature between 25°C and 30°C was considered as optimum for discharge of maximum number of spores. In the fronds of *Hypnea valentiae* treated for short periods at -6°C, 10°C and 40°C, the spore output was less than in the untreated fronds kept at room temperature. In all these cases spore output decreased with increase in the period of temperature treatment (Subba Rangaiah, 1978). The frequency of oospores in *Sargassum muticum* was shorter at 17.8°C and 28 $\mu Em^{-2}s^{-1}$ than in the refrigerated room (9 days) at 16°C and 85 $\mu Em^{-2}s^{-1}$. The receptacles at higher temperatures ripened earlier than those at lower temperatures (Norton, 1981). Peak shedding of spores in *Gracilaria corticata, G textorii* and *Hypnea valentiae* was obtained at 30°C. The pattern of diurnal periodicity

of tetraspore shedding varied with water temperature but not with other environmental conditions tested in *G. corticata* and *H. valentiae*. In these studies, the peak shedding of spores was delayed by 4,8 or 12 hours at temperatures below 30°C in *G. corticata* and below 25°C in *H. valentiae*. Considerable delay in the peak liberation of tetraspore was observed in *G. corticata, G. textorii, Gracilariopsis sjoestedtii* and *H. valentiae* exposed for short periods from 2 to 8 hours at 10°C. (Umamaheswara Rao and Subba Rangaiah, 1981; Subba Rangaiah, 1985 c).

In *Dictyota dichotoma* maximum liberation of tetraspores was found at 25-30°C temperature (Umamaheswara Rao and Reddy, 1982). In *Pterocladia heteroplatos, Gelidium pusillum* and *Gelidiopsis variabilis,* maximum spore shedding was observed at 25-30°C (Umamaheswara Rao and Kaliaperumal, 1983). In *Gracilaria foliifera* var. *angustissima,* carpospore release was highest at 20°C either in the dark or under low light ($8\mu Em^{-2}s^{-1}$). Release of carpospores was negatively correlated with temperature under dark or low light conditions. Attachment of the spores appeared unaffected by temperature although the largest number of attached spores were observed at a temperature of 18°C (Friedlander and Dawes, 1984). Spore production varied in different temperatures with maximum spore output at 25°C in *Gelidiella acerosa,* at 30°C in *Hypnea musciformis* and at 25°C and 30°C in *Gracilaria corticata* and *Gracilaria edulis* (Shoba, 1985).

Another mainly temperature dependent phenology was reported by Novaczek *et. al.* (1986) for the two annual *Chorda* spp. in Novascotia. The gametophyte of *C. tomentosa* readily reproduced at 5°C, not at 10°C or 15°C and those of *C. filum* reproduced in the wider range of 5-15°C. In an experiment on the tetraspore release of *Gracilaria asiatica* along the Qingdao coast of China, initial release occurred in May when seawater temperature was at about 21°C. As seawater temperature increased, the spores were released continuously and the fronds of tetrasporophytes gradually degenerated (Li Xiuliang and Li Meizhan, 1988). The optimal temperature period for carpospore release was from the end of June to early July when the water temperature ranged from 21.9 to 22.5°C (Li Xiuliang and Li Meizhan, 1989). In *Sargassum vulgare* and *S. ilicifolium*, oospore liberation was maximum at 25°C (Umamaheswara Rao, 1990)

The diurnal periodicity of spore shedding was altered significantly in *Wrangelia argus* and *Centroceras clavulatum* in the fronds treated for short periods at 0°C and 10°C. In the fronds treated for short periods at 0°C, the normal peak period of shedding of tetraspores was obtained between 14.00 and 18.00 hours, whereas in the fronds treated for 30 and 60 to 90 minutes, 4 and 8 hours delay was observed respectively in the peak period of shedding of spores in *Wrangelia argus*. In *Centroceras clavulatum* also, the normal peak period of shedding of tetraspores (i.e. between 02.00 and 06.00 hours) was obtained in the control (untreated fronds) but in the fronds treated for 30 minutes, four hours delay was observed and in the fronds treated for 60 and 90 minutes, 8 hours delay had been observed. In contrast

to the above two genera, the normal peak period of shedding of tetraspores was obtained between 14.00 and 18.00 hours in the control as well as in the fronds treated for 30 minutes in *Polysiphonia platycarpa*. In the fronds treated at 10°C also, considerable delay in the peak shedding of tetraspores and carpospores was observed in *Wrangelia argus, Centroceras clavulatum* and *Polysiphonia platycarpa*. These experiments clearly revealed that temperature plays an important role in the diurnal periodicity of spore shedding in a day (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1997 a and 1997 b).

In *Fucus vesiculosus*, no correlation was found with temperature and pattern of egg release (Andersson *et al.,* 1994). Many tetraspores were liberated in the thallus grown at 26°C in *Gracilariopsis bailinae* and no tetraspores were formed at a higher temperature of 30°C (Rabanal *et al.,* 1997). Spore output varied at different temperatures tested in *Padina boergesenii*. At 0°C and 20°C, peak sporulation was observed after 60 minutes of exposure and afterwards it decreased. At 10°C, spore liberation decreased sharply upto 90 minutes exposure and slight increase was observed at 120 minutes. At 40°C and 50°C, maximum output was observed at 30 minutes exposure and decreased suddenly upto 120 minutes. Temperature shock (ranging from 0°C to 50°C upto 120 minutes) did not enhance the spore discharge (Ganesan *et al.,* 1999). Temperatures had a highly significant effect on the spore release in *Gracilaria cornea*. The maximum number of carpospores released per cystocarp was observed at 25°C. In general, the number of spores released at 25°C was higher than those observed at 28 or 31°C regardless of the irradiance (Orduna Rojas and Robledo, 1999).

Light

Light intensity seems to have a great role in the control of reproduction in many species and maximum spore release occurred in dark while in other species at different light intensities. Katada (1955) studied the effect of light on shedding of carporspores in *Gelidium amansii*. No variation was observed in the time of shedding in plants kept under dark and lighted conditions. In *Enteromorpha intestinalis*, there was no liberation from the plants kept in dark (Christie and Evans, 1962). In *Porphyra umbilicalis*, higher light intensities enhanced spore or gamete liberation (Kurogi and Sato, 1967). Effect of light intensity was studied by White and Boney (1969) on the production of monospores in *Achrochaetium endophyticum*. Spore output was obtained in the light intensity ranging from 50 to 110 lumens/sq.ft. (538-1184 lux).

In *Monostroma nitidum*, gamete liberation was observed between 500 and 5000 lux and at intensities higher than 10,000 lux liberation was not found although gamete formation was observed (Ohno, 1972). Abundant monosporangia formation was obtained at 1500-3000 lux in *Porphyra suborbiculata* and the release of spores was induced by increasing light intensity (Iwasaki and Sasaki, 1972). However, Ohno and Nozawa (1972) observed gamete liberation in *Monostroma nitidum* at 10,000 and 30,000 lux light intensity. The tetraspore output was found to be maximum at 0 lux (darkness) in *Gracilaria corticata, G. textorii* and *Gracilariopsis sjoestedtii* and at 750±50 lux in *Hypnea valentiae* (Subba Rangaiah, 1978;

Umamaheswara Rao and Subba Rangaiah, 1986). Brown algae needed very low irradiance for spore liberation (Chapman and Chapman, 1980). In *Porphyra rosengurtii* the formation of monospores was noticed in light intensities of 430-2580 lux (Kapraun and Luster, 1980). Maximum number of monospore release from conchocelis stage of *P. rosengurtii* was noticed with increased illumination. According to Dawes (1981), light quality and day length (photoperiod) influence reproduction. In *Dictyota dichotoma, Padina tetrastromatica, Sargassum vulgare* and *Sargassum ilicifolium*, the maximum number of tetraspore and oospore liberation was seen at 500 lux light intensity (Umamaheswara Rao and Reddy, 1982; Umamaheswara Rao, 1990). Low light intensity (500 lux) favoured the maximum liberation of tetraspores in *Gelidium pusillum, Pterocladia heteroplatos* and *Gelidiopsis variabilis* (Umamaheswara Rao and Kaliaperumal, 1983).

Carpospore release in *Gracilaria foliifera* var. *angustissima* was highest in dark or under low light of 8 $\mu Em^{-2}s^{-1}$ (Friedlander and Dawes, 1984). Peak sporulation was observed at low light intensity of 500 lux in *Gelidiella acerosa, Gracilaria edulis* and *G. corticata* and at 1000 lux in *Hypnea musciformis*. Spore output decreased in high light intensities (Shoba, 1985). In *Aglaothamnion cordatum*, the maximum shedding of tetraspores was seen at 2000 lux (Subba Rangaiah, 1985 b) and at 2,500 lux maximum liberation of monospores and carpospores of *Porphyra vietnamensis* and monospores of *Bangiopsis subsimplex* was seen (Subba Rangaiah, 1986; Narasimha Rao and Subba Rangaiah, 1991). In *Ulva fasciata* and *Enteromorpha compressa*, the maximum liberation of swarmers

were observed at 1,300 and 3,400 lux respectively (Naidu, 1987). The maximum number of plurispores was liberated at 1500 lux in *Ectocarpus mitchellae* (Narasimha Rao and Subba Rangaiah, 1991). In *Wrangelia argus,* gradual decrease in the tetraspore and carpospore shedding was seen from 23-52 $\mu Em^{-2}s^{-1}$. In *Centroceras clavulatum* the tetrasporophytes and carposperophytes liberated maximum number of spores in dark condition and considerable number of spores was also seen at 23$\mu Em^{-2}s^{-1}$ but a sudden decrease of spore shedding was seen in this alga at 34 $\mu Em^{-2}s^{-1}$ onwards. In *Polysiphonia platycarpa*, maximum number of tetraspores and carpospores was noticed at 34 and 23 $\mu Em^{-2}s^{-1}$ respectively (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1997 a). The tetrasporophytes of *P. platycarpa* were more resistant to different photon flux densities than carposporophytes. The quantity of spores liberated at different light intensities in *Padina tetrastomatica* also varied and the maximum shedding was observed at 1000 lux light intensity (Appa Rao, 1995).

In *Jania rubens, Amphiroa fragilissima* and *Grateloupia lithophila,* gradual increase in the tetraspore and carpospore liberation was observed from dark and maximum shedding of both types of spores were observed at 54$\mu Em^{-2}s^{-1}$. Sudden decrease of spore shedding was noticed in all the three algae after 54 $\mu Em^{-2}s^{-1}$ and almost equal number of tetraspores and carpospores was seen at 90 $\mu Em^{-2}s^{-1}$ and dark (Vanilla Kumari, 1997). In *Gracilariopsis bailinae*, many tetraspores were produced at 100 $\mu Em^{-2}s^{-1}$ while those exposed to lower light had fewer tetraspores (Rabanal *et al.,* 1997). Maximum discharge of tetraspores in *Padina boergesenii* was

observed in the alga kept in 26 $\mu Em^{-2}s^{-1}$ light intensity and thereafter it declined (Ganesan *et al.*, 1999). In *Gracilaria cornea*, maximum number of carpospores released per cystocarp was observed at 10 $\mu mol^{-2}s^{-1}$. The number of carpospores released at 10, 25, 50 $\mu mol^{-2}s^{-1}$ were significantly higher than those at 75 and 100 $\mu mol^{-2}s^{-1}$ (Orduna - Rojas and Robledo, 1999).

Photoperiod

Photoperiodic response has recently been demonstrated in seaweeds where it has been shown that the day length and photoperiod regulate the onset of fertility and also influences the liberation of spores. Katada (1955) studied the effect of light on the time of shedding of carpospores in *Gelidium amansii*. No variation was observed in the time of shedding in plants kept under dark and light conditions. Fronds kept under illumination throughout the night did not liberate gametes in *Monostroma* (Shihira, 1958) and this phenomenon was often verified by field observation and after sufficient period of darkness, light appeared to act solely as a trigger agent. In *Porphyra tenera* (Iwaswaki, 1961), monospore formation and release of fertile monospores were induced by short day conditions of 8-11 hours light period.

Sagromsky (1961) also studied the effects of light and dark periods on *Nitophyllum punctatum*. Much work was done by Kurogi and his associates on the photoperiodic induction and liberation of monospores by

the conchocelis phase of *Porphyra* spp.. Short day conditions (12-16 hours of dark period) enhanced spore production in *Porphyra tenera, P. yezoenensis, P. angusta* and *P. pseudolinearis* and long day conditions (less than 12 hours of dark period) in *P. umbilicalis* (Kurogi and Sato, 1962). Photoperiodic effects on the monospore release by the conchocelis phase of *Porphyra tenera* were described by Dring (1967) and Rentschler (1967). Darkness promoted the zoospore production as compared to cool-white illumination in *Protosiphon botryoides* (Durant *et al.,* 1968). Illumination after a period of darkness did not accelerate liberation of spore in *Gloiopeltis tenax* and dark had a pronounced influence on the rhythm (Matsui, 1969). In the experiments conducted by White and Boney (1969) with *Achrochaetium endophyticum*, plants kept under long day conditions (18:6 LD cycle) produced large number of monospores at all light intensities ranging from 30-50 lumens/sq.ft. (323-5382 lux).

Studies on the combining effects of light intensity and photoperiod indicated that the amount of energy received by the plants affected their growth and reproduction and while reviewing the earlier works, Dixon and Richardson (1970) described this interacting effect as photosynthetic effect. Long day conditions (18-24 hours light period at 3000 lux) favoured faster gamete liberation than a normal light period or short day treatment in *Monostroma nitidum* (Ohno, 1972). Srinivasa Rao (1971) reported variations in the spore output in the dark and light conditions in *Gelidiella acerosa*. Thalli under dark conditions liberated less number of spores than those kept under continuous light.

Release of spores in *Porphyra suborbiculata* was induced by short day conditions (Iwasaki and Sasaki, 1972). Spore formation and release were delayed by decreasing day length in *Bangia fuscopurpurea* (Sommerfeld and Nichols, 1973), whereas long day conditions favoured earlier spore formation and release. In *Gelidiella acerosa* (Umamaheswara Rao, 1974) increase in spore output was observed in fertile ramuli exposed to 8 to 16 hours light period rather than 0 hours light period. In *Gracilaria corticata* release of tetraspores and carpospores was observed in different light and dark periods. Tetraspore shedding was maximum in 24 hours dark period and with increasing light period spore output decreased gradually. The carpospere output varied under different light and dark cycles and maximum number of spores were liberated at 4:20 LD cycle (Umamaheswara Rao, 1976). In *Falkenbergia rufolanosa*, shedding of spores was noticed at short day conditions of 6:18 LD cycle (Oza, 1977).

Maximum shedding of tetraspores was also observed by Subba Rangaiah (1978) in *Gracilaria corticata, G. textorii, Gracilariopsis sjoestedtii* and *Hypnea valentiae* at 0:24 LD cycle and the spore output declined with increase in the duration of photoperiod. The values obtained at 4:20 LD regime were also higher than in other photoperiods. The red alga *Porphyra* formed carpospores under long day conditions, whereas the conchocelis phase of *Porphyra* (filamentous, shell boring phase) produced only spores with short day condition (Dawes, 1981). In darkness, emission of oospores were repeated at nine day intervals but in continuous light subsequent emissions were rudimentary or absent in *Sargassum muticum*. Transferring illuminated plants to dark or a photoperiod of 16:8 LD stimulated expulsion within a few days but after 27 days receptacles cultured in the dark began to decay and renewed emission was not induced by transference to either

continuous light or the photoperiodic regime. In continuous light also the branches began to decay, but the receptacles themselves not only remained healthy, but also increased in length by an average of 40% in 27 days (Norton, 1981).

Long day conditions at low illumination was found to be optimum conditions for the maximum shedding of spores in *Gelidium pusillum, Pterocladia heteroplatos* and *Gelidiopsis variabilis* (Umamaheswara Rao and Kaliaperumal, 1983). In *Porphyra abottae* and *P. perforata*, exposure of conchocelis filaments to short days (8:16 LD) for several days induced maturation and release of viable conchospores (Waaland and Duckson, 1983). Numerous examples of environmental triggers controlling algal seasonality were reported mainly on photoperiodic induction of reproduction and often restricted to certain temperature range (Dring, 1984 and 1988; Breeman, 1988). Guiry (1984) reported that in the red alga *Gigartina acicularis* at 16°C, the alga reduced its elongation rate and formed tetrasporangia after 9 weeks in short day conditions (8 or 10 hours light per day), whereas in long day (14 hours light per day or more) high growth rates were maintained and tetrasporogenesis was largely blocked.

Mairh *et al.* (1985) observed swarmer liberation soon after sunrise in the submerged plants of *Enteromorpha flexuosa*. Short day conditions was found to be favourable for the maximum shedding of tetraspores in *Aglaothammion cordatum* where 4:20 LD regime was found to be suitable conditions for maximum liberation (Subba Rangaiah, 1985b). In *Gelidiella acerosa*, tetraspores showed maximum liberation at 12:12 LD cycle. The tetraspores of *Gracilaria corticata* had maximum liberation at 24:0 LD cycle. The carpospores and tetraspores of *G. edulis* showed maximum

liberation at 20:4 LD cycle. In *Hypnea musciformis*, peak carpospore liberation was at 16:8 LD cycle while the peak tetraspore output was at 24:0 LD cycle (Shoba, 1985).

In *Ulva fasciata* and *Enteromorpha compressa*, the maximum spore liberation was found at 12:12 LD and 16.8 LD regime respectively (Naidu, 1987). In experiments conducted on *Wrangelia argus, Centroceras clavulatum* and *Polysiphonia platycarpa*, peak output of spores varied with the duration of irradiance received in different light and dark regimes (Sudhakar, 1992, Sudhakar and Subba Rangaiah, 1997 a). The maximum liberation of spores was observed at 24:0 LD cycle in *Padina tetrastromatica* (Appa Rao, 1995). Many tetraspores were released at 11:13 LD photoperiod in *Gracilariopsis bailinae* and no tetraspores were formed at a longer photoperiod of 13:11 LD cycle (Rabanal *et al.,* 1997). In *Jania rubens, Grateloupia lithophila* and *Amphiroa fragilissima*, the number of tetraspores and carpospores increased gradually from dark to 24:0 LD photoperiod except in the case of tetrasporophytes of *Grateloupia lithophila* where a gradual increase in the tetraspore shedding was noticed from dark upto 20:4 LD. At 24:0 LD, decrease in tetraspore shedding was seen at most light intensities (Vanilla Kumari, 1997). At 26 and 52 $\mu Em^{-2}s^{-1}$ light intensity, tetraspore shedding peaks were at 8:16 and 20:4 LD regime respectively in *Padina boergesenii* (Ganesan *et al.,* 1999).

SPORE SIZES

The spore size in marine algal species are different and such variability in size may be related to variations in spore formation. An account of some studies made by workers on spores sizes is given below. Variabilty in spore size or lack of variability is a species characteristic. Yamanouchi (1912) reported that the female gamete of *Cutleria multifida*

measured about 26 µm in length. Yamanouchi (1913) also reported that the zoospore of *Zanardinia collaris* measured about 22 µm in length. Mature carpospores were found to be elongate to spherical and had a diameter of 30-45 µm in *Arthrocardia gardnerii* (Ganesan, 1967). In *Polysiphonia platycarpa*, ripe carpospores were found to be pyriform, 100 µm long and 54-60 µm broad and gradually tapering towards one end (Krishnamurthy, 1967 a). In *Sargassum swartzii,* the oospores were 200 µm long (Chauhan & Krishnamurthy 1967). The egg of the genus *Cystoseira* was reported to be 75-90 µm along its longest dimension and ovoid in shape (Krishnamurthy and Mairh, 1967). In *Polysiphonia kappannai*, carpospores were elongate and pyriform and in *P. parthasarathyae* carpospores were elongate and pyriform and 26-33 µm broad and 85-102 µm long (Sreenivasa Rao, 1967).

In *Gracilaria verrucosa* carpospores were spherical with a single nucleus and about 27-28 µm in diameter with dense pigments (Oza and Krishnamurthy, 1967). In *Ectocarpus* species, the zoospore size ranged from 10-12 µm in length (Baker and Evans, 1973). In *Derbesia clavaeformis* multiflagellate zoospores having 30-40 µm diameter were seen (MacRould and Womersley, 1974). Umamaheswara Rao (1974) reported that in *Gelidiella acerosa* the tetraspores were globular and 22-26 µm in diameter. Mshigeni (1976 a) reported spore sizes for two Hawaiin *Hypnea* spp. In *Hypnea cervicornis* carpospores were 23.8±0.3 µm and tetraspores were 21.2±0.9 µm in diameter. In *H. cordacea* the corresponding values were 28.4±0.6 µm and 23.4±0.5 µm. In *Gracilaria corticata*, carpospores were 18-20 µm in diameter (Oza, 1976). In *Gracilaria corticata,* carpospores were reddish brown in colour and 20-30 µm in diameter (Mohan Joseph and

Krishnamurthy, 1977). In *Hypnea musciformis,* the diameter of carpospores and tetraspores were 26.9±0.6 µm and 24.2±0.4 µm respectively (Mshigeni and Lorri, 1977). Boney (1978) reported that in the red alga *Rhodymenia pertusa* the diameter of carpospores was in the range of 25-32 µm.

In *Alaria tenuifolia*, zoospore measured 7 µm in length (Henry and Cole, 1982). In *Acanthophora, Chondria, Laurencia* and *Leveillea,* spores were large sized ranging from 50 to 135 µm. (Ngan and Price, 1983). The flagellate egg of *Laminaria angustata* measured about 25 µm diameter (Motomura and Sakai, 1988). In *Ulva rigida*, zoospores were of 11x7 µm size (Phillips, 1988). Subba Rangaiah (1988) reported that in *Hypnea valentiae* the spores were spherical and were about 28 to 30 µm in diameter. In *Gymnogongrus furcellatus*, the tetraspores and carpospores were 8.5±0.7 µm and 10.7±1 µm in diameter respectively with a pale pink colour (Lewis *et. al.* 1991). Shyam Sunder *et. al.* (1991) reported that the carpospores of *Gracilaria crassa* measured about 22 to 27 µm in diameter. In *Dilophus fastigiatus,* the size of the non-motile spores were 165x83 µm (Phillips, 1992). Typically Phaeophycean spores were small (5-15 µm in length), pear shaped, heterokont and motile. *Homeostrichus olsenii* had biflagellate zoopores which were ovoid and 40-45 µm in diameter. They were the largest motile reproductive cells reported for any macroalgae (Phillips and Clayton, 1994). In *Champia compressa*, the tetraspores were pyramidal in shape and 50-70 µm in diameter and carpospores were pyriform in shape, 76-80 µm long and 25-30 µm broad (Kalimuthu, 2000).

Materials & Methods

MATERIALS AND METHODS

Mandapam is situated (9°17'N; 79°8'E) on a narrow piece of land projecting from the southern part of the east coast of India. To the south of this peninsular extension is the Gulf of Mannar and Palk Bay is on the northern side. Boulders and platforms of compressed sandstones with rough and uneven surfaces occur at different levels from high water to low water along the Mandapam coast. The sea in the Gulf of Mannar side becomes rough with heavy/strong wave action during the south - west monsoon season (May to August) and calm during the north-east monsoon season (September to February/March).

Along the Mandapam coast, plants of *Gracilaria crassa* (Harvey) J.Agardh, *Hypnea valentiae* (Turner) Montagne and *Sargassum wightii* (Greville) J. Agardh grow in the intertidal and subtidal region while *Turbinaria conoides* (J.Agardh) Kuetzing occurs only in the subtidal area. The tetrasporic and cystocarpic plants of *Gracilaria crassa* from Thonithurai (Station I) and *Hypnea valentiae* from Mandapam Camp (Station III) were collected. The reproductive plants of *Sargassum wightii* from Mandapam (Station II) and Pudumadam (Station IV) and *Turbinaria conoides* from Thonithurai (Station I) and Kilakkarai (Station V) were collected (Fig 1). Plates I to VI show the photographs of fresh specimens of the above four algae. The plants were washed thoroughly in the sea at the collection localities and transported to the laboratory in plastic buckets containing seawater. The materials thus collected and brought to the laboratory were used to conduct the spore shedding experiments.

Fig.I Coastline of Mandapam showing five collection localities.

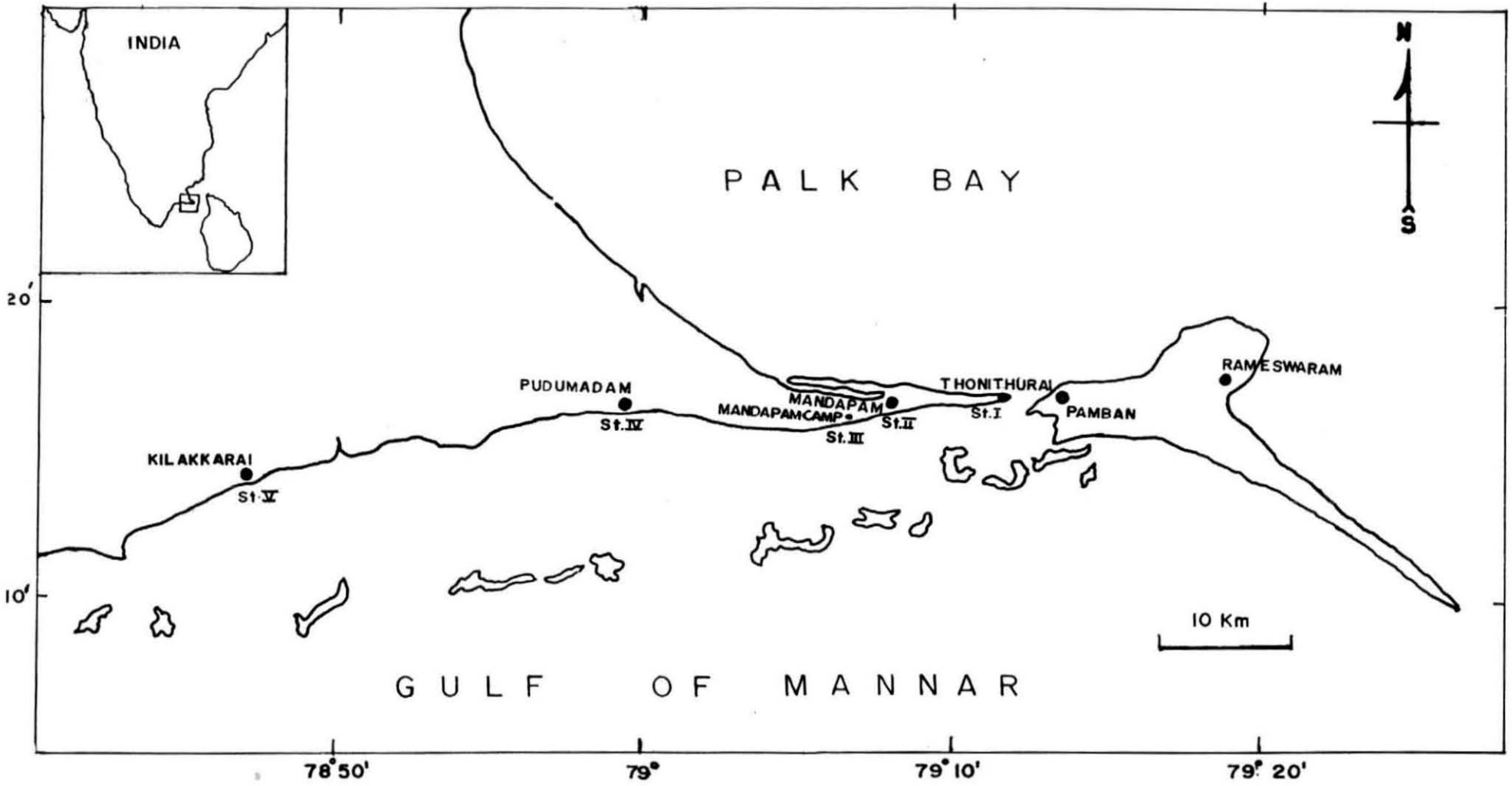

INDIA
PALK BAY
N
S
20'
10'
PUDUMADAM
St.IV
MANDAPAM
MANDAPAM CAMP
St.III
St.II
THONITHURAI
St.I
PAMBAN
RAMESWARAM
KILAKKARAI
St.V
10 Km
GULF OF MANNAR
78°50'
79°
79°10'
79°20'

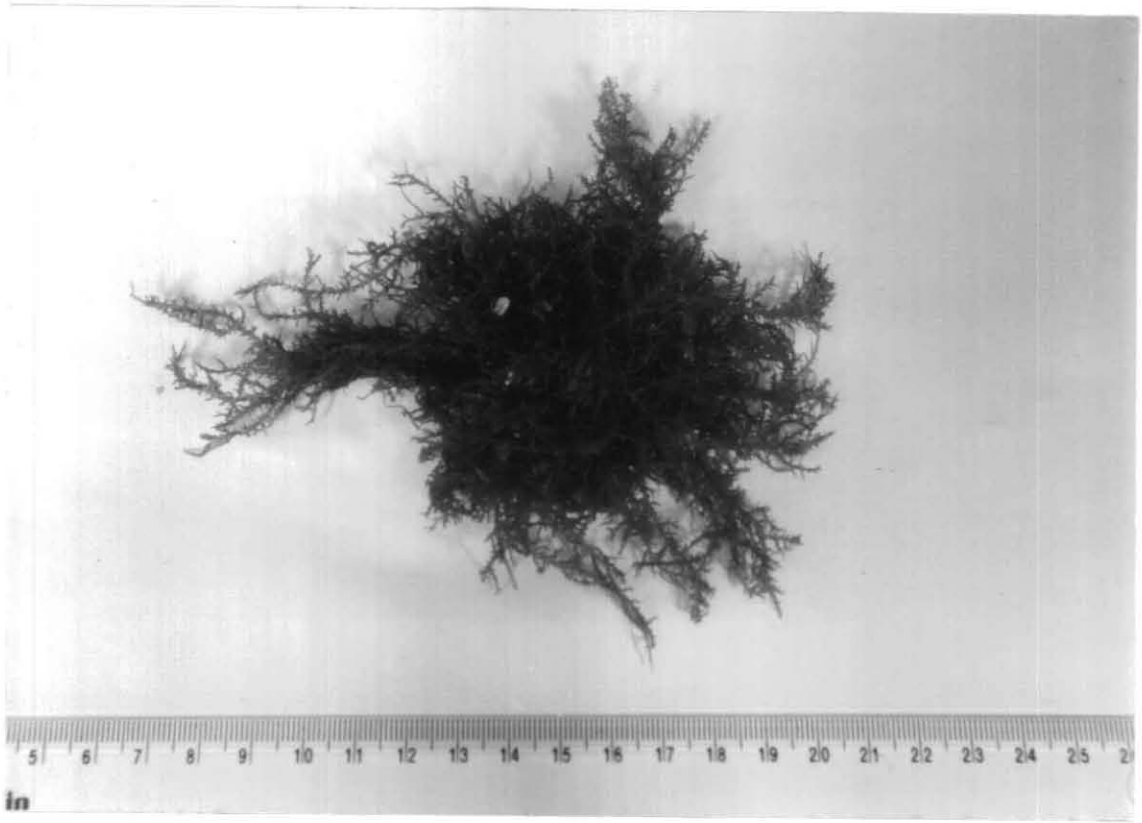
Fig. 1

Plate I - Tetrasporic plant of *Gracilaria crassa* (Harvey) J.Agardh

Plate II - Cystocarpic plant of *Gracilaria crassa* (Harvey) J.Agardh

Plate III - Tetrasporic plant of *Hypnea valentiae* (Turner) Montagne.

Plate IV - Cystocarpic plant of *Hypnea valentiae* (Turner) Montagne.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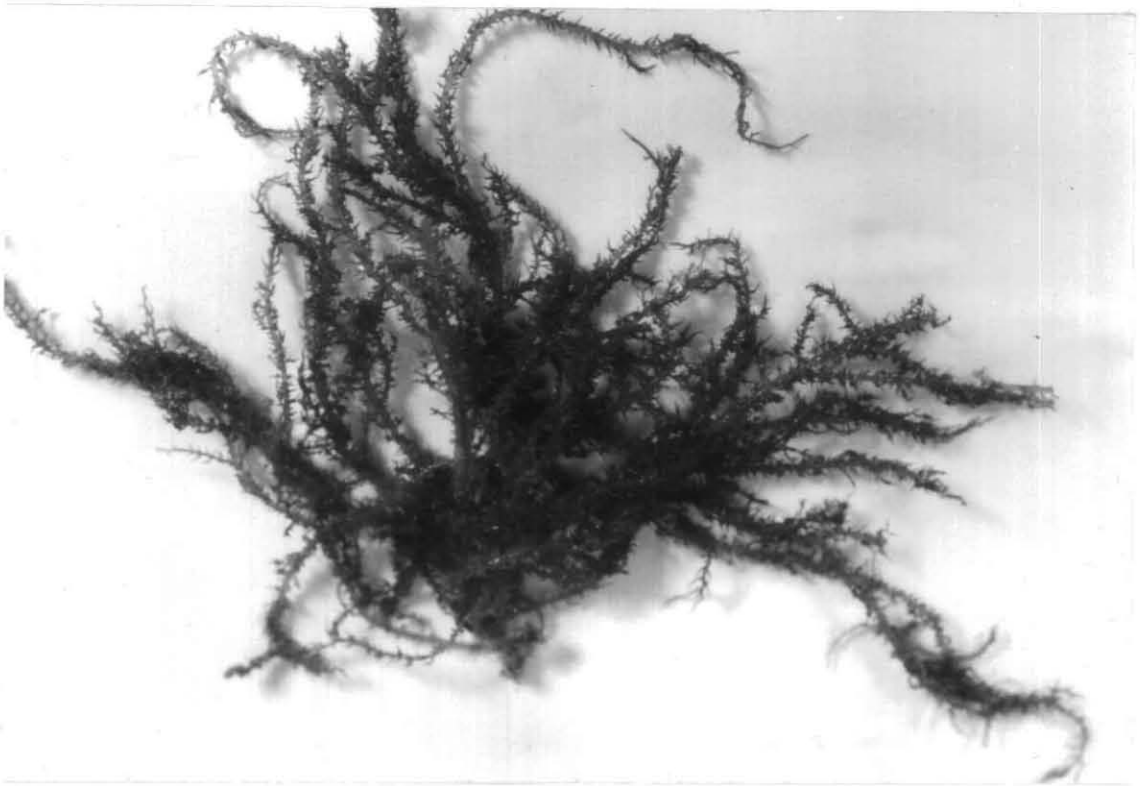
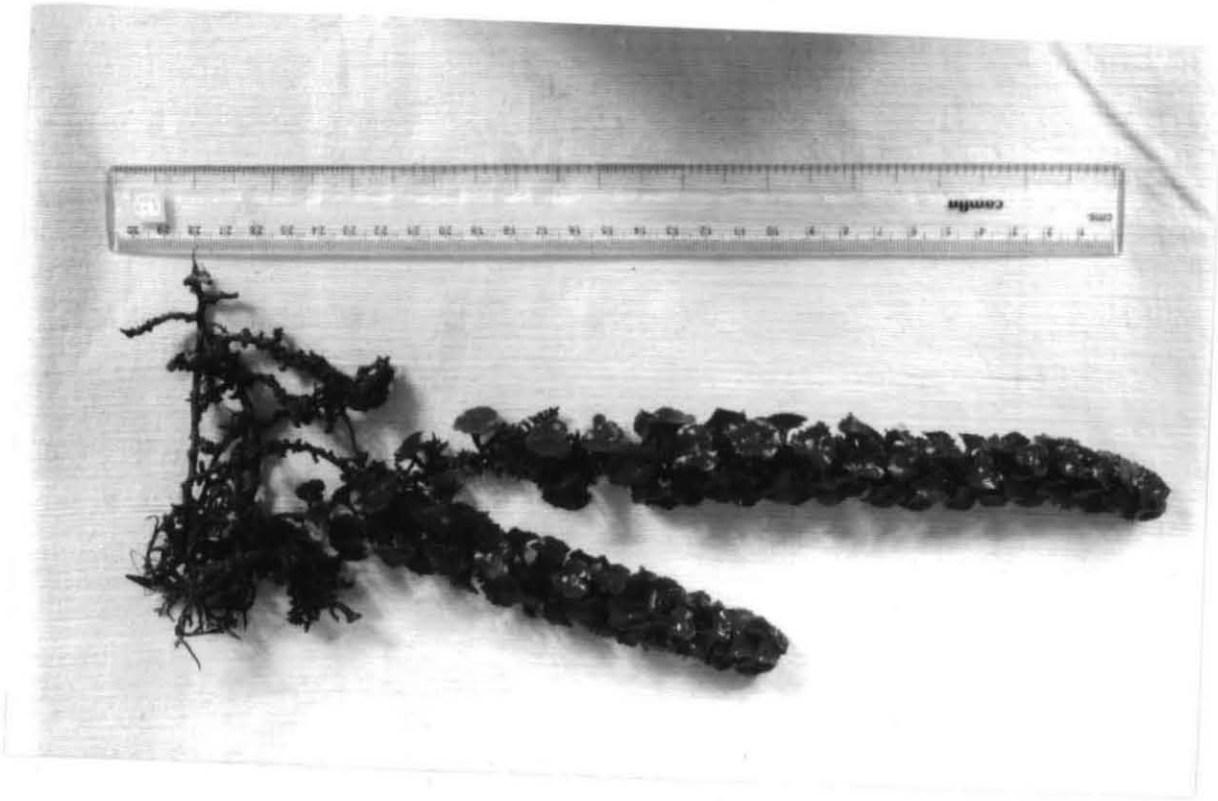




FRUITING BEHAVIOUR

The fruiting behaviour of *Gracilaria crassa, Sargassum wightii* and *Turbinaria conoides* was studied by observing the reproductive conditions in the population of these algae at the collection localities during the period of study from November, 1997 to October, 1999.

SPORE OUTPUT

In the experiments carried out to study the seasonal charges, diurnal periodicity and also effects of environmental factors on spore output, small clumps of *Gracilaria crassa* and *Hypnea valentiae* with good tetrasporangial sori and cystocarps and 8 to 10 healthy well developed mature receptacles of *Sargassum wightii* and *Turbinaria conoides* were used for each experiment.

The materials thus selected for the experiments were washed thoroughly several times with sterile seawater, placed in petridishes of 5 cm diameter and filled with 20 ml of sterile seawater. Spore liberation experiments were started at 6PM in room temperature (30 ± 2°C). The petridishes were illuminated by a fluorescent cool white tube light at 20 $\mu Em^{-2}s^{-1}$ for 8 hours during the daytime from 9 AM to 5 PM except in the case of temperature and light intensity experiments. Tetraspores, carpospores and oospores liberated were counted daily (after 24 hours) to study the seasonal changes and effect of environmental factors on the spore shedding and after every four hours to study the diurnal changes in spore liberation.

Tetraspores, carpospores and oospores liberated in the petridishes were counted as follows: A spore suspension was prepared by thoroughly mixing the spore contents in the petridish with a fine brush and transferred to a measuring cylinder. The petridishes were rinsed 2 or 3 times with small quantity of sterile seawater and the washings were also transferred to the measuring cylinder. The spore suspension was made upto a known volume depending on the spore quantity. A subsample of 1ml of spore suspension was pipetted into a plankton counting chamber and the spores present in all the squares of the chamber were counted using monocular microscope and hand tally counter. The degenerating spores were not counted. Average values of two counts and the total volume of spore suspension were taken into account for computing the spore output. When the spore shedding was very less, the counting was made by keeping the petridishes on a transparent grid sheet under the microscope. When the experiment was completed, fresh weight of the tetrasporic and cystocarpic fronds was taken and the number of receptacles kept in each petridish was also noted. The spore output was expressed as spores/g fresh weight for *Gracilaria crassa* and *Hypnea valentiae* and oospores / receptacle for *Sargassum wightii* and *Turbinaria conoides*. The procedures followed for seasonal and other studies on spore output are outlined below.

SEASONAL CHANGES IN SPORE OUTPUT

Following the methods given above, every month 8 experiments each with tetrasporic plants and cystocarpic plants of *Gracilaria crassa* were conducted by making collections at fortnightly intervals for a period of one year from April, 1998 to March, 1999 to know the seasonal changes in sporulation. The tetraspores and carpospores liberated daily (every 24

hours) for 5 days were counted to understand the variations in the output of tetraspores and carpospores in different days under laboratory conditions. Data on the seasonal changes in the spore output were expressed as spores/g fr.wt. / day.

DIURNAL PERIODICITY IN SPORE OUTPUT

Experiments on the diurnal changes in tetraspore and carpospore shedding of *Gracilaria crassa*, were conducted by transferring the materials at every four hours from one petridish to another petridish containing sterile seawater. These diurnal changes in spore production was followed for one year from April, 1998 to March, 1999 by making collections at every 15 days intervals and conducting 8 experiments with tetrasporic and cystocarpic thalli. The spores liberated at every 4 hourly intervals i.e. from 6 to 10 PM, 10 PM to 2 AM, 2 to 6 AM, 6 to 10 AM, 10 AM to 2 PM and 2 to 6 PM were counted and presented as spores / g fr. wt. These experiments were conducted at room temperature (30±2°C) and at a light intensity of $20\mu Em^{-2}s^{-1}$ during the daytime for 8 hours from 9 AM to 5 PM.

EFFECTS OF ENVIRONMENTAL FACTORS ON SPORE OUTPUT

For assessing the effects of different environmental factors on sporulation, experiments were conducted with tetrasporic thallus of *Gracilaria crassa*, tetrasporic and cystocarpic thalli of *Hypnea valentiae* and receptacles of *Sargassum wightii* and *Turbinaria conoides*. Since very few cystocarpic plants of *Gracilaria crassa* occurred in the field, experiments could not be conducted on carpospore shedding at various environmental factors. Ten experiments were conducted for each factor with *Gracilaria*

crassa, Sargassum wightii and *Turbinaria conoides* whereas only 5 experiments were conducted with *Hypnea valentiae*. These experiments were carried out for a period of 2¼ years from October, 1997 to December, 1999.

Exposure to air and desiccation

For studying the influence of desiccation or exposure to air, tetrasporic thallus of *Gracilaria crassa,* tetrasporic and cystocarpic thalli of *Hypnea valentiae* and receptacles of *Sargassum wightii* and *Turbinaria conoides* were exposed to air in shade and in the sun. The materials were blotted using blotting paper to remove the water on their surfaces before exposing to air. The period of exposure to air varied in shade in the laboratory and outside in the sun. The materials exposed to air in the laboratory upto 2 hours (15 minutes interval upto 1 hour and then ½ hour interval) and upto 1 hour (for 5, 10, 15, 30, 45 and 60 minutes) in the sun, were transferred to petridishes containing sterile seawater. Controls (0 minutes exposure) were also maintained in all these experiments. The spores liberated were counted after 24 hours. During the time of conducting these experiments, the temperature in the shade was 30 ± 2°C and the relative humidity varied from 48 to 61%. In the open air where these experiments were conducted, the temperature was 33±2°C and the relative humidity ranged from 41% to 46%.

Salinity

A stock solution of 100‰ salinity was prepared by adding common salt to the seawater collected from the inshore area and sterilizing it. The salinity was determined using a salinometer (Atago Hand Refractometer). The lower grades were prepared from the stock solution by adding requisite

quantity of distilled water. The spore output in the four algae was estimated at 0, 10, 20, 30, 40, 50, 60, 70 and 80‰ salinities and by maintaining the experimental sets at room temperature (30±2°C) and providing 20 $\mu Em^{-2}s^{-1}$ day light fluorescent illumination for 8 hours from 9AM to 5 PM. The spores liberated were counted after 24 hours.

Temperature

The influence of 9 different temperatures 0,10,15,20,25,30,35,40 and 45°C on sporulation was studied by maintaining the petridishes with fruiting materials for 24 hours in a temperature controlled dark incubator or refrigerator. The spores liberated were counted daily after 24 hours.

Light

Light intensity experiments were conducted with *Gracilaria crassa*, *Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides* at 0, 10, 20, 30, 40, 60, 80 and 100 $\mu Em^{-2} s^{-1}$. The room temperature was 30±2°C while conducting these experiments. The spores liberated were counted after every 24 hours.

Photoperiod

For studying the effect of photoperiod on spore shedding, petridishes with fruiting materials were subjected to 0:24, 4:20,8:16,12:12,16:8,20:4 and 24:0 light and dark cycles by keeping them in separate light and dark chambers. These experiments at seven different light and dark regimes were conducted at 20 $\mu Em^{-2}s^{-1}$. The spores liberated were counted after 24 hours.

The experiments on effect of environmental factors on sporulation were conducted with *Gracilaria crassa* for only one day since the spore output on the second day was very less. In the case of *Hypnea valentiae* experiments were conducted for 2 days except for salinity. Experiments were conducted for 5-7 days with *Sargassum wightii* and *Turbinaria conoides* depending on the spore output.

SPORE STUDIES

The shape and size of spores in the four algae were studied by taking random samples from the spore suspension in different months of the year. The shape of tetraspores and carpospores of *Gracilaria crassa* and *Hypnea valentiae* and oospores of *Sargassum wightii* and *Turbinaria conoides* were noted by observing them in high power under monocular microscope. The sizes of the spores were measured using ocular micrometer.

HYDROLOGICAL AND ENVIRONMENTAL PARAMETERS

Data on hydrological and environmental parameters such as atmospheric temperature, bottom seawater temperature, salinity and light intensity were collected from one of the collection localities namely Thonithurai to correlate the results with the environmental conditions existing in the field and also to know the optimal environmental conditions required for maximum spore output. The air temperature and bottom seawater temperature were measured using thermometer (Jennson Delux) and the salinity was determined using a salinometer (Atago Hand Refractometer). The light intensity in the intertidal and subtidal region from where the samples were collected was measured using an underwater uxmeter (EMCON).

Results

RESULTS

Results obtained on the fruiting behaviour of *Gracilaria crassa, Sargassum wightii* and *Turbinaria conoides;* daily and monthly changes in the tetraspore and carpospore output in *Gracilaria crassa*; effect of environmental factors such as exposure to air (desiccation), salinity, temperature, light intensity and photoperiod on the tetraspore shedding of *Gracilaria crassa*, tetraspore and carpospore output of *Hypnea valentiae* and oospore liberation of *Sargassum wightii* and *Turbinaria conoides* are presented in this chapter. Data collected on the shape and size of different kinds of spores in these four algae and hydrological and environmental parameters from the collection locality are also presented in this chapter.

FRUITING BEHAVIOUR

The tetrasporic plants were very common in the population of *Gracilaria crassa* and they occurred abundantly throughout the year with maximum number during the period August to October. The cystocarpic plants occurred in small quantity throughout the year. Maximum number of plants with cystocarps were observed during the period March to June. The reproductive plants of both *Sargassum wightii* and *Turbinaria conoides* occurred in the population during the period October to February with maximum numbers in the months of December and January.

SPORE OUTPUT

Data obtained on spore output at different days in *Gracilaria crassa* under laboratory conditions are given in Fig.2 to show the trend in the daily liberation of tetraspores and carpospores. In the observations made for 5 days, maximum shedding of both tetraspores and carpospores was seen on first day and the spore output per gram fresh weight of the plant per day decreased rapidly from second day onwards. There was no periodicity in the liberation of tetraspores and carpospores during the observations made for 5 days.

SEASONAL CHANGES IN SPORE OUTPUT

The quantity of tetraspores and carpospores liberated from *Gracilaria crassa* in the laboratory experiments for five days was used for estimating the monthly changes in spore production. Monthly data collected from April, 1998 to March, 1999 on the number of tetraspores and carpospores per gram fresh weight of the plant are shown in Figs.3 and 4 respectively. During the period of this study, maximum quantity of tetraspores was liberated on the first day between August and October and afterwards peak output of spores was seen in the months of February and March. The quantity of tetraspore liberation on the first day varied seasonally from a low value of 1,205 spores/g fr.wt. to a maximum of 40,746 spores/g fr.wt. In general, sudden decline in sporulation was observed from second day onwards in some months (Fig.3). The spore output varied from 17 to 899, 1 to 69, 2 to 64 and 1 to 83 spores/g fr.wt. on the second to fifth day respectively.

Fig.2 Daily liberation of tetraspores and carpospores in *Gracilaria crassa*.

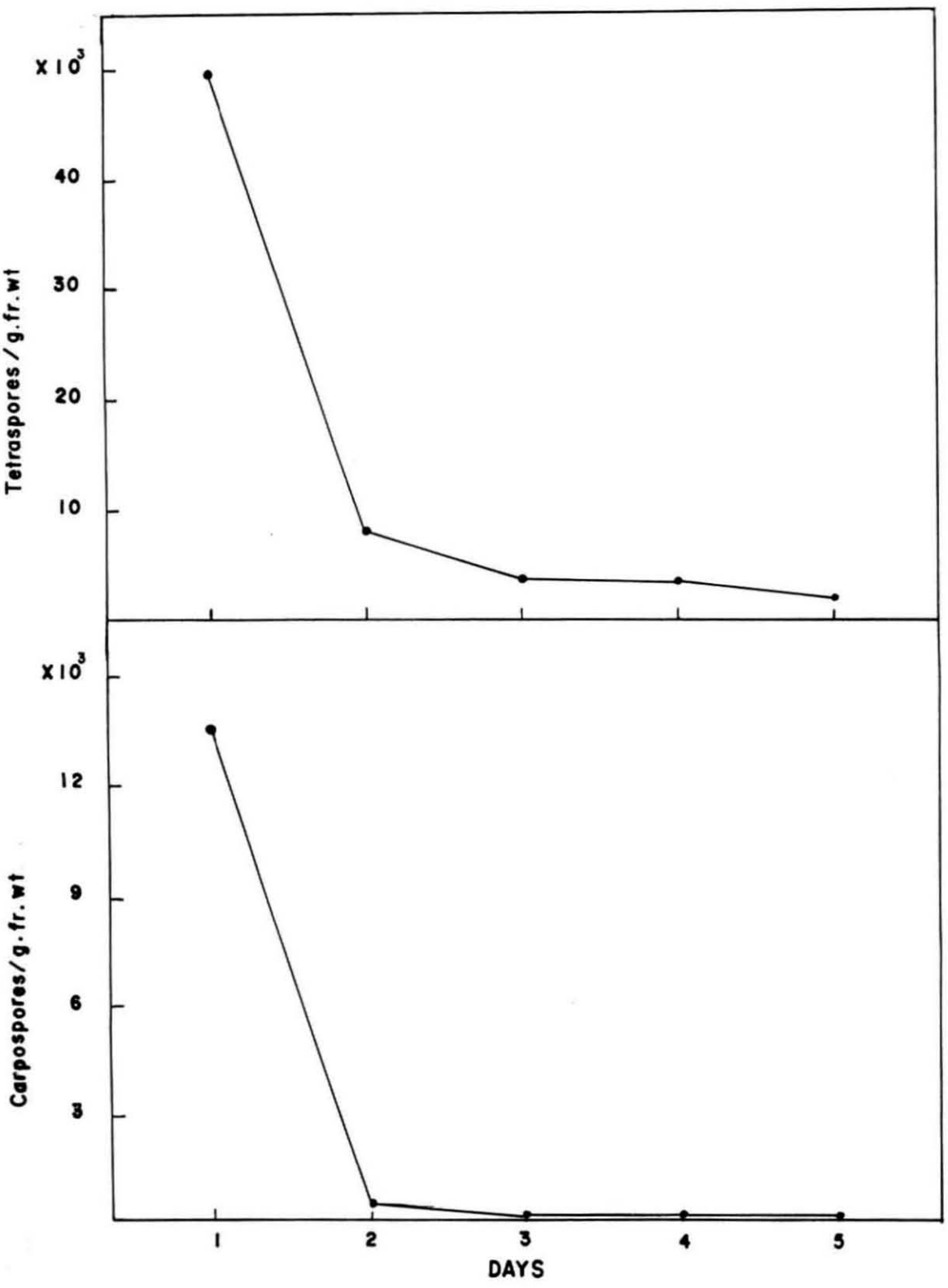

GRACILARIA CRASSA
X 10³
40
30
20
10
Tetraspores / g.fr.wt
X 10³
12
9
6
3
Carpospores / g.fr.wt
1
2
3
4
5
DAYS

Fig. 2

Fig.3 Seasonal variation in tetraspore shedding in *Gracilaria crassa*.

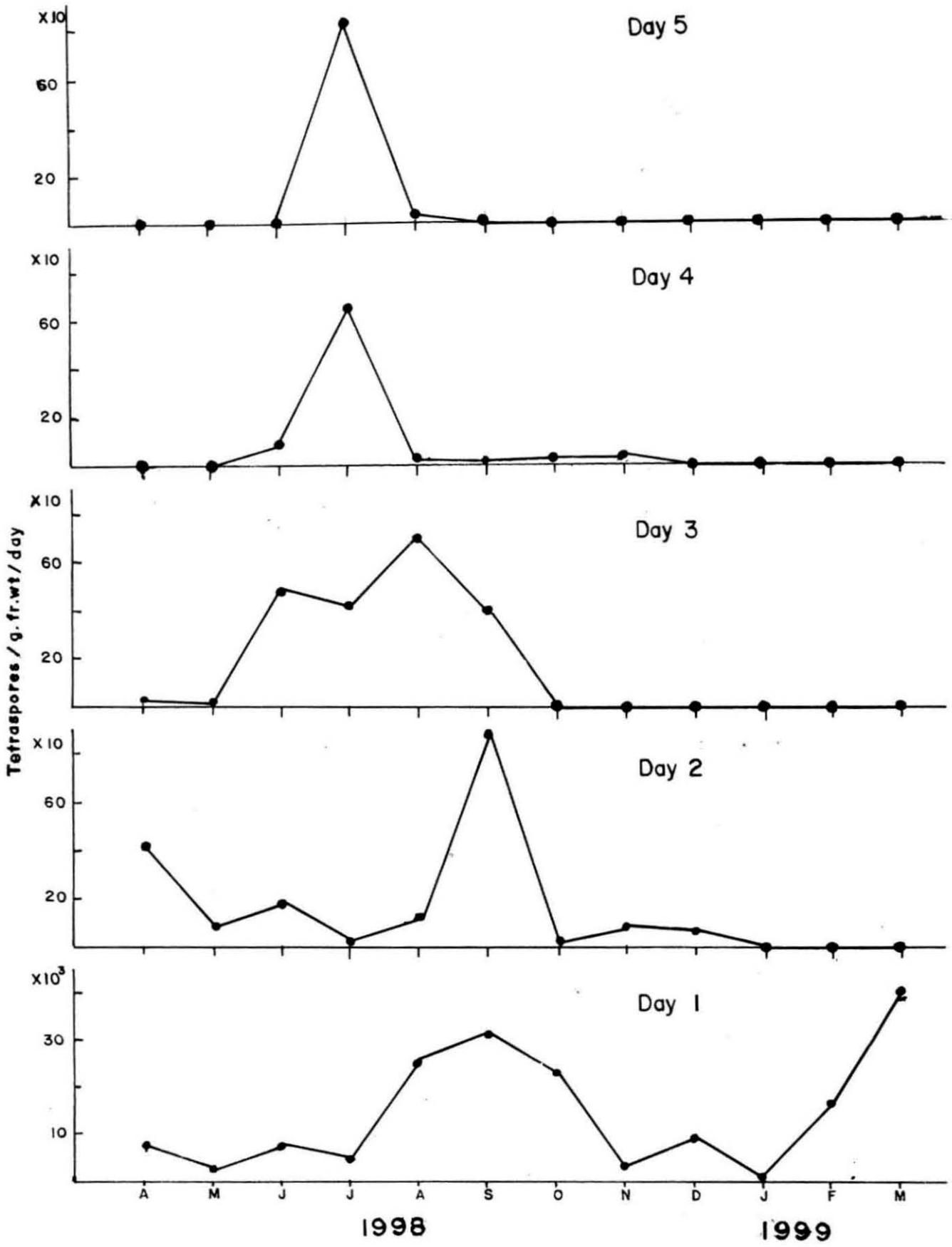

Day 5
Day 4
Day 3
Day 2
Day 1
X10
X10³
60
20
30
10
Tetraspores / g. fr. wt / day
A
M
J
J
A
S
O
N
D
J
F
M
1998
1999

Fig.3

Fig.4 Seasonal variation in carpospore shedding in *Gracilaria crassa*.

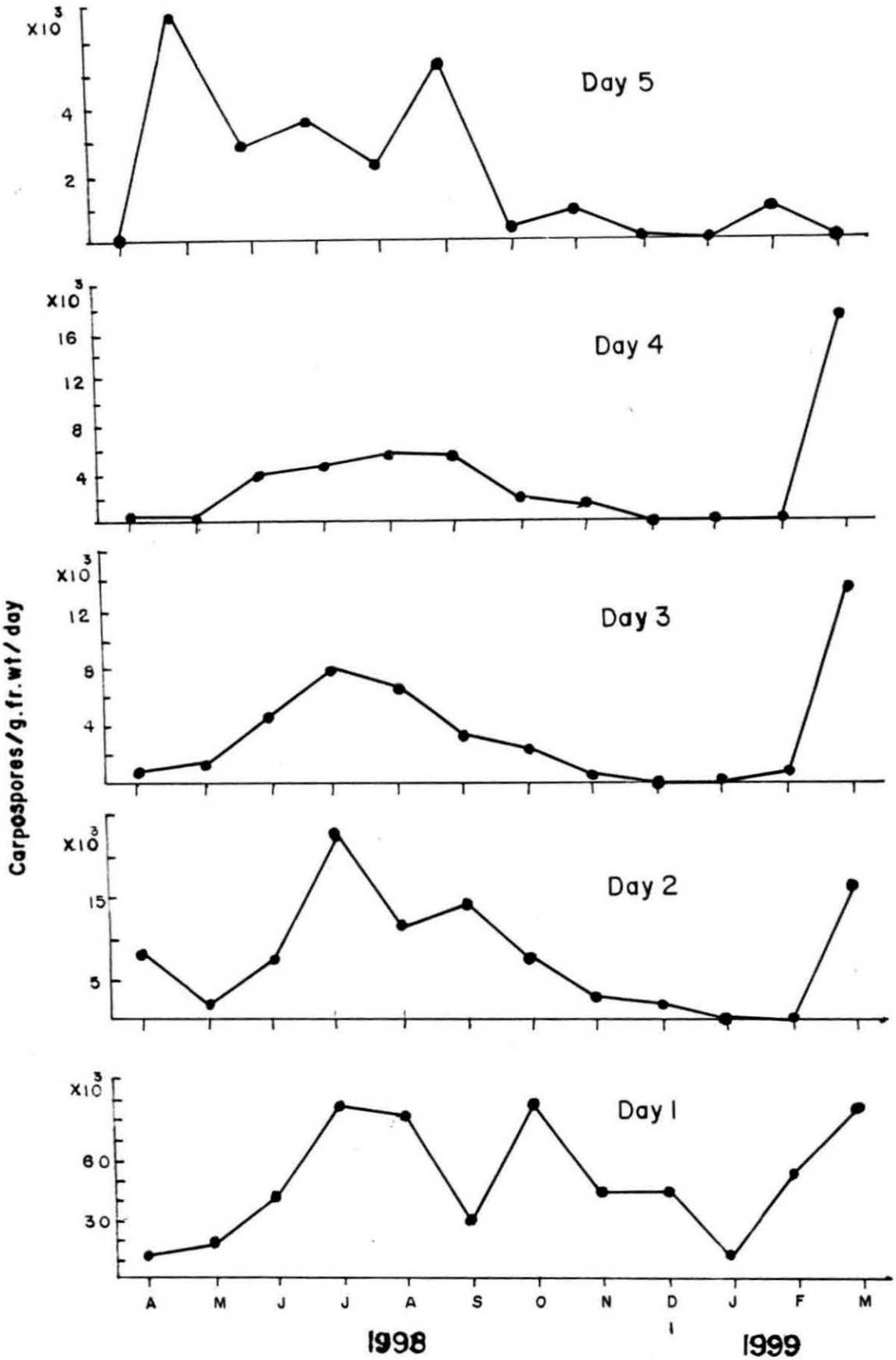

Day 5
Day 4
Day 3
Day 2
Day 1
X10 3
Carpospores/g.fr.wt/day
A M J J A S O N D J F M
1998
1999

Fig. 4

In *Gracilaria crassa* peak output of carpospores on the first day was observed from July to October with low values in September and again with maximum spores during February and March. The number of carpospores liberated on the first day ranged from 11,047 to 87,754 spores/g fr.wt. There was a decline in spore shedding from 2nd day to 5th day. The number of carpospores liberated during the second day to fifth day was found to be higher than that of tetraspores. There was no carpospore output after the first day in few months. The spore output varied from 4 to 22,763, 5 to 13,379, 245 to 17,353 and 849 to 6666 spores/g fr.wt. on the 3rd to 5th day respectively (Fig.4).

SEASONAL CHANGES IN DIURNAL PERIODICITY OF SPORE OUTPUT

Data obtained with *Gracilaria crassa* on the liberation of tetraspores and carpospores at different times of the day during the months from April, 1998 to March, 1999 are given in Figs.5 and 6 respectively to show the trend in the daily periodicity in the liberation of these spores at different months of the year. Data presented in Figure 5 clearly show that the time of peak liberation of tetraspores changed in certain months of the year. Peak output of tetraspores was observed during six months from March to August in the midnight hours i.e. 10 PM. to 2 AM. In the other six months from September to February the diurnal rhythm was different with four hours delay in the liberation of maximum tetraspores (Fig.5). In these six months peak liberation of spores was observed between 2 AM and 6 AM. In

Fig.5 Diurnal periodicity in the liberation of tetraspores in *Gracilaria crassa*.

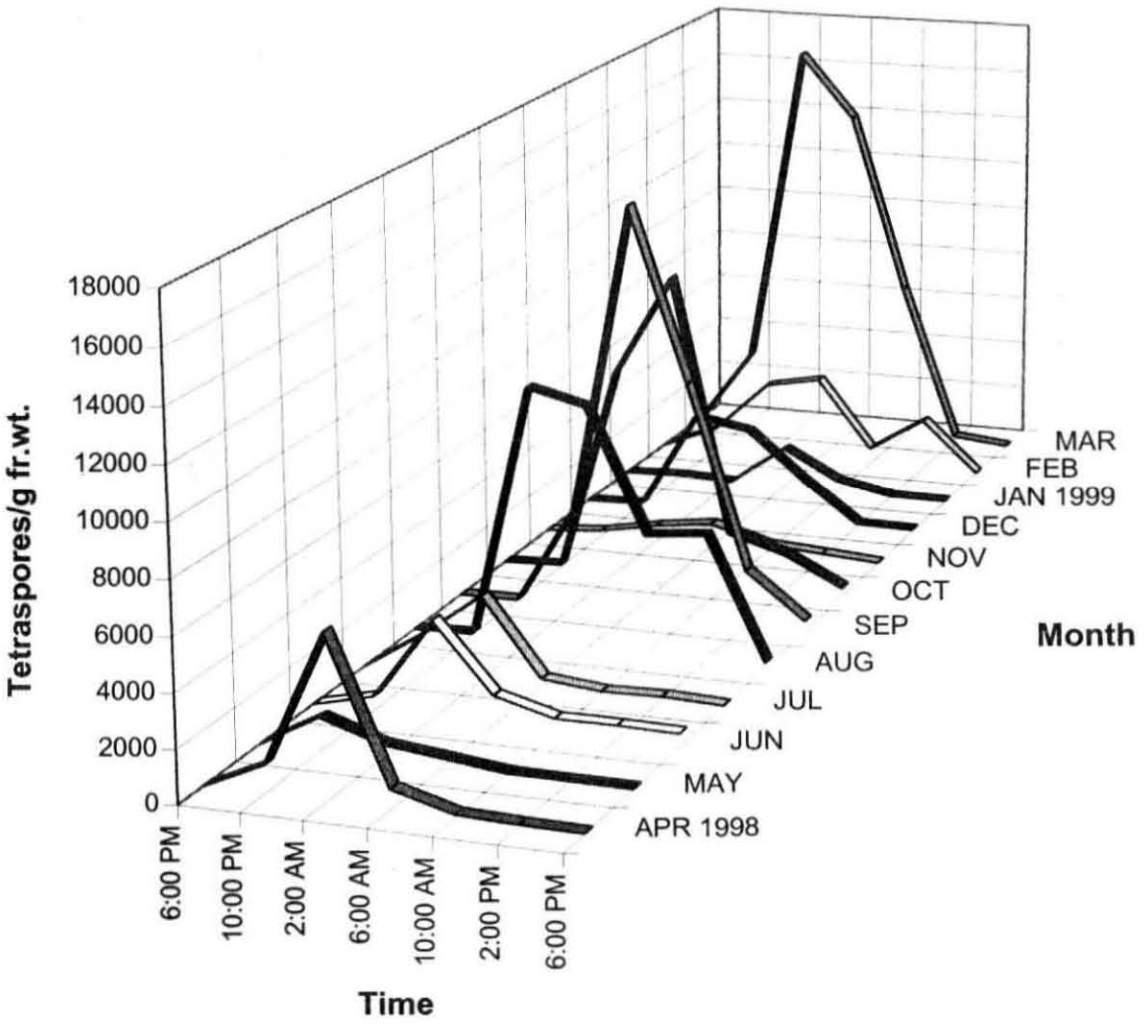

Gracilaria crassa
Tetraspores/g fr.wt.
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
6:00 PM
10:00 PM
2:00 AM
6:00 AM
10:00 AM
2:00 PM
6:00 PM
Time
MAR
FEB
JAN 1999
DEC
NOV
OCT
SEP
AUG
JUL
JUN
MAY
APR 1998
Month

Fig. 5

the liberation of carpospores prominent peak at one particular period of the day was not seen in different months of the year. In general, the quantity of spores liberated was more within the first four hours after commencing the experiments ie. between 6 PM and 10 PM in most of the months (August to December and February to May). This irregular trend in the daily liberation of carpospores can be seen in Fig.6.

EFFECT OF ENVIRONMENTAL FACTORS ON SPORE SHEDDING

Results were obtained on the effects of environmental factors such as exposure to air (desiccation), salinity, temperature, light and photoperiod on spore liberation in *Gracilaria crassa* , *Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides.*

Exposure to air and desiccation

These experiments were designed not only to study the effect of exposure during low tides and the resultant desiccation of plants on spore production, but also to understand the spore release in shaded and in areas directly exposed to sunlight. Changes observed in the tetraspore output of *Gracilaria crassa*, tetraspore and carpospore shedding of *Hypnea valentiae* and oospore liberation of *Sargassum wightii* and *Turbinaria conoides* in controls (O min exposure) and at different periods of exposure to air in the shade (temp. 30±2°C and R.H 48 - 61%) and in the sun (temp.33±2°C and R.H.41 - 46%) are shown in Figs. 7 to 11.

Fig.6 Diurnal periodicity in the liberation of carpospores in *Gracilaria crassa*.

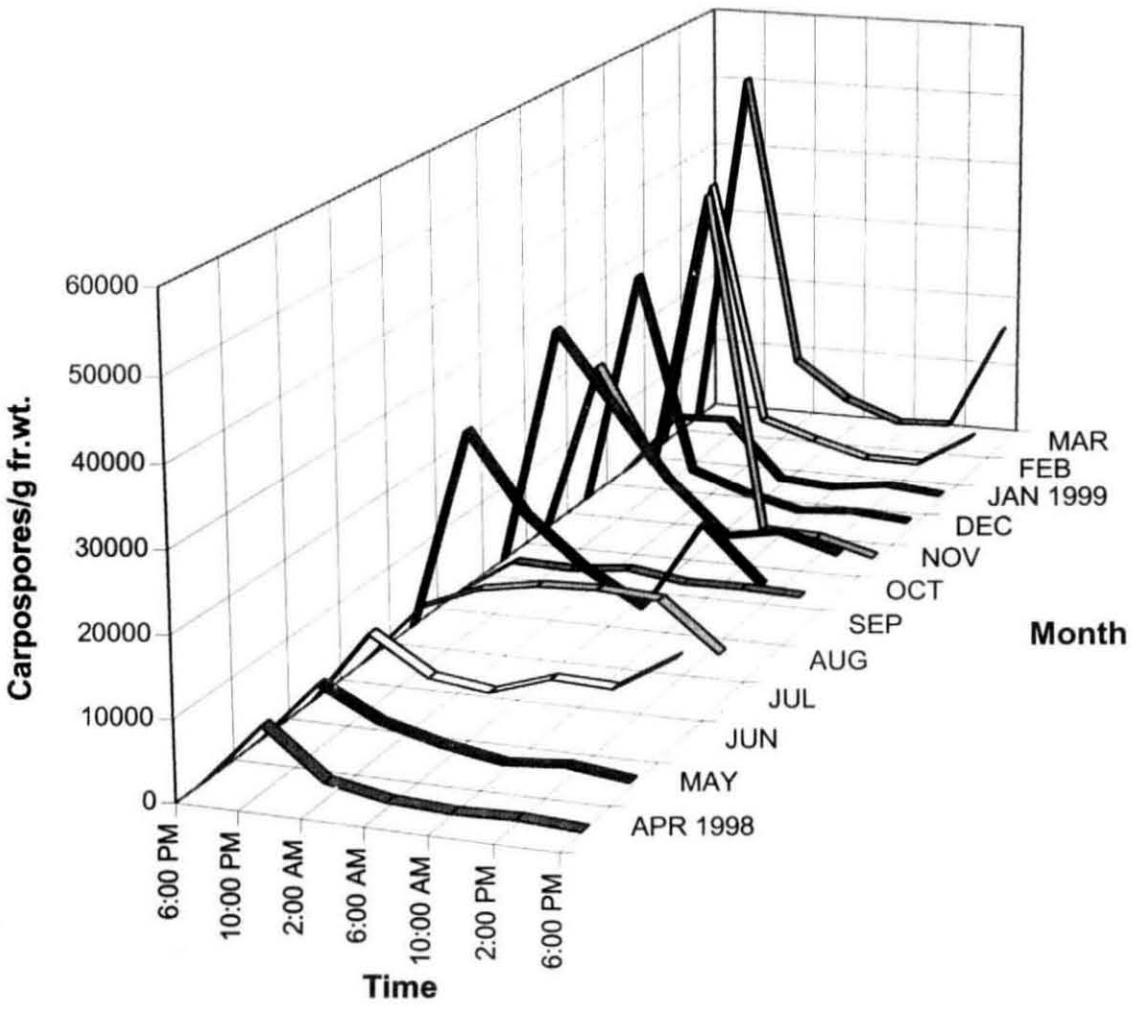

Gracilaria crassa
Carpospores/g fr.wt.
60000
50000
40000
30000
20000
10000
0
6:00 PM
10:00 PM
2:00 AM
6:00 AM
10:00 AM
2:00 PM
6:00 PM
Time
MAR
FEB
JAN 1999
DEC
NOV
OCT
SEP
AUG
JUL
JUN
MAY
APR 1998
Month

Fig. 6

Exposure to air in shade

In experiments conducted with *Gracilaria crassa*, sporulation was seen upto 120 minutes with maximum liberation of tetraspores in control and decline in spore output was found from 15 minutes to 120 minutes exposure (Fig. 7 A). In the experiments conducted with *Hypnea valentiae* for 2 days by exposing the tetrasporic thalli in shade, peak tetraspore output was observed in control both on the first day and second day with decline in spore output from 15 minutes to 90 minutes on the first day and 15 minutes to 30 minutes on the second day (Fig.8 A&B). In the case of carpospores of *Hypnea valentiae*, maximum shedding occurred in the control in the first day whereas on the second day maximum output of carpospores was observed in the thalli exposed for 15, 30 and 45 minutes than in the controls. The carpospore liberation was found in the fronds exposed upto 90 minutes on the first day and only upto 45 minutes on the second day (Fig.8 C&D).

In the experiments conducted for a period of 3 days after exposing the receptacles of *Sargassum wightii* in shade for different durations, maximum oospore shedding was found from the receptacles kept under submerged condition (O minute exposure) in all the three days and thereafter the number of spores liberated declined with increase in the duration of drying of the receptacles in shade. Spore output on the first day was observed from the thalli exposed for 15,30 and 45 minutes duration and only at 15 and 30 minutes exposure on the second day. There was no liberation of oospores

from any of the receptacles exposed to shade for different periods except in control on the third day. There was no liberation of oospore on the 4th day as the receptacles decayed (Fig.9 A).

In *Turbinaria conoides* data were collected only for one day as the receptacles decayed on the second day. The maximum oospore discharge was seen in receptacles submerged for 24 hours and decline in spore output were noticed upto 90 minutes exposure with more number of spores in the receptacles exposed to 45 and 60 minutes. There was no spore liberation from the receptacles exposed for 120 minutes (Fig.9 B).

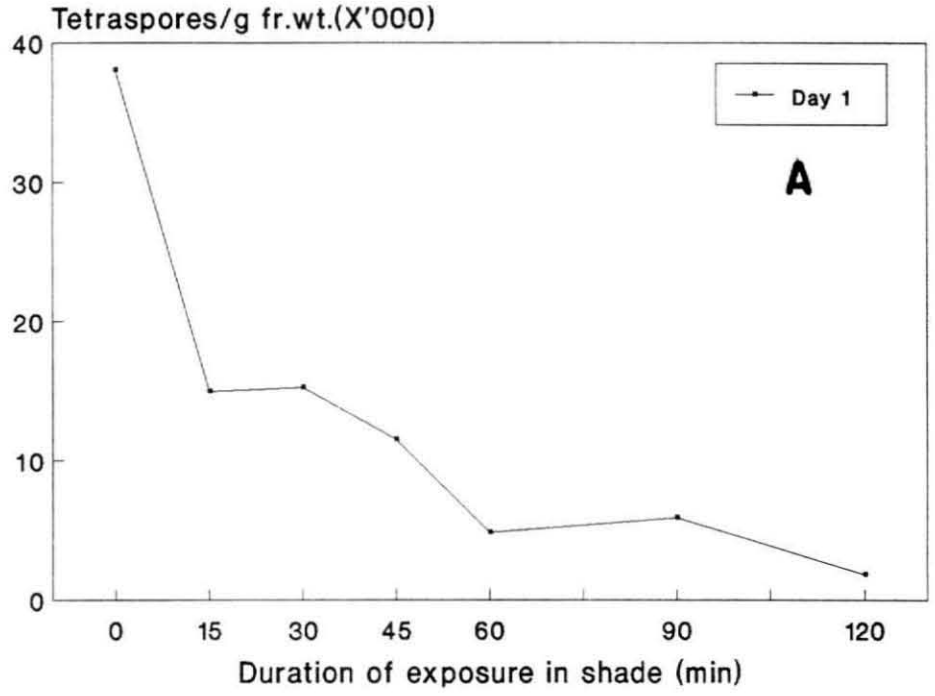
Exposure to air in sun

Changes in spore output were more marked in the fruiting materials of all four algae exposed for even short periods of 5, 10 and 15 minutes in the sun due to high temperature and lowhumidity (Figs.7, 10 and 11). In general, maximum shedding of spores was observed in submerged condition (O minute exposure) in all the experiments conducted with different species except in the case of carpospore output in *Hypnea valentiae* on the second day from the cystocarpic thalli exposed for 5, 10, 15 and 30 minutes.

In *Gracilaria crassa* the tetraspore output was observed from the thalli exposed upto 15 minutes (Fig.7 B). In the case of *Hypnea valentiae* tetraspore output was found upto 30 minutes exposure on the first day and upto 15 minutes exposure on the second day (Fig.11 A&B) whereas

Fig.7 Effect of desiccation in the sun and shade on the tetraspore output of *Gracilaria crassa*.

Gracilaria crassa



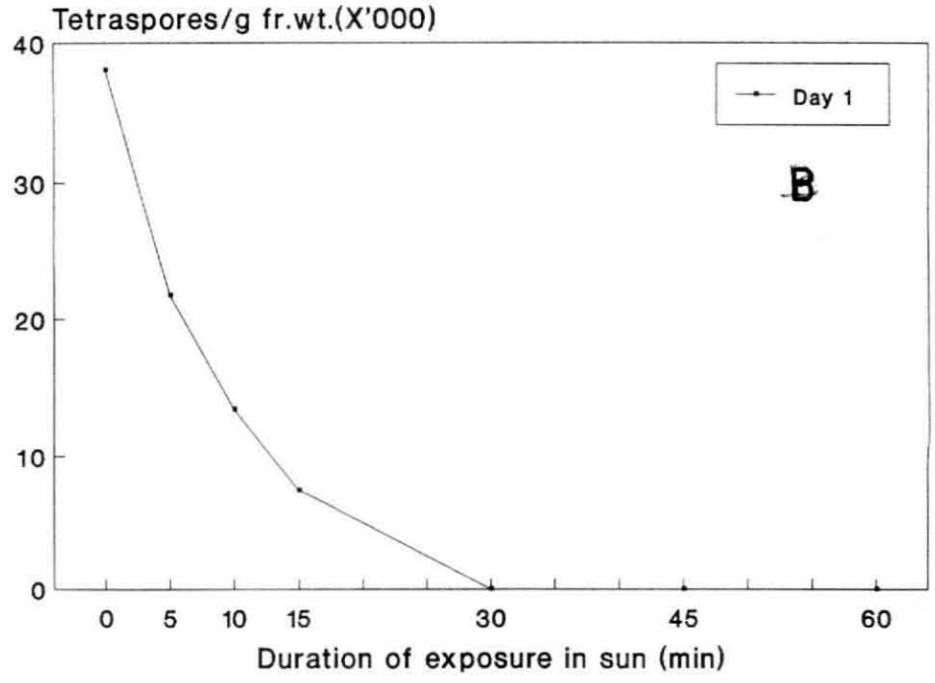
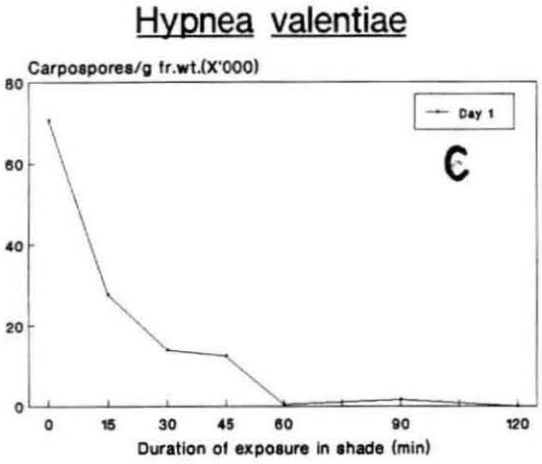
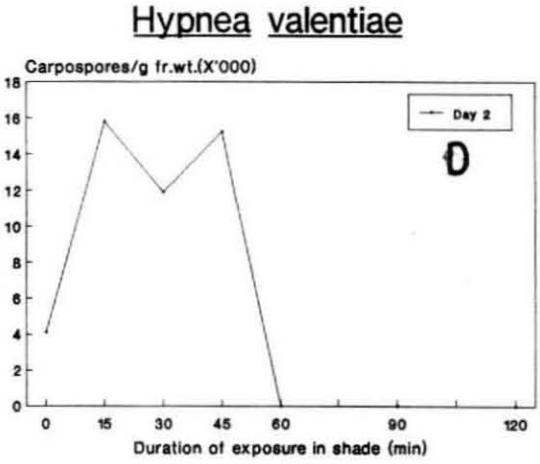
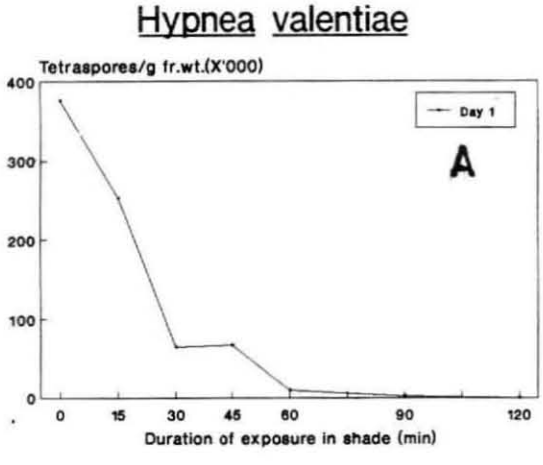


Fig. 7

Fig.8 Effect of desiccation in shade on the tetraspore and carpospore output of *Hypnea valentiae*.


Hypnea valentiae
Carpospores/g fr.wt.(X'000)
Day 1
C
0
20
40
60
80
0
15
30
45
60
90
120
Duration of exposure in shade (min)


Hypnea valentiae
Carpospores/g fr.wt.(X'000)
Day 2
D
0
2
4
6
8
10
12
14
16
18
0
15
30
45
60
90
120
Duration of exposure in shade (min)


Hypnea valentiae
Tetraspores/g fr.wt.(X'000)
Day 1
A
0
100
200
300
400
0
15
30
45
60
90
120
Duration of exposure in shade (min)

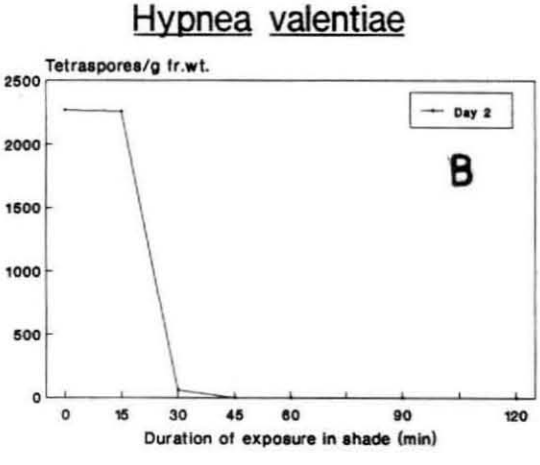
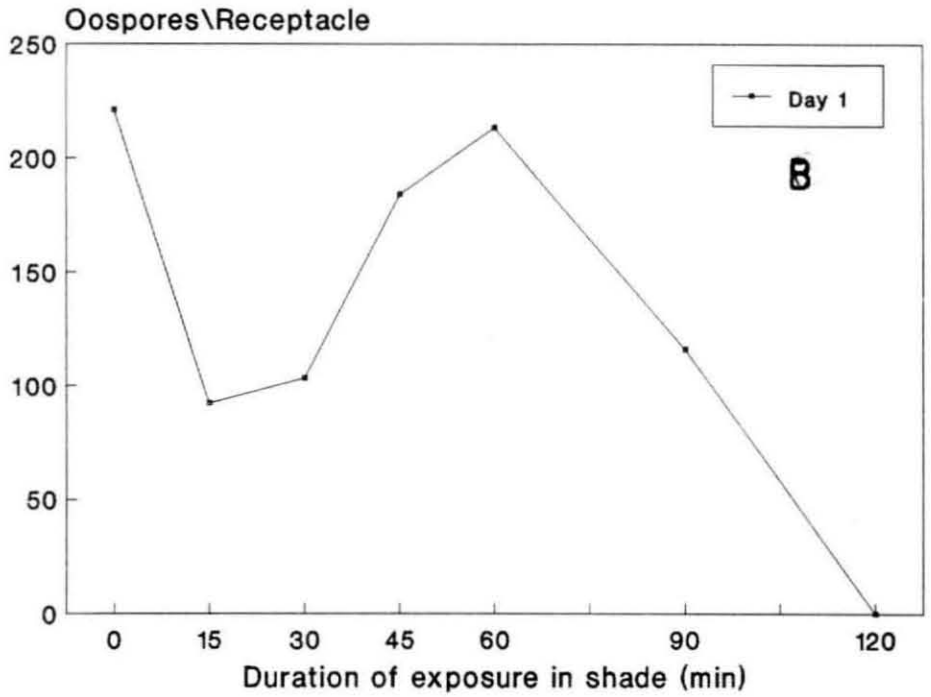

Hypnea valentiae
Tetraspores/g fr.wt.
Day 2
B
0
500
1000
1500
2000
2500
0
15
30
45
60
90
120
Duration of exposure in shade (min)

Fig. 8

Fig.9 Effect of desiccation in shade on the oospore output of *Sargassum wightii* and *Turbinaria conoides*.

Turbinaria conoides



Sargassum wightii

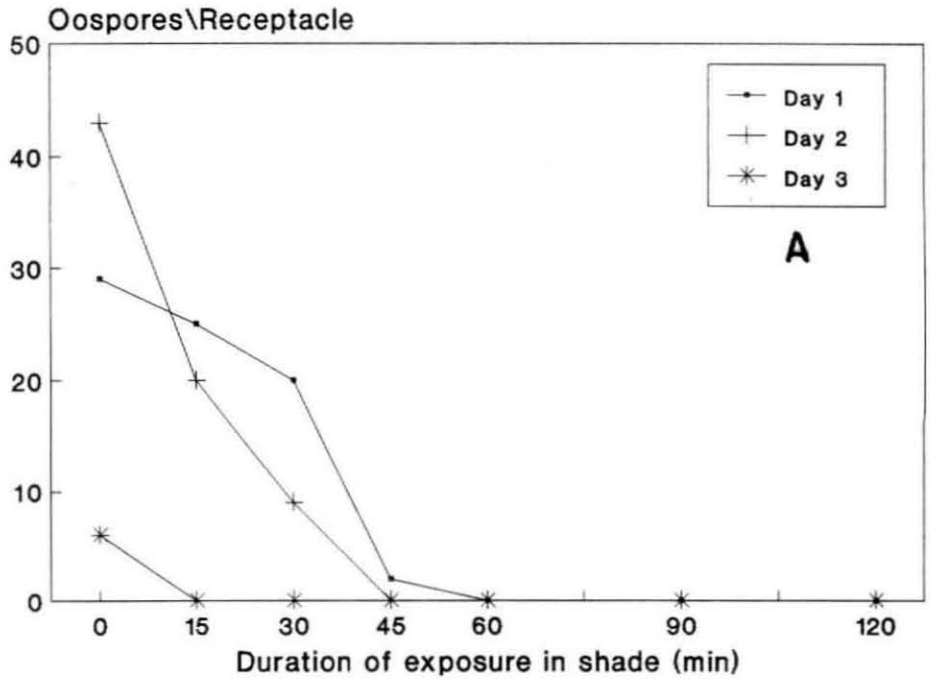
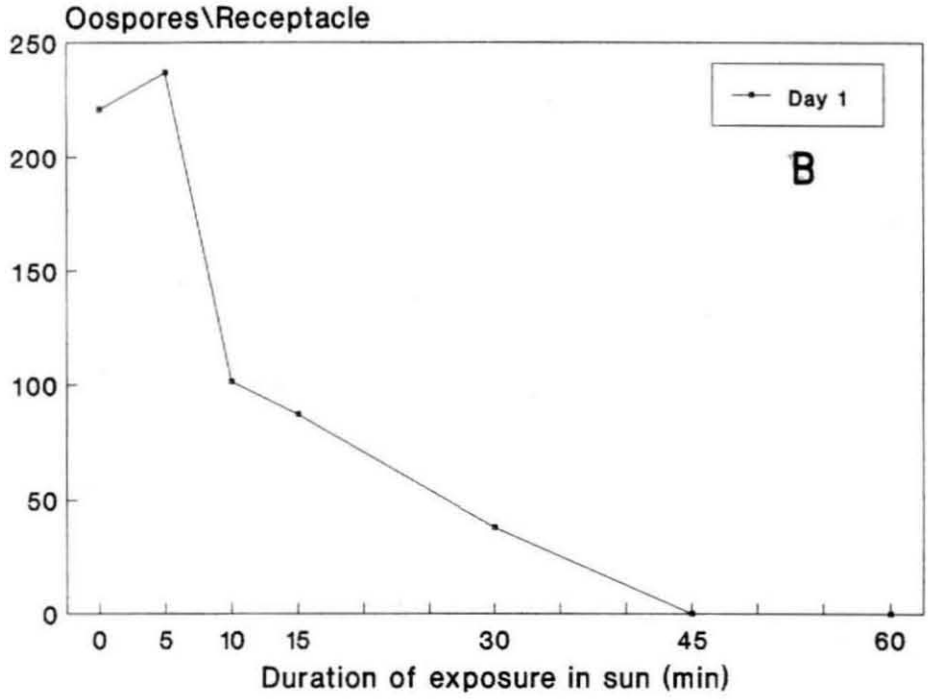


Fig. 9

Fig.10 Effect of desiccation in sun on the oospore output in *Sargassum wightii* and *Turbinaria conoides*.

Turbinaria conoides



Sargassum wightii

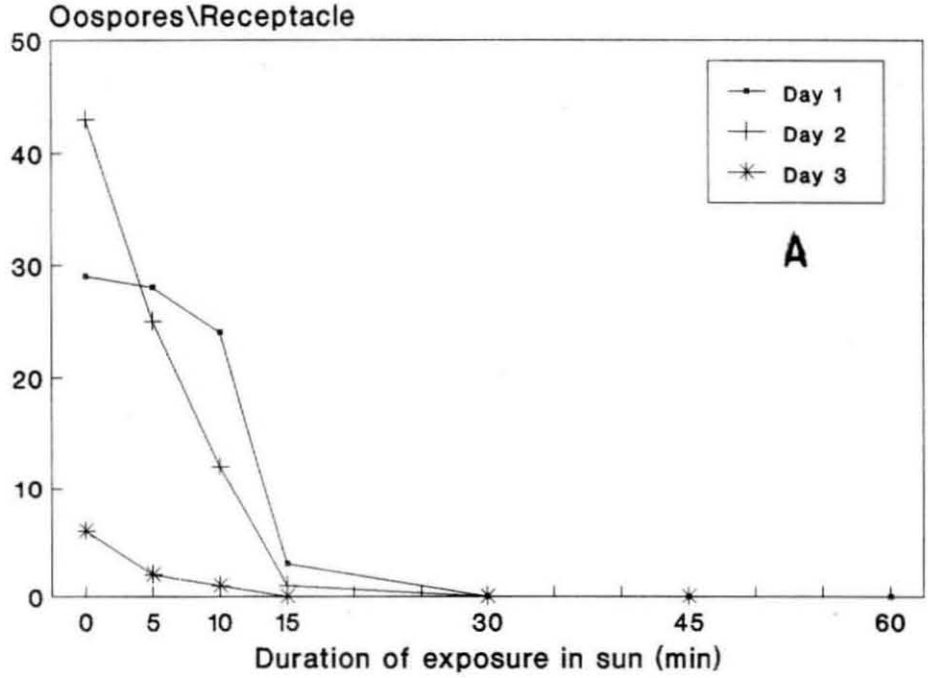
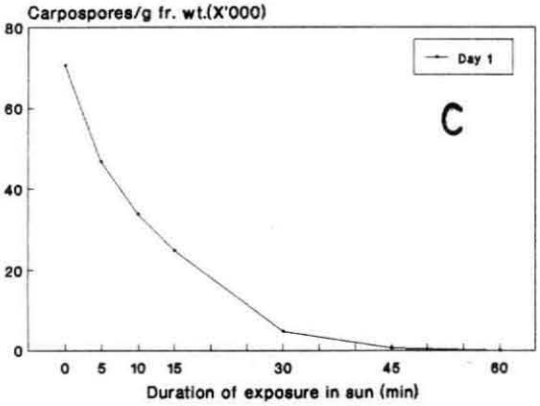


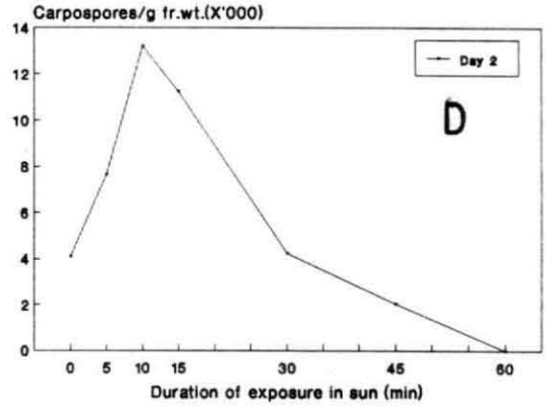
Fig. 10

Fig.11 Effect of desiccation in sun on the tetraspore and carpospore output of *Hypnea valentiae*.

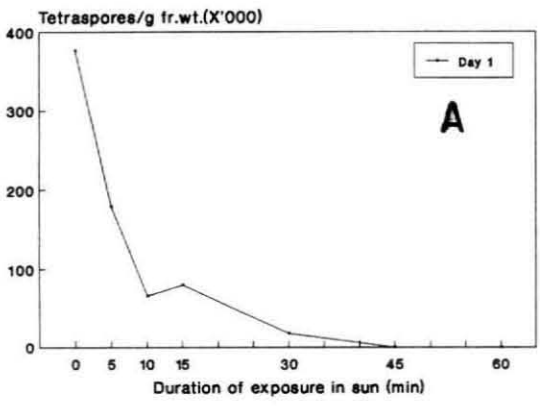
Hypnea valentiae



Hypnea valentiae



Hypnea valentiae



Hypnea valentiae

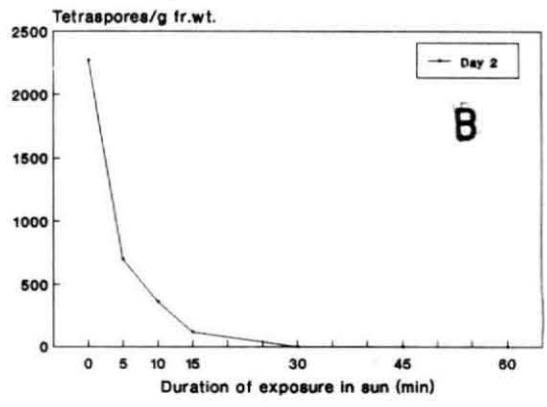


Fig.11

carpospore liberation was observed upto 45 minutes on the first day and second day (Fig.11 C&D). The oospore output in *Sargassum wightii* was found upto 15 minutes exposure on the first and second day and upto 10 minutes exposure on the third day (Fig.10 A). In *Turbinaria conoides* spore liberation was noticed upto 30 minutes exposure with slightly more number of spores at 5 minutes exposure than that of control (Fig.10 B).

Salinity

Data obtained on the effects of different salinities (0, 10, 20, 30, 40, 50, 60, 70 and 80‰) on spore output in *Gracilaria crassa Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides* are shown in Figs.12 to 14. These experiments were conducted for one day with *Gracilaria crass*a and *Hypnea valentiae* and for 4-6 days with *Sargassum wightii* and *Turbinaria conoides*.

Spore output varied markedly in different salinities of the seawater tested with each of the four algae. In *Gracilaria crassa* tetraspore liberation was observed from 10 to 40‰ with peak output of spores at 30‰ (Fig.12). In *Hypnea valentiae* both tetraspore (Fig.13 A) and carpospore (Fig.13 B) shedding was found from 20 to 50‰ with maximum liberation at 30‰.

In the experiments conducted with *Sargassum wightii* at different salinities, there was no oospore output on the first two days and spore shedding was observed from the third day onwards upto the sixth day with peak shedding at 30‰. There was no sporulation on the seventh day in any of the salinities due to the degeneration of receptacles. On the third and

Fig.12 Effect of salinity on the tetraspore output of *Gracilaria crassa*.

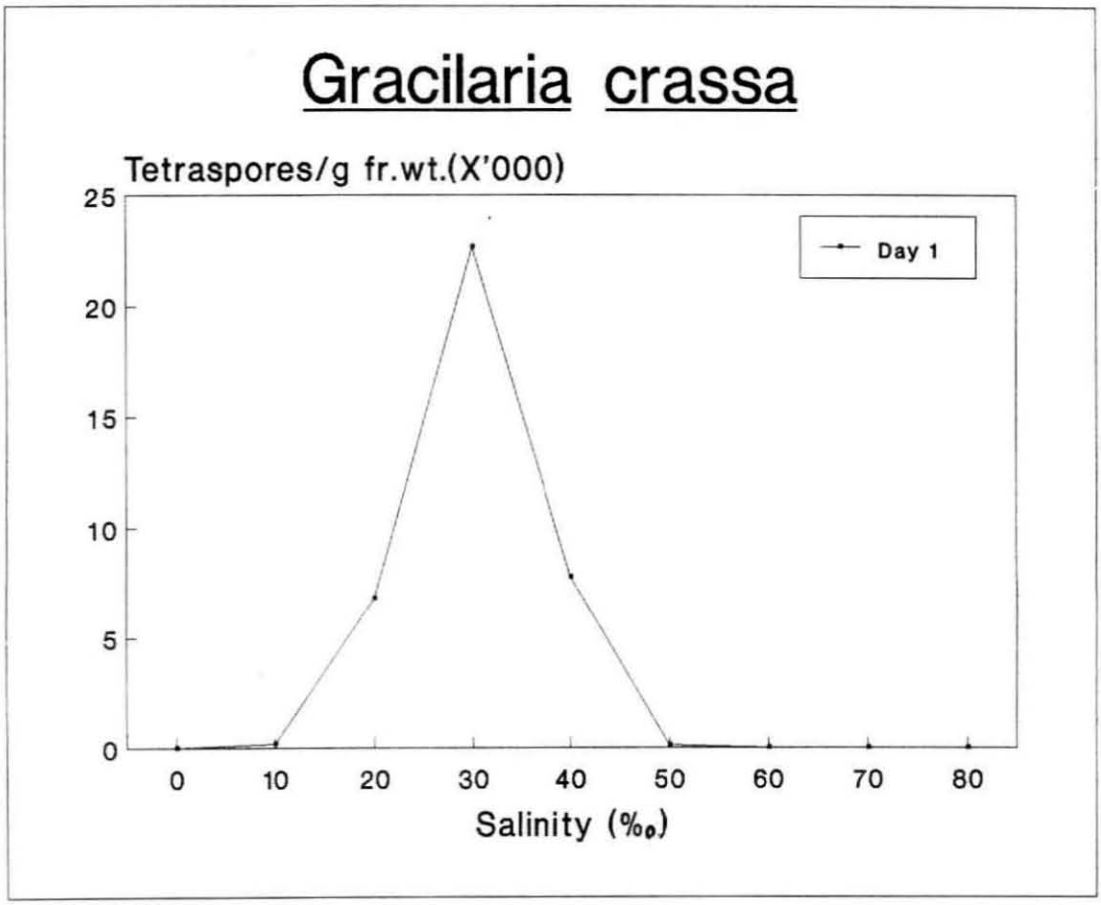
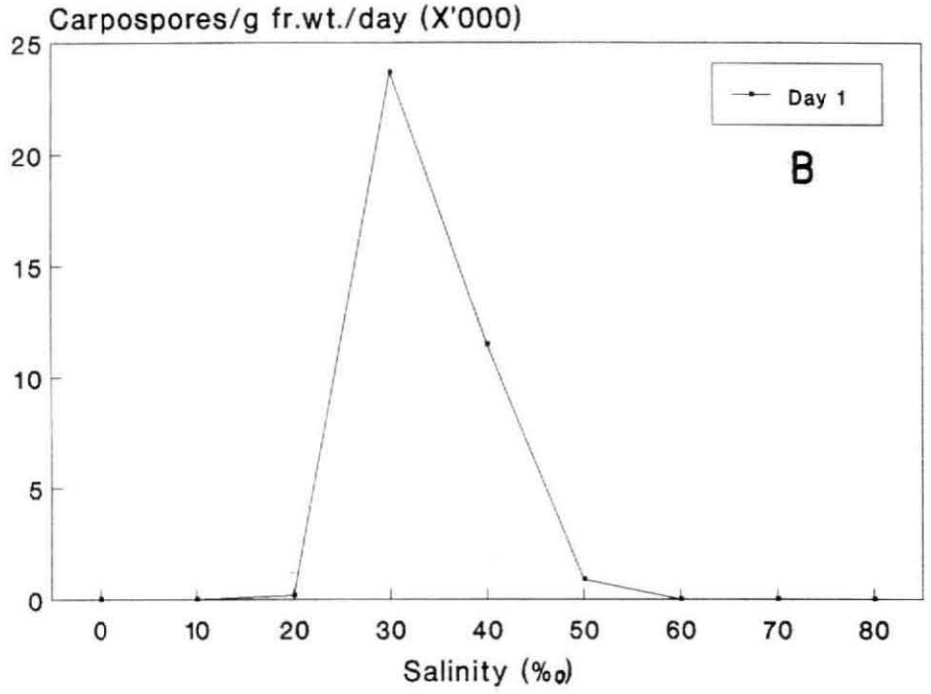

Gracilaria crassa
Tetraspores/g fr.wt.(X'000)
25
20
15
10
5
0
Day 1
0
10
20
30
40
50
60
70
80
Salinity (‰)

Fig. 12

Fig.13 Effect of salinity on the tetraspore and carpospore output of *Hypnea valentiae*.

Hypnea valentiae



Hypnea valentiae

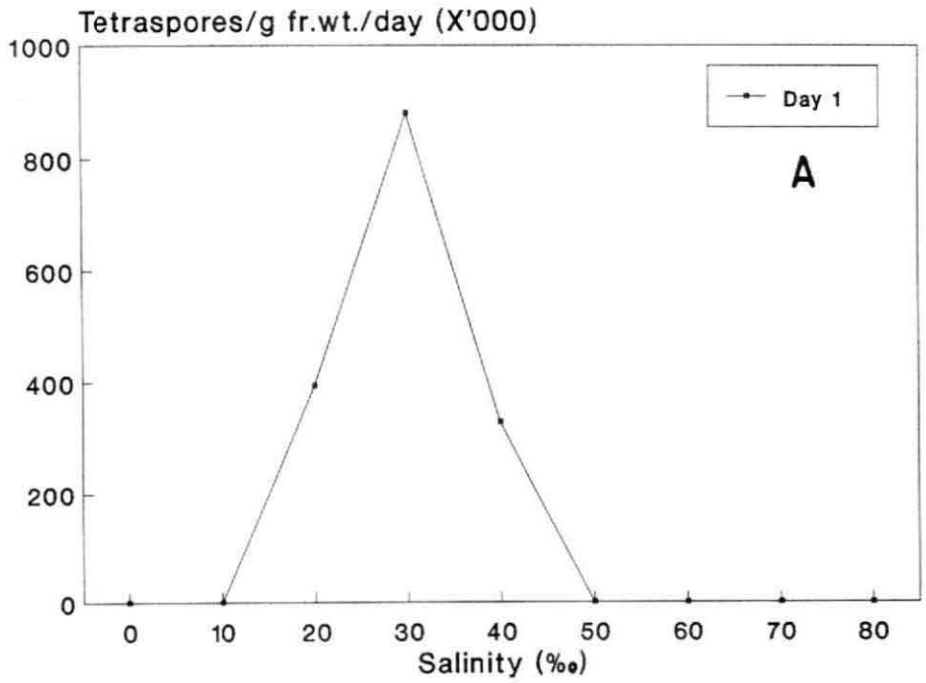


Fig. 13

fourth day spore output was found at 20-40‰ and on the fifth and sixth day at 30 - 40‰ (Fig.14 A). Spore shedding was seen in *Turbinaria conoides* only at two salinities i.e. 30 and 40‰ with maximum shedding at 40‰ in all the four days. The receptacles degenerated after 4 days (Fig. 14 B).

Temperature

Changes observed in the tetraspore output of *Gracilaria crassa* tetraspore and carpospore output of *Hypnea valentiae* and oospore output of *Sargassum wightii* and *Turbinaria conoides* at different temperatures are given in Figs.15 to 17. These experiments were conducted for one day with *Gracilaria crassa*, two days with *Hypnea valentiae*, 4-6 days in *Sargassum wightii* and *Turbinaria conoides*. Spore shedding occurred at different temperature ranges with peak output at a particular temperature in each alga.

In *Gracilaria crassa* tetraspore discharge was found at temperatures ranging from 20° to 40°C with maximum liberation at 25°C (Fig.15). In *Hypnea valentiae* the liberation of tetraspores was observed on the first day between 20°and 40°C with maximum spore output at 30°C, whereas on the second day the tetraspore output occurred between 20°and 30°C with peak output at 25°C (Fig. 16 A). The carpospore output of *Hypnea* was found between 20° to 30°C on the first day with peak liberation at 30°C, while on the second day spore output was observed only at 20° and 25°C with maximum shedding at 20°C (Fig. 16 B).

Fig.15 Effect of temperature on the tetraspore output of *Gracilaria crassa*.

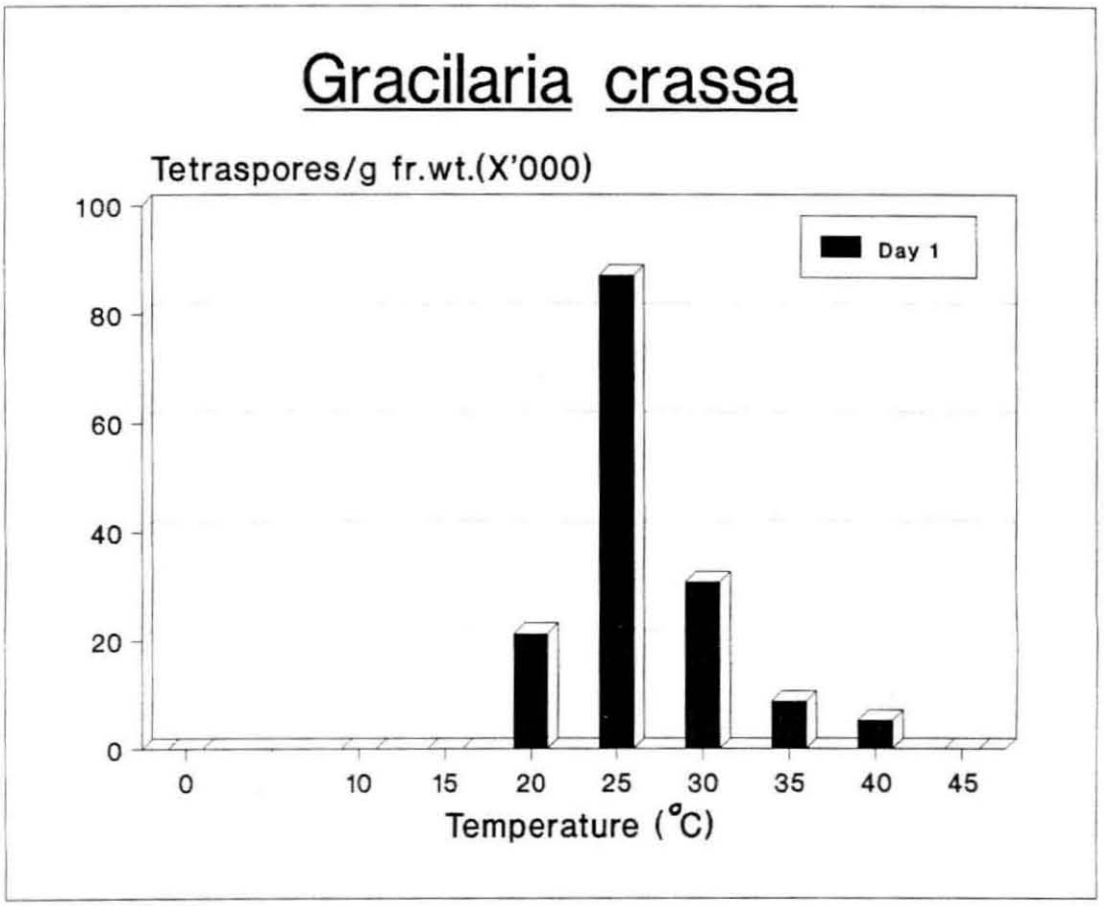
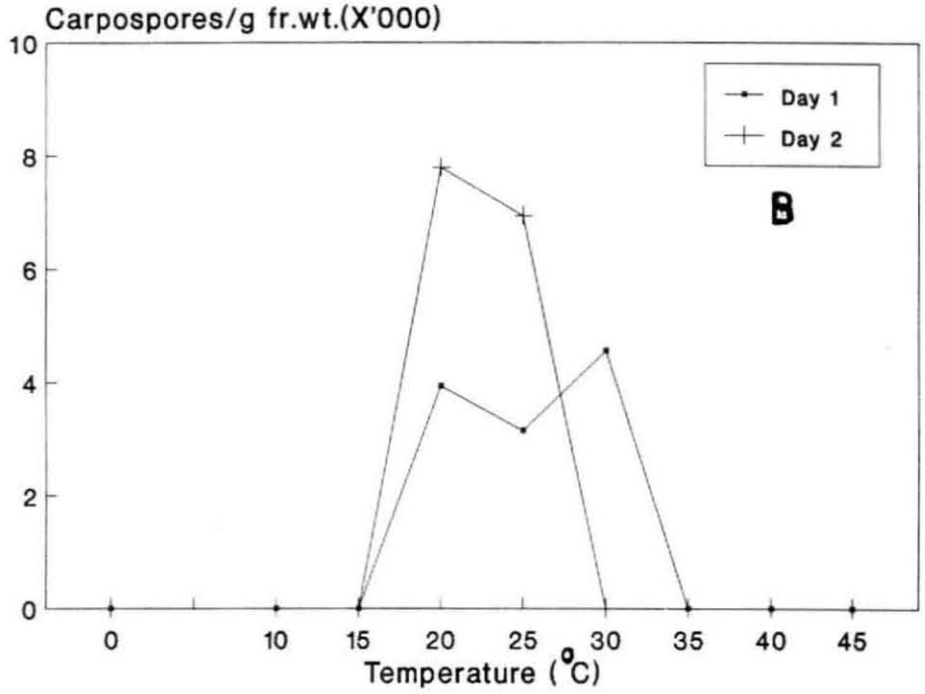

Gracilaria crassa
Tetraspores/g fr.wt.(X'000)
100
80
60
40
20
0
Day 1
0
10
15
20
25
30
35
40
45
Temperature (°C)

Fig. 15

Fig.16 Effect of temperature on the tetraspore and carpospore output of *Hypnea valentiae*.

Hypnea valentiae



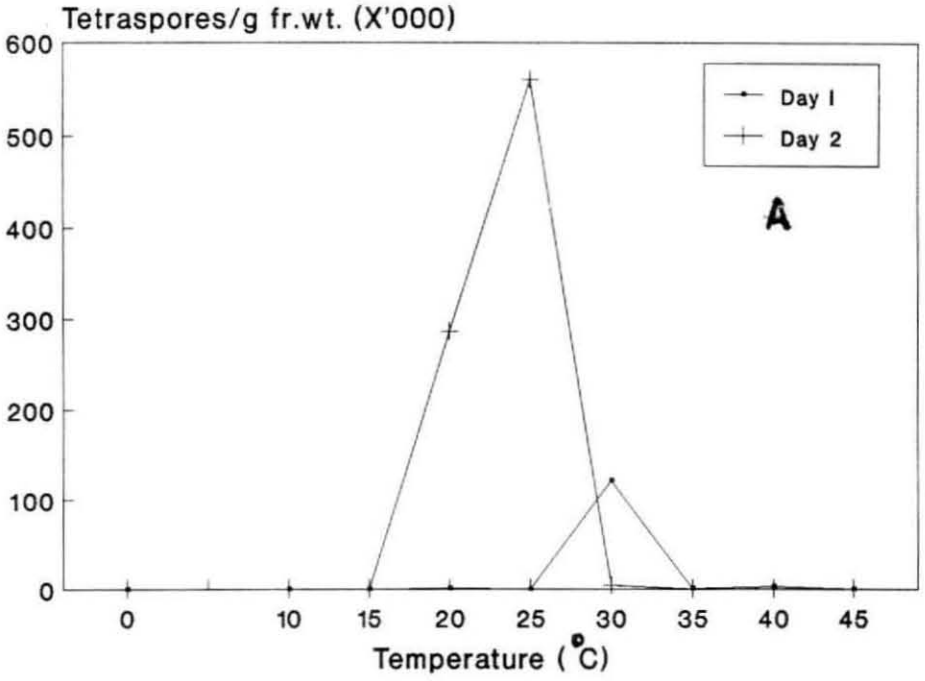
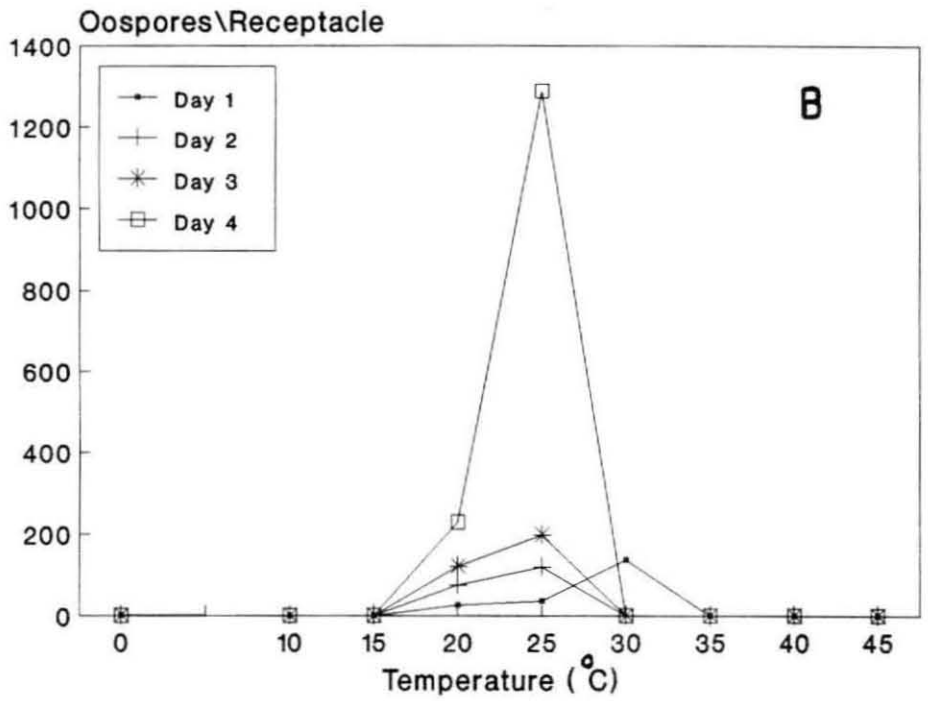


Fig. 16

Fig.17 Effect of temperature on the oospore output in *Sargassum wightii* and *Turbinaria conoides*.

Turbinaria conoides



Sargassum wightii

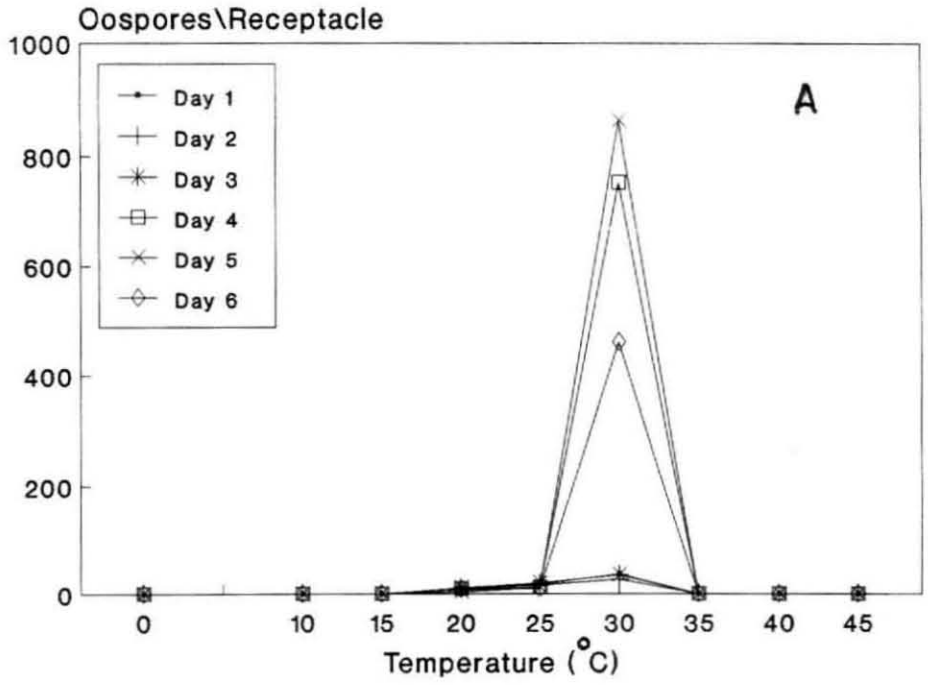


Fig. 17

In *Sargassum wightii* oospore output was recorded between 20° and 30°C in all the six days with peak liberation at 30°C (Fig. 17 A). In *Turbinaria conoides* shedding of oospores occurred at 20° and 30°C with peak liberation at 30°C on the first day. In all the other three days sporulation was observed only at 20° and 25°C with maximum liberation at 25°C (Fig.17 B).

Light

The quantity of spores liberated from the four algae in dark (O light intensity) and at seven different light intensities ranging from 10 to 100 $\mu Em^{-2}s^{-1}$ are shown in Figures 18 to 20. These experiments were conducted with tetrasporophytes of *Gracilaria crassa* for 1 day, tetrasporophytes and carposporophytes of *Hypnea valentiae* for two days and with receptacles of *Sargassum wightii* and *Turbinaria conoides* for five to seven days. The light intensities at which spore liberation occurred differed from species to species.

In *Gracilaria crassa* tetraspore shedding was observed at all light intensities with peak liberation at 20 $\mu Em^{-2}s^{-1}$ (Fig.18). In *Hypnea valentiae* tetraspore output occurred at the light intensities ranging from 0 to 30 $\mu Em^{-2}s^{-1}$ with peak spore output at 30 $\mu Em^{-2}s^{-1}$ on the first day and at 20 $\mu Em^{-2}s^{-1}$ on the second day (Fig. 19 A). The carpospore liberation was found at the light intensities ranging from 0 to 30 $\mu Em^{-2}s^{-1}$ with maximum shedding of spores at 20 $\mu Em^{-2}s^{-1}$ on both days (Fig. 19 B).

Fig.18 Effect of light intensity on the tetraspore output of *Gracilaria crassa*.

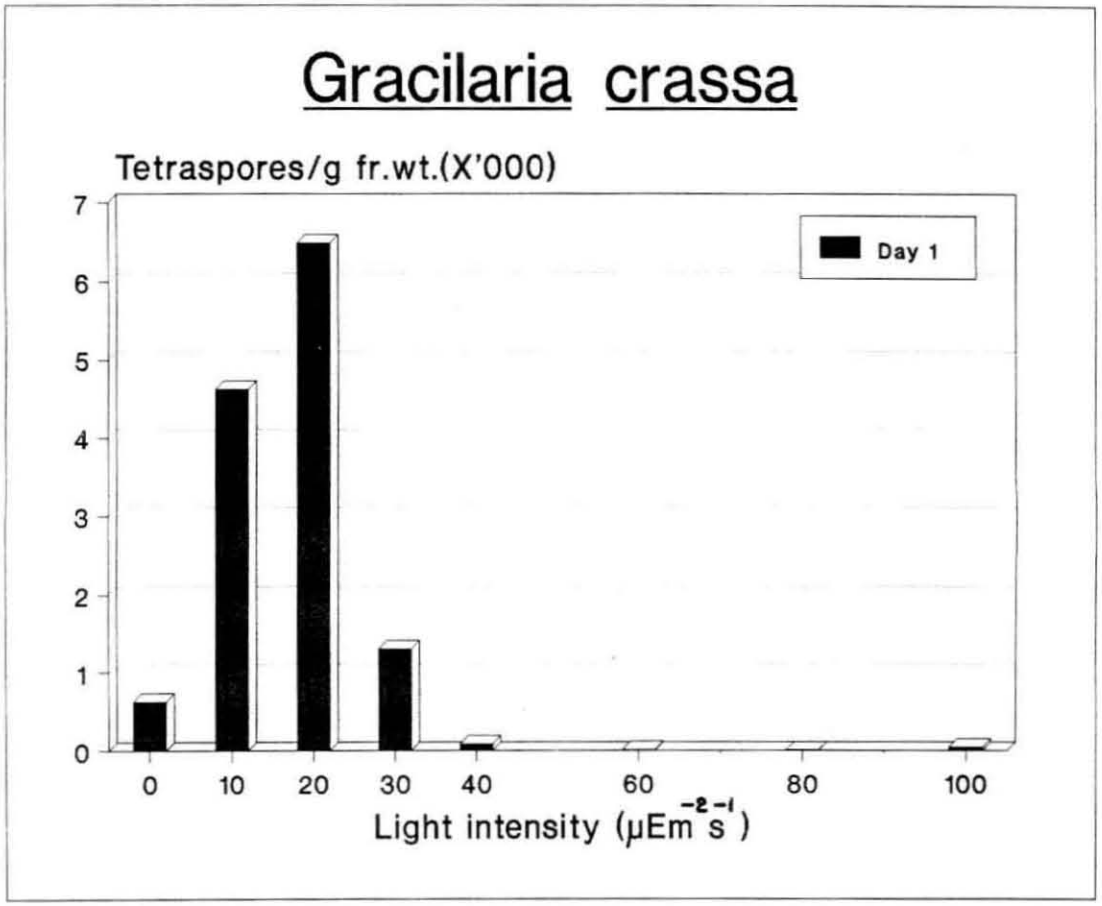
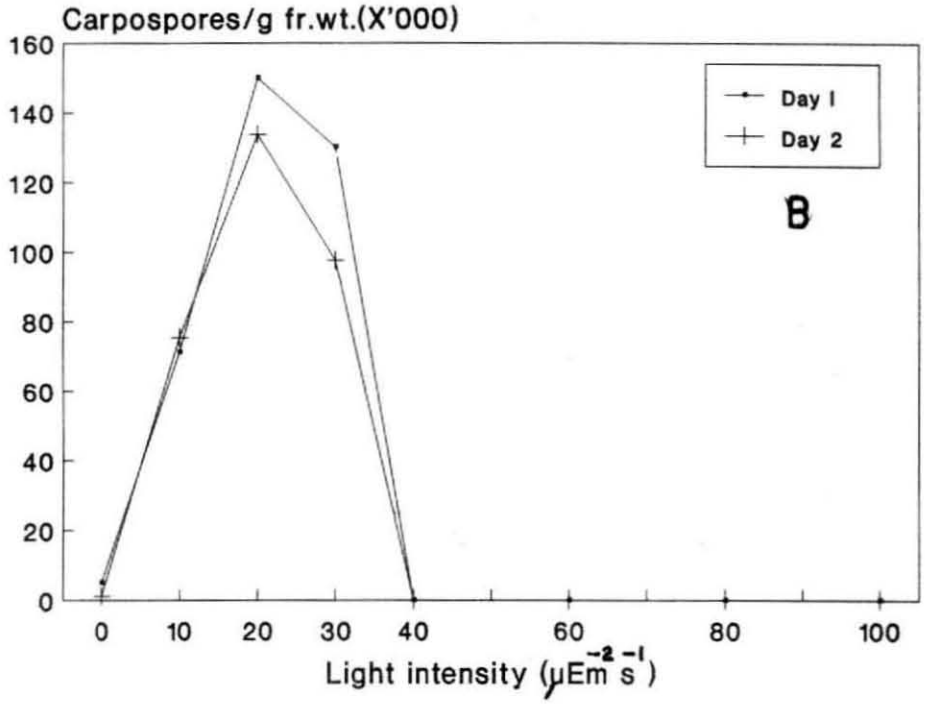

Gracilaria crassa
Tetraspores/g fr.wt.(X'000)
7
6
5
4
3
2
1
0
Day 1
0
10
20
30
40
60
80
100
Light intensity (µEm-2-1s)

Fig. 18

Fig.19 Effect of light intensity on the tetraspore and carpospore output of *Hypnea valentiae*.

Hypnea valentiae



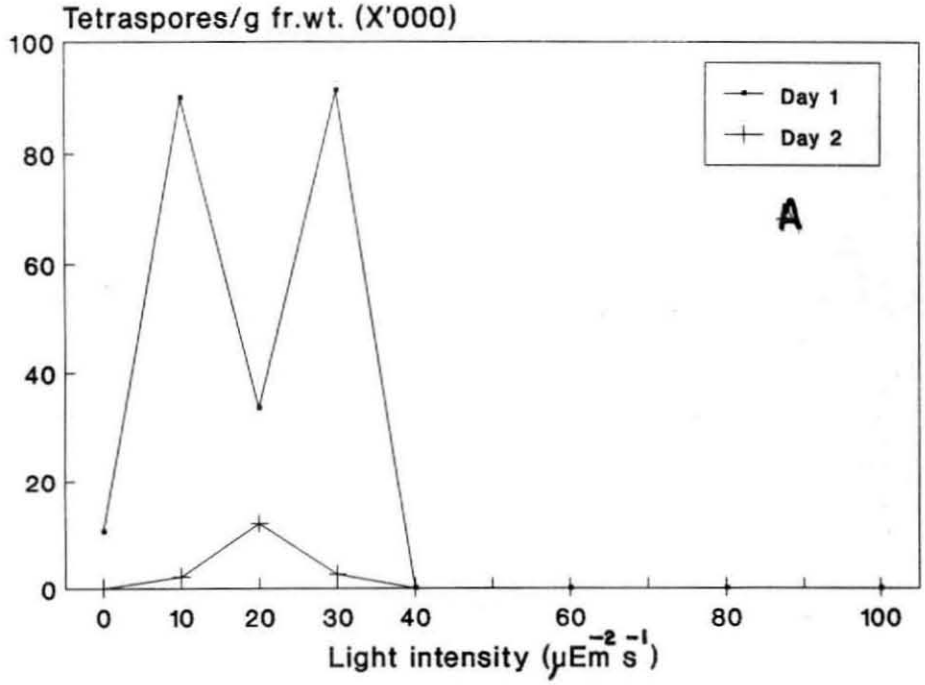
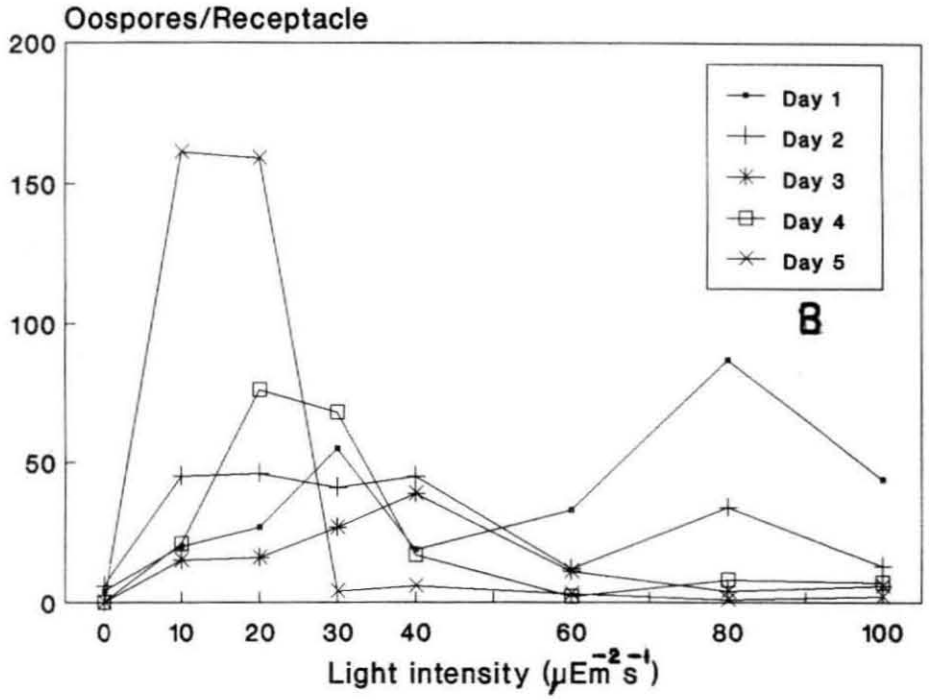


Fig. 19

Fig.20 Effect of light intensity on the oospore output in *Sargassum wightii* and *Turbinaria conoides*.

Turbinaria conoides



Sargassum wightii

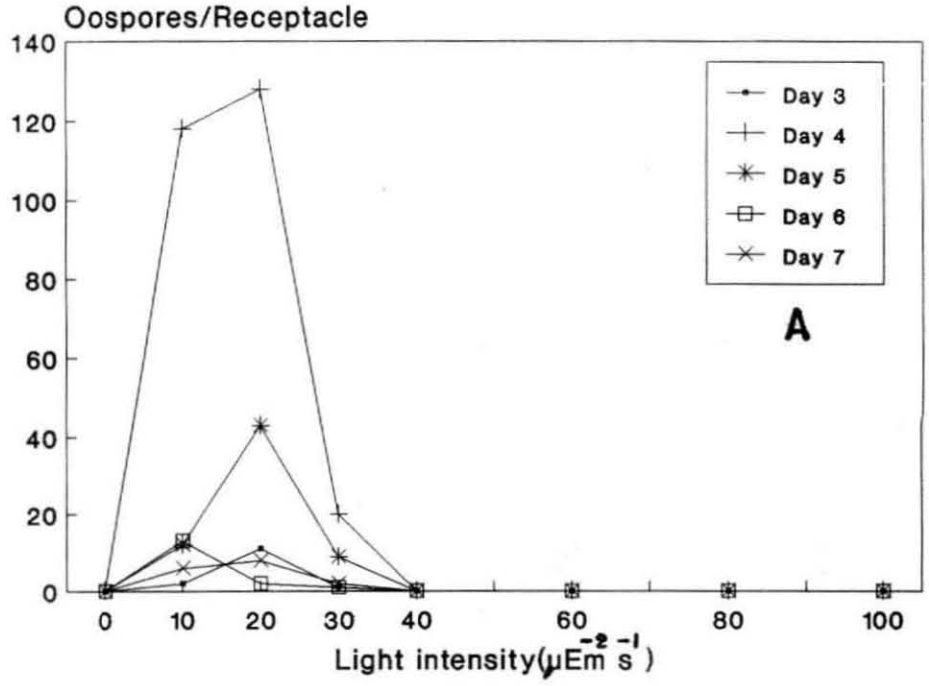


Fig.20

In *Sargassum wightii* oospore output occurred only from third day onwards upto seventh day and thereafter the receptacles decayed. During the five days, oospore output was observed only at three light intensities i.e. 10, 20 and 30 $\mu Em^{-2}s^{-1}$with maximum number of spores at 20 $\mu Em^{-2}s^{-1}$ in all days except on the sixth day at 10 $\mu Em^{-2}s^{-1}$ (Fig.20 A).

In the case of *Turbinaria conoides, oospore* output occurred at all light intensities ranging from 0 to 100 $\mu Em^{-2}s^{-1}$ with maximum liberation of spores at various light intensities during different days i.e. 80 $\mu Em^{-2}s^{-1}$on the first day, 20 $\mu Em^{-2}s^{-1}$ on the second and fourth day, 40 $\mu Em^{-2}s^{-1}$ on the third day and 10 $\mu Em^{-2}s^{-1}$ on the fifth day (Fig. 20 B).

Photoperiod

The effect of different light and dark cycles on tetraspore shedding in *Gracilaria crassa,* tetraspore and carpospore shedding in *Hypnea valentiae* and oospore liberation in *Sargassum wightii* and *Turbinaria conoides* at 20 $\mu Em^{-2}s^{-1}$ light intensity is shown in Figures 21 to 23. These experiments were conducted for one day with *Gracilaria crassa,* two days with *Hypnea valentiae* and five days with *Sargassum wightii* and *Turbinaria conoides.*

In experiments conducted with *Gracilaria crassa* tetraspore output was seen at all photoperiods with maximum spore output at 12:12 LD cycle (Fig. 21). In *Hypnea valentiae* tetraspore output was found at all photoperiods on both days except at 0:24 LD on the second day. The maximum number of spores were liberated at 16:8 LD cycle on the first day. Though the quantity of tetraspores liberated was less on the second day,

Fig.21 Effect of photoperiod on the tetraspore output of *Gracilaria crassa*.

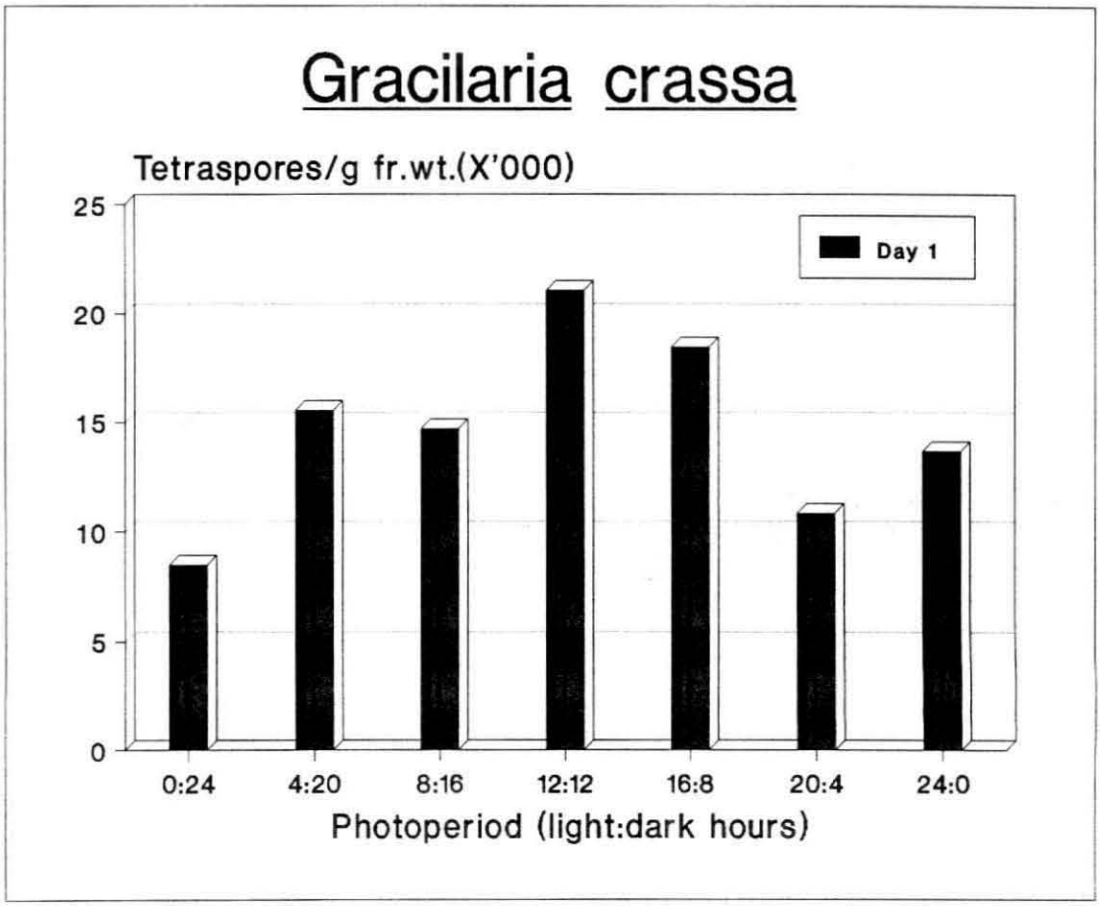
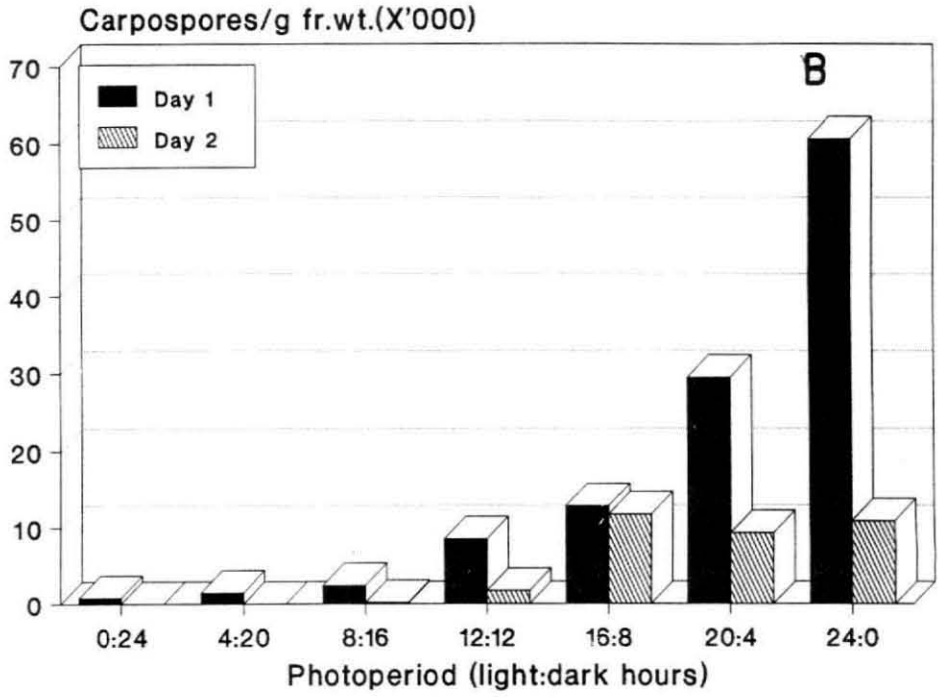

Gracilaria crassa
Tetraspores/g fr.wt.(X'000)
25
20
15
10
5
0
Day 1
0:24
4:20
8:16
12:12
16:8
20:4
24:0
Photoperiod (light:dark hours)

Fig. 21

Fig.22 Effect of photoperiod on the tetraspore and carpospore output of *Hypnea valentiae*.

Hypnea valentiae



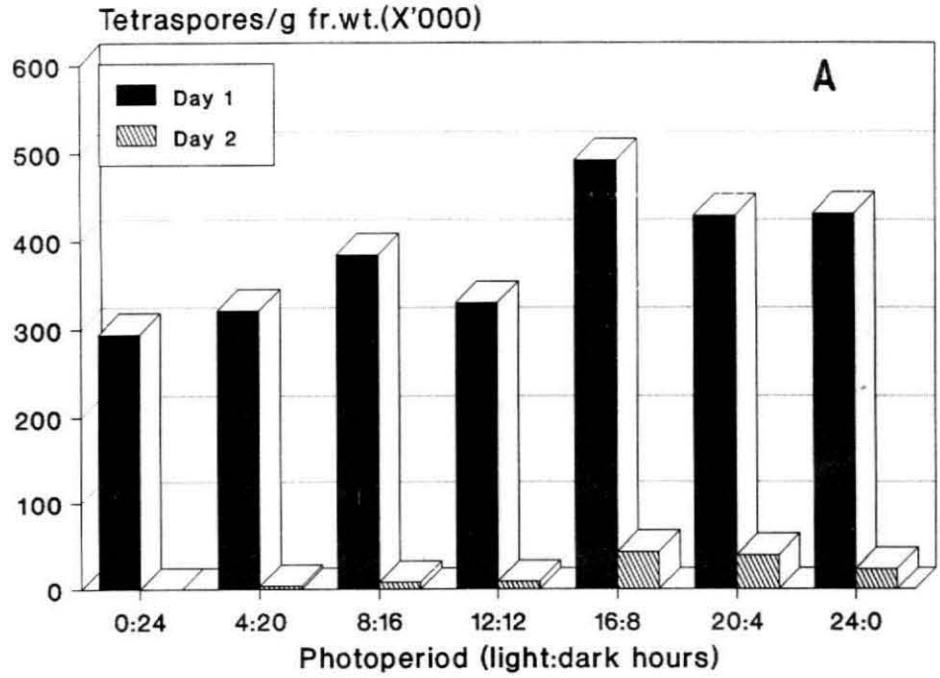
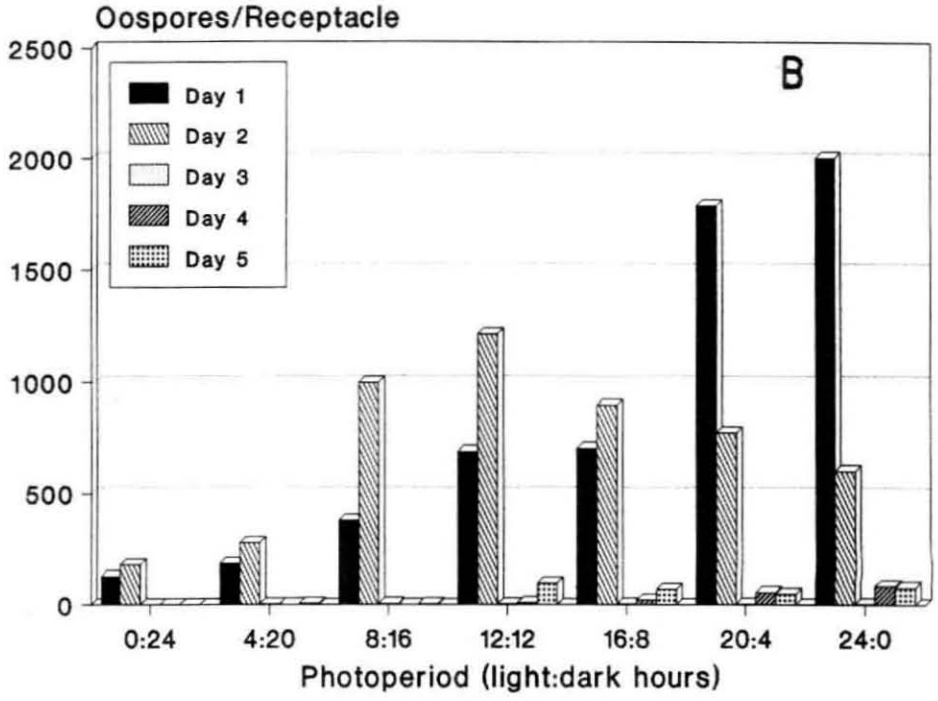


Fig. 22

Fig.23 Effect of photoperiod on the oospore output in *Sargassum wightii* and *Turbinaria conoides*.

Turbinaria conoides



Sargassum wightii

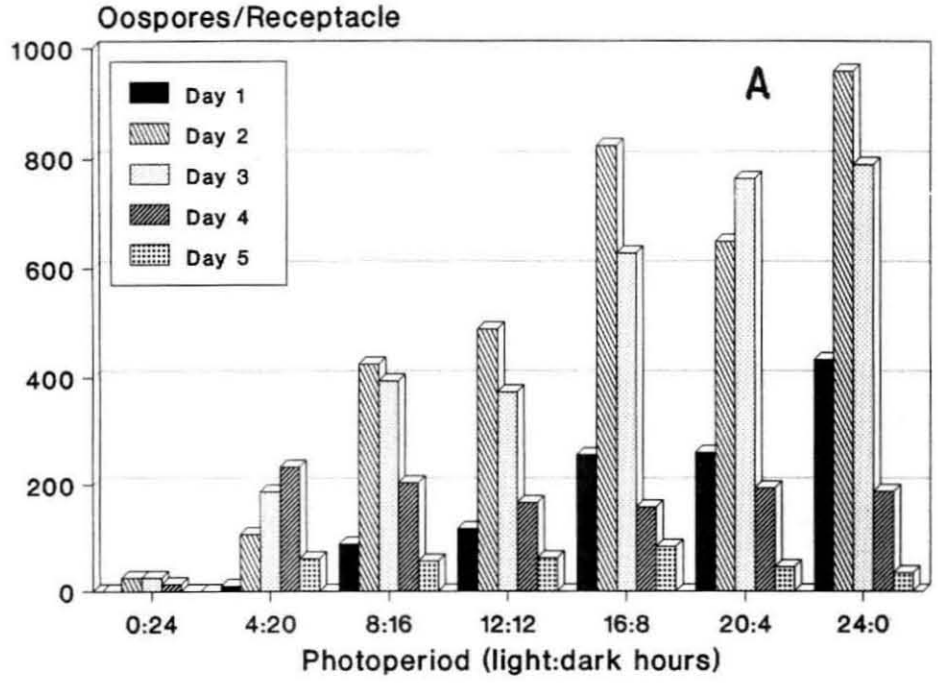


Fig. 23

maximum sporulation was observed at 16:8 LD cycle as recorded on the first day (Fig. 22 A). The liberation of carpospores on the first day was found at all photoperiods with gradual increase in spore output from 0:24 LD cycle onwards and reaching the peak at 24:0 LD cycle. During the second day, there was no carpospore output at 0:24 and 4:20 LD cycle while sporulation was observed at all the other five LD regimes with peak shedding at 16:8 LD cycle (Fig. 22 B).

The oospore output was observed in *Sargassum wightii* almost in all the five days at seven different photoperiods except at 0:24 LD cycle on the first and second day. The peak output of oospores was recorded at 24:0 LD regime from the first day to third day, 4:20 LD cycle on the fourth day and 16:8 LD cycle on the fifth day. The production of oospores was found to be low on the fifth day at all the photoperiods (Fig.23 A). In *Turbinaria conoides* oospore output was seen at all seven photoperiods almost in all five days. Maximum shedding of oospores was observed at 24:0 LD cycle on the first and fourth day, 12:12 LD cycle on the second and fifth day and 8:16 LD regime on the third day. The quantity of oospores liberated was low after the second day at all the photoperiods (Fig.23 B).

SPORE STUDIES

The shape and size of different kinds of spores in the four algae were studied. In *Gracilaria crassa* the shape of tetraspores as well as carpospores was spherical and their size was 18µm and 29µm diameter respectively. The size of carpospores was larger than tetraspores. In *Hypnea valentiae* also both tetraspores and carpospores were spherical in shape and they measured 18µm and 29µm diameter respectively. As observed in *Gracilaria crassa*, the carpospore size was larger than tetraspores in *Hypnea valentiae.*

In *Sargassum wightii* and *Turbinaria conoides,* the oospores were ovoid in shape. The length and breadth of oospores in *Sargassum wightii* were 174 - 232µm and 131 - 160 µm respectively. In *Turbinaria conoides* the length of the oospores was 160 - 189 µm and breadth was 116 - 145 µm. In general, the size of oospores in *Sargassum wightii* was larger than that of *Turbinaria conoides.*

HYDROLOGICAL AND ENVIRONMENTAL PARAMETERS

Data were collected for a period of one year from April, 1998 to March, 1999 on hydrological and environmental parameters from one of the collection localities namely Thonithurai. The mean values obtained on atmospheric temperature, seawater temperature and seawater salinity are given in Table 2. The atmospheric temperature varied from 28.0°C in September to 32.6°C in November. The bottom seawater temperature varied from 27.0°C in January to 32.5°C in October. The salinity of seawater varied from a minimum of 25‰ in January to a maximum of 35‰ in August and October. The underwater light intensity ranged from 2 $\mu Em^{-2}s^{-1}$ to 408 $\mu Em^{-2}s^{-1}$ during the period of this study.

Table - 2

Data collected on hydrological and environmental parameters from the collection locality (Thonithurai)

Month	Atmospheric temperature (°C)	Bottom seawater temperature (°C)	Salinity (‰)
April, 1998	32.0	30.0	33.0
May	32.0	30.0	33.0
June	30.8	30.5	30.5
July	31.0	30.5	33.5
August	31.0	29.7	35.0
September	28.0	29.2	34.0
October	30.5	32.5	35.0
November	32.6	31.7	31.7
December	28.3	28.0	28.5
January, 1999	29.0	27.0	25.0
February	29.8	29.0	29.0
March	30.0	30.5	30.0

Discussion

DISCUSSION

In the present study, data were collected on the fruiting behaviour and spore shedding of the red algae *Gracilaria crassa* and *Hypnea valentiae* and the brown algae *Sargassum wightii* and *Turbinaria conoides* growing along the Mandapam coast. Experiments were carried out under laboratory conditions to show the variations in spore production during different months of the year in *Gracilaria crassa*. Studies were also made to know the effects of environmental factors such as exposure to air (desiccation), salinity, temperature, light and photoperiod on spore shedding in *Gracilaria crassa, Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides*. Information was also gathered on hydrological and environmental parameters from the collection locality.

FRUITING BEHAVIOUR

Fertile plants (tetrasporophytes and carposporophytes) occurred in the population of *Gracilaria crassa* growing at Mandapam throughout the year as reported for *Gracilaria verrucosa* (Jones, 1959) , *G. edulis* (Rama Rao and Thomas, 1974; Atmadja, 1988), *G. foliifera* (Atmadja, 1988) and *G.bursapastoris* (Marinho Soriano *et al.,* 1998). The tetrasporic plants of *G.crassa* occurred abundantly than the vegetative and cystocarpic plants as observed in *G. verrucosa* (Whyte *et al.,* 1981), *G. tikvahiae* (Bird, 1976), *G. edulis* (Rama Rao and Thomas, 1974); *G. bursapastoris* and *G. coronopifolia* (Hoyle, 1978), *G. corticata* (Subba Rangaiah, 1983 a), *G. foliifera* (Chennubhotla *et al.,* 1986) and *G. blodgetii* (Gerung *et al.,* 1997). In *G. foliifera* (Chennubhotla *et al.,* 1986), *G. tikvahiae* (Penniman *et al.,* 1986), *G. verrucosa* (Oza *et al.,* 1989) and *G. heteroclada* (Luhan, 1996), tetrasporic

plants occurred seasonally in the population. But in the present study the tetrasporophytes of *G. crassa* were found in all month as observed in *G. edulis* (Rama Rao and Thomas, 1974; Shoba, 1985), *G. corticata* (Oza, 1979 and 1984; Subba Rangaiah, 1983 a; Shoba, 1985), *G. arcuata var.arcuata* and *G. corticata var. cylindrica* (Kaliaperumal *et al.,* 1986).

In *G. crassa*, cystocarpic plants were seen throughout the year as reported in *G. edulis* (Rama Rao and Thomas, 1974; Shoba, 1985) and *G. corticata* (Subba Rangaiah, 1983a and Shoba, 1985). But in *G. foliifera* (Umamaheswara Rao, 1973), *G. corticata* (Oza 1979 and 1984), *G. tikvahiae* (Penniman *et al.,* 1986), *G. verrucosa* (Oza *et al.,* 1989) and *G. heteroclada* (Luhan, 1996) carposporophytes occurred seasonally.

De Wreede (1976), Ang (1985) Shunula (1988) and Arenas and Fernandez (1998) studied the fruiting behaviour of *Sargassum* spp. growing in other areas. As reported by these workers in *Sargassum oligocystum, S. tenerrimum, S. siliquosum, S. paniculatum, S. aquifolium, S. asperifolium* and *S. muticum*, plants with receptacles were found during the period October - February in *Sargassum wightii* growing at Mandapam coast. This is in agreement with the earlier findings of Umamaheswara Rao and Kaliaperumal (1976) on *S. wightii*. In *T. conoides* also fruiting plants with receptacles were seen during the period October - February. This is in conformity with the observations made earlier in *T. conoides* (Chennubhotla *et al.,* 1978 b), *T. decurrens* (Kaliaperumal and Umamaheswara Rao, 1975; Kaliaperumal and Kalimuthu, 1976) and *T. ornata* (Umamaheswara Rao and Kalimuthu, 1972).

SPORE OUTPUT

Much work has been carried out on the spore output in marine algae of different classes and a perusal of these informations can be used for a comparision of the spore output among the algae of different groups (Table 3). It is clear from the table that there is a wide range in the spore output of different species irrespective of their groups and geographical distribution. The spore output depends largely on the environmental conditions existing at the time of collection. It can also be inferred from Table 3 that the algae having large sized spores *(Sargassum wightii, Turbinaria decurrens* etc) produced lesser number of spores than those which have small sized spores (*Gracilaria edulis, G. corticata* etc.) Intensive studies are necessary to understand the ecological significance of the relative difference in the output of reproductive elements among different classes of algae and among different orders within a class.

Maximum and minimum quantity of spore production in *Gracilaria crassa* during the period of this study from April, 1998 to March, 1999 are given below to know the spore producing capacity of this agar yielding seaweed.

Day	Tetraspores/g fr.wt./day		Carpospores/g fr.wt./day	
	Minimum	Maximum	Minimum	Maximum
1.	1,205	40,746	11,047	87,754
2.	17	899	4	22,763
3.	1	69	5	13,379
4.	2	64	245	17,353
5.	1	83	849	6,666

Table - 3

Spore output in marine algae

Species	Minimum Spore Output	Maximum Spore Output	Type of Spores	Authors
Chlorophyceae				
Enteromorpha compressa	8,31,550	24,14,800	Swarmers/g fr.wt./day	Naidu (1987)
Ulva fasciata	6,15,730	19,16,120	Swarmers/g fr.wt./day	Naidu (1987)
U. fasciata	-	1,15,34,400	Swarmers/plant	Subbaramaiah (1970)
Phaeophyceae				
Cystoseira indica	-	5,11,251	Oospores/plant	Mairh & Krishnamurthy (1968)
Ectocarpus mitchellae	12,00,000	22,00,000	Plurispores/g fr.wt./day	Narasimha Rao (1989a)
Fucus spiralis	-	285	Eggs/m^2	Robertson (1987)
Giffordia mitchellae	6,93,478	13,291,278	Plurispores/g ft.wt./day	Umamaheswara Rao (1990)
Padina tetrastromatica	22,070	81,965	Tetraspores/plant/day	Umamaheswara Rao (1990)
Rosenvingea nhatrangensis	9,70,000	16,00,000	Plurispores/plant/day	Umamaheswara Rao (1990)
Sargassum ilicifolium	94	5,225	Oospores/plant/day	Umamaheswara Rao (1990)
S. swartzii	-	5,53,331	Oospores/plant	Chauhan & Krishnamurthy (1967)
S. vulgare	136	31,284	Oospores/plant/day	Umamaheswara Rao (1990)
S. wightii	15,642	52,896	Oospores/plant/day	Umamaheswara Rao (1990)

Species	Minimum Spore Output	Maximum Spore Output	Type of Spores	Authors
S. wightii	-	3,70,272	Oospores/plant	Umamaheswara Rao & Kaliaperumal (1976)
Turbinaria conoides	56	11,312	Oospores/plant	Chennubhotla *et al.* (1978b)
T. decurrens	1260	28,196	Oospores/plant	Kaliaperumal and Umamaheswara Rao (1975)
T. decurrens	8	1,616	Oospores/plant/day	Umamaheswara Rao (1990)
T. ornata	-	33,810	Oospores/plant	Kaliaperumal *et al.* (1977)
T. ornata	56	11,312	Oospores/plant	Chennubhotla *et al.* (1978b)
Rhodophyceae				
Amphiroa fragilissima	4,240	5,28,461	Tetraspores/g fr.wt./day	Vanilla Kumari (1997)
Asparagopsis delilei	390	11,917	Carpospores/g wet wt.	Vasuki *et al.* (1999)
Bangiopsis subsimplex	12,00,000	24,00,000	Tetraspores/g fr.wt./day	Narasimha Rao (1989a and 1989b)
Centroceras clavulatum	16,338	1,89,949	Carpospores/g fr.wt./day	Sudhakar (1992); Sudhakar & Subba Rangaiah (1993).
C. clavulatum	6,081	84,731	Tetraspores/g fr.wt./day	Sudhakar (1992); Sudhakar & Subba Rangaiah (1993).
Ceramium ciliatum	-	10,512	Tetraspores/sorus	Boney (1960a)
Chondrus crispus	29,000	48,000	Monospores/g fr.wt./day	Mathieson (1989)
Gelidiella acerosa	-	20,000	Tetraspores/plant	Sreenivasa Rao (1971; 1974)
G. acerosa	5,000	10,000	Tetraspores/g fr.wt./day	Umamaheswara Rao (1974)
G. acerosa	5,744	3,89,793	Tetraspores/g. fr.wt.	Shoba (1985)

Species	Minimum Spore Output	Maximum Spore Output	Type of Spores	Authors
G. acerosa	-	50,000	Spores/g/day	Banumathi & Subbaramaiah (1990)
Gelidiopsis variabilis	20	2,60,940	Tetraspores/g fr.wt./day	Kaliaperumal & Umamaheswara Rao (1982)
Gelidium sp.	1,00,000	10,00,000	Spores/g fr.wt./day	Suto (1950a; 1950b)
Gelidium pusillum	1,149	10,78,505	Tetraspores/g fr.wt./day	Kaliaperumal & Umamaheswara Rao (1986)
G. pusillum	1,176	,99,943	Carpospores/g fr.wt./day	Kaliaperumal & Umamaheswara Rao (1986)
G. robustum	-	2,99,072	Carpospores/month	Guzman del Pro *et al.* (1972)
G. robustum	-	27,453	Tetraspores/month	Guzman del Pro *et al.* (1972)
Gigartina canaliculata	2,08,000	20,50,000	Tetraspores/specimen	Pacheco Ruiz (1989)
G. canaliculata	-	27,34,000	Carpospores/specimen	Pacheco Ruiz (1989)
Gracilaria arcuata var. arcuata	43	28,291	Tetraspores/g fr.wt./day	Kaliaperumal *et al.* (1986)
G. arcuata var. arcuata	10	40,055	Carpospores/g fr.wt./day	Kaliaperumal *et al.* (1986)
G. asiatica	52,187	86,250	Carpospores/g fr.wt./day	Li Xiuliang & Li Meizhan (1989)
G. asiatica	-	1,72,089	Tetraspores/g plant	Li Xiuliang & Li Meizhan (1988)
G. corticata	239	53,200	Carpospores/g fr.wt	Mohan Joseph & Krishnamurthy (1977)
G. corticata	947	2,35,000	Carpospores/month	Oza (1979; 1984)
G. corticata	13,700	3,33,300	Tetraspores/g fr.wt./day	Subba Rangaiah (1983a)
G. corticata	300	3,100	Carpospores/g fr.wt./day	Subba Rangaiah (1983a)

Species	Minimum Spore Output	Maximum Spore Output	Type of Spores	Authors
G. corticata	26,500	1,44,000	Tetraspores/g fr.wt./day	Umamaheswara Rao (1976)
G. corticata	1,183	2,374	Carpospores/cystocarp/day	Umamaheswara Rao (1976)
G. corticata	8,181	92,277	Tetraspores/g fr.wt./day	Shoba (1985)
G. corticata	8,086	4,87,178	Carpospores/g fr.wt./day	Shoba (1985)
G. crassa	12	40	Carpospores/g/day	Shyam Sunder *et al.* (1991)
G. crassa	1,205	40,746	Tetraspores/g fr.wt./day	Present Study
G. crassa	11,047	87,754	Carpospores/g fr.wt./day	Present Study
G. corticata var cylindrica	43	28,291	Tetraspores/g fr.wt./day	Kaliaperumal *et al.* (1986)
G. corticata var cylindrica	10	40,055	Carpospores/g fr.wt./day	Kaliaperumal *et al.* (1986)
G. edulis	6,919	6,49,873	Carpospores/plant	Rama Rao & Thomas (1974)
G. edulis	2,135	1,09,565	Tetraspores/g fr.wt./day	Shoba (1985)
G. edulis	28,652	3,27,833	Carpospores/g fr.wt./day	Shoba (1985)
G. edulis	1,696	6,715	Carpospores/cystocarp/day	Mal & Subbaramaiah (1990b)
G. edulis	44	6,439	Tetraspores/g plant/day	Mal & Subbaramaiah (1990b)
G. foliifera	500	11,508	Tetraspores/g fr.wt./day	Chennubhotla *et al.* (1986)
G. foliifera	1,015	26,368	Carpospores/g fr.wt./day	Chennubhotla *et al.* (1986)
G. millardetii	-	68,520	Tetraspores/plant	Krishnamurthy (1967b)
G. millardetii	-	42,782	Carpospores/plant	Krishnamurthy (1967b)
G. textorii	8,50,390	12,30,380	Tetraspores/g fr.wt./day	Subba Rangaiah (1984)

Species	Minimum Spore Output	Maximum Spore Output	Type of Spores	Authors
G. textorii	1,127	2,646	Carpospores/cystocarp/day	Subba Rangaiah (1984)
G. verrucosa	-	19,700	Carpospores/plant/day	Oza & Krishnamurthy (1968)
G. verrucosa	200	2000	Carpospores/cystocarp	Kin (1970)
Gracilariopsis sjoestedtii	3,20,506	5,72,150	Tetraspores/g fr/wt./day	Subba Rangaiah (1985a)
G. sjoestedtii	3,867	6,807	Carpospores/g fr.wt./day	Subba Rangaiah (1985a)
G. sjoestedtii (Pamban)	1,197	3,15,636	Tetraspores/g fr.wt./day	Chennubhotla *et al.* (1986)
G. sjoestedtii (Pamban)	2,700	1,42,672	Carpospores/g fr.wt./day	Chennubhotla *et al.* (1986)
G. sjoestedtii (Kilakkarai)	52	3,27,791	Tetraspores/g fr.wt./day	Chennubhotla *et al.* (1986)
G. sjoestedtii (Kilakkarai)	14	2,52,151	Carpospores/g fr.wt./day	Chennubhotla *et al.* (1986)
Grateloupia filicina	50,000	4,00,000	Tetraspores/g fr.wt./day	Umamaheswara Rao (1987)
G. lithophila	17,090	8,60,435	Tetraspores/g fr.wt./day	Vanilla Kumari (1997)
G. lithophila	5,458	11,64,258	Carpospores/g fr.wt./day	Vanilla Kumari (1997)
Hypnea musciformis	2,662	5,04,958	Tetraspores/g fr.wt./day	Shoba (1985)
Hypnea musciformis (Pudumadam)	16,112	6,46,385	Carpospores/g fr.wt./day	Shoba (1985)
Hypnea musciformis (Kilakkarai)	2,814	2,83,745	Carpospores/g fr.wt./day	Shoba (1985)
H. valentiae	-	3,14,000	Tetraspores/plant	Rama Rao (1979)
H. valentiae	-	7,01,000	Carpospores/plant	Rama Rao (1979)

Species	Minimum Spore Output	Maximum Spore Output	Type of Spores	Authors
H. valentiae	1,63,200	8,49,140	Tetraspores/g fr.wt./day	Subba Rangaiah & Umamaheswara Rao (1983)
H. valentiae	280	1,954	Carpospores/g fr.wt./day	Subba Rangaiah & Umamaheswara Rao (1983)
Jania rubens	84	1,597	Tetraspores/g fr.wt./day	Vanilla Kumari (1997)
J. rubens	36	1,170	Carpospores/g fr.wt./day	Vanilla Kumari (1997)
Polysiphonia platycarpa	43,513	1,78,697	Tetraspores/g fr.wt./day	Sudhakar (1992)
P. platycarpa	16,580	86,994	Carpospores/g fr.wt./day	Sudhakar (1992)
P. platycarpa	43,513	1,78,697	Tetraspores/g fr.wt./day	Vanilla Kumari (1997)
P. platycarpa	16,580	86,994	Carpospores/g fr.wt./day	Vanilla Kumari (1997)
Porphyra vietnamensis	1,40,000	8,20,2000	Monospores/g fr.wt./day	Narasimha Rao (1989a)
P. vietnamensis	-	9,00,000	Carpospores/g fr.wt./day	Narasimha Rao (1989a)
Pterocladia heteroplatos	1,427	7,94,055	Tetraspores/g fr.wt./day	Kaliaperumal & Umamaheswara Rao (1985)
P. heteroplatos	39,996	1,67,040	Carpospores/g fr.wt./day	Kaliaperumal & Umamaheswara Rao (1985)
Wrangelia argus	3,928	1,91,940	Tetraspores/g fr.wt./day	Sudhakar (1992); Sudhakar & Subba Rangaiah (1993;1997a)
W. argus	523	39,706	Carpospores/g fr.wt./day	Sudhakar (1992); Sudhakar & Subba Rangaiah (1993;1997a)

The above values reveal that the spore shedding capacity is high in *Gracilaria crassa* and the spore output estimates can be compared favourably with the values reported on spore production in *Gracilaria corticata* (Mohan Joseph and Krishnamurthy, 1977) and *Gracilaria asiatica* (Li Xiuliang, 1989). The spore output estimated in *G. crassa* (Shyam Sunder *et al.,* 1991) and in other *Gracilaria* species viz *Gracilaria millardetii* (Krishnamurthy, 1967 b), *G. verrucosa* (Oza and Krishnamurthy 1968), *G. corticata* (Oza, 1979), *G. foliifera (*Chennubhotla *et al.,* 1986), *G. edulis* (Mal and Subbaramaiah, 1990 b), *G. arcuata var. arcuata* and *G. corticata* var. *cylindrica* (Kaliaperumal *et al.,* 1986) were lesser than that now estimated in *G.crassa* (Figs.3&4). On the contrary, the quantity of spores released in *Gracilaria textorii* (Subba Rangaiah, 1984), *G. edulis, G. corticata* (Shoba, 1985) and other Gigartinales member *Gracilariopsis sjoestedtii* (Chennubhotla *et al.,* 1986) were higher than the spore output estimated in the present study.

Maximum shedding of tetraspores and carpospores was seen in *Gracilaria crassa* on the first day (Fig. 2) and it is in agreement with the trend reported by Rama Rao and Thomas (1974) in *G. edulis*, Umamaheswara Rao (1976), Mohan Joseph and Krishnamurthy (1977) and Subba Rangaiah (1983 a) in *G. corticata*, Subba Rangaiah (1984) in *G. textorii,* Shyam Sunder *et. al.* (1991) in *G. crassa*, Kaliaperumal *et. al.* (1986) in *G. arcuata* var. *arcuata* and *G. corticata* var. *cylindrica*, Chennubhotla *et. al.* (1986) in *Gracilaria foliifera* and *Gracilariopsis sjoestedtii*, Umamaheswara Rao (1987) in *Grateloupia filicina*, Subba

Rangaiah (1985 a) and Umamaheswara Rao (1987) in *Gracilariopsis sjoestedtii* and Subba Rangaiah and Umamaheswara Rao (1983) in *Hypnea valentiae.* But, maximum liberation of spores was observed on the third day in *Gracilaria verrucosa* (Oza and Krishnamurthy, 1968) and *Gigartina canaliculata* (Pacheco Ruiz *et al.,* 1989).

In *Gracilaria foliifera* and *Gracilariopsis sjoestedtii* (Chennubhotla *et al.,* 1986), *Gracilaria edulis* (Shoba, 1985; Mal and Subbaramaiah, 1990b), *G. arcuata* var. *arcuata* and *G. corticata* var. *cylindrica* (Kaliaperumal *et al.,* 1986) cystocarpic plants released larger number of spores than the tetrasporic plants. In the present study also, the output of carpospores was always higher than that of tetraspores during different days of liberation. But in *Gracilaria millardetii* (Krishnamurthy, 1967 b), *G. corticata* (Subba Rangaiah, 1983 a; Shoba, 1985) and *G. textorii* (Subba Rangaiah, 1984) tetraspore output was always higher than carpospore output.

SEASONAL CHANGES IN SPORE OUTPUT

As reported by Rama Rao and Thomas (1974) in *Gracilaria edulis,* Umamaheswara Rao (1976) and Subba Rangaiah (1983 a) in *G. corticata*, two peaks in a year were observed in the liberation of tetraspores and carpospores (Figs.3 and 4). But only a single peak in a year in the shedding of spores was observed in *Gracilaria verrucosa* (Jones, 1959; Oza and Krishnamurthy, 1968).

In *Gracilaria crassa*, tetraspore and carpospore shedding were seen throughout the year with a bimodal peak in spore discharge. Seasonal variations were also found with peak discharge of both type of spores in the months from July/August to October and another peak in February and March. Minimum quantity of spores were seen in the months of April - May and November to January (Figs.3&4). Similarly, seasonal variations in sporulation was reported in *Gracilaria corticata* (Umamaheswara Rao 1976; Mohan Joseph and Krishnamurthy 1977; Subba Rangaiah, 1983 a; Oza, 1984), *G. crassa* (Shyam Sundar *et al.,* 1991), *G. verrucosa* (Jones, 1959; Oza and Krishnamurthy, 1968; Mohanty, 1982), *G. arcuata* var. *arcuata* (Kaliaperumal *et al.,* 1986), *G. textorii* (Subba Rangaiah, 1984), *G. edulis* (Rama Rao and Thomas, 1974), *G. foliifera* and *Gracilariopsis sjoestedtii* (Chennubhotla *et al.,* 1986). Unlike in the present study, there were no seasonal variations in the spore output in *Gracilariopsis sjoestedtii* (Subba Rangaiah, 1985a), *Gracilaria corticata* var. *cylindrica* (Kaliaperumal *et al.,* 1986), *G. corticata, G. edulis* and *Hypnea musciformis* (Shoba, 1985).

SEASONAL CHANGES IN DIURNAL PERIODICITY OF SPORE OUTPUT

Fukuhara (1957) in *Iridophycus cornucopiae*, Kaliaperumal *et. al.* (1986) in *Gracilaria arcuata* var *arcuata* and *G. corticata* var. *cylindrica,* Umamaheswara Rao and Kaliaperumal (1987) in *Pterocladia heteroplatos*, Chennubhotla *et. al.* (1986) in *Gracilaria foliifera* and *Gracilariopsis sjoestedtii,* Shoba (1985) in *Gracilaria corticata* , *G. edulis* and *Hypnea*

musciformis did not recognise any diurnal periodicity in spore shedding. Several workers have described well defined periodicity in the daily liberation of spores in members of Gelidiales (Suto, 1950 a and 1950 b; Katada *et al.,* 1953; Katada, 1955; Umamaheswara Rao, 1974; Umamaheswara Rao and Kaliaperumal, 1987) , Gigartinales (Matsui, 1969; Umamaheswara Rao, 1976; Umamaheswara Rao and Subba Rangaiah, 1981; Subba Rangaiah and Umamaheswara Rao, 1983; Subba Rangaiah, 1983 a; 1984 and 1985 a), Ceramiales (Subba Rangaiah, 1985 b; Sudhakar, 1992, Sudhakar and Subba Rangaiah, 1993 and 1997 a), Bangiales (Narasimha Rao and Subba Rangaiah, 1991), Cryptonemiales (Vanilla Kumari, 1997), other red algae (Dring, 1974; Ngan and Price, 1983), Dictyotales (Umamaheswara Rao and Reddy, 1982), Fucales (Umamaheswara Rao, 1990; Subba Rangaiah, 1992; Appa Rao, 1998) and Ulotrichales (Naidu, 1987).

A well defined diurnal periodicity with a peak liberation of spores at certain times of the day was found in *Gracilaria crassa* (Figs.5 and 6). In *Gelidium amansii* (Katada *et al.,* 1953 and Katada, 1955), *Hypnea musciformis* (Shoba, 1985) and *H. valentiae* (Subba Rangaiah,1978; Umamaheswara Rao and Subba Rangaiah, 1981), the time of peak shedding of carpospores was found to be 3 to 4 hours earlier than tetraspores. Similarly in present study on *Gracilaria crassa,* the peak output of carpospores was found 4 to 8 hours earlier than tetraspores. There was no difference in the time of peak shedding of carpospores and tetraspores in *Gelidium pusillum* and *Pterocladia heteroplatos* (Kaliaperumal and

Umamaheswara Rao, 1985 and 1986), *Gloiopeltis* spp. (Matsui, 1969), *Gracilaria corticata, G. textorii* and *Gracilariopsis sjoestedtiii* (Subba Rangaiah, 1978; Subba Rangaiah, 1983 a; 1984 and 1985 a). Ngan and Price (1983) also reported after studying 48 tropic benthic algae belonging to 25 genera, that for a particular taxon the pattern of spore discharge over a 24 hours period was essentially similar for carpospores and tetraspores. Similar trend was seen in *Grateloupia filicina* (Umamaheswara Rao, 1987), *Wrangelia argus, Centroceras clavulatum* and *Polysiphonia platycarpa* (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1993 and 1997 a), *Amphiroa fragilissima, Jania rubens* and *Grateloupia lithophila* (Vanilla Kumari, 1997; Subba Rangaiah and Vanilla Kumari, 1999).

The diurnal periodicity of carpospore shedding exhibited by *Gracilaria crassa* did not vary with the season of the year (Fig. 6). Such a diurnal periodicity in the liberation of spores was reported earlier in some members of Gigartinales (Subba Ranagaiah, 1983a; Subba Rangaiah and Umamaheswara Rao, 1983; Subba Rangaiah, 1984 and 1985 a), Ceramiales (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1993 and 1997 a) and Cryptonemiales (Vanilla Kumari, 1997). But the peak tetraspore liberation was seen four hours later (2AM to 6AM) during September to February than the time of peak shedding (10PM to 2PM) from March to August. Similar trend was also reported in *Gelidium amansii* (Katada *et al.,* 1953) *G. pusillum* (Umamaheswara Rao and Kaliaperumal, 1987), *Gelidiopsis variabilis* (Umamaheswara Rao and Kaliaperumal, 1987) and *Asparagopsis delilei* (Vasuki *et al.,* 1999).

Umamaheswara Rao and Subba Rangaiah (1981) also reported that the peak shedding of spores was delayed by 4,8 or 12 hours in *Gracilaria corticata* and *Hypnea valentiae*. The above studies provide evidence that seasonal variations in the diurnal periodicity are brought about by variations in seawater temperature in the field. Data collected on the monthly bottom seawater temperature in the intertidal and subtidal region at Thonithurai (Table 2) and the two periods of peak shedding of tetraspores observed during the one year period from April, 1998 to March, 1999 clearly show the influence of seawater temperature on the seasonal variation in the diurnal periodicity of tetraspore liberation in *Gracilaria crassa*. Peak liberation of tetraspores were seen between 10PM and 2AM from March to August when the seawater temperature was generally more than 30°C and 4 hours delay in the peak liberation was seen in this alga from September to February when the water temperature was mostly less than 30°C. These findings reveal that temperatures higher than 30°C hasten the liberation of spores and temperatures below 30°C delay the liberation of tetraspores in *Gracilaria crassa*.

The time of peak shedding of different kinds of spores varied in several algae studied (Table 4). The time of peak liberation of carpospores in *Gracilaria crassa* duing the present study coincides with the time of peak shedding of tetraspores in the agarophyte *Gelidium pusillum* (Umamaheswara Rao and Kaliaperumal, 1987) and eggs in the alginophyte, *Fucus vesiculosus* (Andersson *et al.*, 1994). The maximum tetraspore shedding in *Gracilaria crassa* from 2 to 6 AM during September to

Table - 4

Diurnal periodicity in spore output in marine algae

Type of spores	Algae	Locality	Authors
Time of peak shedding : 6 to 10 AM			
Swarmers	*Enteromorpha compressa*	Visakhapatnam	Naidu (1987)
Swarmers	*Ulva fasciata*	Visakhapatnam	Naidu (1987)
Tetraspores & carpospores	*Amphiroa fragilissima*	Visakhapatnam	Vanilla Kumari (1997)
Carpospores	*Asparagopsis delilei*	Mandapam	Vasuki *et al.* (1999)
Tetraspores	*Gelidiopsis variabilis (Apr.-Nov.)*	Visakhapatnam	Umamaheswara Rao & Kaliaperumal (1987)
Tetraspores & carpospores	*Jania rubens*	Visakhapatnam	Vanilla Kumari (1997)
Tetraspores	*Padina tetrastromatica*	Visakhapatnam	Umamaheswara Rao (1990); Appa Rao (1995)
Time of peak shedding : 10 AM to 2 PM			
Plurispores	*Ectocarpus mitchellae*	Visakhapatnam	Narasimha Rao & Subba Rangaiah (1991)
Carpospores	*Asparagopsis delilei*	Mandapam	Vasuki et al. (1999)
Monospores	*Bangiopsis subsimplex*	Visakhapatnam	Narasimha Rao & Subba Rangaiah (1991)
Monospores	*Porphyra vietnamensis*	Visakhapatnam	Narasimha Rao & Subba Rangaiah (1991)
Tetraspores	*Gelidiopsis variabilis (Dec.-Mar.)*	Visakhapatnam	Umamaheswara Rao & Kaliaperumal (1987)
Tetraspores & carpospores	*Grateloupia lithophila*	Visakhapatnam	Vanilla Kumari (1997)
Time of peak shedding : 2 to 6 PM			
Tetraspores & carpospores	*Polysiphonia platycarpa*	Visakhapatnam	Sudhakar & Subba Rangaiah (1997b)
Tetraspores	*Gelidiella acerosa*	Mandapam	Shoba (1985)
Tetraspores	*G. acerosa*	Mandapam	Umamaheswara Rao (1974)
Tetraspores & carpospores	*Gracilaria textorii*	Visakhapatnam	Subba Rangaiah (1984)
Tetraspores & carpospores	*Wrangelia argus*	Visakhapatnam	Sudhakar & Subba Rangaiah (1993)

Type of spores	Algae	Locality	Authors
Time of peak shedding : 6 and 10 PM			
Eggs	*Fucus vesiculosus*	Baltic sea	Andersson *et al.* 1994
Tetraspores	*Gelidium pusillum (Mar.-Nov.)*	Visakhapatnam	Umamaheswara Rao & Kaliaperumal (1987)
Time of peak shedding : 10 PM to 2 AM			
Tetraspores & monospores	*Aglaothamnion cordatum*	Visakhapatnam	Subba Rangaiah (1985b)
Tetraspores	*Gelidium pusillum (Dec.-Feb)*	Visakhapatnam	Umamaheswara Rao & Kaliaperumal (1987)
Tetraspores & carpospores	*Gracilaria corticata*	Mandapam	Umamaheswara Rao (1976)
Carpospores	*Hypnea valentiae*	Visakhapatnam	Subba Rangaiah & Umamaheswara Rao (1983)
Tetraspores	*Pterocladia heteroplatos*	Visakhapatnam	Umamaheswara Rao & Kaliaperumal (1987)
Time of peak shedding : 2 to 6 AM			
Oospores	*Sargassum ilicifolium*	Visakhapatnam	Appa Rao (1998)
Oospores	*S. vulgare*	Visakhapatnam	Appa Rao (1998)
Tetraspores & Carpospores	*Centroceras clavulatum*	Visakhapatnam	Sudhakar & Subba Rangaiah (1993)
Tetraspores & Carpospores	*Gracilaria corticata*	Visakhapatnam	Subba Rangaiah (1983a)
Tetraspores & Carpospores	*Gracilariopsis sjoestedtii*	Visakhapatnam	Subba Rangaiah (1985a)
Tetraspores	*Grateloupia filicina*	Visakhapatnam	Umamaheswara Rao (1987)
Tetraspores	*Hypnea valentiae*	Visakhapatnam	Subba Rangaiah & Umamaheswara Rao (1983)
Tetraspores	*Rosenvingea nhatrangensis*	Mandapam	Narasimha Rao (1995)

February can be compared favourably with the peak tetraspore release in *Gracilaria corticata* (Umamaheswara Rao and Subba Rangaiah, 1981; Subba Rangaiah, 1983 a), *Hypnea valentiae* (Subba Rangaiah and Umamaheswara Rao, 1983), *Gracilariopsis sjoestedtii* (Subba Rangaiah, 1985 a), *Grateloupia filicina* (Umamaheswara Rao, 1987) and *Centroceras clavulatum* (Sudhakar and Subba Rangaiah, 1993).

The periods of peak shedding of spores in the different algae give an idea that the spore liberation in the marine environment is a continuous process and one or the other algae may liberate spores throughout the day. Nature induces different species to select different timings for their peak liberation so that the spores liberated are evenly distributed for better settlement and germination (Vanilla Kumari, 1997; Subba Rangaiah and Sudhakar, 1999). It can be concluded that most algae prefer late night hours or morning hours for maximum spore liberation and the reason may be that lower temperature is conducive for maximum spore liberation.

EFFECTS OF ENVIRONMENTAL FACTORS ON SPORE SHEDDING

Exposure to air (desiccation), salinity, light, day length, wavelength of light and seawater temperature are considered as important factors controlling growth and reproduction of intertidal and subtidal algal populations. Detailed studies on these ecophysiological parameters have been made only on some littoral and sublittoral algae growing along the Indian shores. The information available on spore shedding indicates that the response to various environmental factors varies in different algae.

Much information is not available on the influence of these environmental factors on the algae, particularly the members of Fucales. The response of *Gracilaria crassa, Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides* to different environmental factors is discussed below.

Exposure to air and desiccation

The spore output declined when the fertile fronds of *Gracilaria crassa, Hypnea valentiae* and receptacles of *Sargassum wightii* and *Turbinaria conoides* were exposed to air and subjected to desiccation indicating that exposure of fruiting plants adversely affects spore liberation. Submerged condition is favorable for maximum spore release in these four algae (Figs.7 to 11). The same effect was described in some members of Gelidiales (Katada, 1955; Sreenivasa Rao, 1971; Umamaheswara Rao and Kaliaperumal, 1983), Gigartinales (Shoba, 1985; Umamaheswara Rao and Subba Rangaiah, 1986), Ceramiales (Subba Rangaiah, 1985 b; Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1993 and 1997 a) Bonnemaisoniales (Ganesan and Subba Rao, 1997) Bangiales (Narasimha Rao and Subba Rangaiah, 1991), Cryptonemiales (Vanilla Kumari, 1997), Ectocarpales (Narasimha Rao and Subba Rangaiah, 1991), Dictyotales (Umamaheswara Rao and Reddy 1982; Appa Rao, 1995; Ganesan *et al.,* 1999), Scytosiphonales (Narasimha Rao, 1989 a and 1989 c) Fucales (Andersson *et al.,* 1994; Umamaheswara Rao, 1990) and Ulotrichales (Naidu, 1987).

But according to Lüning (1980), Sheath and Cole (1980) and Henry and Cole (1982 a and 1982 b), the release of spores/ gametes in seaweeds is often induced by desiccating and then dehydrating the fertile thalli. Exposure to air and desiccation accelerated the emission of reproductive elements in *Gloiopeltis tenax* and *G. furcata* (Matsui, 1969), *Ceramium* spp. (Chamberlain and Evans, 1973), *Gracilaria verrucosa* and *Iridaea ciliata* (Infante and Candia, 1988), *Ascophyllum nodosum* (Baker, 1910), *Sargassum muticum* (Fletcher and Fletcher, 1975) and *Padina boergesenii* (Ganesan *et al.,* 1999).

The adverse effect of exposure was more distinct in the fertile thalli/receptacles of the four algae exposed in the sun than in the shade because of high temperature and low humidity (Figs.7, 10 & 11). These observations agree with the results obtained in *Gelidium amansii* (Katada, 1955), *Gelidiella acerosa* (Sreenivasa Rao, 1971), *Gracilaria corticata* and other Gigartinales members (Umamaheswara Rao, 1976; Subba Rangaiah, 1978; Umamaheswara Rao and Subba Rangaiah, 1986), *Gelidium pusillum, Pterocladia heteroplatos* and *Gelidiopsis variabilis* (Umamaheswara Rao and Kaliaperumal, 1983), Ceramiales (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1993), Bangiales (Narasimha Rao and Subba Rangaiah,1991), Cryptonemiales (Vanilla Kumari, 1997) and Ulotrichales (Naidu 1987).

The present study and earlier studies reveal that the duration of exposure of fertile thalli to air and desiccation, which affected spore production, varied in different algae. From all these studies it is clear that plants occurring in mid-littoral region like *Bangiopsis subsimplex, Porphyra vietnamensis, Ulva fasciata* and *Enteromorpha compressa* can withstand longer periods of desiccation than infralittoral and sublittoral species belonging to the orders Gelidiales, Cryptonemiales, Gigartinales, Ceramiales and Fucales. Members of Gigartinales and Fucales lie in between Gelidiales on one hand and Ulotrichales and Bangiales on the other hand.These variations are in agreement with the vertical distribution of different algal species along the Mandapam coast (Umamaheswara Rao, 1972 a).

In the present study, sporulation occurred only for fewer days in the algae exposed to sun, besides a sharp decline in spore liberation, than those exposed to air in shade. In *Turbinaria conoides*, the receptacles exposed to air in shade liberated oospore upto 90 minutes and upto 45 minutes in *Sargassum wightii.* This could be because of the rough texture of the receptacles of *Turbinaria conoides* when compared to that of *Sargassum wightii.* The differences in the nature of receptacles in *Turbinaria conoides* could explain the higher capacity for resisting desiccation (slower dehydration rate) when compared with *Sargassum wightii.*

Salinity

Salinity of the seawater influenced sporulation in the present study on *Gracilaria crassa, Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides* and spore output decreased markedly below 30‰ and above 40‰ in all these four algae. Compared to the brown algae, the red algae could tolerate wider ranges of salinity as both carpospores and tetraspores of *Hypnea valentiae* are released at 20 - 50‰ and tetraspores of *Gracilaria crassa* at 10 -50‰ . The red algae had peak liberation only at 30‰, while *Turbinaria conoides* had peak liberation at 40‰ and *Sargassum wightii* at 30‰ (Figs.12 - 14).

Similar observation in the peak release of reproductive elements between the salinity range of 30 - 40‰ were made in a number of red, brown and green algae by Yamasaki *et al.* (1957), White and Boney (1969), Mohsen *et al.* (1972), Subba Rangaiah *et al.* (1975), Subba Rangaiah (1978), Umamaheswara Rao and Reddy (1982), Umamaheswara Rao and Kaliaperumal (1983), Subba Rangaiah (1985 b and 1986), Shoba (1985), Naidu (1987), Narasimha Rao (1989a;1989b and 1989c) Umamaheswara Rao (1990), Narasimha Rao and Subba Rangaiah (1991), Narasimha Rao and Umamaheswara Rao (1991), Sudhakar (1992), Appa Rao (1995), Rabanal *et al.* (1997), Ganesan and Subba Rao, (1997), Vanilla Kumari (1997) and Ganesan *et al.* (1999). It is evident from all these studies that

salinity between 20 - 40‰ is optimum for peak spore discharge in the algae of tropical waters. In *Gloiopeltis tenax* and *G. furcata*, no significant variation was observed in the liberation of spores between 17 and 52‰ salinity (Matsui, 1969). In *Ascophyllum nodosum* and *Audoniella purpurea* reduced salinity favoured propagule discharge (Baker, 1910; West 1972).

The optimum salinity range observed in the present study for maximum shedding of spores in all four algae was 20 to 40‰. The optimum range of salinity found in the laboratory experiments is nearer to the annual range of 25 to 35‰ recorded in the inshore waters of Mandapam (Table 2). These findings indicate that salinity of the seawater along the Mandapam coast is suitable for liberation of maximum number of spores throughout the year from the algae growing in the intertidal and subtidal region.

Temperature

Studies on the effect of temperature on spore shedding were made on a number of marine algae by various workers. In all these investigations spore shedding was affected conspicuously at near low and very high temperatures tested and the optimum temperature range for shedding of spores varied in different algae. In the present study, spore out put was observed between 20 and 40°C in *Gracilaria crassa* and *Hypnea valentiae*

and from 20 to 30 °C in *Sargassum wightii* and *Turbinaria conoides*. The optimal temperature range observed for spore shedding in these four algae was 20 - 30°C (Figs.15 to 17). This can be favourably compared with the results obtained with *Gracilaria* spp. (Umamaheswara Rao and Subba Rangaiah, 1981; Friedlander and Dawes, 1984; Shoba 1985; Li Xiuliang and Li Meizhan, 1988 and 1989; Orduna Rojas and Robledo, 1999), *Hypnea* spp. (Subba Rangaiah, 1978; Umamaheswara Rao and Subba Rangaiah, 1981; Shoba, 1985), *Gracilariopsis bailinae* (Rabanal *et al.,* 1997), *Pterocladia heteroplatos, Gelidiopsis variabilis* (Umamaheswara Rao and Kaliaperumal, 1983) and brown algae *Dictyota dichotoma* (Umamaheswara Rao and Reddy, 1982), *Sargassum vulgare* and *S. ilicifolium* (Umamaheswara Rao, 1990).

In contrast to this, spore release occurred at low temperatures (3 to 25°C) in *Porphyra* spp. (Kurogi and Akiyama, 1966; Chen *et al.,* 1970), *Gloiopeltis tenax, G. furcata* (Matsui, 1969) and *Chorda* (Novaczek *et al.,* 1986) while at higher temperatures in *Bangia fuscopurpurea* (Sommerfeld and Nichols, 1973). The optimal temperature range found for maximum spore output in the laboratory experiments conducted coincided with the annual rate of water temperature (27 to 32.5°C) recorded in the field (Table2).

Light

While reviewing the information available on the effects of light period on the growth and reproductive processes, Dixon (1970) pointed out that there were no clear cut examples in red algae showing the influence of the amount of light energy received by plants on the formation and release of reproductive bodies. The changes observed in the present attempt clearly suggest that the amount of light energy (mean daily illuminance) received by the plants controls spore release.

In *Sargassum wightii* and *Hypnea valentiae*, spores were found under light intensities above 30 $\mu Em^{-2}s^{-1}$. In *Sargassum wightii*, there was no sporulation at 0 $\mu Em^{-2}s^{-1}$. Experiments conducted at different light intensities indicate that more number of spores were liberated in *Gracilaria crassa, Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides* at light intensities form 10 - 40 $\mu Em^{-2}s^{-1}$ (Figs.18 to 20). These observation agree with the results obtained on spore shedding in *Gracilaria foliifera* var. *angustissima* (Friedlander and Dawes, 1984), *G. corticata, G. edulis* (Shoba, 1985), *G. cornea* (Orduna Rojas and Robledo, 1999), *Hypnea valentiae* (Umamaheswara Rao and Subba Rangaiah, 1986), *H. musciformis* (Shoba, 1985), other Gigartinales members *Gracilariopsis bailinae* (Rabanal *et al.,* 1997), other red algae *Gelidiella acerosa* (Shoba, 1985), *Gelidium pusillum, Pterocladia heteroplatos, Gelidiopsis variabilis* (Umamaheswara

Rao and Kaliaperumal, 1983), Acrochaetium endophyticum (White and Boney, 1969), *Aglaothamnion cordatum* (Subba Rangaiah, 1985 b), *Porphyra vietnamensis, Bangiopsis subsimplex* (Narasimha Rao and Subba Rangaiah, 1991), *Wrangelia argus* and *Polysiphonia platycarpa* (Sudhakar, 1992; Sudhakar and Subba Rangaiah, 1997 a), *Porphyra rosengurtii* (Kapraun and Luster, 1980), *Jania rubens, Amphiroa fragilissima* and *Grateloupia lithophila* (Vanilla Kumari, 1997), brown algae *Ectocarpus mitchellae* (Narasimha Rao and Subba Rangaiah, 1991), *Dictyota dichotoma* (Umamaheswara Rao and Reddy, 1982), *Padina tetrastromatica* (Umamaheswara Rao, 1990; Appa Rao, 1995), *Padina boergesenii* (Ganesan *et al.,* 1999), *Sargassum ilicifolium* and *S. vulgare* (Umamaheswara Rao 1990) and green algae *Ulva fasciata* and *Enteromorpha compressa* (Naidu, 1987).

The response in the liberation of spores at various light intensities for *Gracilaria crassa, Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides* is different from *Gracilaria corticata, G. textorii, Gracilariopsis sjoestedtii* (Subba Rangaiah, 1978) and *Centroceras clavulatum* (Sudhakar, 1992) in which peak discharge of spores was observed in complete darkness. On the other hand, spore formation occurred at higher light intensities of 10,000 - 30,000 lux in *Monostroma nitidum* (Ohno and Nozawa, 1972) and higher light intensities enhanced spore liberation in *Porphyra umbilicalis* (Kurogi and Sato, 1967) and *P. suborbiculata* (Iwasaki and Sasaki, 1972).

Inhibition of spore emission was seen in *Monostroma nitidum* (Ohno, 1972) at 10,000 and 20,000 lux. In the present study also at high light intensities of above 30 $\mu Em^{-2}s^{-1}$ though spores were found in the fertile thalli of *Hypnea valentiae* and receptacles of *Sargassum wightii*, spore emission did not occur.

The light intensity had a varying effect on the liberation of spores in the four red algae studied during the present investigation. In *Gracilaria crassa* and *Turbinaria conoides* spore discharge was found from 0 - 100 $\mu Em^{-2}s^{-1}$ whereas in *Hypnea valentiae* and *Sargassum wightii* from 0-30 $\mu Em^{-2}s^{-1}$. This may be due to the tough and rigid condition of the thallus / receptacles of *Gracilaria crassa* and *Turbinaria conoides* when compared to the delicate nature of thallus / receptacle of *Hypnea valentiae* and *Sargassum wightii*.

Photoperiod

Some information is available on the effect of photoperiod in the release of reproductive elements in a number of marine algae. In the present study, peak shedding of spores was found under long day conditions at 20 $\mu Em^{-2}s^{-1}$ light intensity in the experiments conducted with *Gracilaria crassa, Hypnea valentiae, Sargassum wightii and Turbinaria conoides* (Figs.21 to 23). Similar trend in the release of reproductive elements under

long day conditions was observed in *Gracilaria corticata, G. edulis, Hypnea musciformis* (Shoba, 1985), *Gracilariopsis bailinae* (Rabanal *et al.,* 1997), *Porphyra umbilicalis* (Kurogi and Sato, 1962), *Porphyra spp.* (Dawes, 1981), *Gelidiella acerosa* (Sreenivasa Rao , 1971; Umamaheswara Rao, 1974; Shoba 1985), *Gelidium pusillum, Pterocladia heteroplatos, Gelidiopsis variabilis* (Umamaheswara Rao and Kaliaperumal, 1983), *Jania rubens, Amphiroa fragilissima, Grateloupia lithophila* (Vanilla Kumari, 1997) *Acrochaetium endophyticum* (White and Boney, 1969), *Bangia fuscopurpurea* (Sommerfeld and Nichols, 1973), *Wrangelia argus* and *Polysiphonia platycarpa* (Sudhakar 1992; Sudhakar and Subba Rangaiah, 1997a), *Padina tetrastromatica* (Appa Rao, 1995), *Sargassum muticum* (Norton, 1981), *Monostroma nitidum* (Ohno, 1972) *Ulva fasciata* and *Enteromorpha compressa* (Naidu, 1987).

In contrast to this, peak shedding of spores was found under short day conditions in *Gracilaria corticata* (Umamaheswara Rao, 1976), *Gigartina acicularis* (Guiry, 1984), *Porphyra tenera* (Iwasaki, 1961), *P.suborbiculata* (Iwasaki and Sasaki, 1972), *P. abottae, P. perforata* (Waaland and Duckson, 1983) and *Porphyra spp.* (Kurogi and Sato, 1962; Dawes, 1981), *Falkenbergia rufalanosa* (Oza, 1977), *Aglaothamnion cordatum* (Subba Rangaiah, 1985 b), and *Padina boergesenii* (Ganesan *et al.,* 1999) and in complete darkness in *Gracilaria corticata, G. textorii, Hypnea valentiae* and *Gracilariopsis sjoestedtii* (Subba Rangaiah, 1978; Umamaheswara Rao and Subbarangaiah, 1986) and *Centroceras clavulatum* (Sudhakar, 1992).

The interacting effects of light intensity and photoperiod clearly show that the amount of energy received by plants influences spore release which is due to photosynthetic effect as described by Dixon and Richardson (1970). Murray and Dixon (1973) observed similar photosynthetic effect in the division of apical cells in *Plenosporium squarrulosum*. The results obtained in the present and earlier studies on the combining effect of light intensity and day length or photoperiod clearly indicate that the Mean Daily Illuminance (Light Intensity x Day length in hours per day) is an important factor in growth and reproduction.

SPORE STUDIES

Studies were made by several workers on the shape and size of spores in some marine algae. The shape and size of spores varied in the four algae studied during the present investigation. In *Gracilaria crassa* and *Hypnea valentiae*, the shape of tetraspores and carpospores was spherical and their size was 18 and 29 µm in diameter respectively. These observations almost agree with the shape and size of the spores recorded in *Gracilaria crassa* (Shyam Sunder *et al.*, 1991), *G. verrucosa* (Oza and Krishnamurthy, 1967), *G. corticata* (Mohan Joseph and Krishnamurthy, 1977; Oza, 1976), *Hypnea cervicornis, H.cordacea* (Mshigeni, 1976 a), *H.musciformis* (Mshigeni and Lorri, 1977) and *H. valentiae* (Subba Rangaiah, 1988). In both the species of *Sargassum wightii* and *Turbinaria*

conoides oospores were ovoid in shape. But the size of oospores in *Sargassum wightii* was bigger (174 - 232µm long and 131 - 160 µm broad) than the oospores in *Turbinaria conoides* (160 - 189 µm long and 116 - 145 µm broad). The shape and size of the oospores observed in *Sargassum wightii* and *Turbinaria conoides* resemble that of *S. swartzii* (Chauhan and Krishnamurthy, 1967) and also larger than that of *Cystoseira sp.* (Krishnamurthy and Mairh, 1967) and *Cutleria multifida* (Yamanouchi, 1912).

The present study reveals that the intertidal and subtidal algae experience a variety of potentially stressful environmental conditions which include exposure to air and desiccation, high and low light and temperature, osmotic stress etc. and the role of these environmental factors in the ecology and physiology of marine algae.

From the above studies on different environmental factors, it can be concluded that the submerged condition of the algae, light intensity of 10-40 $\mu Em^{-2}s^{-1}$, salinity around normal seawater 20-40‰ and water temperatures of 20-30°C are favourable for obtaining maximum sporulation in *Gracilaria crassa, Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides.* These experimental findings agree with the environmental conditions prevailing in the nearshore areas of the Mandapam coast.

Summary

SUMMARY

Studies on sporulation were made for a period of 2¼ years from October, 1997 to December, 1999 in two red algae viz. *Gracilaria crassa* and *Hypnea valentiae* and two brown algae viz. *Sargassum wightii* and *Turbinaria conoides* growing at Mandapam coast. The healthy tetrasporic and cystocapric plants of *Gracilaria crassa* and *Hypnea valentiae* and reproductive plants of *Sargassum wightii* and *Turbinaria conoides* with well developed receptacles were collected at fortnightly intervals and experiments were conducted in the laboratory to know the fruiting behaviour and the spore producing capacities of these four algae.

Seasonal and diurnal changes in tetraspore and carpospore shedding in *Gracilaria crassa* were studied. The effects of environmental factors such as exposure to air and desiccation, salinity, temperature, light intensity and photoperiod on tetraspore shedding in *Gracilaria crassa,* tetraspore and carpospore shedding in *Hypnea valentiae* and oospore shedding in *Sargassum wightii* and *Turbinaria conoides* were studied under laboratory conditions in detail. The results obtained on these aspects together with the data collected on the shapes and sizes of spores, hydrological and environmental parameters from the collection locality are presented in this thesis.

Tetrasporic and cystocarpic plants of Gracilaria *crassa* occurred throughout the year with maximum number during August - October and March - June respectively. Reproductive plants of *Sargassum wightii* and *Turbinaria conoides* occurred during October to February with more number of plants having receptacles in December and January.

Tetraspore and carpospore output were estimated in *Gracilaria crassa*. Spore shedding was found in all months of the year. Maximum shedding of tetraspores and carpospores was seen on the first day and the spore output decreased rapidly from the second day onwards. There was no periodicity in the liberation of tetraspores and carpospores during the observations made for 5 days. The spore output in the tetrasporophytes and carposporophytes varied seasonally with peak shedding of spores during the periods from July / August to October and February to March. The quantity of tetraspores and carpospores liberated varied form 1,205 to 40,746 and 11,047 to 87,754 spores / g fr.wt. respectively on the first day.

Diurnal periodicity with peak liberation of tetraspores during night hours was observed in *Gracilaria crassa*. In the diurnal experiments conducted under laboratory conditions, maximum shedding of tetraspores was found during the period 10 PM to 2 AM from March to August and 2 AM to 6 AM from September to February. The maximum carpospore output

was seen during early night hours i.e. between 6 PM and 10 PM in most of the months i.e. from August to December and February to May. The peak output of carpospores was found 4-8 hours earlier than tetraspore shedding.

Effects of environmental factors were studied on the spore shedding in *Gracilaria crassa, Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides*. Spore shedding decreased with increase in the duration of exposure to air in shade and sun and maximum quantity of all types of spores were liberated from the fruiting thalli / receptacles under submerged condition. The spore shedding also varied in the different salinities tested and the optimum range observed for more quantity of spores liberation was 20-40‰. Peak output of tetraspores in *Gracilaria crassa* and tetraspores and carpospores in *Hypnea valentiae* was recorded at 30‰. Maximum oospore shedding was seen at 30‰ and 40‰ in *Sargassum wightii* and *Turbinaria conoides* respectively.

The effect of different temperatures on spore liberation was also quite evident. *Gracilaria crassa* liberated maximum number of tetraspores at 25°C. In *Hypnea valentiae* maximum shedding of tetraspores was seen at 25-30°C and carpospores at 20-30°C. Maximum oospore output was recorded at 30° and 25°C in *Sargassum wightii* and *Turbinaria conoides* respectively.

In the experiments conducted with different light intensities, spore shedding declined in high light intensities and peak spore output was observed in low light intensities. Peak discharge of tetraspores in *Gracilaria crassa* and tetraspore and carpospore shedding in *Hypnea valentiae* was found at 20 $\mu Em^{-2}s^{-1}$ light intensity. Maximum oospore output was seen in *Sargassum wightii* at 20 $\mu Em^{-2}s^{-1}$ and at 10-20 $\mu Em^{-2}s^{-1}$ in *Turbinaria conoides*.

Peak spore output was recorded in long day condition at 20 $\mu Em^{-2}s^{-1}$ light intensity in all the four algae studied. Maximum shedding of tetraspores in *Gracilaria crassa* was seen at 12:12 LD cycle. In *Hypnea valentiae*, maximum tetraspore ouput was observed at 16:8 LD cycle and carpospore output at 16:8 and 24:0 LD cycle. In *Sargassum wightii*, maximum oospore shedding was found at 16:8 LD cycle and above and in *Turbinaria conoides* at 12:12 LD cycle and above. The shape and size of the different kinds of spores in the above four algae were also studied. In both *Gracilaria crassa* and *Hypnea valentiae*, the tetraspores and carpospores were spherical in shape and 18 and 29 µm in diameter respectively. *Sargassum wightii* produced ovoid oospores and they were 174-232 µm long and 131 - 160 µm broad. The oospores of *Turbinaria conoides* were also ovoid in shape and measured 160-189 µm length and 131-145 µm breadth.

Data on the hydrological parameters from the study area were also collected. During the period of this investigation, the atmospheric temperature varied from 28.0°C to 32.6°C, the bottom seawater temperature from 27°C to 32.5°C, salinity from 25‰ to 35‰ and underwater light intensity from 2 $\mu Em^{-2}s^{-1}$ to 408 $\mu Em^{-2}s^{-1}$

The present study reveals that submerged condition of the algae, light intensity of 10-40 $\mu Em^{-2}s^{-1}$, long day condition at low illuminance (20 $\mu Em^{-2}s^{-1}$), salinities around normal seawater (20-40‰) and water temperature of 20-30°C are favourable for obtaining maximum quantity of spores in the four algae, *Gracilaria crassa*, *Hypnea valentiae, Sargassum wightii* and *Turbinaria conoides* and for taking up large scale cultivation of these commercially important seaweeds by spore culture method. These experimental findings closely agree with the hydrological and environmental conditions existing in the intertidal and subtidal region of Mandapam coast.

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