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A review of the life history, reproduction and phenology of *Gracilaria*

Joanna M. Kain (Jones)[1,*] & Christophe Destombe[2]
[1] *Port Erin Marine Laboratory (University of Liverpool), Port Erin, Isle of Man, IM9 6JA, UK*
[2] *Laboratoire de Génétique et Evolution des Populations Végétales, URA CNRS 1185, GDR 'Algues' 1002, Bât SN2, Université des Sciences et Technologies de Lille, F-59655 Villeneuve d'Ascq Cedex, France*
*(*Author for correspondence)*

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Abstract

The basic life history of the red alga *Gracilaria* is of the three-phase *Polysiphonia* type but a number of species show deviations. Plants can bear both gametangia and tetrasporangia, either on separate parts of the thallus or on the same. Explanations include the *in situ* germination of tetraspores (allowing gametophytic thalli to be epiphytic on tetrasporophytes), the coalescence of spores or developing discs (resulting in chimaeras), mitotic recombination during cell division in the mature diploid thallus (resulting in patches of diploid male and female cells on the tetrasporophyte), a mutation eliminating the repression of female expression allowing haploid male plants to be bisexual and initial failure of cell walls to form during the development of tetraspores. Polyploids can be produced from plants with diploid gametangia. The sexes and phases are usually morphologically identical but gametophytes or their parts may be smaller. The growth rates of the sexes may differ and diploid juveniles may survive better than haploid. Neither polyploidy nor hybridization results in superior growth. The sex ratio is probably 1:1 but females may appear to be more abundant. Diploid and haploid phases are usually either about equal or diploids predominate, often depending on the type of substratum. At high latitudes reproduction peaks in late summer whereas in the tropics it may be high all year. In temperate regions growth rate is fastest and biomass highest in late summer; in the tropics peak biomass is mainly in the winter. Spermatia are effective for only a few h. Spores vary in size around 25 μm, diploid ones usually being larger. Cystocarps or tetrasporangia in the field may not currently be releasing spores. In the laboratory spore release shows a diurnal rhythm, peaking during the night or day according to the species. All the above attributes are potentially important in planning and executing *Gracilaria* cultivation.

Introduction

Species of *Gracilaria* are some of the most useful algae in the world, combining the production of the valuable polysaccharide agar with a fast growth rate, ease of vegetative reproduction and other attributes favouring their cultivation. When planning to farm these red algae in new areas such as Europe, it is essential to be aware of the biology of the species considered.

For optimal exploitation of a crop species, efficient seeding, a fast growth rate and genetic improvement are of prime importance to the farmer. Growth rate can be affected by the life history phase and by the season while genetic improvement and seeding from spores can be achieved only if the methods of reproduction are properly understood. This review aims to cover these important aspects of the biology of the genus which are pertinent to cultivation.

Most of the species considered here belong to *Gracilaria* itself but information on the morphologically similar *Gracilariopsis*, only recently separated from *Gracilaria* (Fredericq & Hommersand, 1989), is also included. Other free-living members of the Gracilariaceae (see Bird, 1995), although closer to *Gracilaria* taxonomically (Bird *et al.*, 1994) are not farmed commercially.

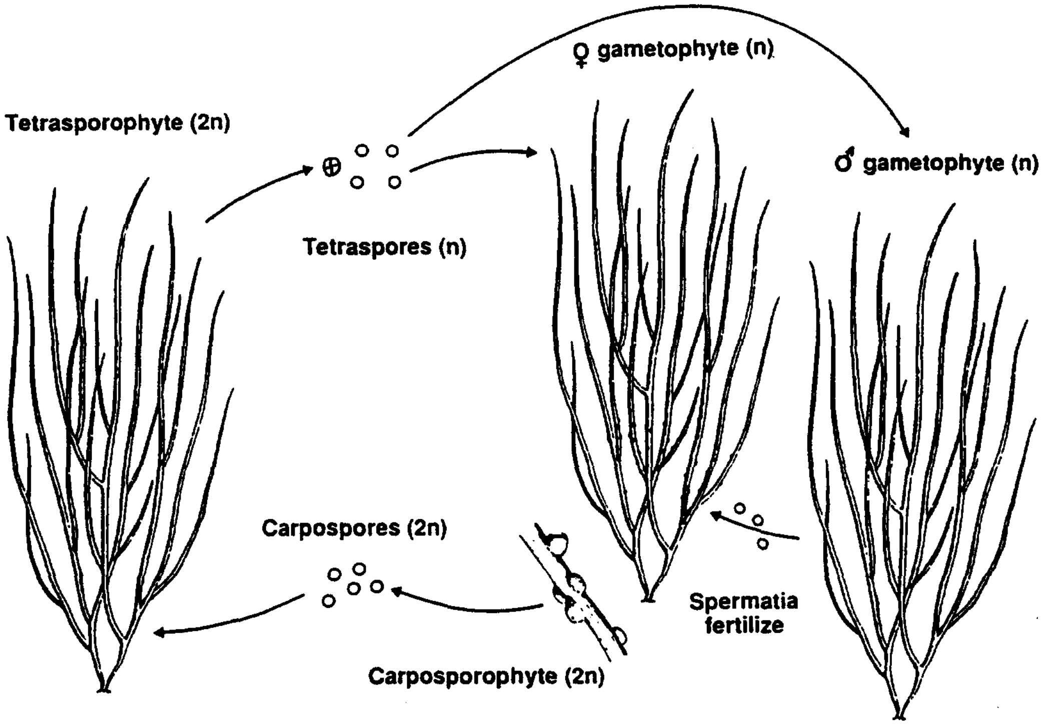

Fig. 1. The life history of *Gracilaria*. Reproduced from Kain (1991) by permission of John Wiley & Sons.

The nomenclature follows Bird and Kain (1995). The subject has been recently reviewed by Oliviera & Plastino (1994).

Life history

In most populations of *Gracilaria* the life history is of the *Polysiphonia* type, i.e. having morphologically identical diploid tetrasporophyte and haploid gametophyte phases, the latter consisting of equal numbers of male and female plants (Fig. 1). The female gamete is fertilized *in situ* and the zygote develops as a third phase, the diploid carposporophyte, a spore-producing structure entirely dependent on the female gametophyte. The resulting carpospores, the product of a single fusion of gametes, are numerous and genetically identical. Each spore can develop into a diploid tetrasporophyte in which reproduction involves meiosis, resulting in haploid genetically variable tetraspores. This life history has been completed in culture, taking 5–12 months, in several *Gracilaria* species: *G. gracilis* (as *G. verrucosa*) (Ogata *et al.*, 1972; Rueness *et al.*, 1987), *G. tikvahiae* (as *Gracilaria* sp.) (N Bird *et al.*, 1977), *G. multipartita* (as *G. foliifera*) (McLachlan & Edelstein, 1977) *G. debilis* (Oliveira & Plastino, 1984), *G. chilensis* (Bird *et al.*, 1986; Plastino & Oliveira, 1988) and a *Gracilariopsis* species (as *Gracilaria verrucosa*) (Bird *et al.*, 1982). From these *in vitro* demonstrations one would expect only male and female gametophytic and tetrasporophytic individuals in natural populations but in many cases in nature this is not so, indicating variations to this clear-cut sequence.

In some cases small gametophytic thalli develop as epiphytes on parental tetrasporophytes of *G. tikvahiae* (as *Gracilaria* sp.) (CJ Bird *et al.*, 1977), *G. debilis* and *Gracilaria* sp. in Brazil (Oliveira & Plastino, 1984) and *G. gracilis* (as *G. verrucosa*) in northern France (Destombe *et al.*, 1989). In other cases male and/or female organs occur on the same thallus with or without tetrasporangia: in *G. gracilis* (as *G. verrucosa*) in France (Cabioch, 1972; Destombe *et al.*, 1989; Kling, 1978; Oliveira, 1968) and India (Oza *et al.*, 1989; Umamaheswara Rao, 1972) and in *G. blodgettii* and *G. chouae* (as *G. bursa-pastoris*) in Japan (Ohmi, 1958). Similar observations have been made on *G. chilensis* in culture (Plastino & Oliveira, 1988; Prieto *et al.*, 1991). Also in culture, tetrasporic thalli have apparently changed to males and females (Candia, 1991).

Two groups of possible explanations for deviations from the straightforward life history have been proposed: (1) mechanical and (2) genetical or cytological. The first mechanical explanation is that tetraspores germinate *in situ*, allowing the development of male gametangia on a diploid thallus (Cabioch, 1972) or causing the epiphytic gametophytes mentioned above (CJ Bird *et al.*, 1977; Oliveira & Plastino, 1984; Destombe *et al.*, 1989). The second mechanical possibility is that basal discs arising from spores which germinate close to each other may coalesce and apparently become one plant (a chimaera). This has been recorded in *G. gracilis* (as *G. verrucosa*) (Jones, 1956), a Chinese species (Ren & Chen, 1986), *G. tikvahiae* and *G. chilensis* (Maggs & Cheney, 1990; Muñoz & Santelices, 1994). Sporelings of the last two species even coalesced with each other (Maggs & Cheney, 1990). Thirdly, during their development, cystocarps close to each other may fuse and the resulting single cystocarp will contain carpospores that are not genetically identical. However, this event, shown in *G. chilensis*, is fairly rare (3%) (Santelices & Varela, 1993).

Three genetical explanations are all based on *in vitro* experiments and may not be pertinent to field populations. They do, however, show what is possible in the genus and may be helpful in understanding and planning crops. Firstly, in the well studied *G. tikvahiae* (as *Gracilaria* sp.) of the northwest Atlantic, tetrasporophytes sometimes produce functional diploid male (van der Meer & Todd, 1977) and female (van der Meer, 1981) gametes which, when appropriately mated, can produce polyploids. The mechanism for this was shown (van der Meer & Todd, 1977) to be mitotic recombination, a switching of parts of chromosomes during normal nuclear division, allowing a heterozygous condition to become homozygous for mating type in resulting cells and their progeny. Sporophytes must normally have both male and female alleles (thus being heterozygous) but when either are doubled they become effective in determining sexual reproduction. Patches of such cells resulting from localized cell division are responsible for gamete production on the diploid plant. This phenomenon probably explains one of the types of abnormal individuals of *G. gracilis* (as *G. verrucosa*) of the northeast Atlantic in which tetrasporophytes bear male and female gametes (Destombe *et al.*, 1989).

Secondly, another variation in *G. tikvahiae* is the result of a naturally occurring mutation, probably at a locus where female expression is repressed in males. This allows carpogonia to be formed on male plants which are therefore bisexual (van der Meer, 1986; van der Meer *et al.*, 1984). Self-fertilization in such plants produces carpospores developing into diploid bisexual individuals. This life history anomaly again allows the production of polyploids.

Finally, in the same species, it has been observed that in tetrasporangia, in which meiosis normally occurs, the formation of cross-walls is not always complete, resulting in spores of unequal size (van der Meer, 1977). These spores may be medium-sized and presumably binucleate, or large and presumably quadrinucleate, as well as small and uninucleate. There is thus an absence of cytokinesis (separation of cytoplasm). During sporeling development extra walls are created so that all cells are uninucleate but the basal disc so formed from medium or large spores is a mosaic or chimaera, composed of patches of tissue of different genetic and sexual makeup. From such a disc male and female fronds usually arise separately but branches on one frond may be mixed (van der Meer, 1977).

An aberration not easy to explain occurs in the Indian Ocean. In India and Sri Lanka only cystocarpic and vegetative plants of *G. edulis* could be found (Jayasuriya, 1993; Krishnamurthy *et al.*, 1969) and carpospores gave rise to plants which again bore cystocarps (Krishnamurthy *et al.*, 1969; Jayasuriya, pers. comm.).

There is evidence for intrinsic differences between 'strains' which might be assumed to be genotypically identical because they came from the same plant or developed from carpospores from the same cystocarp (Lignell & Pedersén, 1989; Santelices & Varela, 1993). This topic is discussed in the present volume by Santelices *et al.* (1995).

Considerable attention has been given to the genetics of *Gracilaria* and to the possibility of developing fast growing strains. These aspects have been reviewed by Patwary & van der Meer (1992).

Sexes and phases

In most cases the two sexes of gametophyte and the tetrasporophyte are morphologically identical and of the same size, e.g. *G. domingensis* (Pinheiro-Joventino & Bezerra, 1980). In some cases however, male plants have been reported to be smaller, e.g. (*G. gracilis*) (as *G. confervoides*) in South Africa (Isaac, 1956), India (Durairatnam, 1965) and France (Destombe, 1987) or, in the case of *G. chilensis* (as *G. sordida*), it can be deduced from the data presented that they were smaller (Nelson, 1989). A more subtle difference between the phases is shown by *G. gracilis* (as *G. verrucosa*) in France where, although the number of upright thalli per plant is similar, the holdfasts of female plants are smaller than those of the other phases, resulting in their bearing a higher density of upright thalli (Destombe, 1987).

Even when the sexes and phases look identical it is possible that there are physiological differences between them. An important attribute is growth rate and some differences have been reported. In *Gracilariopsis lemaneiformis* (as *Gracilaria sjoestedtii*) from China, females grew much faster than the other two free phases when grown in separate culture vessels (Zhang & van der Meer, 1988a). This was attributed to the fact that, because the plants were isolated from males, carposporophytes failed to appear and growth remained mainly vegetative, whereas in males and tetrasporophytes reproduction was followed by senescence. In a field population of *G. gracilis* (as *G. verrucosa*) in France, growth in male plants decreased less after reproduction than in females and tetrasporophytes (Destombe, 1987). In two species from Hawaii, *G. parvispora* (as *G. bursapastoris*) and *G. coronopifolia*, the relative growth rate of female plants was lower than that of either males or tetrasporophytes (Hoyle, 1978). Survival and development of haploid and diploid juvenile individuals of *G. gracilis* (as *G. verrucosa*) under different artificial conditions have been shown to be different (Destombe *et al.*, 1993). Such differences could help to explain phase imbalances in populations.

Polyploidy in *G. tikvahiae* is of no advantage in growth which is no faster and may actually be inhibited by the extra set(s) of chromosomes (Patwary & van der Meer, 1984; Zhang & van der Meer, 1988b). Nor has hybrid vigour (heterosis) been detected in this species; crosses between inbred clones grew no faster than their parents (Zhang & van der Meer, 1987). On the other hand mutations may influence growth; several mutant clones have been shown to grow faster than the wild type (Patwary & van der Meer, 1983) though some colour mutants grow more slowly (van der Meer, 1979).

The chemical constituents of *Gracilaria* plants may be influenced by the sex or phase. In *G. chilensis* (as *G. sordida*) in New Zealand the gel strength of agar in male plants was weaker than from the other two but the actual agar content was similar in the three (Pickering *et al.*, 1990). The mean agar content of tetrasporophytes of wild *G. gracilis* (as *G. verrucosa*) in France was higher than that of gametophytes but this situation was reversed, for females, after one month of cultivation (Destombe, 1987). It was suggested that, in *G. chilensis* (as *G. verrucosa*), the agar yield was higher and the gel strength lower in cystocarpic than tetrasporic plants (Kim & Henríques, 1979). Differences in agar viscosity and gel strength were claimed for *G. pacifica* (as *G. verrucosa*-type) in British Columbia (Whyte *et al.*, 1981) but in the absence of consistency and an indication of variation these are doubtful. No differences between females and tetrasporophytes in any constituents, including agar content, were found in *G. tikvahiae* (Penniman & Mathieson, 1987).

The presumed method of genetic control of sex in *Gracilaria*, mentioned above (van der Meer & Todd, 1977), should prescribe males and females in a 1:1 ratio. Proportions of sexes can only be determined precisely when all the plants are fertile simultaneously, which is rarely the case. When many of the plants are vegetative it is necessary to sample the population all through the fertile seasons because the sexes may be apparent at different times. The best method of determining sex ratios is to map individuals and follow them through the year (Destombe *et al.*, 1989). Male plants may be expected to be under-represented because they are less obvious than spore-producing plants, partly because they may be smaller and partly because spermatangia are not easy to see. The relationships of the sexes in populations observed over the seasons are represented in Table 1; only in three was there a clear 1:1 ratio. In the vast majority of populations fewer males than females were observed but there were non-reproductive plants which could have contained enough spent or otherwise unrecognized males to bring their number up to that of the females. This was not the case in the Brazilian population of *G. domingensis* and no males were observed in *G. arcuata* and *G. corticata* in India. In *G. coronopifolia* in Hawaii there were more males than females. These observations are unexplained.

Natural populations of *Gracilaria* may not contain gametophytes and tetrasporophytes in equal proportions. Assessing the ratio is subject to the same constraints as with the sexes but, in the absence of evidence to the contrary, it will be assumed that carpospores and tetraspores, even when seasonal, are borne for similar periods of time (Destombe *et al.*, 1989). If haploids and diploids are equal and the sex ratio is 1:1, the num-

Table 1. The relative abundance of males in relation to females in populations of *Gracilaria* at various latitudes. O, no males; F, very few males; F, fewer males than females but the balance could be contained in the apparently vegetative plants; =, sex ratio of 1:1, M, more males than females.

Species	Country	Lat	O	F	F'	=	M	Reference
G. domingensis	Brazil	3°S			+			Pinheiro-Joventino & Benzerra 1980
G. edulis	India	9°N			+			Umamaheswara Rao 1973
G. foliifera	India	9°N			+			" " "
G. corticata	India	9°N			+			Umamaheswara Rao 1975
G. arcuata	India	9°N	+					Kaliaperumal *et al.* 1986
G. corticata	India	9°N	+					Kaliaperumal *et al.* 1986
G. corticata	India	9°N	+					Krishnamurthy *et al.* 1969
G. sp # 1	Panama	9°N			+			Hay & Norris 1984
G. sp # 2	Panama	9°N			+			Hay & Norris 1984
G. sp # 3	Panama	9°N			+			Hay & Norris 1984
G. domingensis	Panama	9°N			+			Hay & Norris 1984
G. cuneata	Panama	9°N			+			Hay & Norris 1984
G. changii	Thailand	12°N			+			Chirapart *et al.* 1992
G. gracilis (as *G. verrucosa*)	Philippines	15°N			+			Trono & Azanza-Corrales 1981
G. coronopifolia	Hawaii	21°N					+	Hoyle 1978
G. parvispora (as *G. bursapastoris*)	Hawaii	21°N				+		Hoyle 1978
G. gracilis (as *G. verrucosa*)	India	22°N			+			Oza *et al.* 1989
G. pacifica	Mexico	32°N			+			Aguilar Rosas *et al.* 1993
G. chilensis	Chile	37°S	+					Candia 1988
G. chilensis (as *G. sordida*)	New Zealand	41°S				+		Nelson 1989
G. gracilis (as *G. verrucosa*)	Argentina	43°S			+			Boraso de Zaixso 1990
G. tikvahiae	NH, USA	43°N			+			Penniman *et al.* 1986
G. chilensis (as *G. sordida*)	New Zealand	46°S			+			Pickering *et al.* 1990
G. pacifica (as *G. verrucosa*-type)	BC, Canada	49°N			+			Whyte *et al.* 1981
G. gracilis (as *G. verrucosa*)	France	51°N				+		Destombe *et al.* 1989

ber of tetrasporangia-bearing plants (0.50) should be double that of cystocarpic plants (0.25). If, in a population, there is a significant departure from this ratio (2:1) throughout the year then the two phases are not equal. This interpretation has been used on the data concerning the populations in Table 2. In two-thirds of these the phases are either about equal or tetrasporophytes predominate. Variations in the frequencies of haploid and diploid individuals in populations are due to differences in their fertility and survivorship (De Wreede & Klinger, 1988; Santelices, 1990; Richerd *et al.*, 1993a). If equal numbers of spores of each generation survive then gametophytes should slightly predominate (Destombe *et al.*, 1989; Kain & Bates, 1993) because in haploids only females produce spores, resulting in what has been termed the 'cost of males' (Maynard Smith, 1978). The predominance of tetrasporophytes in *Gracilaria* seems to indicate that there is something in this genus that makes the diploid phase fitter. This fitness has been demonstrated at the juvenile stage in *G. gracilis* (as *G. verrucosa*) in France where diploids had twice the survival rate of haploids (Destombe *et al.*, 1989). Two extremes, however, demonstrate the difficulty in predicting this phase balance. Firstly *G. pacifica* was found with a predominance of gametophytes in one site and an absence of them in another about 6 km away in Mexico. Secondly *G. edulis* was composed of only gametophytes in Sri Lanka and virtually only tetrasporophytes just across the Gulf of Mannar in India. In both these cases the habitats were very different; the local conditions are clearly of greater importance than species or latitude in determining which phase survives better. One interpretation of the effect of habitat is that the substratum is important in determining the type of reproduction (Aguilar Rosas *et al.*, 1993). When plants are growing on a soft bottom development from spores is unlikely and reproduction is vegetative, favouring a single phase.

Table 2. The relative abundance of haploid and diploid phases in populations of *Gracilaria* at various latitudes. G, all gametophytes; g, more gametophytes than tetrasporophytes; =, no significant difference between gametophytes and tetrasporophytes; t, more tetrasporophytes than gametophytes; T, all tetrasporophytes.

Species	Country	Lat	G	g	=	t	T	Reference
G. domingensis	Brazil	3° S				+		Pinheiro-Joventino & Bezerra 1980
G. edulis	Sri Lanka	8° N	+					Jayasuriya 1993
G. edulis	India	9° N					+	Umamaheswara Rao 1973
G. foliifera	India	9° N				+		" " "
G. corticata	India	9° N				+		Umamaheswara Rao 1975
G. foliifera	India	9° N				+		Chennubhotla *et al.* 1986
G. arcuata	India	9° N				+		Kaliaperumal *et al.* 1986
G. corticata	India	9° N				+		" " "
G. corticata	India	9° N	+					Krishnamurthy *et al.* 1969
G. edulis	India	9° N	+					" " "
G. sp # 1	Panama	9° N		+				Hay & Norris 1984
G. sp # 2	Panama	9° N				+		Hay & Norris 1984
G. sp # 3	Panama	9° N			+			Hay & Norris 1984
G. domingensis	Panama	9° N			+			Hay & Norris 1984
G. cuneata	Panama	9° N			+			Hay & Norris 1984
G. changii	Thailand	12° N				+		Chirapart *et al.* 1992
G. gracilis (as *G. verrucosa*)	Philippines	15° N		+				Trono & Azanza-Corrales 1981
G. coronopifolia	Hawaii	21° N				+		Hoyle 1978
G. parvispora (as *G. bursapastoris*)	Hawaii	21° N			+			Hoyle 1978
G. corticata	India	21° N		+				Oza 1984
G. gracilis (as *G. verrucosa*)	India	22° N		+				Oza *et al.* 1989
G. pacifica[1]	Mexico	32° N		+			+	Aguilar Rosas *et al.* 1993
G. gracilis (as *G. confervoides*)	SouthAfrica	33° S		+				Isaac 1956
G. chilensis (as *G. verrucosa*)	Chile	37° S					+	Romo & Alveal 1979
G. chilensis	Chile	37° S	+					Candia 1988
G. chilensis (as *G. verrucosa*)	Chile	40° S				+		Ramirez *et al.* 1981
G. chilensis (as *G. sordida*)[1]	New Zealand	41° S			+	+		Nelson 1989
G. gracilis (as *G. verrucosa*)	Japan	42° N			+			Yamamoto & Sasaki 1987
G. chilensis	Chile	42° S			+			Prieto *et al.* 1991
G. chilensis	Chile	42° S					+	Bird *et al.* 1986
G. gracilis (as *G. verrucosa*)	Argentina	43° S			+			Boraso de Zaixso 1990
G. tikvahiae	NH, USA	43° N			+			Penniman *et al.* 1986
G. tikvahiae	NS, Canada	46° N				+		CJ Bird *et al.* 1977
G. chilensis (as *G. sordida*)	New Zealand	46° S			+			Pickering *et al.* 1990
G. pacifica (as *G. verrucosa*-type)	BC,Canada	49° N			+			Whyte *et al.* 1981
G. gracilis (as *G. verrucosa*)	France	51° N			+			Destombe *et al.* 1989

[1] Two sites

Hard substrata, however, are suitable for spore settlement and the alternating life cycle can be completed, allowing a mixture of phases in the population. Another interpretation is that substratum affects the presence of holdfasts: gametophytes, but not tetrasporophytes of the temperate *G. tikvahiae* tend to degenerate after reproducing in the summer and new thalli regenerate from holdfasts but in unattached populations there are no such holdfasts so the diploid plants have a competitive advantage (CJ Bird *et al.*, 1977). Other unattached populations are sterile (Causey *et al.*, 1946; Simonetti *et al.*, 1970; Stokke, 1957) as are most cultivated crops (Santelices & Doty, 1989).

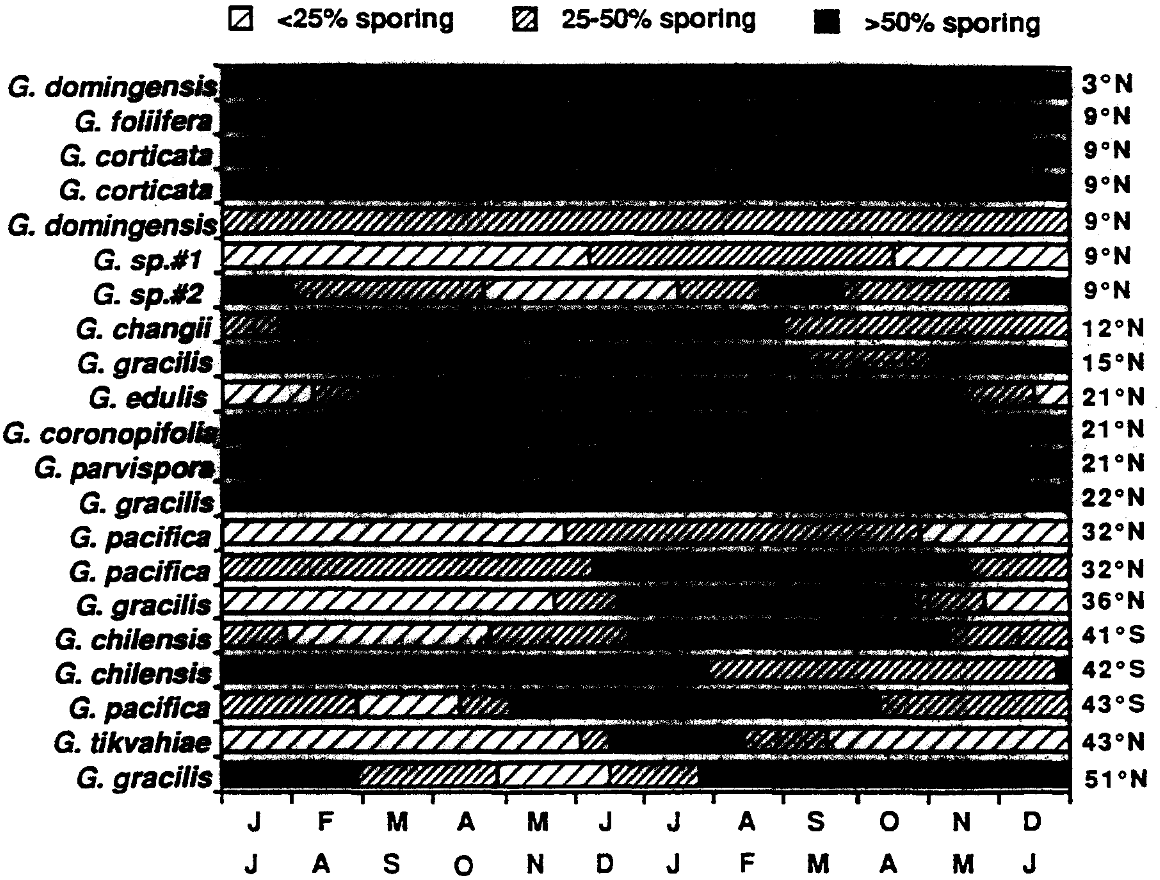

Fig. 2. An indication of the percentage of plants in various populations that were sporing (bearing carpospores or tetraspores) throughout the year at various latitudes. Replotted from (in order of increasing latitude) Pinheiro-Joventino & Bezerra (1980), Umamaheswara Rao (1973), Umamaheswara Rao (1975), Kaliaperumal *et al.* (1986), Hay & Norris (1984), Chirapart *et al.* (1992), Trono & Azanza-Corrales (1981), Oza (1984), Hoyle (1978), Oza *et al.* (1989), Aguilar Rosas *et al.* (1993), Wang & Zhang (1981), Nelson (1989), Prieto *et al.* (1991), Boraso de Zaixso (1990), Penniman *et al.* (1986) and Destombe *et al.* (1989). Upper month initials, northern hemisphere; lower month initials, southern hemisphere.

Reproductive phenology

Seasonal changes in the proportions of plants with reproductive organs have been determined for a number of species of *Gracilaria* from widely different geographical areas. In order to simplify the information sufficiently for easy comparison the percentages of spore-bearing (tetraspores and carpospores) plants have been added together and the interpolated time of changing between the categories 1–25%, 26–50% and >50% recorded. (Single months in a different category were ignored.) Those populations for which there are sufficient data are shown graphically with increasing latitude in Fig. 2. In all species there were some spore-bearing plants at every one of the sampling dates. This is probably partly a reflection of the populations selected for attention. As mentioned above, in some habitats some species are sterile and as such would be unlikely to be selected for a phenological study.

It might be expected, however, that there would be increasing seasonal change with increasing latitude; this seems partly true (Fig. 2). Outside the tropics fertility was seasonal with a summer peak. Within the tropics most plants were fertile throughout the year in most of the populations. One exception was the pair of unidentified species in Panama where winds during the dry season cause water and sediment disturbance, markedly reducing the light penetration (Hay & Norris, 1984). Another exception was *G. gracilis* (as *G. verrucosa*) in the Philippines where seasonally reduced salinity was thought to inhibit reproduction (Trono & Azanza-Corrales, 1981).

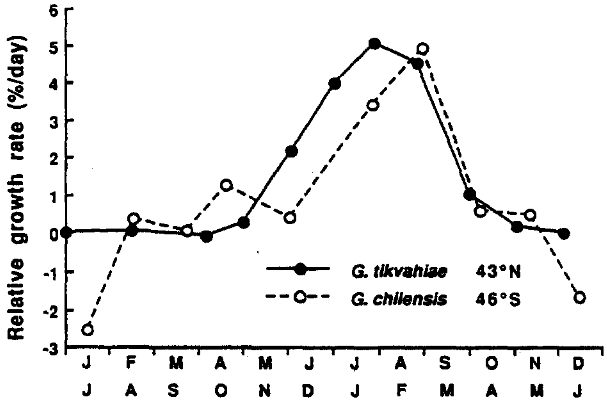

Fig. 3. Relative growth rates through the year in two populations of *Gracilaria* at similar latitudes. Upper month initials, northern hemisphere; lower month initials, southern hemisphere. Replotted from Penniman *et al.* (1986) and Nelson (1989).

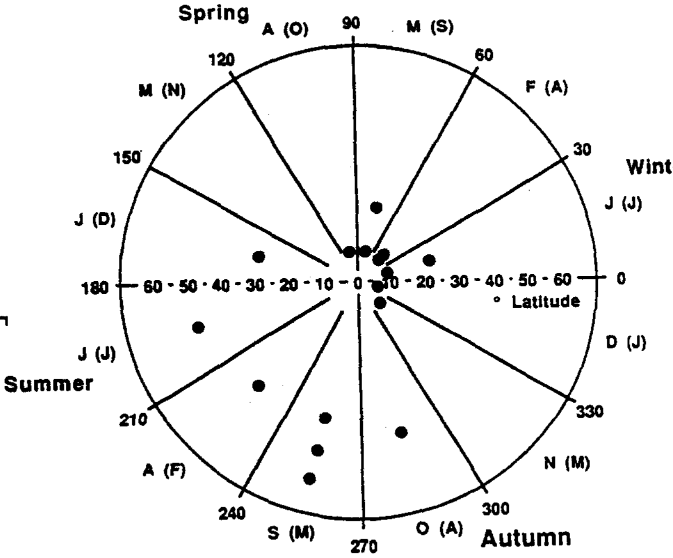

Fig. 4. The month (as the angle of a circle) in which the biomass or the mean plant length was at its seasonal peak in various populations plotted against the latitude (as the radius). Southern hemisphere month initials in brackets. Replotted from CJ Bird *et al.*, (1977), Black & Fonck (1981), Boraso de Zaixso (1990), Castro *et al.* (1991), Chennubhotla *et al.* (1986), Conover, 1958), Dellarossa *et al.* (1980), Destombe *et al.* (1988), Jayasuriya (1993), Kaliaperumal *et al.* (1986), Nelson (1989), Oza (1984), Oza *et al.* (1989), Pizarro (1986), Romo & Alveal (1979), Rueness *et al.* (1987), Santelices *et al.* (1984), Umamaheswara Rao (1973), Wang *et al.* (1984), Whyte *et al.* (1981).

Seasonal growth

There are difficulties associated with the measurement of the growth rate of individual plants of *Gracilaria* in natural populations. Some measurements have been made by placing weighed plants in plastic mesh containers, returning them to their habitat and weighing them at intervals. The relative growth rates of such plants in two widely separated populations of different species are compared in Fig. 3. At equivalent latitudes the phenologies are remarkably alike, with zero or negative growth in the winter and peak growth rate after the summer solstice. The growing season is limited to about 6 months of the year. At the lower latitude of 30 °S in Chile regrowth after cutting was apparent for about 7 months (Santelices, 1989: p. 190).

Seasonal observations of biomass and plant length in natural populations have been made more often. The timing of the peak in either of these two attributes is plotted against latitude in Fig. 4. At higher latitudes the peak mainly occurs in late summer or autumn, after growth in response to long days and before autumnal storms or decay due to reproduction (Destombe *et al.*, 1988; Jones, 1959). At low latitudes, in the populations considered, monsoons control seasonality and the peak occurs mainly in the 'winter' but may be bimodal (Jayasuriya, 1993; Kaliaperumal *et al.*, 1986; Umamaheswara Rao, 1973). There is no evidence of species of *Gracilaria* anticipating the seasons by being triggered by a repeatable seasonal condition such as daylength or water temperature for optimal exploitation of predictable conditions. It seems that they are responders (Kain, 1989); they grow when they can, when the environment allows.

Spermatia, spores and sporelings

The difficulty in achieving fertilization when the male gametes are non-motile (Searles, 1980) is exacerbated by the fact that time is limited: spermatia of *G. gracilis* (as *G. verrucosa*) are effective for less than 5 h after release (Destombe *et al.*, 1990). As with most algae, mates are likely to be close in space though in an intertidal population of this species fertilization was achieved over a distance of 80 m (Destombe *et al.*, 1990). In this species the reproductive success of females was reported to be favoured by an increased distance between the populations containing the parent plants (Richerd *et al.*, 1993b).

The presence of fertile plants in the field does not mean that spore shedding is taking place, e.g. at certain times of year Indian populations of *G. arcuata* (Kaliaperumal *et al.*, 1986) and *Gracilariopsis lemaneiformis* (as *Gracilaria sjoestedtii*) (Chennubhotla *et al.*, 1986) contained both tetrasporic and cystocarpic plants but neither shed spores in the laboratory. Thus spore shedding can be more seasonally confined than apparent fertility. In the same area *G. corticata* sheds both types of spore all through the year with variable apparent peaks (Kaliaperumal *et al.*, 1986; Umamaheswara Rao, 1976).

When fertile plants are brought into the laboratory for observation of spore shedding the highest number seems to be shed within the first three days in five different species (Chennubhotla *et al.*, 1986; Oza, 1984; Oza & Krishnamurthy, 1968; Shyam Sundar *et al.*, 1991). In *G. edulis* there is thereafter a decline in daily output, reaching nil at between 5 and 30 days according to season (Oza, 1984; Rama Rao & Thomas, 1974). This presumably depends partly on laboratory conditions. A single cystocarp of *G. gracilis* (as *G. verrucosa*) emits carpospores rhythmically for about a month (Lefebvre *et al.*, 1987).

Interesting features of spore liberation are that there can be marked diurnal variation and that different species of *Gracilaria* show peak output at different times. Whether there is an endogenous rhythm does not seem to have been established. In *G. corticata* peak emission of both carpospores and tetraspores is at the end of the night (Fig. 5) and a lengthened night or continuous darkness results in a higher output (Umamaheswara Rao, 1976; Umamaheswara Rao & Subbarangaiah, 1981). The same pattern is shown by *Gracilariopsis lemaneiformis* (as *G. sjoestedtii*) (Fig. 5). In *Gracilaria edulis* the peak in carpospore shedding is around the middle of the night (Fig. 5) and extending the day by 5 h significantly reduces output (Jayasuriya, 1993). In contrast, *G. edulis* in Australia sheds mainly at the end of the night (Ngan & Price, 1983). In *G. textorii* peak shedding is at the end of the day (Fig. 5) (Rangaiah, 1984a). The timing of peak spore output is affected by temperature but not by irradiance, desiccation or salinity (Umamaheswara Rao & Subbarangaiah, 1981). Darkness increases the carpospore output of *Gracilaria* sp. (as *G. foliifera*) (Friedlander & Dawes, 1984).

The effect of environmental factors on the magnitude of spore output can be of considerable interest to cultivators. Traditionally, mild desiccation followed by re-immersion in seawater is the recipe for spore release and this was the recommended method for *G. chilensis* (as *G. verrucosa*) carpospores (Infante & Candia, 1988). However, even 15 min of exposure to air inhibited subsequent tetraspore release by *G. corticata*, *G. textorii* and *Gracilariopsis lemaneiformis* (as *G. sjoestedtii*) (Umamaheswara Rao & Subbarangaiah, 1981). Increasing irradiance had the same effect on these spores in these species (Umamaheswara Rao & Subbarangaiah, 1981) and on carpospore release by *Gracilaria* sp. (as *G. foliifera*) (Friedlander & Dawes, 1984).

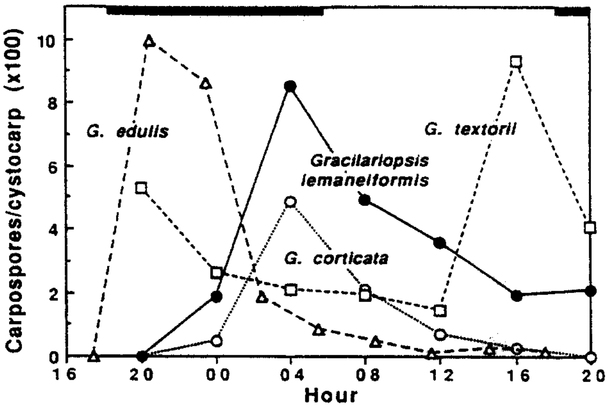

Fig. 5. The number of carpospores shed in the laboratory in three or four h periods (shown at the mid-point of each period) during the first 24 h after collection in three species of *Gracilaria* and one of *Gracilariopsis*. Numbers for *G. edulis* should be multiplied by three. Black bars indicate the night. Replotted from Umamaheswara Rao & Subbarangaiah (1981) and Mal & Subbaramaiah (1990).

After release, spores may be dispersed and the distance travelled may depend on the spore size. Carpospores, even when measured without the mucilage sheath, vary considerably in size within the genus, from 12 to 42 μm in diameter (Ngan & Price, 1979). In *Gracilariopsis lemaneiformis* (as *Gracilaria sjoestedtii*) and *G. gracilis* (as *G. verrucosa*) tetraspores were found to be smaller (Coon *et al.*, 1972; Destombe *et al.*, 1992; Okuda & Neushul, 1981) but tetraspores were reported to be larger than carpospores in *G. corticata* (Trono & Azanza-Corrales, 1981) and *G. cervicornis* (Oliveira & Plastino, 1984). In *G. gracilis* (as *G. verrucosa*) spore size did not affect the distance travelled in a water current which, in an experimental chamber, was the same for haploid and diploid spores (Destombe *et al.*, 1992).

Both types of spores can survive for some weeks in the dark (N Bird *et al.*, 1977). They can also survive a few days of desiccation (Aste & Alveal, 1988). Viability, as measured by the germination rate, may be influenced by season and favoured at the time of peak sporulation (Rangaiah, 1984b).

Conclusions pertinent to cultivation

Gracilaria plants are usually males, females or tetrasporophytes but for various reasons they may be mixed and changes may take place during vegetative growth.

Sexes and phases may differ in their growth rates and other attributes; diploids are often favoured. The phase balance and therefore the type of reproduction depends on habitat. Reproduction may interfere with growth. The output of spores follows a diurnal rhythm peculiar to the species.

Plants respond directly to prevailing conditions and therefore respond to rather than anticipate the seasons. Peak biomass and reproduction are mainly in late summer at higher latitudes.

References

Aguilar Rosas R, Marcos Ramírez R, Lobo Niembro JM, Zertuche González JA (1993) Variacion estacional de fases reproductoras y vegetativa de *Gracilaria pacifica* Abbott, en el Estero de Punta Banda, Baja California, Mexico. Cienc. mar. 19: 219–228.

Aste A, Alveal K (1988) Resistenciade las esporas de *Iridaea laminarioides*, *Gigartina chamissoi* y *Gracilaria gracilis* (as *G. verrucosa*) (Rhodophyta, Gigartinales) a la desecacion. Gayana Bot. 45: 345–349.

Bird CJ (1995) A review of recent taxonomic concepts and developments in the Gracilariaceae (Rhodophyta). J. appl. Phycol. 7: 255–267.

Bird CJ, Kain JM (1995) Recommended names of included species of Gracilariaceae. J. appl. Phycol. 7: 335–338.

Bird CJ, Edelstein T, McLachlan J (1977) Studies on *Gracilaria*. Occurrence in Atlantic Canada, with particular reference to Pomquet Harbour, Nova Scotia. Naturaliste can. 104: 257–266.

Bird CJ, McLachlan J, Oliveira EC (1986) *Gracilaria chilensis* sp. nov. (Rhodophyta, Gigartinales), from Pacific South America. Can. J. Bot. 64: 2928–2934.

Bird CJ, van der Meer JP, McLachlan J (1982) A comment on *Gracilaria verrucosa*) (Huds.) Papenf. (Rhodophyta: Gigartinales). J. mar. biol. Ass., U.K. 62: 453–459.

Bird CJ, Ragan MA, Critchley AT, Rice EL, Gutell RR (1994) Molecular relationships among the Gracilariaceae (Rhodophyta): further observations on some undetermined species. Eur. J. Phycol. 29: 195–202.

Bird N, McLachlan J, Grund D (1977) Studies on *Gracilaria*. 5. In vitro life history of *Gracilaria* sp. from the Maritime Provinces. Can. J. Bot. 55: 1282–1290.

Black HJ, Fonck E (1981) On the vegetation dynamics of *Gracilaria* spec. in Playa Changa, Coquimbo, Chile. In Levring T (ed.), Xth International Seaweed Symposium. Walter de Gruyter, Berlin: 223–228.

Boraso de Zaixso AL (1990) Ecological considerations for the possibility of culturing *Gracilaria verrucosa* in Argentina. In Oliveira EC, Kautsky N (eds), Cultivation of Seaweeds in Latin America. Universidade de São Paulo, São Paulo: 51–58.

Cabioch J (1972) Un nouveau cas d'anomalie du cycle des Gigartinales. C. r. Acad. Sci. Paris 275: 1979–1981.

Candia AI (1988) Ciclo reproductivo *in vitro* de dos poblaciones de *Gracilaria* Greville (Rhodophyta, Gracilariaceae) de Lenga, Bahia San Vicente. Gayana Bot. 45: 357–364.

Candia A (1991) El ciclo de vida de *Gracilaria* (Rhodophyta, Gracilariaceae): variaciones en el patrón reproductivo e implicancias genéticas. Rev. Chil. Hist. nat. 64: 331–334.

Castro TR, Guanzon NG, Luhan MRJ (1991) Assessment of stocks of a natural *Gracilaria* population on Panay Island, Philippines. Bot. mar. 34: 383–386.

Causey NB, Prytherch JP, McCaskill J, Humm HJ, Wolf FA (1946) Influence of environmental factors upon the growth of *Gracilaria* confervoides. Duke Univ. mar. Stn Bull. 3: 19–24.

Chennubhotla VSK, Kaliaperumal N, Ramalingam JR, Kalimuthu S (1986) Growth, reproduction and spore output in *Gracilaria folifera* (Forsskal) Boergesen and *Gracilariopsis sjoestedtii* (Kylin) Dawson around Mandapam. Ind. J. Fish. 33: 76–84.

Chirapart A, Lewmanomont K, Ohno M (1992) Seasonal variation of reproductive states of the agar-producing seaweed, *Gracilaria changii* (Xia & Abbott) Abbott, Zhang & Xia in Thailand. Bull. mar. Sci. Fish., Kochi Univ. 12: 9–16.

Conover JT (1958) Seasonal growth of benthic marine plants as related to environmental factors in an estuary. Contr. mar. Sci. 5: 97–147.

Coon DA, Neushul M, Charters AC (1972) The settling behaviour of marine algal spores. In Nisizawa K (ed.), Proceedings of the Seventh International Seaweed Symposium. University of Tokyo Press, Tokyo: 237–242.

De Wreede RD, Klinger T (1988) Reproductive strategies in algae. In Lowett Doust J, L (eds), Plant Reproductive Ecology: Patterns and Strategies. Oxford U.P., Oxford: 267–284.

Dellarossa V, Romo H, Alveal K (1980) Avances en el conocimiento ecologica de *Gracilaria verrucosa* en el area de Concepcion, Chile. Bolm Inst. oceanogr., S. Paulo 29: 149–155.

Destombe C (1987) Biologie des populations de l'algue rouge *Gracilaria verrucosa* (Hudson) Papenfuss, intérêt et implication en aquaculture. Thèse de doctorat, Université de Lille Flandre-Artois, 263 pp.

Destombe C, Godin J, Bodard M (1988) The decay phase in the life history of *Gracilaria verrucosa*: the consequences in intensive cultivation. In Stadler T, Mollion J, Verdus M-C, Karamanos Y, Morvan H, Christiaen D (eds), Algal Biotechnology. Elsevier Applied Science, London: 287–303.

Destombe C, Godin J, Remy J-M (1990) Viability and dissemination of spermatia of *Gracilaria verrucosa* (Gracilariales, Rhodophyta). In Lindstrom SC, Gabrielson PW (eds), Thirteenth International Seaweed Symposium. Developments in Hydrobiology 58. Kluwer Academic Publishers, Dordrecht. Reprinted from Hydrobiologia 204/205: 219–223.

Destombe C, Godin J, Lefebvre C, Vernet P (1992) Differences in dispersal abilities of haploid and diploid spores of *Gracilaria verrucosa* (Gracilariales, Rhodophyta). Bot. mar. 35: 93–98.

Destombe C, Valero M, Vernet P, Couvet D (1989) What controls haploid-diploid ratio in the red alga, *Gracilaria verrucosa*? J. evol. Biol. 2: 317–338.

Destombe C, Godin J, Nocher M, Richerd S, Valero M (1993) Differences in response between haploid and diploid isomorphic phases of *Gracilaria verrucosa* (Rhodophyta: Gigartinales) exposed to artificial environmental conditions. In Chapman ARO, Brown MT, Lahaye M (eds), Fourteenth International Seaweed Symposium. Developments in Hydrobiology 85. Kluwer Academic Publishers, Dordrecht. Reprinted from Hydrobiologia 260/261: 131–137.

Durairatnam M (1965) The ecology of *Gracilaria verrucosa* (Hudson) Papenfuss [formally *G. confervoides* (L.) Greville] in Koddiyar Bay, Trincomalee. Bull. Fish. Res. Stn, Ceylon 18: 29–34.

Fredericq S, Hommersand MH (1989) Comparative morphology and taxonomic status of *Gracilariopsis* (Gracilariales, Rhodophyta). J. Phycol. 25: 228–241.

Friedlander M, Dawes CJ (1984) Studies on spore release and sporeling growth from carpospores of *Gracilaria foliifera* (Forsskål) Børgesen var. *angustissima* (Harvey) Taylor. 1. Growth response. Aquat. Bot. 19: 221–232.

Hay ME, Norris JN (1984) Seasonal reproduction and abundance of six sympatric species of *Gracilaria* Grev. (Gracilariaceae; Rhodophyta) on a Caribbean subtidal sand plain. In Bird CJ, Ragan MA (eds), Eleventh International Seaweed Symposium. Developments in Hydrobiology 22. Dr W Junk Publishers Dordrecht. Reprinted from Hydrobiologia 116/117: 63–72.

Hoyle MD (1978) Reproductive phenology and growth rates in two species of *Gracilaria* from Hawaii. J. exp. mar. Biol. Ecol. 35: 273–283.

Infante R, Candia A (1988) Cultivo de *Gracilaria verrucosa* (Hudson) Papenfuss e *Iridaea ciliata* Kützing (Rhodophyta, Gigartinaceae) en laboratorio: esporulacion inducida y colonizacion de carposporas en diferentes sustratos. Gayana Bot. 45: 297–304.

Isaac WE (1956) The ecology of *Gracilaria confervoides* (L.) Grev. in South Africa with special reference to its ecology in the Saldanha-Langebaan Lagoon. In Braarud T, Sørensen NA (eds), Second International Seaweed Symposium. Pergamon, London: 173–185.

Jayasuriya PMA (1993) Seaweed Resources in Sri Lanka: Culture of *Gracilaria* and Intertidal Surveys. PhD, Liverpool: 116 pp.

Jones WE (1956) Effect of spore coalescence on the early development of *Gracilaria verrucosa* (Hudson) Papenfuss. Nature, Lond. 178: 426–427.

Jones WE (1959) The growth and fruiting of *Gracilaria verrucosa* (Hudson) Papenfuss. J. mar. biol. Ass. U.K. 38: 47–56.

Kain JM (1989) The seasons in the subtidal. Br. phycol. J. 24: 203–215.

Kain JM (1991) Cultivation of attached seaweeds. In Guiry MD, Blunden G (eds), Seaweed Resources in Europe: Uses and Potential. John Wiley & Sons, Chichester: 309–377.

Kain JM, Bates MJ (1993) The reproductive phenology of *Delesseria sanguinea* and *Odonthalia dentata* off the Isle of Man. Eur. J. Phycol. 28: 173–182.

Kaliaperumal N, Chennubhotla VSK, Kalimuthu S, Ramalingam JR (1986) Growth, phenology and spore shedding in *Gracilaria arcuata* var. *arcuata* (Zanardini) Umamaheswara Rao and *G. corticata* var. *cylindrica* (J. Agardh) Umamaheswara Rao (Rhodophyta). Indian J. mar. Sci. 15: 107–110.

Kim DH, Henriques NP (1979) Yields and gel strengths of agar from cystocarpic and tetrasporic plants of *Gracilaria verrucosa* (Florideophyceae). In Jensen A, Stein JR (eds), Proceedings of the Ninth International Seaweed Symposium. Science Press, Princeton: 257–262.

Kling R (1978) Observation d'un cas de monoecie chez *Gracilaria verrucosa* (Huds) Papenfuss (Gigartinales). Bull. Soc. Bot. M. Fr. 31: 59–60.

Krishnamurthy V, Venkataraju P, Venugopal R (1969) An aberrant life-history in *Gracilaria edulis* (Gmel.) Silva and *Gracilaria corticata*. J. Agric. Curr. Sci. 14: 343–344.

Lefebvre CA, Destombe C, Godin J (1987) Le fonctionnement du carposporophyte de *Gracilaria verrucosa* et ses répercussions sur la stratégie de reproduction. Cryptogamie, Algol. 8: 113–126.

Lignell Å, Pedersén M (1989) Agar composition as a function of morphology and growth rate. Studies on some morphological strains of *Gracilaria secundata* and *Gracilaria verrucosa* (Rhodophyta). Bot. mar. 32: 219–227.

Maggs CA, Cheney DP (1990) Competition studies of marine macroalgae in laboratory culture. J. Phycol. 26: 16–24.

Mal TK, Subbaramaiah K (1990) Diurnal periodicity of carpospore shedding in the red alga *Gracilaria edulis* (Gmel.) Silva (Rhodophyta). Indian J. mar. Sci. 19: 63–65.

McLachlan J, Edelstein T (1977) Life history and culture of *Gracilaria foliifera* (Rhodophyta) from south Devon. J. mar. biol. Ass. U.K. 57: 577–586.

Maynard Smith J (1978) The Evolution of Sex. Cambridge U.P., Cambridge, 209 pp.

Muñoz AA, Santelices B (1994) Quantification of the effects of sporeling coalescence on the early development of *Gracilaria chilensis* (Rhodophyta) J. Phycol.30: 387–392.

Nelson WA (1989) Phenology of *Gracilaria sordida* W. Nelson populations. Reproductive status, plant and population size. Bot. mar. 32: 41–51.

Ngan Y, Price IR (1979) Systematic significance of spore size in the Florideophyceae (Rhodophyta). Br. phycol. J. 14: 285–303.

Ngan Y, Price IR (1983) Periodicity of spore discharge in tropical Floridophyceae (Rhodophyta). Br. phycol. J. 18: 83–95.

Ogata E, Matsui T, Nakamura H (1972) The life cycle of *Gracilaria verrucosa* (Rhodophyceae, Gigartinales) *in vitro*. Phycologia 11: 75–80.

Ohmi H (1958) The species of *Gracilaria* and *Gracilariopsis* from Japan and adjacent waters. Mem. Fac. Fish. Hokkaido Univ. 5: 1–66.

Okuda T, Neushul M (1981) Sedimentation studies of red algal spores. J. Phycol. 17: 113–118.

Oliveira JC (1968) Recherches sur le développement et les organes reproducteurs de *Gracilaria* de la Manche. Thèse 3ème Cycle de Biologie Végétale, Univérsité de Paris VI: 49 pp.

Oliveira EC, Plastino EM (1984) The life history of some species of *Gracilaria* (Rhodophyta) from Brazil. Jap. J. Phycol. 32: 203–208.

Oliveira EC de, Plastino EM (1994) Gracilariaceae. In Akatsuka I (ed.), Biology of Economic Algae. SPB Academic Publishing, The Hague: 185–226.

Oza RM (1984) Studies on Indian *Gracilaria* III. Seasonal variation in growth and reproduction in *Gracilaria corticata* J. Ag. occurring on the coast of Veraval (Gujarat). Seaweed Res. Util. 7: 1–20.

Oza RM, Krishnamurthy V (1968) Studies on carposporic rhythm of *Gracilaria verrucosa* (Huds.) Papenf. Bot. mar. 11: 118–121.

Oza RM, Tewari A, Rajyaguru MR (1989) Growth and phenology of red alga *Gracilaria verrucosa* (Huds.) Papenf. Indian J. mar. Sci. 18: 82–86.

Patwary MU, van der Meer JP (1983) Improvement of *Gracilaria tikvahiae* (Rhodophyceae) by genetic modification of thallus morphology. Aquaculture 33: 207–214.

Patwary MU, van der Meer JP (1984) Growth experiments on autopolyploids of *Gracilaria tikvahiae* (Rhodophyceae). Phycologia 23: 21–27.

Patwary MU, van der Meer JP (1992) Genetics and breeding of cultivated seaweeds. Korean J. Phycol. 7: 281–318.

Penniman CA, Mathieson AC (1987) Variation in chemical composition of *Gracilaria tikvahiae* McLachlan (Gigartinales, Rhodophyta) in the Great Bay Estuary, New Hampshire. Bot. mar. 30: 525–534.

Penniman CA, Mathieson AC, Penniman CE (1986) Reproductive phenology and growth of *Gracilaria tikvahiae* McLachlan (Gigartinales, Rhodophyta) in the Great Bay Estuary, New Hampshire. Bot. mar. 24: 147–154.

Pickering TD, Gordon ME, Tong LJ (1990) Seasonal growth, density, reproductive phenology and agar quality of *Gracilaria sordida* (Gracilariales, Rhodophyta) at Mokomoko Inlet, New Zealand. In Lindstrom SC, Gabrielson PW (eds), Thirteenth International Seaweed Symposium. Developments in Hydrobiology 58. Kluwer Academic Publishers, Dordrecht. Reprinted from Hydrobiologia 204/205: 253–262.

Pinheiro-Joventino F, Bezerra CLF (1980) Estudo de fenologia e regeneração de *Gracilaria domingensis* Sonder (Rhodophyta – Gracilariaceae), no estado do ceará. Arq. Ciên. mar. 20: 33–41.

Pizarro A (1986) Conocimiento actual y avances recientes sobre el manejo y cultivodo *Gracilaria* spp. in Chile. Monograf. biol. 4: 63–96.

Plastino EM, Oliveira EC (1988) Deviations in the life-history of *Gracilaria* sp. (Rhodophyta, Gigartinales), from Coquimbo, Chile, under different culture conditions. Hydrobiologia 164: 67–74.

Prieto I, Westermeier R, Müller D (1991) Variacion de fenofases de *Gracilaria chilensis* Bird, McLachlan y Oliveira (Rhodophyta, Gigartinales), en condiciones de cultivo en laboratorio y terreno. Presencia de fases mexcladas. Rev. Chil. Hist. nat. 64: 345–352.

Rama Rao K, Thomas PC (1974) Shedding of carpospores in *Gracilaria edulis* (Gmel.) Silva. Phykos 13: 54–59.

Ramirez C, Rivera P, Stegmaier E, Contreras D (1981) Prospeccion de *Gracilaria verrucosa* en la Bahia Corral y Ensenada do Don Juan (Valdivia, Chile). Rev. Biol. mar. 17: 389–404.

Rangaiah GS (1984a) Effect of environmental factors on germination and growth in *Gracilaria corticata* J. Agardh. Indian J. Bot. 7: 234–239.

Rangaiah GS (1984b) Growth, reproduction and spore shedding in *Gracilaria textorii* (Sur.) J. Ag. along the Visakhapatnam coast. Phykos 23: 246–253.

Ren G-Z, Chen M-Q (1986) On the coalescence phenomenon during the disc stage of young sporeling in *Gracilaria*. (In Chinese). Mar. Sci. 10: 49–50.

Richerd S, Couvet D, Valero M (1993a) Evolution of alternation of haploid and diploid life cycles. II. Maintainance of the haplodiplontic cycle. J. evol. Biol. 6: 263–280.

Richerd S, Destombe C, Cuguen J, Valero M (1993b) Variation of reproductive success in a haploid-diploid red alga. *Gracilaria verrucosa*: effects of parental identities and crossing distance. Am. J. Bot. 80: 1379–1391.

Romo DH, Alveal VK (1979) Estudlos poblacionales en la pradera de *Gracilaria verrucosa* (Hudson) Papenfuss de Isla de Los Reyes, Bahia de Conception. Cienc. Tecnol. mar. 4: 15–26.

Rueness J, Mathisen HA, Tananger T (1987) Culture and field observations on *Gracilaria verrucosa* (Huds.) Papenf. (Rhodophyta) from Norway. Bot. mar. 30: 267–276.

Santelices B (1989) Algas Marinas de Chile. Ediciones Universidad Católica de Chile, Santiago, 399 pp.

Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanogr. mar. Biol. ann. Rev. 28: 177–276.

Santelices B, Doty MS (1989) A review of *Gracilaria* farming. Aquaculture 78: 95–133.

Santelices B, Varela D (1993) Intra-clonal variation in the red seaweed *Gracilaria chilensis*. Mar. Biol. 116: 543–552.

Santelices B, Aedo D, Varela D (1995) Causes and implication of intra-clonal variation in *Gracilaria chilensis*. J. appl. Phycol. 7: 283–290.

Santelices B, Vasquez J, Ohme U, Fonck E (1984) Managing wild crops of *Gracilaria* in central Chile. In Bird CJ, Ragan MA (ed.), Eleventh International Seaweed Symposium. Developments in Hydrobiology 22. Dr W. Junk Publishers, Dordrecht. Reprinted from Hydrobiologia 116/117: 77–89.

Searles RB (1980) The strategy of the red algal life history. Amer. Nat. 115: 113–120.

Shyam Sundar KL, Subba Rao PV, Subbaramaiah K (1991) Studies on carpospore shedding in the red alga *Gracilaria crassa* (Gigartinales, Rhodophyta). Indian J. mar. Sci. 20: 70–71.

Simonetti G, Giaccone G, Pignatti S (1970) The seaweed *Gracilaria confervoides*, an important object for autecologic and cultivation research in the northern Adriatic Sea. Helgoländer wiss. Meeresunters. 20: 89–96.

Stokke K (1957) The red alga *Gracilaria verrucosa* in Norway. Nytt Mag. Bot. 5: 101–111.

Trono GC, Azanza-Corrales R (1981) The seasonal variation in the biomass and reproductive states of *Gracilaria* in Manila Bay. In Levring T (ed.), Xth International Seaweed Symposium. Walter de Gruyter, Berlin: 743–748.

Umamaheswara Rao M (1972) On the Gracilariaceae of the seas around India. J. mar. biol. Ass. India 14: 671–696.

Umamaheswara Rao M (1973) Growth and reproduction in some species of *Gracilaria* and *Gracilariopsis* in the Palk Bay. Ind. J. Fish. 20: 182–192.

Umamaheswara Rao M (1975) Studies on the growth and reproduction of *Gracilaria corticata* near Mandapam in the Gulf of Mannar. J. mar. biol. Ass. India 17: 646–652.

Umamaheswara Rao M (1976) Spore liberation in *Gracilaria corticata* J. Agardh growing at Mandapam. J. exp. mar. Biol. Ecol. 21: 91–98.

Umamaheswara Rao M, Subbarangaiah G (1981) Effects of environmental factors on the diurnal periodicity of tetraspores of some Gigartinales (Rhodophyta). In Levring T (ed.), Xth International Seaweed Symposium. Walter de Gruyter, Berlin: 209–214.

van der Meer JP (1977) Genetics of *Gracilaria* sp. (Rhodophyceae, Gigartinales) II. The life history and genetic implications of citokinetic failure during tetraspore formation. Phycologia 16: 367–371.

van der Meer JP (1979) Genetics of *Gracilaria* sp. (Rhodophyceae, Gigartinales). V. Isolation and characterization of mutant strains. Phycologia 18: 47–54.

van der Meer JP (1981) Genetics of *Gracilaria tikvahiae* (Rhodophyceae). VII. Further observations on mitotic recombination and the construction of polyploids. Can. J. Bot. 59: 787–792.

van der Meer JP (1986) Genetics of *Gracilaria tikvahiae* (Rhodophyceae). XI. Further characterization of a bisexual mutant. J. Phycol. 22: 151–158.

van der Meer JP, Todd ER (1977) Genetics of *Gracilaria* sp. (Rhodophyceae, Gigartinales). IV. Mitotic recombination and its relationship to mixed phases in the life history. Can. J. Bot. 55: 2810–2817.

van der Meer JP, Patwary MU, Bird CJ (1984) Genetics of *Gracilaria tikvahiae* (Rhodophyceae). X. Studies on a bisexual clone. J. Phycol. 20: 42–46.

Wang S, Zhang Y (1981) Observation on the growth and reproductive cycle of *Gracilaria verrucosa* (Hudson) Papenfuss. Mar. Fish. Res. 2: 17–26.

Wang YC, Pan GY, Chen LC-M (1984) Studies on agarophytes II. Field observations and growth of *Gracilaria* cf. *verrucosa* (Rhodophyta) in Shantou District, Guangdong, P.R.C. Bot. mar. 27: 265–269.

Whyte JNC, Englar JR, Saunders RG, Lindsay JC (1981) Seasonal variation in the biomass, quantity and quality of agar, from the reproductive and vegetative stages of *Gracilaria* (*verrucosa*-type). Bot. mar. 24: 493–501.

Yamamoto H, Sasaki J (1987) Crossing experiments between populations of socalled *Gracilaria verrucosa* (Huds.) Papenfuss from two localities. Bull. Fac. Fish. Hokkaido Univ. 38: 335–338.

Zhang X, van der Meer JP (1987) A study on heterosis in diploid gametophytes of the marine red alga *Gracilaria tikvahiae*. Bot. mar. 30: 309–314.

Zhang X, van der Meer JP (1988a) A genetic study on *Gracilaria sjoestedtii*. Can. J. Bot. 66: 2022–2026.

Zhang X, van der Meer JP (1988b) Polyploid gametophytes of *Gracilaria tikvahiae* (Gigartinales, Rhodophyta). Phycologia 27: 312–318.