Cultivation biology of *Gracilaria*

Conveners: I. A. Abbott & B. Santelices

Seasonal reproduction and abundance of six sympatric species of *Gracilaria* Grev. (Gracilariaceae; Rhodophyta) on a Caribbean subtidal sand plain

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Introduction

Only a few studies have focused on the seasonality (Cheney & Dyer, 1974; Schneider, 1976; Bula Meyer, 1983) or reproduction (Peckol, 1982; Peckol & Searles, 1983) of subtidal macroalgal communities in the tropical/subtropical western Atlantic.

Quantitative studies of the reproduction and seasonality of tropical red algal species are also relatively few. *Hypnea* species were studied in Hawaii (Mshigeni, 1976) and India (Rama Rao, 1977), and Ganzon-Fortes & Trono (1982) quantified reproductive periodicity of the recently described *Laurencia tronoi* Ganzon-Fortes (1983) in the Philippines. Each of these studies reported a dominance of tetrasporophytes over other reproductive stages. Similarly, Dawes, *et al* (1974) reported tetrasporophyte dominance in two Florida *Eucheuma* species, *E. isiforme* (C. Ag.) J. Ag. and the 'Bahía Honda plant'; however, for a third species, *E. nudum* J. Ag., they found a dominance of spermatangial plants over both cystocarpic and tetrasporangial plants. In ecological studies of *Spyridia filamentosa* (Wulf.) Harv. from Puerto Rico, a dominance of male plants over both cystocarpic and tetrasporic plants was also reported (Soto, 1980).

Studies on seasonal variation of reproduction in temperate *Gracilaria* species were done by Jones (1959), Kim (1970) and Penniman (1977). The only previous studies of reproductive seasonality in tropical species of *Gracilaria* are those of Hoyle (1978) on *G. bursa-pastoris* (Gmel.) Silva and *G. coronopifolia* J. Ag. from Hawaii, Umamaheswara Rao (1973) on *G. sjoestedii* Kyl. from India, and Trono & Azanza-Corrales (1981) on *G. verrucosa* (Huds.) Papenf., *G. salicornia* (C. Ag.) Daws. and *G. coronopifolia* from the Philippines.

On the subtidal sand plain off the fringing reef at Galeta Point, Caribbean Panama (Fig. 1), there are over 60 species of benthic macroalgae. Up to 12 of these belong to the genus *Gracilaria* Grev. (Gigartinales; Gracilariaceae), a group of taxonomically confusing, but economically important red algae. All 12 can be found growing sympatrically on hard substrata of the sand plain. This may be the largest number of sympatric species of a single red algal genus from any area in the world. Six of these *Gracilaria* species, *G. cuneata* Aresch., *G. cylindrica* Børg., *G. domingensis* Sond., *Gracilaria* sp. #1, *Gracilaria* sp. #2 and *Gracilaria* sp. #3, are among
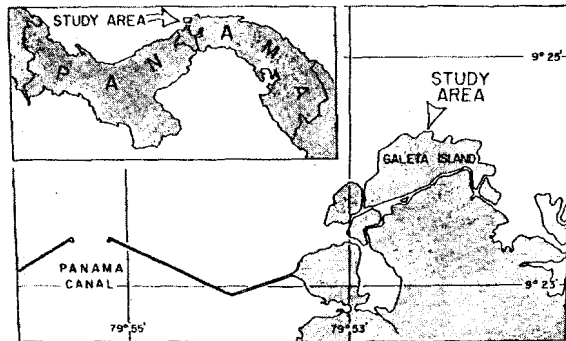
Fig. 1. The Galeta Point study site and its location on the Caribbean coast of the Republic of Panama, Central America.

the most abundant species on the reef's sand-plain system (Hay 1981). These sympatric algae have broad overlapping resource requirements. The sympatric nature of these *Gracilaria* species raises several interesting questions: Are these species partitioning the habitat (attachment sites) by producing spores at different times of the year? Are they achieving reproductive isolation by producing gametophytes at different times of the year? Finally, what is the relation between their abundance and reproductive effort? The present study documents the seasonality of abundance and of gametophytic and tetrasporophytic reproduction of these six tropical species of *Gracilaria*.

Study site and methods

Description of the study site. The study was conducted at the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute located on the Caribbean coast of the Republic of Panama (9° 24' N; 79° 52' W; Fig. 1). The reef is representative of other fringing reefs found on the northern coast of Panama (Glynn, 1972; Macintyre & Glynn, 1976). At a depth of 10–14 m, the reef slope merges with an extensive sand plain that includes sparse fragments of hard substrata (e.g., coral rubble) to which the various species of *Gracilaria* are attached. The low abundance of these substrata limits the abundance of red algae on the sand plain (Hay, 1981).

During the dry-season, usually December-April, strong winds (24–27 km · h⁻¹) blow consistently from the north. In contrast, wet-season winds are

slight (6–12 km · h⁻¹) and variable in direction (Hendler, 1976). Waves, generated by dry-season winds, result in high turbidity that reduces light penetration to the sand plain. At this time, the sand plain can be in complete darkness even at midday. In some years, a 'mini-dry-season' occurs in July-August (Fig. 2). The decreased light available in the dry-season and 'mini-dry-season' may cause algal abundance to decrease by as much as 80%. Thus, during the relatively benign wet-season, algae are limited by the scarcity of attachment sites; during the stressful dry-season (and occasional 'mini-dry-season'), conditions are unsuitable for growth even if attachment sites are available (Hay, 1981).

Methods. Of the six most common *Gracilaria* species (Figs. 3–4), three were identified according to Taylor (1960, 1969), and three may represent undescribed species. These six sand-plain algae were monitored at approximately monthly intervals between October 1978 and September 1979 to determine plant density and reproductive condition. Plant density was measured by counting individuals within 100 1.0-m² quadrats randomly locat-
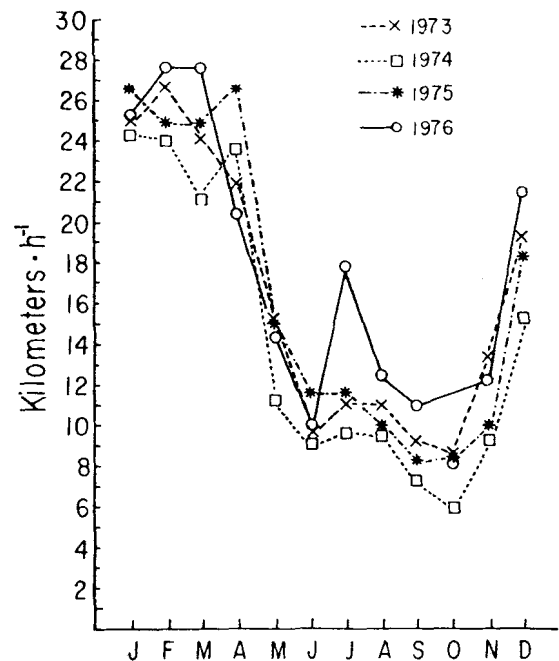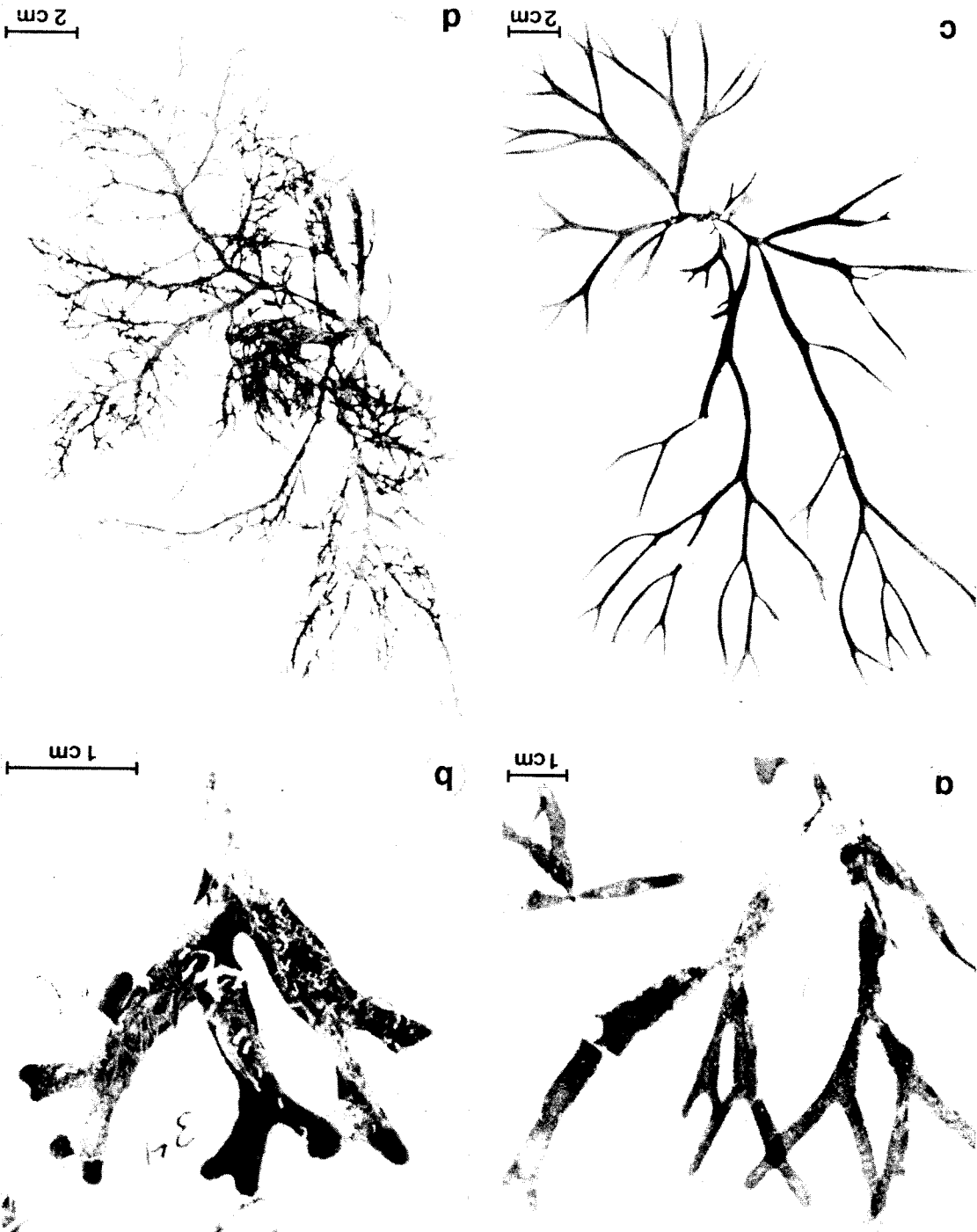

Fig. 2. Average hourly wind speed (kilometers · h⁻¹) per month from 1973 to 1976 for Galeta Point, Republic of Panama. Note the 'mini-dry-season' during July 1976 [data from the Environmental Science Program of the Smithsonian Institution].

Fig. 3. Galeta sand-plain species of *Gracilaria:* (a) *Gracilaria* sp. #1; (b) *Gracilaria* sp. #2; (c) *Gracilaria* sp. #3; (d) *G. domingensis.*
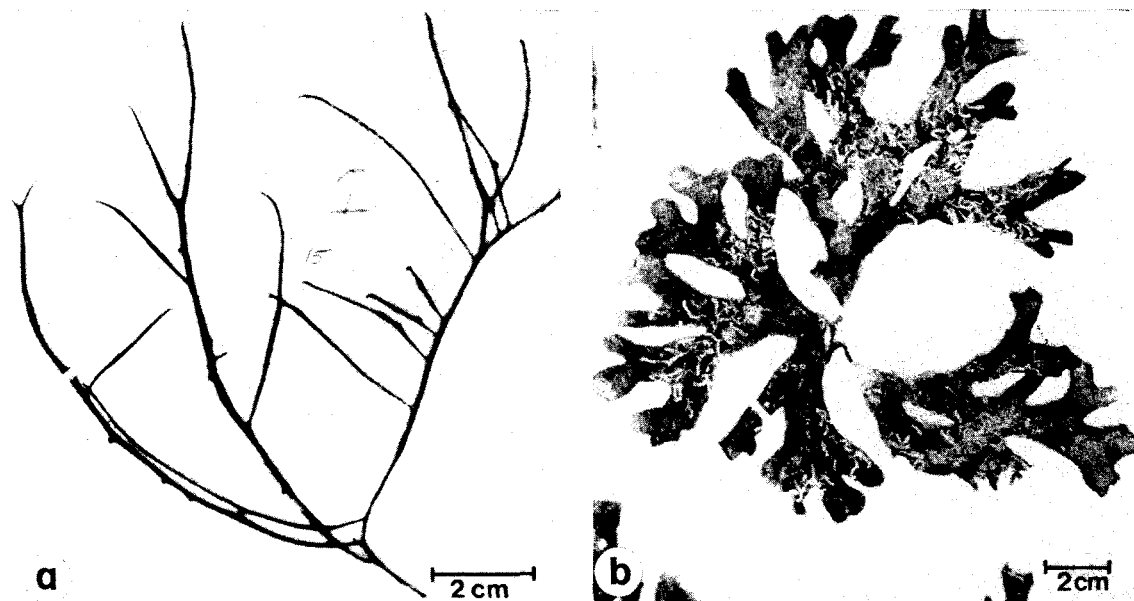
Fig. 4. Galeta sand-plain species of *Gracilaria:* (a) *G. cylindrica;* (b) *G. cuneata.*

ed within a 2 000-m² area of the sand plain. All individuals of each species were counted within each quadrat. The data were recorded with a bone-microphone on a Panasonic cassette tape recorder in an underwater plexiglass housing.

To assess reproductive condition at each sampling, portions of individuals of each *Gracilaria* species were collected from areas immediately adjacent to the 2 000-m² monitoring site (to insure non-destructive sampling of these quadrats). During sampling periods when underwater visibility was 0.5 m or better, portions of *Gracilaria* thalli were collected from 0.15-m² quadrats that were randomly located within this sampling site. When visibility was less than 0.5 m, portions of thalli were collected by swimming haphazardly across the bottom and collecting portions of all algae encountered. The sample size of each species during each sampling period ranged from 5–133 individuals per species (Table 1); the former number reflects the less common species at times of zero visibility.

Portions of approximately 2 400 individuals of the six *Gracilaria* species were collected during the one-year sampling regime. Serial transections were prepared from suspected reproductive areas of each individual specimen. These sections were permanently mounted on microscope slides using Karo syrup (Abbott & Hollenberg, 1976) and labeled with the identifying number of the individual specimen from which they were prepared. All microscope slides and corresponding voucher specimens are deposited in the Algal Collection, US National Herbarium, Department of Botany, Smithsonian Institution (US). We later determined the reproductive condition by examining the sections with a Zeiss Universal microscope. All apparently infertile material was sectioned a second time to confirm its nonreproductivity. Seasonal variation in the number of reproductive plants $\cdot$ m^{-2} was obtained by multiplying the percentage of plants that were reproductive by the mean number of plants $\cdot$ m^{-2} [(% reprod.) (mean no. plants $\cdot$ m^{-2}) = mean no. reprod. plants $\cdot$ m^{-2}].

Results

The percentage of reproductive plants (i.e., spermatangial, cystocarpic, or tetrasporic), as well as the number of plants $\cdot$ m^{-2}, and number of reproductive plants $\cdot$ m^{-2} are shown in Figures 5 & 6. Sample sizes of individuals of *G. cuneata, G. cylindrica, G. domingensis, Gracilaria* sp. #1, *Gracilaria* sp. #2 and *Gracilaria* sp. #3 (Figs. 3-4), for the
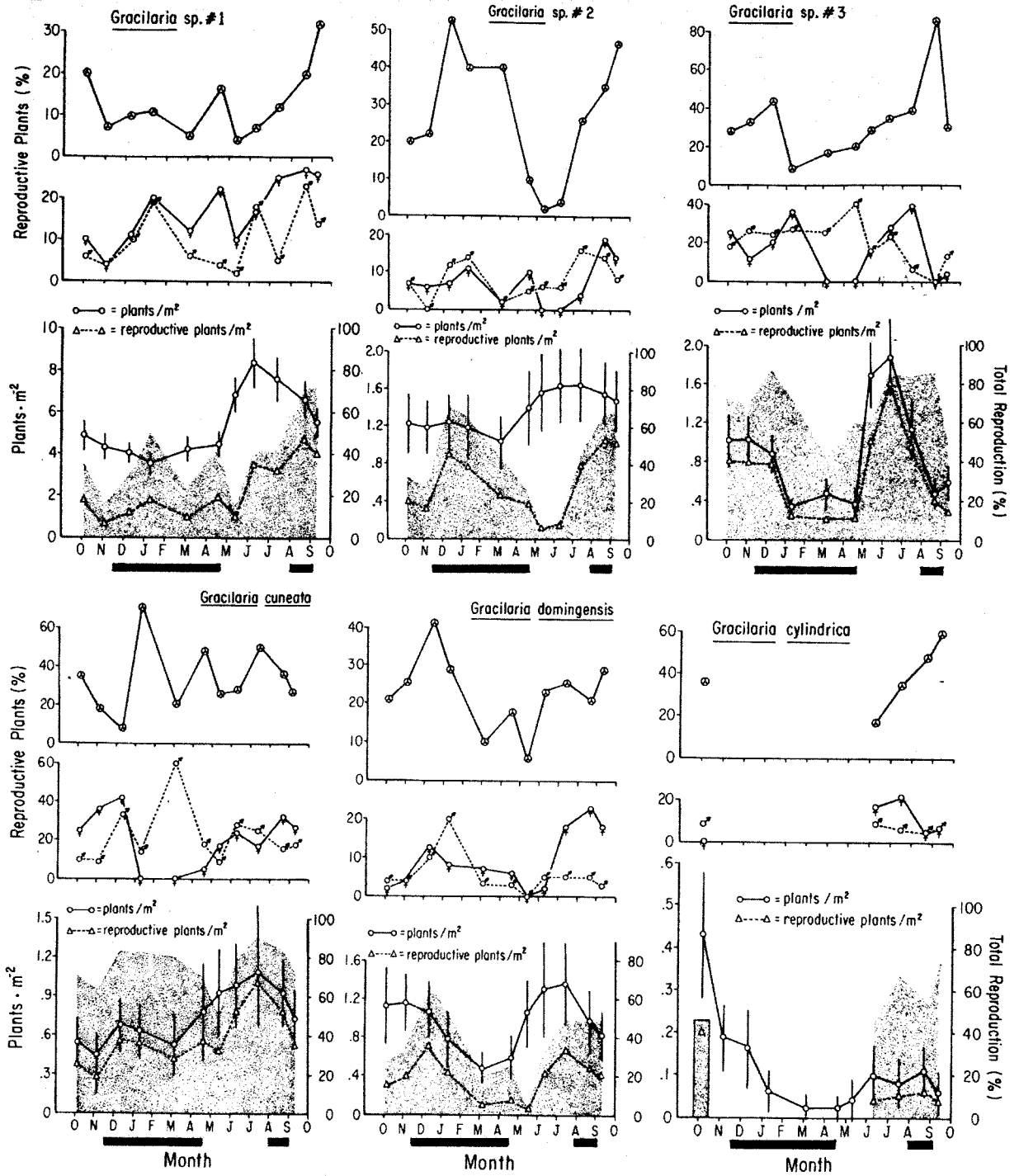
Fig. 5. Reprodution and abundance of sand-plain *Gracilaria*. Black bars represent 'dry-season' (early Dec.-late Apr.), and 'mini-dry-season' (Aug.-Sept.) conditions. The shaded areas show the total % reproductive plants. Vertical lines on graphs of overall plant density represent 95% confidence intervals.
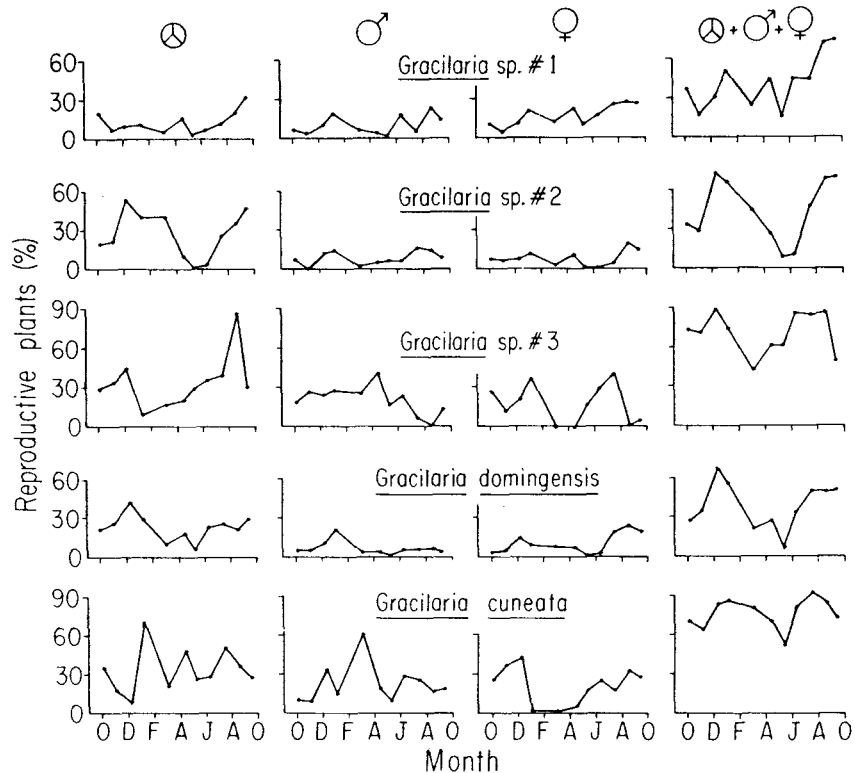
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Fig. 6. Percent tetrasporic, cystocarpic, and spermatangial plants and total % reproductive plants of the five dominant *Gracilaria* species on the Galeta sand plain.

reproductive determination study, are summarized in Table 1. Data on *G. cylindrica* are incomplete for much of the dry-season, and this species is thus excluded from some of the analyses.

All six species exhibited an increase in the percentage of reproductive plants following the onset of the turbid dry-season in late November, and a second reproductive peak occurred during or after the 'mini-dry-season' of August. All species showed

less reproduction sometime between March and June. Reproduction during this period was markedly less for *Gracilaria* sp. #2 and *G. domingensis* (8% and 6% respectively) than was observed in *Gracilaria* sp. #3 or *G. cuneata* (42% and 52% respectively); *Gracilaria* sp. #1 displayed an intermediate pattern.

With the exception of *Gracilaria cuneata*, all species of *Gracilaria* decreased in abundance during

Table 1. The number of individuals of each species examined for reproductive condition during each sampling period.

Species	Month of sampling										
	O	N	D	J	M	A	M	J	J	A	S
Gracilaria											
Gracilaria sp. #1	50	67	63	101	64	67	113	72	40	82	62
Gracilaria sp. #2	30	18	58	37	45	39	50	50	49	37	78
Gracilaria											
domingensis	48	53	38	65	30	34	51	43	39	61	62
Gracilaria sp. #3	28	27	25	11	12	5	58	57	31	7	23
Gracilaria cuneata	20	11	12	7	10	40	23	25	24	25	22
Gracilaria cylindrica	11	0	0	0	0	0	0	23	18	21	15

the dry-season and the 'mini-dry-season'. All species, except *G. cylindrica*, showed maximum abundance in June-July of the wet-season. When both plant density and percent reproduction are taken into account to estimate the number of reproductive plants · m⁻², *Gracilaria cuneata* exhibits a much more constant pattern of reproduction than do any of the other species. The coefficient of variations (standard deviation · mean⁻¹) of reproductive plants · m⁻² are as follows for the different species: *G. cuneata* = 0.36, *G. domingensis* = 0.58, *Gracilaria* sp. #2 = 0.59, *Gracilaria* sp. #1 = 0.61, and *Gracilaria* sp. #3 = 0.67.

The relative proportion of tetrasporophytes to gametophytes showed no consistent pattern for any of the *Gracilaria* species in general (Fig. 5). Using the percentage of gametophytes and tetrasporophytes during each sample period as a paired sample, a Wilcoxon paired-sample rank-sum test (see Zar, 1974) can be used to test for significant differences in incidence between the reproductive stages, in each species. Gametophytes were significantly ($P < 0.05$) more abundant than tetrasporophytes in *Gracilaria* sp. #1 and *Gracilaria* sp. #3, while tetrasporophytes were significantly more abundant than gametophytes in *Gracilaria* sp. #2 and *G. domingensis*. There was no significant difference in frequencies of tetrasporophytes and gametophytes in *G. cuneata*.

In comparing the gametophytic (spermatangial and cystocarpic) thalli of each species, female gametophytes were significantly more abundant than male gametophytes in *Gracilaria* sp. #1 ($P < 0.05$; Wilcoxon paired-sample rank-sum test). All the other *Gracilaria* species showed no significant differences in frequency of males and females (Fig. 5).

The timing of gametophyte reproduction was similar in the five most abundant *Gracilaria* species (Figs. 5-6). Thus there was no indication that hybridization could have been prevented by temporal partitioning of gametophyte fertility. Similarly, the hypothesis that species partition attachment sites by producing spores at different times of the year does not appear valid for these species; all species were reproductive throughout the year (Figs. 5-6).

Discussion

At the sand-plain study site on the Galeta reef, underwater light fluctuates widely on a seasonal basis (Hay, 1981), while temperature and salinity vary only slightly (Hendler, 1976). Most species showed an increased percentage of reproduction just after the onset of the dry-season (Figs. 5-6). This pattern was especially prominent in tetrasporophytes of *G. cuneata, G. domingensis, Gracilaria* sp. #2 and *Gracilaria* sp. #3; *Gracilaria* sp. #1 being the exception (Fig. 5). Reproduction that is associated with or stimulated by the onset of adverse physical conditions is often selected for in plants that have resting stages that are more resistant to physical stress than normal vegetative stages (Williams 1975; Grime 1977). In many species of algae, environmental changes stimulate the formation of gametes (Dring, 1974; Clayton, 1982). For most of the species studied here, there is a 4- to 5-month delay between the reproductive peak in December-January and the increase in plant density that occurs in late April or early May.

As none of the *Gracilaria* species is known to have a spore that functions as a resting stage, the most probable explanation for this lag is that the early developmental stages are able to persist throughout periods that are stressful for the macrothalli. Increased tolerance of early developmental stages has previously been documented for several seaweeds occurring in environments subject to seasonal changes in physical conditions (e.g., Richardson, 1979, 1981). If early developmental stages, which should be most abundant following the onset of the dry-season (Fig. 5), are more resistant to low light intensity, this would be especially important for *Gracilaria cylindrica, G. domingensis* and *Gracilaria* sp. #3 because the macroscopic forms of these species suffer the largest losses coincident with the dry-season darkness (Fig. 5). Loss of macrothalli during the dry-season appears to be related primarily to low light intensity; experimentally, we found that these species will settle and grow to maturity during the turbid dry-season if light levels are artificially raised by providing attachment sites in the higher intensity light regimes near the surface (see Hay, 1981). Perennation by persisting holdfasts (Dixon, 1965, 1973; Dayton, 1975; Sousa, *et al* 1981) should also be considered a possibility for these species.

The reproductive patterns documented in this study differ from most other studies in two respects: ratio of males to females, and of tetrasporophytes to gametophytes. First, only one species, *Gracilaria* sp. #1, exhibited a significantly higher number of

female than male plants (Fig. 5); all others showed no significant differences. Most previous studies found fewer male than female plants (e.g., Powell, 1964; Neushul, 1972; Tveter-Gallagher, et al 1980; Kain, 1982; Peckol, 1982). The low proportion of males in most studies may be the result of the increased difficulty in recognizing males during the early developmental stages, the shorter period of fertility of the males (Tveter-Gallagher, et al 1980), or the inadequacy of the sample size and sampling regime. As in our study, a nearly equivalent proportion of males to females was found by Hoyle (1978) in Gracilaria bursa-pastoris from Hawaii. Hoyle (1978) also recorded significantly more male than female thalli in G. coronopifolia. This phenomenon of a more-or-less equal ratio of gametophytes in some tropical Gracilaria species is difficult to reconcile with the unequal numbers found in other studies. The documentation of uneven ratios of reproductive condition by previous studies appears to have been conducted very thoroughly (e.g., Kilar & Mathieson, 1978; Hoyle, 1978; Kain, 1982). Perhaps the 1:1 male:female ratio recorded at Galeta reflects a phenomenon peculiar to perennial, tropical algae (or uniqueness of the physical conditions of the sand plain). It is not known if these plants have a normal life history; the possibility of their being apomictic, as has been found in the culture of some Gigartinaceae (Polanshek & West, 1977; West, et al 1978; West & Hommersand, 1981), or sexual, should be investigated. Most studies of reproductive seasonality have been conducted in temperate climates where it may be adaptive for male reproduction to the compressed into a smaller portion of the season to allow for maturation of the carposporophyte during the short growing season.

The second finding at variance with published accounts is that, as a whole, tetrasporophytes are not consistently more abundant than gametophytes. In our study, we found tetrasporangial plants not to be dominant over the gametangial plants in three of the five species studied. Gametophytes were in fact significantly more abundant than tetrasporophytes in Gracilaria sp. #1 and Gracilaria sp. #3, and there was no significant difference found in G. cuneata; tetrasporophytes were, however, more abundant than gametophytes in G. domingensis and Gracilaria sp. #2. In the temperate Pacific, Abbott (1980, Table 1, Fig. 1), using biomass (dry wt), reported more gametangial than tetrasporan-

gial plants throughout the year for three intertidal species of Gigartinaceae. In most perennial species of red algae, however, the sporophytic phase in a population dominates the gametangial generation (Hoyle, 1978). Dixon (1965) pointed out that the relative abundance of fertile tetrasporophytes usually increases toward the geographic extremes of a species' distribution. Some other studies of reproductive seasonality may have been done nearer the extremes of the species' ranges (e.g., Kain, 1982); higher proportions of tetrasporophytes are to be expected in these areas (Dixon, 1963, 1965; Kapraun, 1978). Other explanations for this reported phenomenon include: higher mortality of gametangial thalli (Johnstone & Feeney, 1944), response to the sublittoral habitat (Knaggs, 1969), inherent advantages of diploidy over haploidy (Hansen & Doyle, 1976), and periodic development of tetrasporophytes from tetraspores through apomeiosis (Hansen & Doyle, 1976). Tetrasporophytes dominated gametangial plants in two tropical Gracilaria species studied by Hoyle (1978); however, he reported no evidence to support any of the above hypotheses, and suggested that all except Dixon's and Knaggs's were plausible for this site.

Recently Bird & McLachlan (1982) attempted to cross five species of Gracilaria under laboratory conditions and indicated that all were sexually incompatible. While these experiments should be repeated under a wide variety of physical and cultural conditions in the laboratory and field, their negative results are consistent with our findings that fertile gametophytes of several different species can overlap in time (i.e., no temporal reproductive partitioning) and space (i.e., being sympatric) and do not produce obvious hybrids. Because reproductive activity of these tropical Gracilaria species is not separated spatially or temporally, some other mechanism, such as chemical or structural recognition, must be responsible for maintaining reproductive isolation.

The seasonal patterns of reproduction are also inconsistent with the hypothesis that available attachment sites are being partitioned temporally. The seasonal differences in spore production (Figs. 5-6) are insufficient to account for the maintenance of so many sympatric species in this habitat.

It appears that these species of tropical Gracilaria have adapted to unstable environments by being asexually and sexually reproductive throughout the

year, thereby increasing successful recruitment and survival. This is especially evident by their increased reproductive effort at the onset of stressful conditions. Gametophytic and tetrasporic generations differ in the amount of genetic variability expressed (see Maynard Smith, 1971, 1978; Grant, 1971), and these may represent different adaptations for species living in an unstable environment.

This study raises several questions: Could the unusually high diversity [i.e., six competitively competent species (Hay 1981) in the same genus] be due to the continuous disturbance preventing competitive exclusion, or to subtle differences in niches? What is the advantage of sexual versus asexual reproduction in an unstable environment? If these species can persist by perennation, why the large effort in tetrasporangial and carposporangial production? Finally, what is the relationship between the cost of carposporangial and tetrasporangial spore production and successful recruitment and survivorship?

Acknowledgements

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