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Seasonal growth, density, reproductive phenology and agar quality of *Gracilaria sordida* (Gracilariales, Rhodophyta) at Mokomoko Inlet, New Zealand

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Abstract

Growth of mesh-enclosed *Gracilaria sordida* plants was determined monthly for one year at the Mokomoko mudflat, South Island, New Zealand. Growth of plants with permanent water cover was correlated with water temperature and was most rapid during summer months. Plants exposed at low tide grew only during early spring and late autumn. Bimonthly quadrat sampling of a mudflat population showed that all stages of the life cycle were present throughout the year. Spermatangial plant length and biomass were greatest in early spring; cystocarpic and tetrasporic plants were greatest in midsummer. Sterile plants were most numerous in the late summer. Agar yield showed little variation either seasonally or between different stages of the life cycle. Agar gel strengths for all life cycle stages were greatest at the time of peak plant size and abundance. Gels from spermatangial plants generally were weaker than those from other stages.

Introduction

The seaweed *Gracilaria sordida* W. A. Nelson (Gracilariales, Rhodophyta) is of commercial interest in New Zealand as a source of agar and as a food for farmed abalone *Haliotis* spp. The biology of *Gracilaria* spp. lends itself to a variety of cultivation methods, from harvest and management of wild populations, to longline or raft farming or to intensive onshore cultivation systems (Lignell *et al.*, 1987; Pickering, 1989; Santelices & Doty, 1989). However, highly productive intensive systems require large inputs, which may render them uneconomic (McLachlan & Bird, 1986).

The most likely scenario for commercial utilization of *Gracilaria sordida* in New Zealand is harvesting and enhancement of natural populations as in Chile (Santelices *et al.*, 1984; Pizzarro & Barrales, 1986; Poblete & Inostroza, 1987) or extensive, low-input pond farming as in Taiwan (Chiang, 1981). Accordingly there is a need for study of *G. sordida* field populations as a basis for managing and enhancing wild crops and for developing suitable pond-farming methods (Nelson, 1989).

The aim of this study was to find out how the productivity of *Gracilaria sordida* varied in a natural environment between seasons, between micro-environments within a locality, and between two geographically isolated ecotypes of this species. Since productivity is a function of

(1) growth rate and (2) biomass (McLachlan & Bird, 1986), plant growth and density were monitored in experimental plots over a full year. To provide information on reproduction and recruitment processes, sampled plants were grouped according to sex. Lastly, the quantity and quality of extracted agar was determined for plants of each sex at different times of the year. The study location was at the Mokomoko Inlet near Bluff, New Zealand, an area of interest for commercial *Gracilaria* farming.

Materials and methods

Seasonal growth

On 14 June 1987 two experimental sites were established at Mokomoko for a year-long comparison of *Gracilaria* growth rate. Both sites were on a mudflat at the mean low-water mark; one retained about 50 mm depth of water at low tide (Site 1) whereas the other was drained of water for 4–5 hours at each low tide (Site 2). The effect on growth of exposure to the air at each low tide could thus be compared with the effect of permanent water cover. Also, 'Manukau' and 'Mokomoko' ecotypes were being compared as candidates for commercial cultivation. Plants belonging to the 'Manukau' ecotype were collected from Manukau Harbour, North Island, New Zealand (37 °S, 175 °E) in March 1987 and were maintained in indoor culture along with plants from Mokomoko Inlet (46 °30′ S, 168 °E) at the Mahanga Bay Shellfish Hatchery (MAF) in Wellington. The *Gracilaria sordida* plants used in the experiment were weighed into 30 g aliquots (drip-dry fresh weight), and placed in sock-like plastic mesh bags (0.5 m long, 0.1 m wide, mesh size 5 mm). The plants used were predominantly of the tetrasporophyte generation, and although some gametophytes were present, their proportion was not estimated. Four replicate bags of each plant variety were tied between stakes pushed into the mudflat, and lay at ground level on the mud. At the end of each growth period (roughly 4 weeks) the plants were recovered, washed and weighed. They were replaced by bags containing new plants from the stock cultures at the Mahanga Bay Shellfish Hatchery.

For each 4-week growth period, the growth rate of harvested plants was expressed as the 'mean relative growth rate' ($\overline{R}$) in% day^{-1}, using the formula in Hunt (1978):

$$\overline{R} = \frac{(\ln W_2 - \ln W_1)}{t_2 - t_1} \cdot 100$$

where W_2 is the fresh weight at time t_2, and W_1 is the fresh weight at time t_1.

Seasonal density

Two further sampling sites were marked at Mokomoko Inlet, one a 20 × 5 m area in a rocky-bottom channel with 100 mm water depth at low tide (Site 3), and one a 20 × 20 m intertidal mudflat area exposed for 4–5 hours at each low tide (Site 4). The sampling method was similar to that described by Nelson (1989). Plants were collected from randomly selected 0.5 × 0.5 m quadrats at each sampling site until 10 (Site 3) or 25 (Site 4) quadrats containing plants had been sampled. The number of quadrats sampled ensured that at least 300 plants were collected at each sampling date. Sampling at these sites began in July 1987 and continued at roughly two-month intervals until July 1988. Plant samples were washed and the drip-dry fresh weight recorded.

For samples from Site 4 only, individual plants were classified according to sex. The length of each plant was measured to the nearest mm from thallus base to most distal tip. Plants of each sex were grouped from all quadrats and dried to constant weight at 60 °C for determination of % dry weight and for agar analysis.

By combining growth-rate data with reasonable assumptions for plant density, estimates of yield (as defined by Sorokin, 1973) were calculated as follows:

$$Y = \frac{X_1 - X_0}{A}$$

where 'A' is the area under cultivation, 'X_0' is the initial biomass (equivalent to 'W_1' in the $\overline{R}$ formula), and 'X_1' is the final biomass. This final biomass can be estimated by rearranging the $\overline{R}$ formula as follows:

$$\ln W_2 = \ln W_1 + \frac{\overline{R} \cdot (t_2 - t_1)}{100}$$

Yield was estimated firstly by assuming an initial plant density half that found naturally at Site 3, in accordance with the recommendation by Luxton (1977) that standing stocks be harvested to 50% so rapid regeneration is possible. A second estimate used an initial density of 500 kg (dry wt) ha^{-1}, a figure often used when stocking culture ponds in Taiwan (Chiang, 1981).

Agar extraction method

Batches of seaweed (10 g dry wt) were washed in running distilled water for 2 h to extract cold-water solubles, then redried and weighed. A 5% stock solution of sodium dihydrogen phosphate was used as a buffer in an extraction medium consisting of 10 mL buffer and 290 mL distilled water. The medium was adjusted to pH 6.00 with dilute NaOH, then added to the dried plant material and autoclaved at 120 °C for 30 min. The hot gel solutions were filtered first through muttoncloth, then through Whatman 541 filter paper under suction. Gels were frozen and allowed to thaw. The thaw water was drained, and the cold-water insoluble fraction of agar was washed liberally with distilled water on a 100-μm mesh sieve, dried to constant weight at 60 °C, and weighed. This weight was the 'agar yield' and was expressed as a percentage of the initial 10 g dry weight. The dry agar was ground in a hammer mill and reconstituted into 1.5% solutions. The rupture strength of agar gels was measured at 20 °C using a cylindrical hollow plunger (cross-sectional area = 1.0 cm^2) balanced on the gel surface. Water was added to the plunger at a constant rate of 200 mL min^{-1}. When the gel ruptured the water flow was stopped, and the plunger removed and weighed. This weight was recorded as the 'gel strength' in g cm^{-2}. Four replicate measurements were recorded for each batch.

Environmental factors

The maximum and minimum water temperature was recorded weekly at Sites 1–3 during the study. Every second week a water sample was collected and frozen for subsequent measurement of salinity, pH, and nitrate, nitrite, and ammonium concentrations. The monthly duration of bright sunshine was recorded by the New Zealand Meteorological Office using a Campbell-Stokes sunshine recorder at Invercargill Airport, 12.5 km to the north.

Statistical analysis

Differences between treatments were tested using one-way ANOVA. For the sake of brevity F-values have not been shown.

Results

The weight of *Gracilaria* plants placed in bags at the submerged outplanting site (Site 1) decreased from July to September 1987, increased from October to March 1988, and decreased from April to July 1988 (Fig. 1). During the summer growth period 'Manukau' plants often grew faster (5% day^{-1}) than 'Mokomoko' plants (4% day^{-1}) although the difference was not always significant. At the exposed outplanting site (Site 2) plants lost weight at all times of the year except for short periods of slow growth in August-September and March-April.

The beginning and end of the growth season showed a correlation with seasonal patterns in water temperature and sunshine hours. The water temperatures recorded at Sites 1–3 were similar, ranging from 0 °C (winter minimum) to 32 °C (summer maximum). The duration of bright sunshine showed the same seasonal trend as tem-

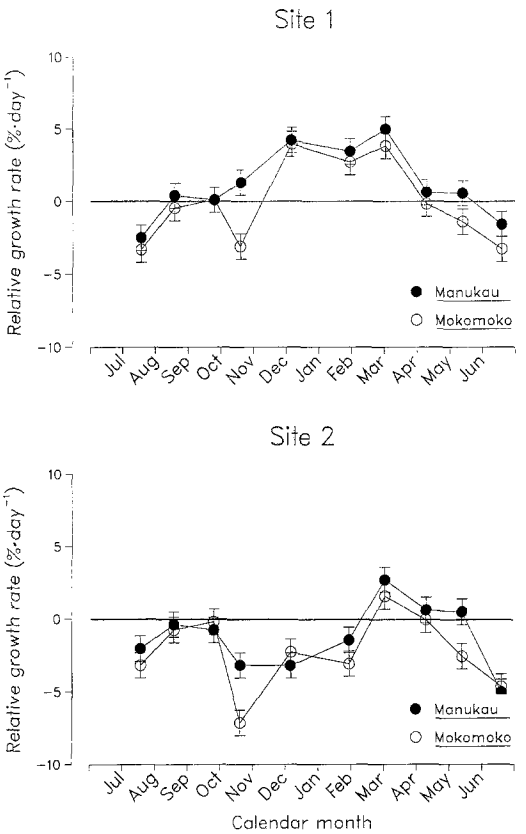

Fig. 1. Seasonal relative growth rate (wet wt day^{-1}) for two ecotypes of *Gracilaria sordida* at the submerged (Site 1) and exposed (Site 2) outplanting sites, recorded from July 1987 to June 1988. Each point represents the mean relative growth rate ($\bar{R}$) over an approximately 4-week period. Error bars represent 95% confidence intervals based on a pooled standard deviation.

perature, ranging from a winter minimum of 60 hours per month to a summer maximum of 200 hours per month. There were no seasonal trends in salinity, pH or nitrogen levels, and levels of these factors fluctuated daily over a wide range in response to tides.

Plant biomass of naturally occurring plants differed greatly between Sites 3 and 4 (Fig. 2). The density of plants at Site 3 (submerged site) rose from a minimum of around 500 g m^{-2} to 2000 g m^{-2} (wet wt) in February and March, then decreased during the following autumn and winter. Plant density at Site 4 (periodically-exposed site) was greatest in December at 112 g m^{-2} and declined over summer to a winter minimum of

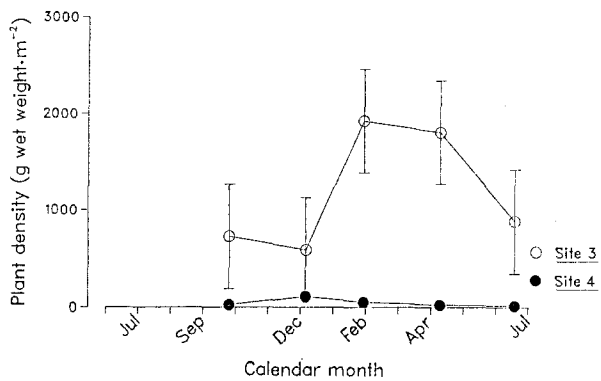

Fig. 2. Seasonal density of *Gracilaria sordida* plants (g fresh wt m^{-2}) at Site 3 (submerged) and Site 4 (periodically-exposed). Error bars represent 95% confidence intervals based on a pooled standard deviation. Confidence intervals for Site 4 ($\pm$ 45 g wet weight m^{-2}) are contained within the closed circles.

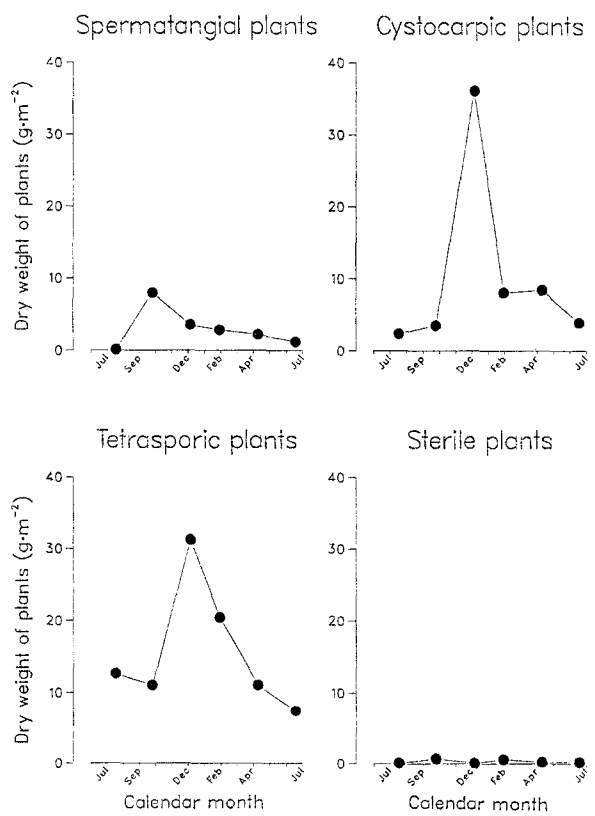

Fig. 3. Seasonal density for different reproductive groups of *Gracilaria sordida* plants (g dry wt m^{-2}) at Site 4 (periodically-exposed). Data points represent a single estimate of plant density after plant material was pooled between quadrats.

15–25 g m^{-2}. The peak in biomass was reached later in the season at the submerged site, where it persisted longer.

The seasonal yield of *Gracilaria sordida* plants at Mokomoko was estimated using two sets of assumed values for plant density, as described above. The 'annual yield' was taken to be the cumulative yield found by summing values estimated over the positive portions of the growth curve of Mokomoko *Gracilaria* in Fig. 1 (upper graph). Assuming an initial density half that observed for each sampling date at Site 3 (submerged site) (Fig. 2), this yield would be 6.7 t (dry wt) ha^{-1} yr^{-1}. If an initial density of 500 kg (dry wt) ha^{-1} were used, the annual yield would be 7 t (dry wt) ha^{-1} yr^{-1}.

The density of spermatangial plants at Site 4 (Fig. 3) formed a peak in September, and a peak in cystocarpic plant density followed in December. Tetrasporic plant density also became highest in December, and this peak persisted through to February. The density of sterile plants remained low throughout the year. The abundance of fertile plants in each quadrat at Site 4 (Fig. 4) did not vary significantly between seasons although they appeared more numerous during the summer months. Sterile plants became very abundant in February and April. The average length of spermatangial plants peaked in September and December (Fig. 5). The average length of cystocarpic and tetrasporic plants peaked in December. Sterile plants did not show any seasonal trend in length. The dry weight of plants at Site 4, as a percentage of their fresh weight, varied seasonally, with plants collected in summer

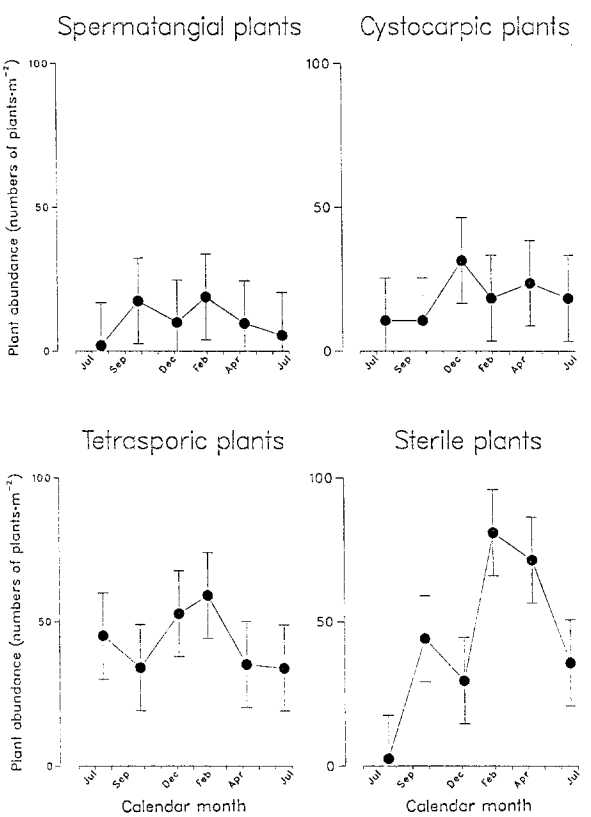

Fig. 4. Seasonal abundance for different reproductive groups of *Gracilaria sordida* plants (numbers of plants m^{-2}) at Site 4. Error bars represent 95% confidence intervals based on a pooled standard deviation.

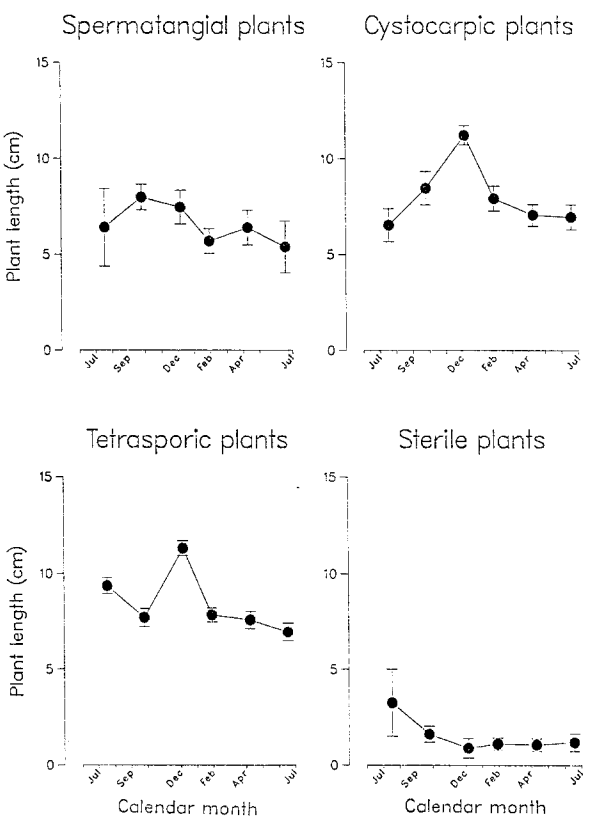

Fig. 5. Seasonal plant length for different reproductive groups of *Gracilaria sordida* plants (cm) at Site 4. Error bars represent 95% confidence intervals based on a pooled standard deviation. Intervals vary because of sample size differences.

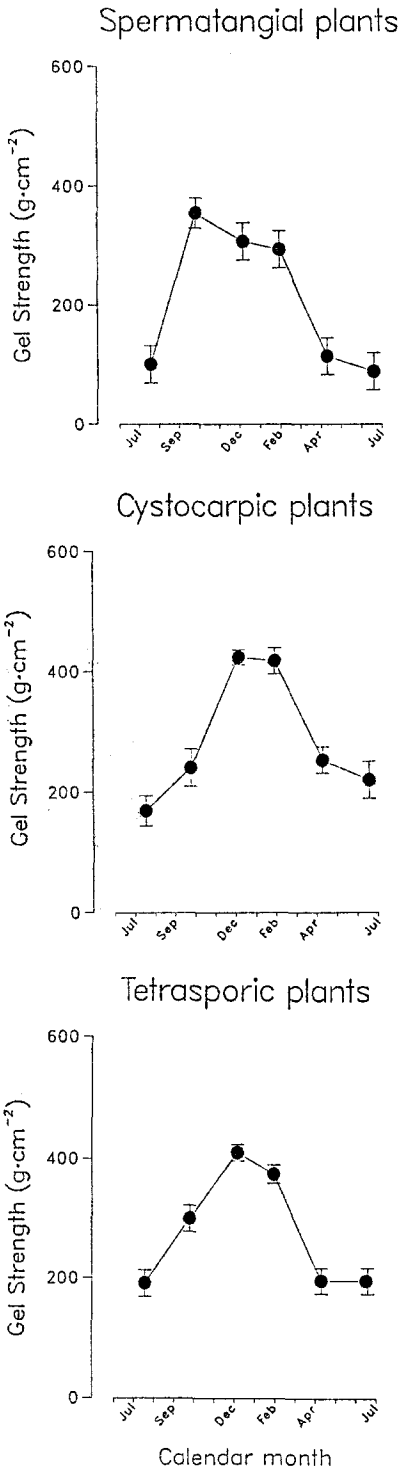

Fig. 6. Seasonal changes in the gel strength (g cm^{-2}) for different reproductive groups of *Gracilaria sordida* plants at Site 4. Error bars represent 95% confidence intervals based on a pooled standard deviation. Intervals vary because of sample size differences.

(December to February) containing a lower proportion of dry matter (9.5–10%) than at other times of the year (13–14%).

The yield of agar in plants at Site 4 followed no particular seasonal trend and was no different between sexes. Values ranged from 16% to 23% of initial plant dry weight. The gel strength of agar (Fig. 6) showed clear differences both between sexes and at different times of the year. Agar gels from spermatangial plants were strongest in September (354 g cm^{-2}), decreased over summer and were low at all other times of the year. Agar gels from cystocarpic and tetrasporic plants were strongest in December and February (423 and 411 g cm^{-2}, respectively). There was no significant difference between cystocarpic and tetrasporic plants. However, agar gels from spermatangial plants were much weaker than those from cystocarpic and tetrasporic plants at all times of the year except September, when there was no difference.

Discussion

Net growth of *Gracilaria sordida* plants occurred during seven months of the year at the site where thalli were permanently immersed (Site 1). The peak mean relative growth rate ($\overline{R}$) values of 4–5% day^{-1} are at the lower end of the 5–10% day^{-1} range considered typical for *Gracilaria* spp. by McLachlan & Bird (1986) and are similar to the 1–4.6% day^{-1} range reported by Luxton (1977) for plants in Manukau Harbour, New Zealand. However these estimates are conservative. Although the effect of density on growth was not known, the plant density in the bags during rapid summer growth often became high, and self-shading may have limited growth.

The loss of biomass in winter was due to regeneration rates being unable to compensate for thallus fragmentation and loss of tissue. Fragmentation could be caused by excessive water movement or by portions of thallus becoming necrotic after experiencing freezing conditions at night during low tides. McLachlan & Edelstein

(1977) reported necrosis in a species of *Gracilaria* at 10 °C and below, though *G. tikvahiae* apparently can tolerate prolonged periods of sub-zero temperatures (Edelstein *et al.*, 1976). Laing *et al.* (1989) and Lignell (1988) reported significant *G. sordida* growth at 10 °C and 8 °C, respectively, and the growth season at Mokomoko probably was initiated when water temperatures rose above these levels. The upper limits to water temperature would have been due to warming at low tide, hence their close coupling to sunshine hours. At high tide, typical sea temperatures prevailed and ranged from 10 to 20 °C between winter and summer.

Growth of the periodically-exposed outplanted thalli (Site 2) also increased in spring as water temperatures rose, but at the height of summer these plants lost weight. The maximum water temperature recorded at both sites during summer was 32 °C, which is beyond the upper limit of the tolerance range for *Gracilaria sordida* plants (Lignell, 1988). The actual temperature experienced by dark-colored thalli exposed to direct sunlight on a summer day may have risen still higher, and such thalli were very warm to the touch. A combination of stress from high temperature and stress from desiccation (Hodgson, 1984) is the most likely cause of this lack of summer growth. Comparison of growth at these two sites highlights the importance of keeping cultivated plants permanently immersed and shows that the productivity of many intertidal *Gracilaria sordida* populations may be greatly increased if water can be retained at low tide.

Of the two *Gracilaria sordida* ecotypes compared here, the 'Mokomoko' variety was expected to be better adapted to local conditions than the transplanted 'Manukau' variety. However, the 'Manukau' variety often grew faster. This may have been due to morphological differences between the two ecotypes. The 'Manukau' plants were bushier and more finely branched than the thicker, coarser-looking 'Mokomoko' plants. Calculation of a 'branching index' showed that 'Manukau' plants had 1050 branches g^{-1} (S.D. = 290) whereas 'Mokomoko' thalli bore 370 branches g^{-1} (S.D. = 140). Since growth is initiated by the apical cell of each branch, a much-branched variety would be expected to gain weight more rapidly.

The large difference in the density of plants occurring naturally at Sites 3 and 4 shows that Site 3 is more like that required for successful farming. At this submerged, rocky site, the density of plants was much greater at all times of the year, and the summer density peak lasted longer compared with the intertidal mudflat (Site 4). The mean size of plants was also much greater (data not shown). The permanent water cover at site 3 may have allowed a longer growing season by preventing stress from heat and desiccation.

The other obvious environmental difference between the two sites was the rocky bottom at Site 3 and the soft mud with scattered clam shells at Site 4. A higher density of plants was apparently due to the far greater surface area available for plant attachment at Site 3. Henriques (1978) documented two growth habits for *Gracilaria sordida* in Manukau Harbour: (1) dense aggregations of loose, vegetatively propagating thalli partially buried in soft bottom sediment, and (2) sparsely distributed fertile single thalli attached by holdfasts to stones or shells. The *G. sordida* populations at Mokomoko are of the latter type. Dense 'meadows' of large plants were found at Mokomoko only where there was an abundance of substratum suitable for spore settlement and where water was retained at low tide. Other experiments at Mokomoko have shown that providing artificial substrata can increase the productivity of a site (Pickering, 1990).

Since the environmental conditions at the submerged-population site were similar to those likely to be provided by a commercial pond, production figures estimated for this site are expected to be realistic. There are several ways of estimating 'production' or harvest 'yield', and such estimates can vary greatly depending on the assumptions for starting density and harvest-season length. It was decided to define 'production' here as the yield a farmer might expect to harvest given assumed values for growth rate, initial density, and dry matter content at different times of the year. The values obtained in this way (6.7 and

7.0 t ha^{-1} yr^{-1}) were similar to values reported in studies reviewed by McLachlan & Bird (1986).

An alternative method of calculating annual yield is to assume that the average standing biomass for the December–April period is cropped to 50% four times during summer. This method was used by Luxton (1977) to estimate the projected yield for a *Gracilaria sordida* 'meadow' in Manukau Harbour, and values in the range of 5.8–6.9 t (dry wt) ha^{-1} yr^{-1} were obtained. The mean density at Site 3 over summer was 216 g (dry wt) m^{-2}, so according to this method the yield should be 4.3 t (dry wt) ha^{-1} yr^{-1}. According to McLachlan & Bird (1986) production of *Gracilaria* spp. in natural environments typically does not exceed 5 t (dry wt) ha^{-1} yr^{-1}, although for pond aquaculture, figures may be as high as 40 t (dry wt) ha^{-1} yr^{-1}.

Reproductive plants were present in the population throughout the year, but they were less dense in winter. Sterile plant density did not change significantly between seasons. This would have caused the proportion of sterile plants in the total biomass to increase in winter as observed by Whyte *et al.* (1981), Penniman *et al.* (1986) and Nelson (1989). Sterile plants tended to be small plants that had not yet become reproductive and thus were juveniles of other reproductive stages.

At the onset of the growing season, spermatangial plants at the exposed site were first to increase in size and density, forming a peak in September and declining over the rest of summer. They always were less dense than other stages. Cystocarpic plants reached their peak in length and density in December and declined over the rest of summer. Whyte *et al.* (1981) also found a lag in the seasonal peak of cystocarpic plants behind that of spermatangial plants. It could be assumed that fertilization occurs chiefly in spring.

Although there were slight springtime peaks in numbers of fertile plants, seasonal differences in abundance were not significant. The spring density peak appeared to be caused by increases in plant length. This contrasts with the central New Zealand *Gracilaria sordida* populations studied by Nelson (1989), where there was little seasonal variation in plant length and where density increases were due to higher plant numbers and a springtime increase in plant bushiness. The drop-off in density and length of fertile plants at Mokomoko as summer progressed was most likely due to thallus fragmentation and necrosis of thallus extremities, induced by heat stress, rather than to any post-reproductive deterioration in condition. Large thalli are higher off the mud and are more vulnerable to damage from wind, sun and water movement.

Sterile plants formed the only category in which variation in plant numbers was more meaningful than length or density. Sterile plants formed an almost insignificant part of the population in terms of size or density at all times of the year. But a late-summer peak in numbers of sterile plants extended from February to April, during which time they outnumbered other categories. Wang *et al.* (1984) and Boraso de Zaixso (1987) also reported an abundance of small plants in summer and suggested that this was the main time of recruitment.

A peak in sterile plant abundance might predictably appear after the spring peaks in cystocarpic and tetrasporic plant density, but one must be wary of assuming that this is due to a springtime increase in spore release from these stages. It could be that late summer is the most favorable time for spore survival and growth; hence the appearance of a cohort of small sterile plants might be a result of either high spore settlement, or high spore survival, or both. Moreover, it is not yet known whether *Gracilaria sordida* has perennial holdfasts that may contribute to the production of new sterile shoots. Unless regeneration is the most important source of new growth, the presence of fertile plants all year round suggests that recruitment might occur whenever conditions are favorable for spore survival. Seeding farm substrata with spores, as described by Santelices & Doty (1989), could be carried out at any time of the year at Mokomoko.

The% dry weight of plants at the exposed site varied seasonally in that values were lowest during summer (9%) and were highest in winter (14%). Similarly Friedlander *et al.* (1987) found that these values varied from 10 to 17% and

Penniman & Mathieson (1987) reported values of 8 to 18% between summer and winter, respectively.

The % yield of agar did not show any obvious trends either seasonally or between categories of plants. Agar yields generally decline during summer or during periods of rapid growth (Rotem *et al.*, 1986; Christiaen *et al.*, 1987; Edding *et al.*, 1987; Friedlander *et al.*, 1987; Penniman & Mathieson, 1987). According to Christiaen *et al.* (1987) either plant growth or agar deposition will be promoted depending on temperature.

Gel strengths commonly have been reported as higher from plants harvested during summer, with the difference caused by lower levels of sulfate substitution on agar polymers (Asare, 1980; Whyte *et al.*, 1981; Friedlander & Zelikovitch, 1984; Rotem *et al.*, 1986; Friedlander *et al.*, 1987; Bird, 1988). Conversely, there also have been reports of lower gel strengths and higher sulfation levels during summer or in high temperatures (Craigie & Wen, 1984; Cote & Hanisak, 1986; Christiaen *et al.*, 1987). The levels of sulfation in agars extracted during this study were lowest during summer, when gel strengths were highest. These sulfation results will be presented in detail elsewhere (Pickering, 1990). Miller & Furneaux (1987) have reported lower sulfation of agar in summer *Gracilaria sordida* plants harvested from the Pauatahanui site studied by Nelson (1989). Another agar parameter with a role in determining gel strength, but so far little studied in relation to environmental changes, is the average molecular weight (polymer length) of agar molecules (Bird *et al.*, 1981).

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