Growth, Survival and Reproduction of Two Species of Marine Algae at Different Densities in Natural Stands
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GROWTH, SURVIVAL AND REPRODUCTION OF TWO SPECIES OF MARINE ALGAE AT DIFFERENT DENSITIES IN NATURAL STANDS

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SUMMARY

(1) Naturally-occurring monospecific stands of two subtidal fucoid species, an annual, Sargassum sinclairii and a perennial, Carphophyllum maschalocarpum, were monitored from recruitment, at high and low densities, in northern New Zealand.

(2) Individuals of both species grew faster and attained a larger size in the high-density stands.

(3) Survivorship rates fluctuated throughout the year for low- and high-density Sargassum sinclairii, but a higher proportion of low-density plants survived at the end of the year. Carphophyllum maschalocarpum plants showed higher survivorship at low density, but all plants in these stands which remained at the end of the study were stunted.

(4) Size-frequency distributions through time tended to be positively skewed for both low- and high-density stands of Sargassum sinclairii. For both species, however, there was little indication that most plants at high density were being trapped under the canopy of a few large individuals.

(5) Ninety-two per cent of the S. sinclairii plants became reproductive in high-density stands, compared with 46% at low density. Forty per cent of the Carphophyllum maschalocarpum plants became fertile after the second year of growth at high-density, while none of the low-density plants became reproductive.

(6) The bearing of receptacles is clearly related to plant size, and most plants of both species at low density did not attain a large enough size to reproduce. For both species, the proportion of plant weight invested in receptacles increased with plant size. In addition, the greatest recruitment for Sargassum sinclairii occurred near dense adult stands.

(7) High density aggregations may be important for the establishment and maintenance of populations of large brown algae. There may be important differences between terrestrial and marine systems with respect to some density effects.

INTRODUCTION

Interactions among plants have received far less attention than those between plants and herbivores in investigations of algal community structure in subtidal marine systems. For example, several studies have shown that the removal of grazers, especially echinoids, can result in a high recruitment of large brown algae (Jones & Kain 1967; Pearse & Hines 1979; Paine & Vadas 1969; Duggins 1980). There are only a few studies, however, which have followed the development of algal populations and community structure in the absence of herbivores (Dayton 1973; Pearse & Hines 1979; Duggins 1980; Reed & Foster 1984). The growth rates of the plants, their reproductive output and survivorship may have important community consequences (e.g. Black 1972, 1974; Chapman 1979).

There are parallels in studies of terrestrial environments, where the structure of plant communities may be the result of grazing (Harper 1977; Dirzo & Harper 1980), as well as events among plant species (Harper & McNaughton 1962; Harper 1977). Terrestrial plant
ecologists, however, have long recognized that the structure of plant communities and the yields of populations may depend on the demography of individual plant species. Because of agronomic uses, the single-species aggregations of many plants and the tractability of experiments using single species, there has been great interest in assessing within-species events in monospecific stands (Donald 1951; Kira, Ogawa & Sakazaki 1953; Yoda et al., 1963; White 1980). In these cases, the abundance of immediate neighbours has been shown to have a great effect on individual plants in a stand. A large body of evidence indicates that, on average, crowded plants should have reduced growth, survivorship and reproductive output compared with those at lower densities. Of particular importance is that these effects are not evenly distributed among the individuals in a population. Size or weight frequency distributions tend to be skewed, with a few dominant individuals having trapped many others beneath their canopy (Mohler, Marks & Sprugel 1978; Ogden 1970). Similar studies have rarely been done in marine algal systems, except for some species of red algae in cultivation (Yoshida 1972; Adams & Austin 1979) and for Egregia menziesii (Turn.) Aresch. (Black 1972, 1974).

Large, predominantly single-species aggregations of brown algae occur both intertidally and subtidally in many boreal and temperate areas of the world (Stephenson & Stephenson 1949, 1972; Kain 1962; Mann 1972; Dayton 1975; Duggins 1980). In subtidal regions of north-eastern New Zealand, stands of fucoid and laminarian algae often show a disjointed distribution with echinoids, the major herbivores (Choot & Schiel 1982; Schiel 1982). These distributions may remain stable and the algae may persist for long periods without being affected by the echinoids. It is of interest, therefore, to assess the patterns of development of natural populations of plants in the absence of these herbivores.

A static sampling programme of plants of known age at different densities indicated that two species of algae did not undergo some of the adverse effects which are common for terrestrial plants in dense stands (Schiel & Choot 1980, 1981). For a laminarian, Ecklonia radiata, and a fucoid, Sargassum sinclairii, plant size was positively correlated with density on a shallow subtidal reef.

This present study is of post-recruitment events. The consequences to individuals of being in natural, monospecific stands at two different densities of recruitment were investigated. Growth, reproduction and survivorship were examined for two species which are common subtidally in northern New Zealand. To reduce the number of confounding factors influencing density effects, stands of these plants were located at similar depths on the same reef, so that general environmental conditions such as exposure, water clarity and temperature were similar, and all plants in these stands were new recruits. Two questions were asked: (i) how do plants respond to different densities of natural recruitment?; and (ii) what are the population and community consequences of these responses? The answers serve as a basis for further studies involving the experimental thinning of stands.

MATERIAL AND METHODS

Study sites and organisms

This work was done near the Auckland University Marine Laboratory in north-eastern New Zealand (36°16'S, 174°48'E). Study sites were in the shallow subtidal areas (3–7 m depth) of Waterfall Reef in the Cape Rodney-Okakari Point Marine Reserve. This reef is in the lee of the prevailing south-westerly winds and is subject to a mean wave rise and fall of about 1 m. Occasional north-easterly storms may generate waves of more than 10 m. The boulders on which the study plants were located were each at least 3 m² in projected
surface area and were distributed over an area of about 3000 m². Boulders with different densities of plants were often adjacent (i.e., c. 1 m apart), but the boulders selected for study were scattered among hundreds of others. Waterfall Reef is described by Jones & Thompson (1980), Ayling (1981) and Kingett & Choot (1981).

The two species of algae investigated are both endemic to New Zealand: *Sargassum sinclairii* Hook. & Harv. and *Carpophyllum maschalocarpum* (Turn.) Grev. In the remainder of this paper they will be referred to by their generic names only. They were chosen because they are very abundant on Waterfall Reef, are common along the north-eastern coast of New Zealand (Choot & Schiel 1982), and are suitable for measurements of growth rates over the period of a year. A further advantage of using these fucoid species is their seasonal development of discrete receptacles, which may be removed from plants to give an assessment of reproductive output. It is assumed that the output of gametes per receptacle is similar for plants of all sizes (Schiel 1981).

Most work for this study was done with *Sargassum*, which is monoecious (Lindauer, Chapman & Aiken 1961), grows quickly relative to the other fucoid species and is deciduous, shedding most of its thallus annually (Schiel 1981). It grows by producing short branches with large basal 'leaves'. Longer, side branches arise from the primary ones and are somewhat slender and delicate. These bear smaller leaves, vesicles and receptacles (Lindauer, Chapman & Aiken 1961). An individual is easily distinguished because of its discrete discoid holdfast, which rarely fuses with that of another plant. *Carpophyllum* is dioecious, perennial and relatively slow-growing. It has flat main axes, up to 9 mm wide and 1.5 m long, which arise from a flattened holdfast with branched haptera. The 'leaves' are regular and alternate, and large vesicles (10–23 mm long) are present. Secondary and tertiary branches often occur (Lindauer, Chapman & Aiken 1961). Entanglement of holdfasts commonly occurs in dense stands of this species, but it is possible to distinguish individual plants at an early age.

*Sargassum sinclairii* stands

On the basis of previous results, which indicate that plant size was positively correlated with natural densities of the stands in which they occurred (Schiel & Choot 1980), the initial densities for this study were chosen at the lower and higher extremes of natural densities, in order to test for differences with time. All the stands were monospecific and the larger herbivores present on the reef, the echinoid *Evechinus chloroticus* (Val.) and the turbinid gastropod *Cookia sulcata* (Gmelin), were kept from the study boulders by removing them from the vicinity and frequent checking of the study site.

During early April 1979, two similar boulders of approximately 12 m² projected area were chosen which had 2200 ± 565 (1 S.D.) newly-recruited plants m⁻² (Table 1a i). Ten other boulders (surface area: $\bar{x} = 9.7$ m², S.D. = 15.7) had 24 ± 5.2 (1 S.D.) newly-recruited plants m⁻² (Table 1a ii). Subsamples of these plants were counted and measured several times during the remainder of 1979. Surge conditions made it impossible to keep account of individually tagged or mapped plants in the dense stands. Therefore density on high density boulders was assessed using ten 25 × 25 cm quadrats, which were placed on the boulders using random coordinates. The lengths of plants were measured within the stands after haphazardly tossing 10 × 10 cm quadrats, in which all of the plants were measured. This assured that adjacent plants, those most likely to have an effect on each other, were measured.

Stands at low density were also subsampled on several dates during 1979. The locations of these plants were mapped, and the plants were selected from the boulders by random
**Effects of density on marine algae**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Density (m⁻²)</th>
<th>Sampling programme</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) <em>Sargassum sinclairii</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(i) 2 boulders (high density)</td>
<td>2200 (initial)</td>
<td>sizes through time; destructive sampling in December 1979</td>
</tr>
<tr>
<td>(ii) 10 boulders (low density)</td>
<td>1–40 (initial)</td>
<td></td>
</tr>
<tr>
<td>(iii) 4 boulders (intermediate densities)</td>
<td>60–1500 (initial)</td>
<td>counts during April, October and December; destructive sampling for size and weight in December 1979</td>
</tr>
<tr>
<td>(iv) 36 boulders (different densities)</td>
<td>0–220 (final)</td>
<td>numbers of adults v. numbers of recruits assessed, March 1980</td>
</tr>
</tbody>
</table>

| (b) _Carpophyllum maschalocarpum_ | | |
| (i) 2 boulders (high density) | 5200 (initial) | sizes, through time |
| (ii) 12 boulders (low density) | 1–10 (initial) | sizes through time; these recruited one year after those in (i) & (ii) |
| (iii) 1 boulder (high density) | 3100 (initial) | |
| (iv) 20 boulders (different densities; different ages of plants) | — | destructive sampling for weight-length relationships. |

placement of a 50 × 50 cm quadrat. Measurements of each plant in both density treatments were the lengths of the main axis plus those of the lateral branches. In each case at least fifty plants were sampled.

To test if growth was related to density in the period prior to maximum increase in plant tissue, an additional sample of plants was measured for total length during early October 1979. Sixteen different plant densities were used for this comparison (Table 1a iii). Plants were measured from the high and low density treatments (Table 1a i, ii), as well as from four boulders with intermediate densities (Table 1a iii) for which initial densities were recorded earlier in the year. Plants on these four additional boulders were also 1979 recruits.

During the period of greatest plant size, when elongation ceased for most individuals (late December), samples were taken from all boulders (Table 1a i, ii, iii) after random placement of 25 × 25 cm quadrats and removing all plants from within them. These plants \((n = 135)\) were brought into the laboratory and measured for total length, the receptacles were dissected from them, and the dry weights of individual plants and their receptacles were obtained. These plants represented sixteen final densities, ranging from 1–272 m⁻².

It was common to find large numbers of drifting plants during the period of greatest growth (November–December). To assess one cause of mortality, 100 drifting plants were sampled following stormy weather and it was noted whether or not their holdfasts were intact.

To determine the relationship between the numbers of adult plants and the numbers of recruits, thirty-six 1-m² quadrats were sampled on the boulders during March 1980 (Table 1a iv). It was then still easy to distinguish older plants from those newly recruited. Sixteen of these samples were from the density treatments (Table 1a i, ii, iii) and twenty were chosen randomly from a map of boulders. All older plants and new recruits within the quadrats were counted.

The following relationships were assessed by regression analysis: (i) plant length on plant density for the October sample; (ii) plant dry weight, receptacle dry weight, and receptacle dry weight per plant dry weight on plant length; (iii) plant length, dry weight and receptacle dry weight on plant density for the December sample; and (iv) numbers of recruited plants on numbers of adult plants. In addition, dry weight v. plant length curves
were compared for the low and high density stands. Appropriate data transformations were used when required.

Size–frequency histograms for plant length were constructed for each sample of low and high density stands. Size–frequency histograms for plant weight were compiled from two types of data. The first and last samples from both low and high density stands represent plants which were removed from the field, dried and weighed. For the other dates, graphs were constructed from plant length data using regressions relating length to dry weight (Schiel 1981; Choat & Schiel 1982). The August low density sample for length and weight was missed, due to storms.

Sokal & Rohlf's (1969) g-tests for skewness were used to detect departures from normality for the size and weight-frequency histograms, and t-tests were used to test the significance of the g values.

**Carpophyllum maschalocarpum stands**

The growth and survivorship of *Carpophyllum* were also assessed in low and high density stands. Dense populations of recruited plants (>5000 m\(^{-2}\)) occurred on two boulders during December 1977 (Table 1b i). Samples of these plants were measured periodically until October 1979. One hundred plants at densities from 1 to 10 m\(^{-2}\), located on several boulders, were mapped and measured periodically for approximately 22 months after their recruitment during December 1977 (Table 1b ii). A second high density recruitment (>3000 m\(^{-2}\)) was located on another boulder during December 1978 (Table 1b iii). These plants were observed periodically, and a sample was measured during July 1979. The sizes of these plants were compared with those which were a year older, located in the low density stands.

Sampling for density was done in dense stands with random 25 × 25 cm quadrats (n = 5), while the sizes of all plants within randomly placed 10 × 10 cm quadrats were measured (n = 50). The boulders on which these plants were located were all >3 m\(^2\) in surface area, and were scattered at depths of 3–5 m. None of the plants in these treatments were overshadowed by other algae, and echinoids did not have access to them.

Large *Carpophyllum* plants occurred at many different densities, but because individuals are long-lived and slow-growing, the ages and previous histories of these plants were not known. Reproductive output was assessed by removing a sample of plants of a range of sizes from adjacent boulders (Table 1b iv) during October, the month of peak reproduction (Schiel 1981). These plants were taken to the laboratory, measured for total length, their receptacles were removed, and the dry weights of individual plants and their receptacles were obtained in the same way as for the final *Sargassum* sample.

Because of the perennial habit of *Carpophyllum*, its variable recruitment, and the great differences evident at the end of the study between low and high density treatments, destructive sampling of these stands was not done. It was not possible to monitor *Carpophyllum* of known age over a range of densities because recruit plants were not encountered at intermediate densities and there were not enough high density stands of recruits to enable thinning experiments.

**RESULTS**

**Sargassum sinclairii stands**

The initial sizes of *Sargassum* plants at low and high density were the same (high density: \(\hat{x} = 5.5\) mm, S.D. = 2.2; low density: \(\hat{x} = 5.1\) mm, S.D. = 2.1). Figure 1 shows
that by the end of July, however, after only 3 months of growth, the high density plants were significantly larger than those at low density ($t = 8.79$, d.f. = 136, $P < 0.001$).

During October (the beginning of the period of rapid growth) there was a significant positive relationship between plant size (total length) and density, over densities ranging from 1 to 1100 m$^2$ (Table 2a). By the end of the year, the high density plants were, on

**Table 2.** Summary of results describing various plant measurements and their relationship to plant length and density for *Sargassum sinclairii* (a–i) and *Carpophyllum maschalocarpum* (j–k) at Waterfall Reef, New Zealand. Appropriate data transformations were used, when required.

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Regression equation</th>
<th>$r^2$</th>
<th>$P (\beta = 0)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a Plant length $v.$ density, October 1979</td>
<td>ln length = $3.60 + 0.27$ (ln density)</td>
<td>0.27</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>b Dry weight of receptacles $v.$ plant length</td>
<td>ln rep. wt = $-2.27 + 0.46$ (ln length)</td>
<td>0.71</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>c Proportion of plant dry weight in receptacles $v.$ plant length</td>
<td>arcsine rep. wt/plant wt = $0.25 + 0.0002$ length</td>
<td>0.44</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>d Numbers of recruits $v.$ numbers of adult plants</td>
<td>recruits = $-28.27 + 11.02$ (adults)</td>
<td>0.80</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>e Plant length $v.$ density, December 1979</td>
<td>ln length = $3.35 + 0.67$ (ln density)</td>
<td>0.39</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>f Plant dry weight $v.$ density, December 1979</td>
<td>ln weight = $-0.19 + 0.33$ (ln density)</td>
<td>0.25</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>g Dry weight of receptacles $v.$ density, December 1979</td>
<td>ln rep. wt = $-0.65 + 0.29$ (ln density)</td>
<td>0.24</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>h Final density (December) $v.$ initial density (April)</td>
<td>Dec. density = $-0.62 + 0.11$ (April density)</td>
<td>0.95</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>i Proportion surviving in December $v.$ April density</td>
<td>Dec. proportion = $0.11 - 0.0001$ (April density)</td>
<td>0.02</td>
<td>N.S.</td>
</tr>
<tr>
<td>j Dry weight of receptacles $v.$ plant length</td>
<td>ln rep. wt = $-1.54 + 0.28$ (ln length)</td>
<td>0.54</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>k Proportion of plant dry weight in receptacles $v.$ plant length</td>
<td>arcsine rep. wt/plant wt = $0.08 + 0.0002$ length</td>
<td>0.22</td>
<td>0.025</td>
</tr>
</tbody>
</table>
average, five times the size of those at low density. Size–frequency histograms (Fig. 2) show that the largest plants invariably occurred at the higher density. The low density size distributions became markedly skewed as the year progressed, with most plants in the smaller size classes. The distributions of high density plants appeared to be normal on most sampling dates, but slightly skewed by the end of the year. The lack of strongly skewed distributions in the high density stands indicates that most of the plants were not being trapped under the canopy of a few large plants, as is often the case with terrestrial plant populations growing at high density (e.g. Mohler, Marks & Sprugel 1978; Schlesinger & Gill 1978).

There were also differences in the distribution of plant weight between the low and high density populations (Fig. 3). The low density distributions were invariably skewed toward the smaller weights. The high density distributions were skewed during the early sampling date (July), were normal for the next three samples, but were skewed at the final sampling date. By December, however, there was a six-fold difference between the mean weights of low and high density plants. In addition, 42% of the high density plants were heavier than the largest individuals at low density.
These differences were also reflected in the reproduction of plants. Only 60% of the low density plants became reproductive, while 94% became reproductive at high density (Figs. 2 and 3). The weight of receptacles was related to plant size (Table 2b). More importantly, however, the proportion of plant weight invested in reproductive structures increased with plant length (Table 2c), even though the weight–length curves were similar for plants at low and high densities (test of slopes: $F_{1,83} = 0.03$, $P > 0.05$). From the amount of reproductive material present, it appeared that plants at lower density had a disproportionately smaller chance of contributing to the next generation. This is supported by two types of evidence. High density plants had a much greater weight of reproductive structures than did those at low density (Fig. 4), and recruitment during the following year was significantly related to adult density (Table 2d). Because Sargassum plants are deciduous, shedding most of the thallus seasonally during the later stages of reproduction (cf. S. muticum, Fletcher & Fletcher 1975; Norton 1977), this effectively removes the canopy, leaving open space which may be colonized by other plants. In the areas of highest adult densities (~250
m\(^{-2}\)), there were over 2000 recruits m\(^{-2}\), which quickly spread their leaves to occupy entirely the available substrata.

On the last sampling date, there were significant positive relationships between plant density and: (i) plant length (Table 2e), (ii) plant weight (Table 2f), and (iii) the weight of reproductive structures (Table 2g). Length, plant weight and the weight of reproductive structures are highly correlated. The equations in Table 2 demonstrate, however, that there was no evident etiolation of plants in stands of higher densities, which might have produced plants of lower weight, as has been shown in some terrestrial studies (e.g. Hodgson & Blackman 1957; Harper 1977).

The survivorship rates for low and high density plants were similar until July (Fig. 5). Between then and September the low density plants declined at a greater rate. After October, however, the plants at high density declined rapidly so that, at the final sampling date in December, a greater proportion of low density plants survived (low, 26·0%; high,
Effects of density on marine algae

11.9% \(; \chi^2 = 6.5, P = 0.01\). Final densities of plants for the two treatments were
262 ± 43.8 (1 S.D.) m\(^{-2}\) and 6.2 ± 6.4 m\(^{-2}\).

The greatest mortality for high density plants occurred after the start of the season of
peak growth. Often there are then large numbers of drift plants, particularly after storms.
This suggested that the sudden increase in plant bulk may have been a contributing factor
to their disappearance from the rock surfaces. Ninety-two per cent of drift plants sampled
had their discoid holdfasts intact, usually with small pebbles or encrusting algae still
attached, suggesting that the plants were merely pulled from the substratum.

By combining data from twelve boulders, a significant positive relationship was found
between final density (December) and initial density (April) (Table 2h). However, there
was no significant relationship between the proportion of plants surviving and initial
density (Table 2i). These tests indicate that, over this range of densities, there was no
proportional increase in survivorship with decreasing density, and that high final densities
were the result of high initial densities of recruits.

Carpophyllum maschalocarpum stands

High density plants were recruited at approximately 5000 m\(^{-2}\) during November 1977;
9.5% of these survived until October 1979 (Fig. 6). From March 1978 onwards, this
represented complete cover of the rock surface. Low density plants were recruited at
approximately 5 m\(^{-2}\) during November 1977, and had 45% survival by the final sampling
date (Fig. 6). Except on the first sampling date (December), when plants were of a similar
size (7.0 ± 2.5 mm; \(t = 0.10, d.f. = 49, P > 0.05\)) there were large differences between
those at low and high density (Fig. 7). During July 1979 high density plants were, on
average, three times the size of those at low density, and by October this difference had
increased to eight-fold (\(t = 7.8, d.f. = 99, P < 0.001\)). The plants at low density had by
this time begun to show signs of frond damage. None of the low density plants in this study
grew to a large size. During July 1979 a younger stand of high density plants, which were

![Fig. 6. Survivorship curves (adjusted to a starting value of 1000) for the Carpophyllum
maschalocarpum plants in the density treatments at a site in northern New Zealand. Mean
number ± 95% C.L. are shown for each sample. Dashed line: low-density plants; solid line:
high-density plants.](image-url)
recruited during early December 1978, had plants of the same length as those in the low density stands which were recruited during the previous year (December 1978 plants: $\bar{x} = 73.9$ mm; December 1977 plants: $\bar{x} = 72.4$ mm; $t = 0.14$, d.f. = 99, $P > 0.05$).

Size--frequency histograms of the plants at high density (Fig. 8) indicate that most plants were able to remain in the developing canopy. The causes of mortality in high density stands could not be identified, but overgrowth of plants was one possibility. This was difficult to assess because the understorey became densely interwoven with holdfasts. However, it appeared that as individual plants came into contact with each other, their thalli responded by growing upwards before their holdfasts became completely entangled. In contrast, fronds of the low density plants remained prostrate until the last sampling date and their holdfasts remained small.

During November 1978, three plants from the stands of high density 1977 recruits became reproductive. These were greater than 60 cm in length, and were the largest plants present in the stands. When the plants were about 2 years old (October 1979), most of the high density plants greater than 60 cm in length became fertile (Fig. 8). None of the low density plants became reproductive. A random sample of Carpophyllum plants from several boulders showed that, with few exceptions, only the larger plants reproduced (Fig. 8). As for Sargassum, both the weight of receptacles and the proportion of plant weight invested in them increased with plant size (Table 2j, k).

These data, although less complete than those for Sargassum, indicate that recruitment at higher densities results in increased growth and reproductive benefits relative to recruitment at low densities.
DISCUSSION

A description of patterns of recruitment, growth and survivorship does not reveal underlying mechanisms. The number of plants in a given area may be both an indication of the suitability of that particular habitat in terms of the physical environment as well as the end product of a series of biotic interactions. The results of this study indicate that the individuals of two algal species, in naturally occurring stands, had an overall higher survivorship at low density. However, plants, on average, grew faster, became larger and had a greater amount of reproductive structures in dense aggregations. This discussion examines several possible explanations for these patterns and their consequences.

Site effects

Terrestrial studies have shown that local soil conditions (Antonovics & Levin 1980) or localized herbivory (Harper 1977) may have large effects on the performance of plants.
Local site effects may also be important for marine plants, but there have been few studies which test for them. Exposure gradients, both on a broad scale (Chapman 1973) and a local scale (Cousens 1982) have been implicated in the differing morphologies and growth rates of conspecific individuals. Without a knowledge of other differences between sites, however, such as the presence of grazers and potentially competing species of algae, the density of stands and the age structure and history of populations, these studies can be difficult to interpret.

In this study, the high density recruitment of Sargassum and Carpophyllum may have been simply a reflection that these particular sites were most suitable for occupation by plants, and their subsequent performance was merely an extension of this. The problems of localized effects were partially countered by using plants at the same depth and similar general exposure from the boulders of one reef. Plants which recruited at the same time were used to offset problems associated with different recruitment histories (e.g. Harper, Williams & Sagar 1965). However, the problem of site effects involves three other types of information affecting the period between settlement (when spores or germlings arrive) and recruitment (when small plants are seen in the field): (i) are propagules arriving in an area, and in what quantities?; (ii) do the biological characteristics of microsites affect germination, growth and survival from settlement to recruitment?; (iii) do the physical characteristics of microsites affect these patterns? The first of these questions could be clarified by settlement studies (e.g. Schonbeck & Norton 1978), substratum scrapings and examination for algal spores (cf. Denley & Dayton 1985). Experimental studies using laboratory-settled germlings placed into different sites would help clarify the second two points. If several stands of densely settled recruits can be found in similar environmental conditions, experimental thinning may reduce localized effects and clarify density responses of algae (D. R. Schiel unpublished).

The survival of individual plants can be affected by small grazers (Gunnill 1980), physical factors and shading by conspecific adults (Schonbeck & Norton 1978; 1980), all of which may change over short distances. The initial problem is to identify survivorship and growth patterns before invoking causative mechanisms of microsite differences (e.g. Cousens & Hutchings 1983), which may not be able to be measured on this fine scale.

**Density dependence**

Despite a long history of research on within-species interactions among terrestrial plants (e.g. Tansley 1917; Donald 1951, 1963; Kira, Ogawa & Sakazaki 1953; Harper 1977), there have been few tests of these effects in marine environments. The best example is by Black (1972, 1974), who determined experimentally that survivorship was density-dependent for very small recruits of Egregia menziesii, but that this was not the case when plants were 3 months older. The growth rates were also significantly greater in three out of eight experimentally thinned stands. In other studies, some species of cultivated red algae have been shown to give reduced yields at higher densities (Yoshida 1972; Adams & Austin 1979). The shading effects of canopy plants have been mentioned in several studies as affecting juvenile growth (Kain 1963; Duggins 1980; Schonbeck & Norton 1980). Other studies have mentioned density as an important variable affecting plant size in naturally occurring stands. However, the lack of knowledge of the histories of plants may confound the effects of other factors such as age composition and different depths and exposures (Luning 1969; Jupp & Drew 1974; Paula & Oliveira 1982; Cousens & Hutchings 1983).

In the present study, the reasons for the ‘better’ performance at higher density are not clear. These results could be expected if: (i) competition for light was reduced, (ii) nutrients
were not differentially limiting, and (iii) some protection was afforded from severe water movement. Light competition reduces the growth of plants beneath canopies in terrestrial stands (e.g. Black 1958; Donald 1963), and of marine plants which have recruited beneath canopies (Kain 1979; Schiel 1981; Reed & Foster 1984). This effect could be reduced where the plants are not trapped beneath the canopies, and where the swaying of algae, induced by water movement, produces light flashes through the stands (Kitching 1941; Kain 1979). Differences in the growth rates of laminarian algae can also be the result of different concentrations of nutrients between seasons and localities (Chapman & Craigie 1977; Gerard & Mann 1979). Within a kelp stand, the plants themselves may affect nutrient flow (Gerard 1982; Wheeler 1982), but this has been shown only for *Macrocystis pyrifera*. Nutrient flow within a locality may not be affected seriously by plants which have adult canopy heights of only 1–2 m, such as fucoids and stipitate laminarians (cf. Neushul 1972; Norton, Mathieson & Neushul 1982). Plants at low density could also suffer from increased water movement and abrasion, with resultant changes in size and morphology (Gerard & Mann 1979), and could be more susceptible to micro-grazers (F.C. Gunnill unpublished).

A frequent problem in algal studies is the inability to observe directly the agents of mortality; in most cases, entire plants disappear between censuses (Gunnill 1980; Schiel 1981). Plants of the genus *Sargassum* are often found drifting on the surface, both before and during the period of reproduction (Yoshida, Sawada & Higaki 1963; Fletcher & Fletcher 1975; Norton 1977; Deysher & Norton 1982). In this study, the period of increased mortality in dense stands began when plants started to attain a large size. A high proportion of the plants found drifting then were entirely intact, suggesting that they were simply dragged from the boulders by water movement. This may be related to density because the larger plants tended to be in high density stands. Density-independent events also occurred, however, since there was mortality in low density stands during the same period. There was no evidence that small plants suffered greater mortality in dense stands of *Sargassum*, although this may have occurred in stands of *Carpophyllum*. Overgrowth of plants probably occurred in dense stands of *Carpophyllum*, but this is difficult to quantify.

The interplay between density-dependent and density-independent effects has had important ecological implications in terrestrial plant studies (Harper 1977; Antonovics & Levin 1980) and will be equally important in understanding the dynamics of marine algal populations.

*Ecological considerations*

The spatial distribution of species can have important consequences to the dynamics of a community. For example, questions concerning the importance of seed dispersal and the effects of host-specific seed predators (Janzen 1970; Connell 1971) have been approached by examining the spatial relationship between adult and juvenile trees, and the aggregations of each species (Hubbell 1979). The dense aggregations of predominantly single species of marine plants, both intertidally and subtidally, reported for many areas worldwide (Kain 1963; Mann 1972; Stephenson & Stephenson 1972; Choat & Schiel 1982) imply that a knowledge of the performance of plants in these types of stands is necessary to an understanding of community organization. Of particular interest is the relationship between the distribution of adult plants and the settlement of germings. Little is known about the distribution of settlers and the relationship between settlement and recruitment (Hruby & Norton 1979). Questions of dispersal have parallels in terrestrial
studies. Cook (1980) concluded, from many terrestrial studies, that most seeds do not disperse very far, and that the emphasis has tended to be on the long-distance tails of distributions. The factors affecting mortality of offspring and how this is related to parent plants are therefore important considerations. Unlike many terrestrial species, which have adaptations for seed dispersal by wind and animals, fucoid and laminarian algae rely on drifting reproductive thalli for long-distance dispersal rather than on the prolonged activity of propagules.

This study showed that for Sargassum sinclairii, dense recruitment occurred very near adult plants which had shed their thalli. The evidence which is available from other studies indicates that S. muticum germlings do not travel far from parent receptacles (Fletcher 1980; Norton 1981), and that for this and other large brown algae, most recruits appear close to adults (Anderson & North 1966; Dayton 1973; Hay & South 1979; Paine 1979; Deysher & Norton 1982). This is somewhat paradoxical in the case of the notoriously invasive species S. muticum, for which long-range dispersal has obviously been important (Fletcher & Fletcher 1975; Farnham 1980; Farnham et al. 1981; Deysher & Norton 1982; Critchley 1983). For both this species and for S. sinclairii, most recruits appear within 2 m of parent plants, despite the fact that these species have a dispersal mechanism in the form of floating, detached branches (Fletcher & Fletcher 1975; Norton 1977; this study).

High density populations may have several advantages over stands at low density. In dioecious species such as Carpophyllum maschalocarpum, it may increase the probability of successful fertilization, thereby providing many more viable germlings per female plant than in sparser stands. When other fucoid species are near, successful fertilization may be rarer (Bolwell et al. 1977). For Sargassum muticum, which is monoecious, Fletcher (1980) suggested that fertilization is much more readily accomplished where there is gamete release en masse, in a short period. Outcrossing may therefore be increased in dense stands.

Higher densities of recruits may be important for the continued occupation of space in marine environments. Paine (1979), for example, found that below a threshold density of about twenty-five plants m⁻², populations of Postelsia palmaeformis were unable to maintain their position against encroaching mussels unless there was physical disturbance. High density recruitment near adult stock for species of Sargassum may also have the important effect of excluding other species of large brown algae (Fletcher & Fletcher 1975; Ambrose & Nelson 1982). Other studies have indicated that survivorship in dense mats of algae may be higher than for isolated plants, because of reduced effects of desiccation, exposure and herbivory (Schonbeck & Norton 1978; Gunnill 1980; Hay 1981). In addition, Gunnill (1980) found that persistent plants in dense aggregations may be an important source of propagules for local populations.

Although there are obvious parallels between terrestrial and marine plant communities, there are also important differences. Marine plants derive nutrients from an ambient medium rather than from their substrata, and even large species of brown algae often colonize previously bare space without obvious successional events. Little is known in marine environments about the incidence and importance of dense concentrations of spores to the settlement and subsequent development of algal stands. There is evidence that these occur in some situations (Hruby & Norton 1979; Norton & Fetter 1981). For larger marine algae, there may be no long term equivalent to the seed banks and ‘safe sites’ which characterize the regeneration process of many terrestrial plants (Harper, Williams & Sagar 1965; Cook 1980). Although laminarian gametophytes may remain viable in the
laboratory for long periods (Kain 1964; Sanbonsuga & Neushul 1980), little is known about the length of time gametophytes and germlings can remain dormant in the field, particularly with the interference of other algae and grazers. There is a growing interest in these problems for marine systems (Denley & Dayton 1985).

The assessment of plant performance with respect to density in marine environments will be modified as more experiments are done. Even if, as in this study, there appear to be few detrimental effects and several advantages to being in dense aggregations, there is obviously a limit to how many individuals may be packed into an area without negative consequences. Consideration of the $-\frac{3}{2}$ thinning law (Harper 1977; White 1980) may also be relevant, once properly controlled experiments are done. In the meantime, it is premature to assume that equivalent processes obtain for terrestrial plants and large marine algae.

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