The suitability of ten South African species of marine macroalgae for establishment in temperate marine aquaria

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Abstract

Ten species of South African marine macroalgal understorey species were investigated to determine their viability over a light gradient, their re-attachment ability, and sporeling recruitment in an indoor aquarium environment. These species were: *Hymenena venosa* ; *Pachymenia carnosa*; *Plocamium corallorhiza*; *Epymenia obtusa*; *Gelidium capense*; *Botryocarpa prolifera* (Rhodophyta); *Axillariella constricta*; *Sargassum heterophyllum* (Phaeophyta); *Caulerpa holmesiana*; and *Caulerpa filiformis* (Chlorophyta). The development of microalgal communities on the tank floor was also observed.

Seaweed productivity was low in a tank lit by artificial light. Productivity was particularly low (usually negative) in plants grown under low light intensities (3.4 μmol.m^{-2}.s^{-1}). After fourteen weeks (the duration of the experiment), positive relative growth rates only occurred under high light conditions (80.9 μmol.m^{-2}.s^{-1}) and these were recorded in the species: *C. holmesiana* (3 % per day); *Pachymenia carnosa* (0.5 % per day); *A. constricta* (0.2 % per day); *G. capense* (0.1 % per day) and *E. obtusa* (0.2 % per day). Although the condition of most species deteriorated initially, new blade and/or holdfast growth was evident in *C. holmesiana*; *C. filiformis*; *E. obtusa*; *Plocamium corallorhiza*; *G. capense* and to a lesser extent in *B. prolifera* and *S. heterophyllum* at week fourteen. *A. constricta* was the only species to remain healthy throughout the experiment, under all light conditions. Re-attachment experiments found that species with rhizome-like spreading holdfasts (*C. holmesiana*, *C. filiformis*, *E. obtusa*, *P. corallorhiza* and *G. capense*) were able to re-attach, whereas species with discoid holdfasts (*S. heterophyllum*, *A. constricta*, and *Pachymenia carnosa*) did not. Sporeling recruitment was more prolific under high light intensities than low light intensities, as was microalgal growth.

The characteristics of species recommended for use in understorey seaweed community in the Kelp Forest Exhibit at the Two Oceans, Aquarium are: robust forms with spreading holdfasts.

Introduction

The Two Oceans Aquarium, at the Victoria and Alfred Waterfront, Cape Town, is due to open in November 1995. With the theme of South African marine ecosystems, it promises to be a major attraction for locals and tourists alike. One of the aims of the Two Oceans Aquarium is to establish a self sustaining living kelp exhibit representative of that found locally in the natural environment. An ecologically important, and aesthetically valuable component of south african kelp forests is the understorey seaweed community. It is therefore necessary to establish such a community in the Kelp Forest Exhibit. The species selected to represent this flora should have some aesthetic appeal as well as the ability to tolerate artificial conditions. Fouling species need to be avoided as far as possible (Phillips *et al.*, (1988). Unfortunately, little information is available on the successful establishment of seaweeds in marine aquaria. It is therefore difficult to predict which species will react favourably to such an environment. In South Africa, and other countries, this problem is aggravated by large gaps in information on the basic biology, ecology and physiology of the subtidal understorey seaweed flora.

The few studies that have been conducted on seaweeds in marine aquaria indicate that too little light may be an important factor adversely affecting growth and development the seaweed flora in aquaria (Linden and Yarish, 1992; Phillips *et al.*, 1988). Frond growth in *Macrocystis pyrifera* (L) C. AG. in the Monterey Kelp Forest Exhibit was lower than in natural populations. The reason for the lower growth in aquarium plants was, in part, attributed to light. Although open to the sky, the vertical orientation of the walls allows sunlight to enter the tank only when the sun is directly overhead. Thus, plants in the tank received less light than they would in natural environments (Watanabe and Phillips, 1986). Furthermore, irradiance levels of 79.3 μmol.m^{-2}.s^{-1} in the North Atlantic Kelp Exhibit at the New York aquarium were the limiting resource for the growth of *Laminaria longicruris* and *L. saccharina* (Linden and Yarish, 1992).

A typical feature of disturbed marine substrates and newly established aquaria is the colonisation of exposed surfaces with a biofilm consisting of microorganisms such as bacteria and microalgae, especially diatoms (Phillips *et al.*, 1988; Keough and Raimondi, 1995). The development of such a community was monitored in the Monterey Bay Kelp Exhibit. The

biofilm that developed consisted mainly of benthic diatoms. After three months, the walls of the exhibit, and many of the kelp fronds become fouled by these and other weedy species of macroalgae (eg. *Gifforidia granulosa* and *Ulva* sp.). The cover of the fouling species started to decrease steadily after about 5 months as a result of manual removal and natural (undetermined) causes (Phillips *et al.*, 1988). Subsequently communities of Californian understorey perennial seaweeds became dominant. These species were introduced to the tank by collecting fertile material of desirable species, and placing this under nets on the rock work in the tank where they were left until thallus material had rotted away, (approximately one month). The dominance of these perennial species was still apparent after three and a half years.

The broad aim of this study was to do a preliminary investigation to establish which South African subtidal understorey seaweeds are appropriate for establishment in the artificial environment of marine aquaria. More specifically the aims were to:

1) Investigate viability, and see if viability varies within and among species, or differs over a light gradient. Such information may indicate the density at which the kelp forest canopy should be maintained, and the depths at which certain seaweeds should be positioned.

2) Determine which species of understorey seaweeds have the ability to re-attach to false substrates used in the aquarium following transplantation from the ocean.

3) To make observations on sporeling recruitment, and the succession of fouling species (ie. microalgal biofilm).

Materials and methods

Study species were ten species occurring around the Cape of Good Hope (Table 1): *H. venosa* (L.) Kylin; *Pachymenia carnosa* (J. Ag.) J. Ag.; *Plocamium corallorhiza* (Turner) Harvey in Hooker et Harvey; *E. obtusa* (Greville) Kuetzing; *G. capense* (S.G. Gmelin) P.C. Silva; *B. prolifera* Greville 1830; *A. constricta* (Harvey) Gruber; *S. heterophyllum* (Turner) C. Agardh, 1820 ; *C. holmesiana* G. Murray 1891: 208; and *C. filiformis* (Suhr) Hering . *H. venosa*, *Pachymenia carnosa*, *Plocamium corallorhiza*, *E. obtusa*, *G. capense*, *B. prolifera* and *A. constricta* were collected from Oudekraal, on the west coast of the Cape Peninsula. *C. holmesiana*, *C. filiformis* and *S. heterophyllum* were collected from Bordjiesrif, on the east coast of the Cape Peninsula.

Table 1. Geographical distributions of species as well as positions on the shore (data taken from Stegenga *et al.*, in press) and the collection site.

Species	Geographical location	Positions on shore	Position collected from
A. constricta	St. Helena Bay - Cape Point	Sublittoral	3-5m
B. prolifera	Namibia- Hangklip.	Sublittoral fringe & down	3m
C. filiformis	False Bay eastward to N. Natal	Lower intertidal & sublittoral fringe	3-5m
C. hobnesiana	South coast	Sublittoral	10m
E. obtusa	Muizenberg-Namibia; New Zealand: Auckland	Sublittoral	3-5m
G. capense	East coast	Sublittoral fringe & downwards	3-5m
H. venosa	Namibia-southern Cape Pen.	Sublittoral	3-5m
Pachymenia carnosa	Southern Africa (endemic): Namibia-Brandfontein	Sublittoral fringe and down	3-5m
Plocamium corallorhiza	Yserfontein eastwards to Natal; N. Namibia	Sublittoral	3-5m
S. heterophyllum	St. Helena Bay - east coat	Sublittoral	3-4m

Divers collected whole plants by carefully removing them from the substrate with knives. The plants were placed in collecting bags until sampling was complete. Collected material was taken to shallow, shady water and transferred into black plastic bags, without emmersing the plants. This was done in order to minimise possible light and dehydration stress. The black bags, containing the collected material and seawater, were placed into white plastic buckets. The buckets were then sealed with lids. Immediately after collection the plants were transported to, and released into, the tank in which the experiments were to be conducted. It was later discovered that various animals, including grazers such as sea urchins, had been introduced into the tank. These animals were evidently brought in on plant material and live

rock temporarily stored in the tank. Some other seaweeds eg. *Ulva* were also noted

The tank that is intended to house the Kelp Forest Exhibit at the aquarium is open to the sky, hence the organisms therein will experience natural fluctuations in ambient light intensity. The tank holds 8×10^5 l of sea water and has a throughput of 8-10m^3 of filtered sea water per hour. The maximum depth of the tank is six meters. Several artificial rock reefs made of concrete and false rock are located across the tank. The false rock used in the tank was made of fibreglass sheeting which is sandblasted before the fibreglass sets. Water movement can be induced by means of a surge generator, which, for most of the time, will be set to maintain moderate levels water movement in the tank. This tank could not be used in the experiment as it was still being built.

The substitute was a 3x4m, 1m deep concrete tank painted with enamel paint, stationed in a temporary holding facility at Granger Bay. The water feeding the tank was filtered through mechanical, biological and protein filter systems. The temperature of the water was maintained between 15-17°C. Two aeration stones, each 3cm^3, continuously supplied the tank with air. Water movement in the experimental tank was very low compared to what the plants experience in their natural environment.

Three light conditions were set up in the experimental tank (high, medium and low). A high light intensity was created by positioning three 400 watt mercury halide lights over one end of the tank, whereas the medium light area was illuminated by two 40 Watt cool white fluorescent light tubes. The low light condition was devised by covering the surface of the water with several layers of 90% shade cloth. Lights were switched on at approximately 8:30am, and switched off between 4:30-5:00pm. Plants therefore effectively experienced a winter day length for the duration of the experiment. This is appropriate as the experiment itself was conducted over the winter season, from May 1995 to September 1995.

Irradiance levels in the experimental tank and the tank intended to support the Kelp Forest Exhibit were determined using a Li-cor meter (LI-1000) with a spherical radiation sensor. Kelp plants were present in the kelp tank when measurements were taken. Kelp forest tank and experimental tank irradiance data are presented in Figure 1 and Table 2 respectively.
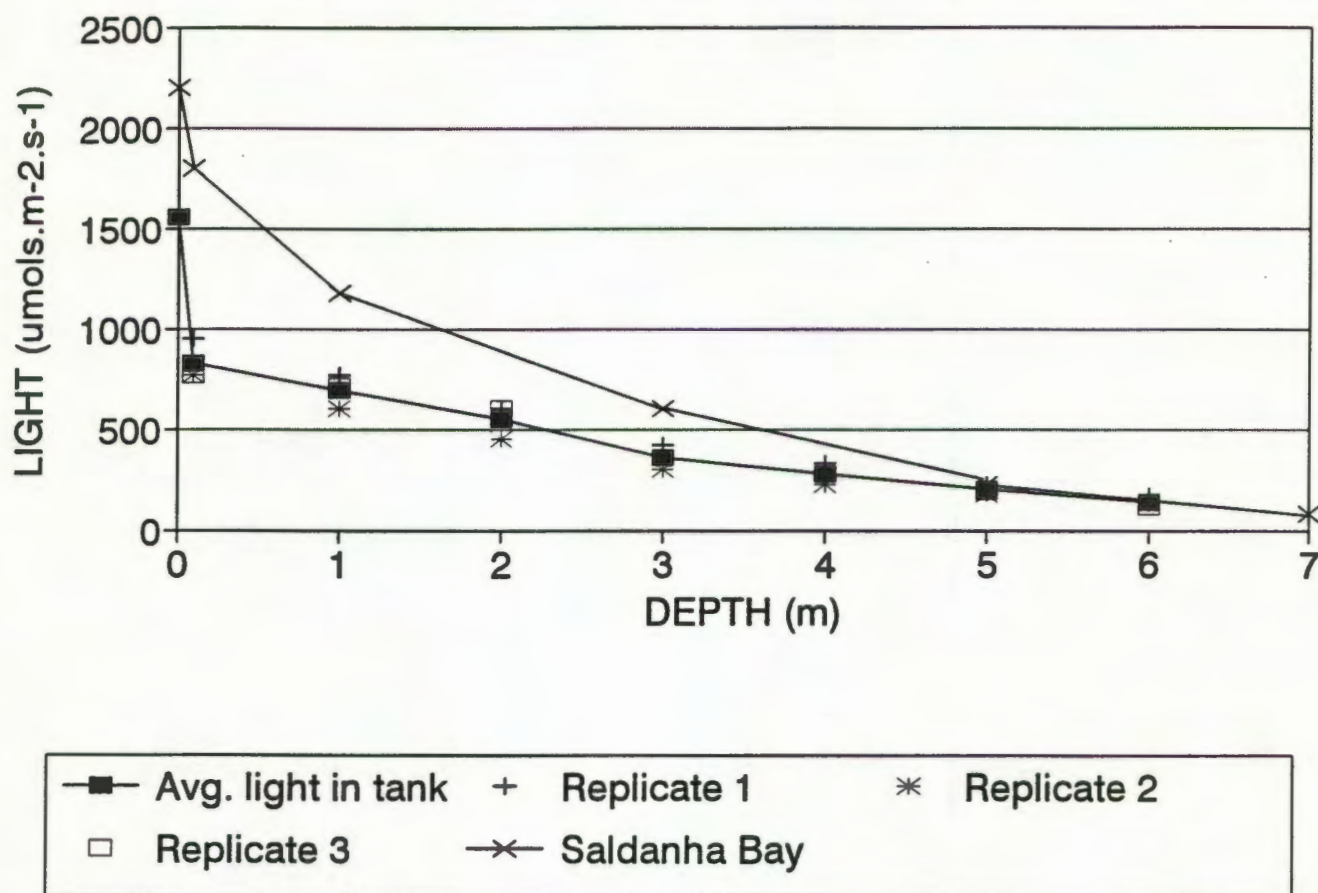
KELP FOREST EXHIBIT
LIGHT PROFILE

Figure 1. Irradiance levels in Saldanha Bay on a clear summer day and the Kelp Forest Exhibit tank at the Two Oceans Aquarium. The measurement at 0m at the aquarium was done in air. Thereafter three replicates, at each depth irradiance was measured at, were taken

Table 2. Means and standard deviation (n=9) of light measurements taken in the experimental tank at 0.2m and 0.8m below the surface of the water.

Light condition	Light in μmol.m^{-2}.s^{-1} at 0.20m	Light in μmol.m^{-2}.s^{-1} 0.80m
High	134.92 ($\pm$ 18.62)	80.88 ($\pm$ 7.20)
Medium	38.19 ($\pm$ 4.97)	30.47 ($\pm$ 5.37)
Low	1.45 ($\pm$ 0.33)	3.37 ($\pm$ 0.60)

Fifteen plants per species were used in the light experiment. This allowed replicates of five plants per species per light condition. The positions of the plants, within each light condition, were random, and plants were spaced in such a way so as to avoid any shading effects. The positions of the plants within each light condition were changed weekly for the first four weeks. Plants were weighted down individually, using clothes pegs attached to lead weights (145 grams) with a rubber bands.
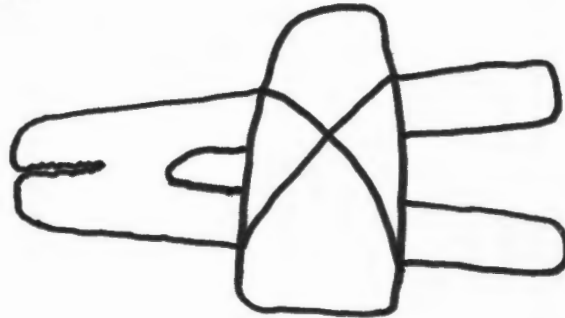

Figure 1. The device used to weight seaweeds down with.

Individual plant biomass (wet) was used as a measure of plant productivity. Initial plant biomass was recorded the day after plants were collected. Thereafter, biomass was recorded on a weekly basis over a period of four weeks. Plants were then left undisturbed for ten weeks. After this period, plants were removed from the tank and final weights were recorded. All weights were determined, after removing excess water, using a Salter spring balance (100g max.). Biomass data were later converted into relative growth rates (RGRs) using the formula RGR= $(^n\sqrt{w2} \otimes w1-1)$x100, where n is time, w2 is weight two and w1 is starting weight.

Change in biomass per week was also calculated for each species. (In the case of biomass data from week fourteen, change in biomass was divided by ten (the number of weeks since last record)). Statgraphics 6.0 (STSC Inc) was used to conduct a multivariate analysis of variance (ANOVA) on data for each of the ten species to determine if time, light or the interaction between and light have a significant effect on biomass. Tukey's HSD test (an *a postiori* multiple-comparison test) was used to compare levels of each treatment and their interactions.

Each time biomass was recorded, plants were examined and their condition classified as being healthy (H), relatively healthy (RH) or deteriorating (D). Representative examples of these three class are shown in Plates 1a-d. Observations of new growth, and possible fertility were also recorded. In order to test whether condition of the seaweeds differed among and within species over the different light conditions, seaweed conditions were ranked as 3,2 or 1 corresponding to the classes H, RH or D respectively. A nonparametric test for ranked data, (Kruskal-Wallis), was then used to determine whether there is a significant effect of time on the condition of each species for each of the three light conditions. Ie. the test was performed on the ranks obtained form the condition data (n=15) for each of the three light conditions, which determined whether the number of individuals in each class (rank) changed significantly over time.
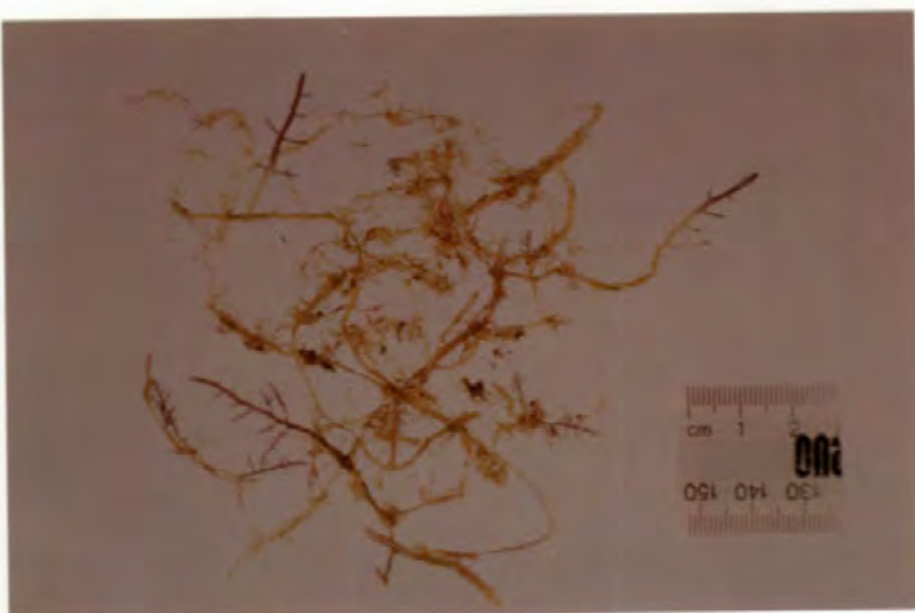

Plates 1a-d. Examples of the three classes: healthy, relatively healthy; and deteriorating. A, *G. capense* (H). B, *G. capense* (RH). C, *G. capense* (D). D, *E. obtusa* (H).

B

C

D

The ability of all the species expect *P. corallorhiza* and *S. heterophyllum* to re-attach to false rock was tested. *P. corallorhiza* and *S. heterophyllum* could not be used in this re-attachment experiment due to shortages in plant material. Five plants from each of the eight species tested were carefully weighted down, as described earlier, on pieces of false rock. The false rock was then placed in the tank under a medium light condition. The plants were left undisturbed for fourteen weeks, then examined for signs of re-attachment.

All the plants used in the light experiment were also examined for signs of re-attachment just prior to their removal on the fourteenth week of the experiment. These plants would have had ten weeks to attach to the tank floor. This supplied re-attachment data for those species not represented in the re-attachment experiment as well as additional data for represented species.

The following were also investigated:

a) whether sporelings of the study species established in the tank during the experiment;

b) if other species of seaweed established;

c) whether there is a difference in sporeling establishment as well as microalgal dominance on the tank floor among the three light conditions.

d) if there are changes in the dominant microalgal communities that establish on the tank floor over time.

This was done by laying glass slides out on the tank floor at the beginning of the experiment. Ten slides per light condition were randomly placed on the tank floor. Two slides from each light condition were collected on weeks one, two, three, four, and fourteen of the experiment. Collected slides were rinsed carefully in a 5% formalin-filtered seawater solution. Thereafter the slides were rinsed quickly with distilled water and excess water was removed. Material on the slides was set in corn syrup, covered with a cover slip and left to dry. The presence of sporelings was recorded, as well as nature and composition of microalgal species. The tank walls were also surveyed carefully on the final day of the experiment for the presence of sporelings.

Results

The relative growth rates (RGRs) of each species under the three different light conditions are shown in Figures 3a-j.
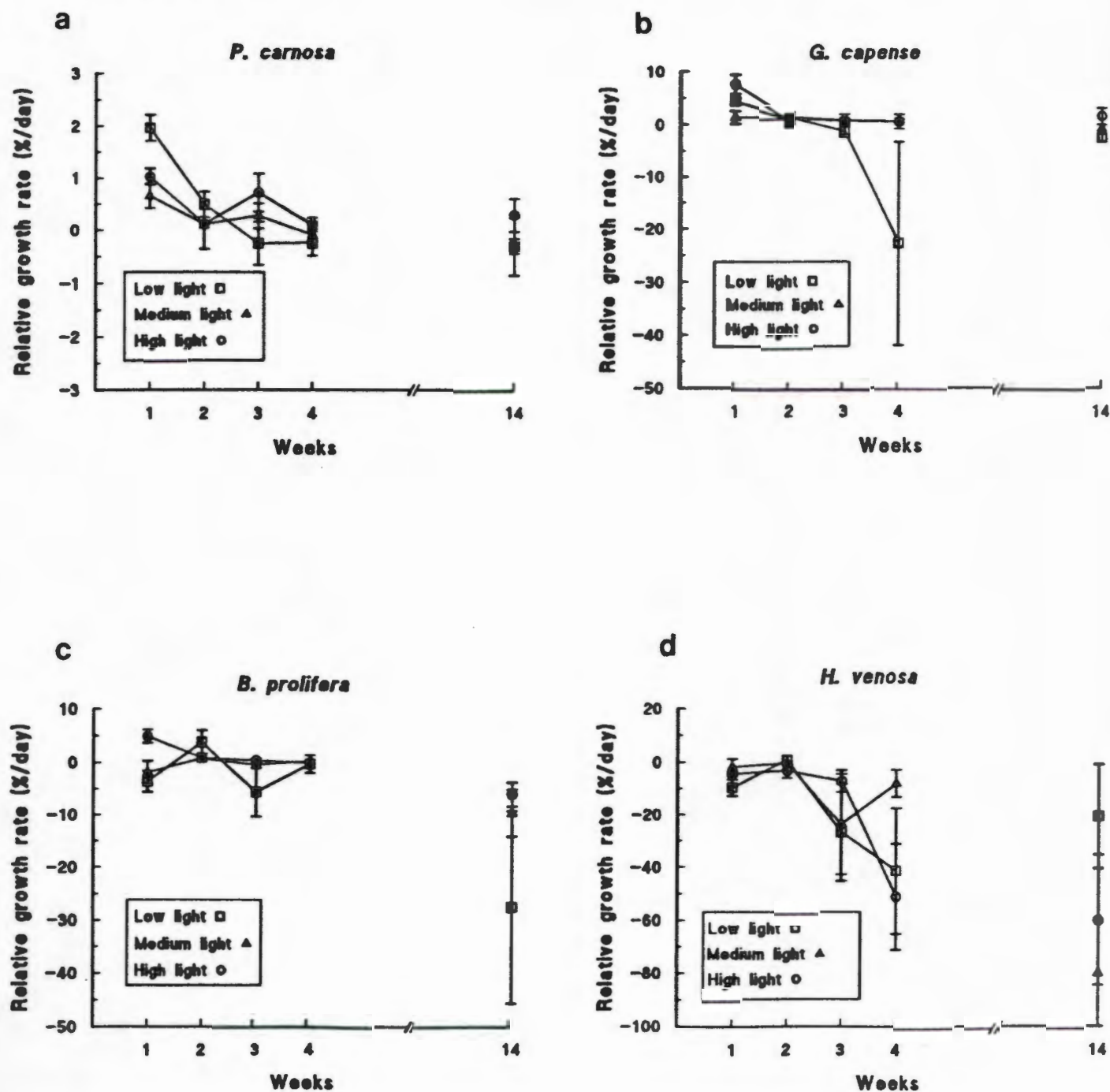
Figures 3a-j. The effect of light on the relative growth rates of ten South African understorey seaweeds. A, *Pachymenia carnosa*. B, *G. capense*. C, *B. prolifera*. D, *H. venosa*. E, *Plocamium corallorhiza*. F, *C. holmesiana*. G, *A. constricta*. H, *S. heterophyllum*. I, *E. obtusa*. J, C. filiformis. Vertical bars indicate standard errors.
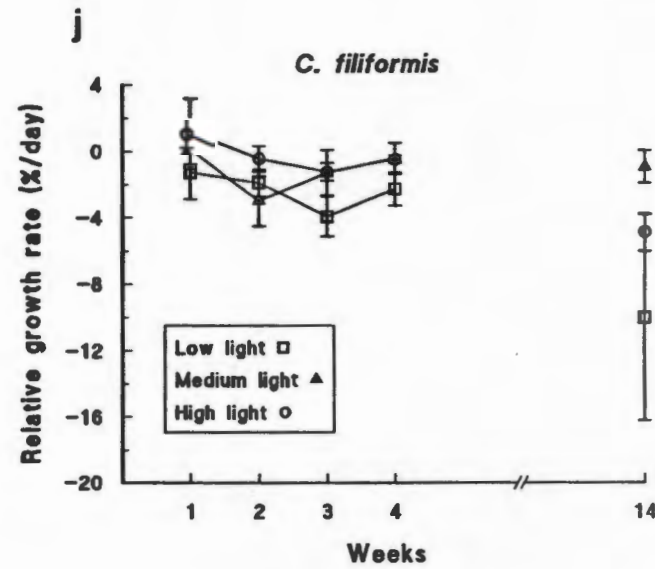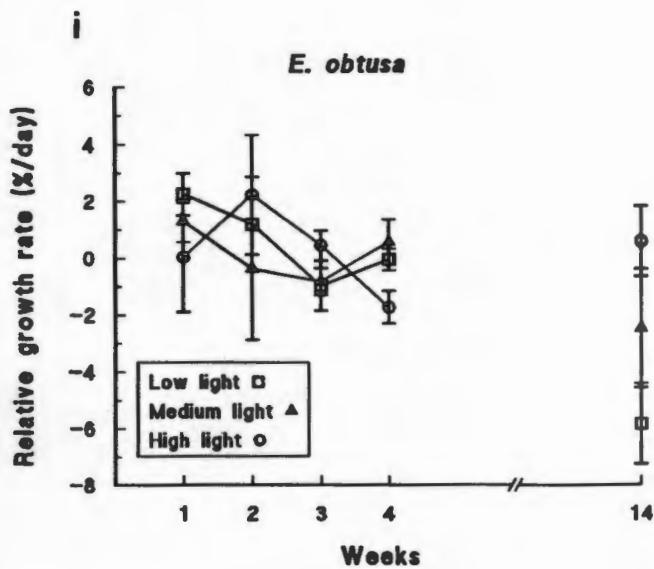
e *P. corallorhiza*

f *C. holmesiana*

g *A. constricta*

h *S. heterophyllum*

i *E. obtusa*
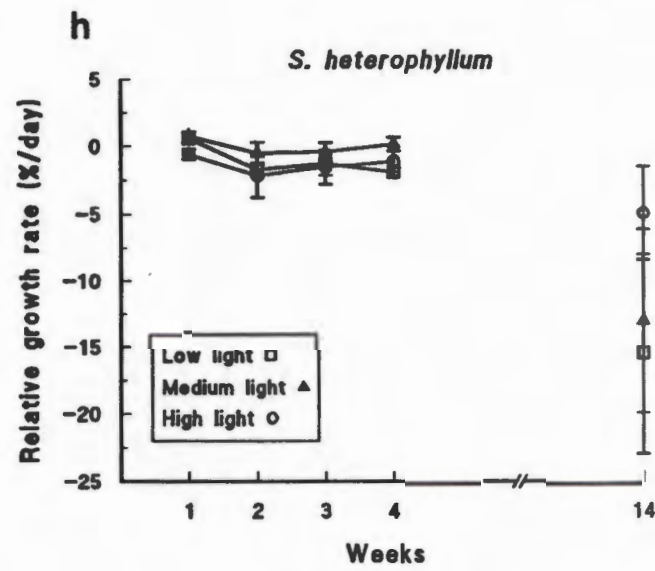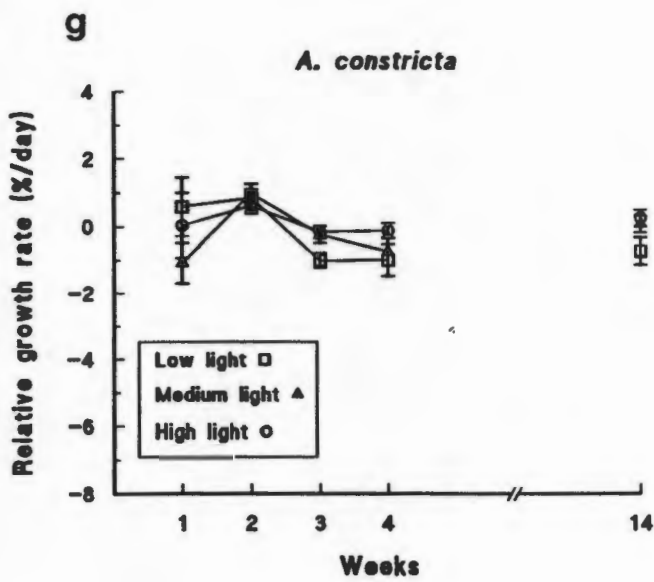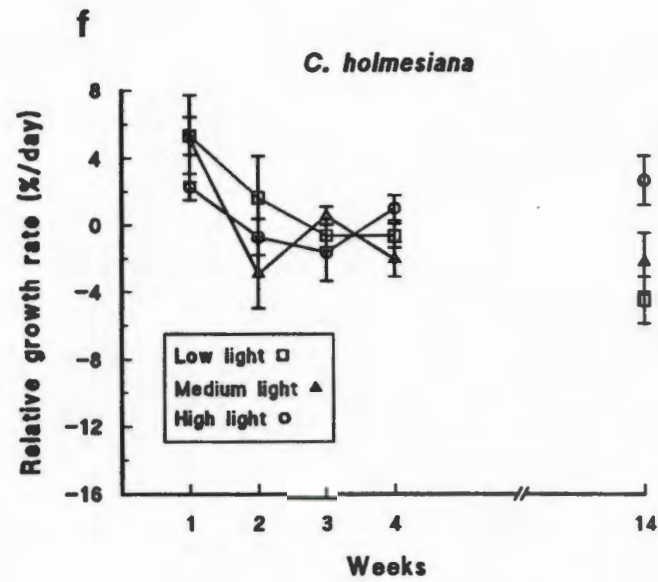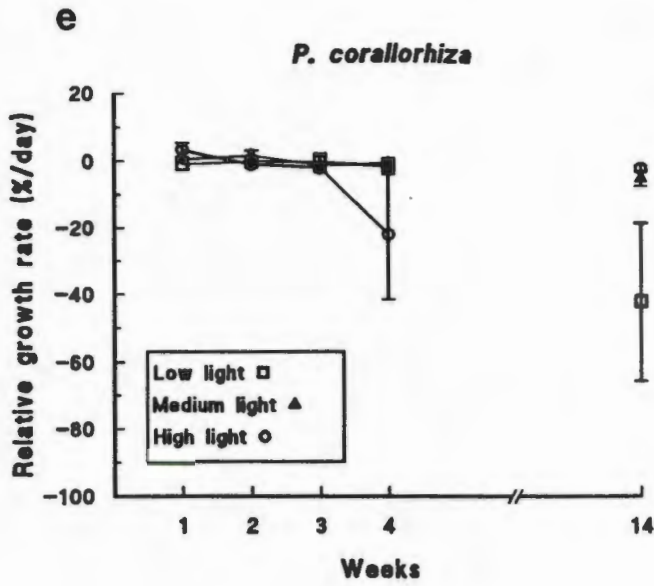
j *C. filiformis*

Table 3. Probabilities of accepting the null hypothesis (no effect or interactions between the treatments on rate of change in biomass). Probabilities generated by multivariate ANOVAs. When asterisk is shown, the null hypothesis is rejected (p < 0.05).

SPECIES	TIME	LIGHT	TIME @ LIGHT
A. constricta	.0031 *	.3459	.0062 *
B. prolifera	.0255 *	.0040 *	.0011 *
C. filiformis	.1353	.0551	.6983
C. holmesiana	.0004 *	.6026	.1569
E. obtusa	.1469	.9526	.4305
G. capense	.0000 *	.0051 *	.0369 *
H. venosa	.0007 *	.1015	.5096
Pachymenia carnosa	.0035 *	.0242 *	.2988
Plocamium corallorhiza	.0029 *	.7715	.2356
S. heterophyllum	.0618	.0016 *	.2125

Time and light have significant effects on the RGR of *Pachymenia carnosa*, *G. capense* and *B. prolifera* (Table 3). The RGR of *P. carnosa* decreased over time (Fig. 3a). This decrease was more rapid in low and medium light conditions than in high light conditions. Unlike replicates under low and medium conditions, the RGR of *P. carnosa* was always positive in plants under high light conditions. The RGR of *G. capense* (Fig. 3b) decreased in the first week, under all light conditions. Thereafter the RGR was maintained at or just above zero in medium and high light intensities until week fourteen. The RGR of plants under the low light decreased dramatically by week four but recovered to some extent by week fourteen to levels similar to those plants grown under high and medium conditions. The difference in RGR response over time to different light conditions was statistically significant (Table 3). The RGR of *B. prolifera* (Fig. 3c) decreased in all light conditions by week fourteen. However, positive growth rates were for plants under the low light condition increased and decreased from week to week. A significant interaction between light and time was found for this species (Table 3).

Time, but not light, had a significant effect on the RGR of *H. venosa*, *Plocamium corallorhiza*, *C. holmesiana* and *A. constricta* (Table 3). The RGR of *H. venosa* (Fig. 3d) plants decreased rapidly over time under all three tight conditions. The RGR of *P. corallorhiza* generally remained zero or became negative with time (Fig. 3e). The RGR of *C. holmesiana* (Fig. 3f) also decreased over time, although periodic increases in growth rate occurred in some cases. The RGR of *A. constricta* (Fig. 3g) fluctuated over time resulting in a statistically significant interaction between light and time. RGRs increased between weeks one and two, decreased from week two to three and remained stable from week three onwards, in replicates under all three light conditions. However the extent to which this occurred differed among light conditions.

Light had a significant effect on the RGR of *S. heterophyllum* (Table 3). Plants in all light conditions maintained relatively stable RGRs over the first four weeks (Fig. 3h). By week fourteen the RGR's of plants in all three light conditions had decreased, however this decrease was not as pronounced in plants under the high light condition as it was in those under medium and low light conditions.

Although there were changes in RGR occurred in *E. obtusa* (Fig. 3i) and *C. filiformis* (Fig. 3j), neither the effect of light or time was statistically significant (Table 3).

The data on the condition of the plants among the three light intensities are presented in Figures 4a-j. Results from the Kruskal-wallis test or shown in Table 4. The condition of *H. venosa* (Fig. 4a), *B. prolifera* (Fig. 4b) and *S. heterophyllum* (Fig. 4c) decreased significantly among all three light conditions (Table 4). Neither time nor light affected the condition of *A. constricta* (Fig. 4d), *E. obtusa* (Fig. 4e) and *Pachymenia carnosa* (Fig. 4f) significantly (Table 4).

The condition *C. filiformis* (Fig. 4g), *C. holmesiana* (Fig. 4h) and *G. capense* (Fig. 4i) deteriorated significantly over time under low light conditions (Table 4). However, at medium and, especially high light intensities, thallus condition remained at healthy to relatively heathy levels over the fourteen weeks of the experiment. The condition of *Plocamium corallorhiza* plants deteriorated significantly at low and medium light conditions

over time (Table 4), but remained a relatively healthy at high light conditions (Fig. 4j). Species that were able to recover after a decline in condition include *C. filiformis*, *C. holmesiana*, *P. corallorhiza*, *B. prolifera*, *S. heterophyllum*, and *G. capense*.
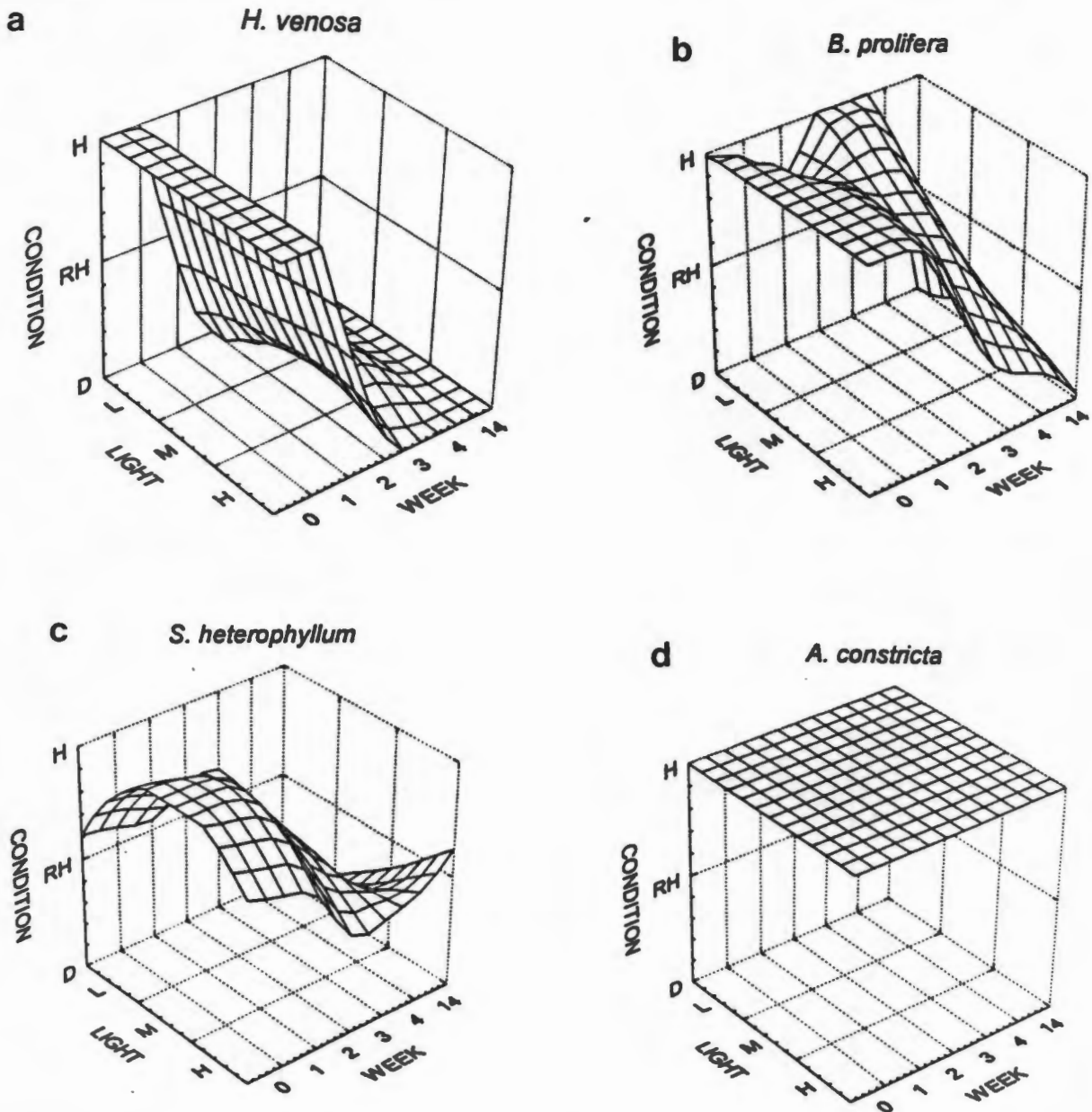
Figures 4a-j. Condition of ten species of South African understorey seaweeds where n=15 for each light condition. A, *H. venosa*. B, *B. prolifera*. C, *S. heterophyllum*. D, *A. constricta*. E, *E. obtusa*. F, *P. carnosa*. G, *C. filiformis*. H, *C. holmesiana*. I, *G. capense*. J, *P. corallorhiza*. H = healthy, RH= relatively healthy, D = deteriorating.
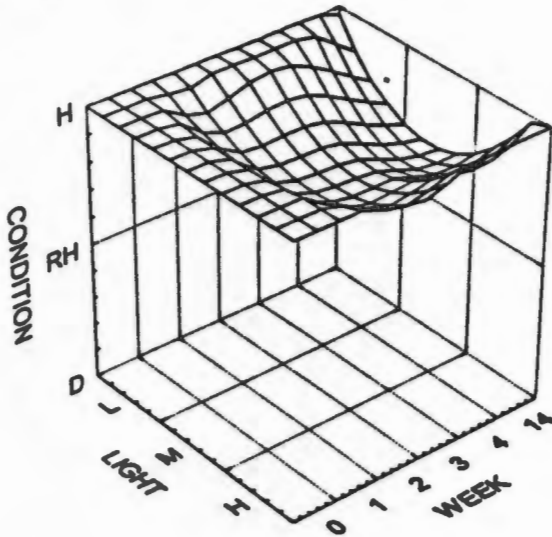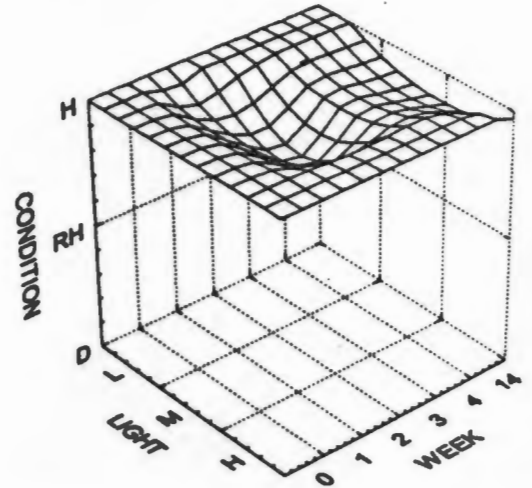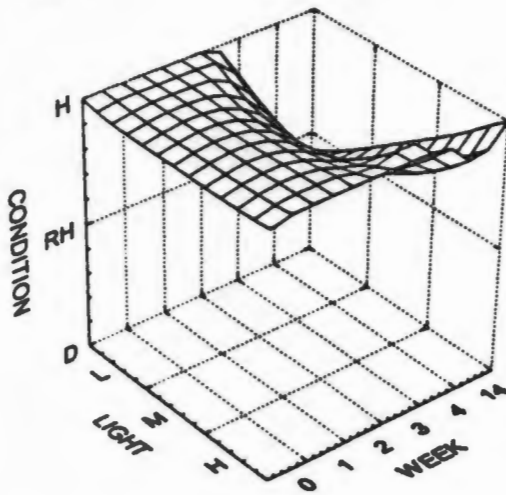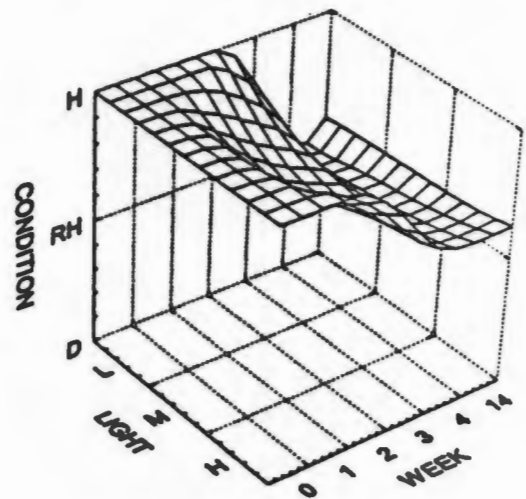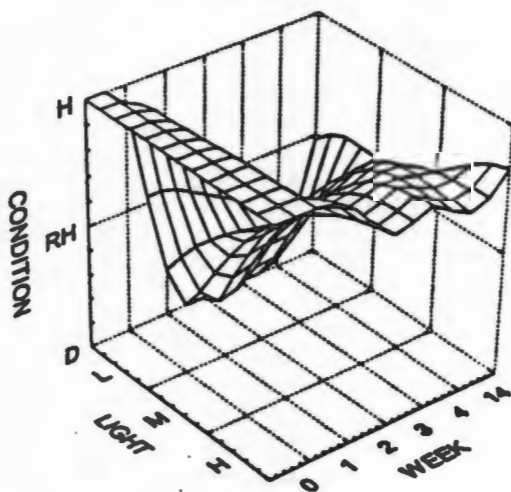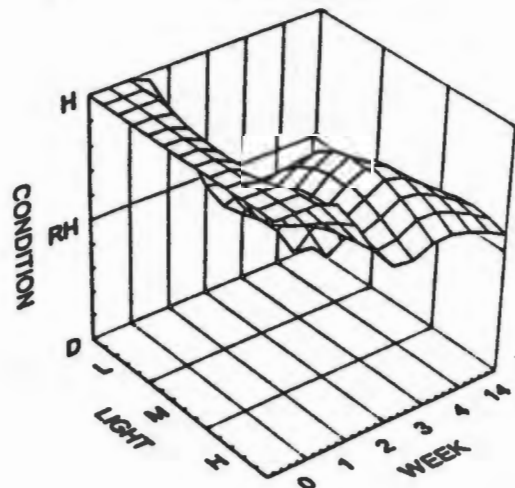
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e   E. obtusa

f   P.carnosa

g   C. filiformis

h   C. holmesiana

i   G. capense

j   P.corallorhiza

Table 4. Probabilities of accepting the null hypothesis (no effect of time among the treatments on plant condition). Probabilities generated by Kruskal-Wallis test. When asterisk is shown, the null hypothesis is rejected ($p < 0.05$).

Species	High light	Medium light	Low light
A. constricta	1.000	1.0000	1.000
B. prolifera	.0005 *	.0009 *	.0005 *
C. filiformis	.0903	.0783	.0145 *
C. holmesiana	.2065	.2473	.0294 *
E. obtusa	.6904	.4366	.3496
G. capense	.2710	.0807	.0052 *
H. venosa	.0002 *	.0005 *	.0001 *
Pachymenia carnosa	.4159	.2027	.4159
Plocamium corallorhiza	.1134	.0033 *	.0014 *
S. heterophyllum	.0411 *	.0029 *	.0103 *

Observations made on the condition of the plants during light experiments indicated that some plants are more susceptible to handling damage than others. This handling damage was either due to the effect of the clip on the plants or the effect of direct handling which caused delicate or brittle plants to break. Plants which showed sensitivity to handling were : *C. holmesiana, C. filiformis, G. capense*, (clip damage) *S. heterophyllum, P. corallorhiza*, and *E. obtusa* (direct handling damage). This negative effect of handling could be considered as a source of experimental error. Most of these species in which damage occurred showed the ability to recover to some extent, depending on the extent of the damage.

Species that showed signs of new blade and holdfast growth by the fourteenth week were: *E. obtusa, C. holmesiana, C. filiformis, G. capense*. Holdfast growth occurred in *P. corallorhiza* and *B. prolifera*. Isolated cases of blade growth and holdfast growth occurred in *S. heterophyllum* and *H. venosa*.

The re-attachment data, (Table 5), indicates that *Plocamium corallorhiza* (Plate 2a), *C. filiformis*, *C. holmesiana* (Plate 2b), *E. obtusa*, and *G. capense* have the ability to re-attach to a substrate. Note that re-attachment ability was generally lower for plants in the low light condition than those in higher light conditions.

Table 5. Percentage of plants that re-attached to the false rock after fourteen weeks and to the tank floor, under the three light conditions after ten weeks.

Species	% of plants attached to false rock	% of plants that attached to the tank floor under each of the three light conditions		
		Low	Medium	High
A. constricta	0	0	0	0
B. prolifera	0(80)*	0	0	0
C. filiformis	80	0	80	100
C. holmesiana	100		60	80
E. obtusa	80	20	60	60
G. capense	60		60	60
H. venosa	0	0	0	20
Pachymenia carnosa	0	0	0	0
Plocamium corallorhiza	-	0	80	40
S. heterophyllum	-	0	0	0

* Denotes that although plants were not attached, holdfasts were growing and plants were likely to attach if left for longer.

Only one individual out of a total of 20 *H. venosa* plants re-attached. *B. prolifera* had not attached to the false rock after fourteen weeks, although new holdfast growth was evident and it is likely that given more time this species would re-attach and grow new blades. The species *A. constricta*, *Pachymenia carnosa*, and *S. heterophyllum* (Plate 2c) showed absolutely no signs of holdfast growth after ten or fourteen weeks.
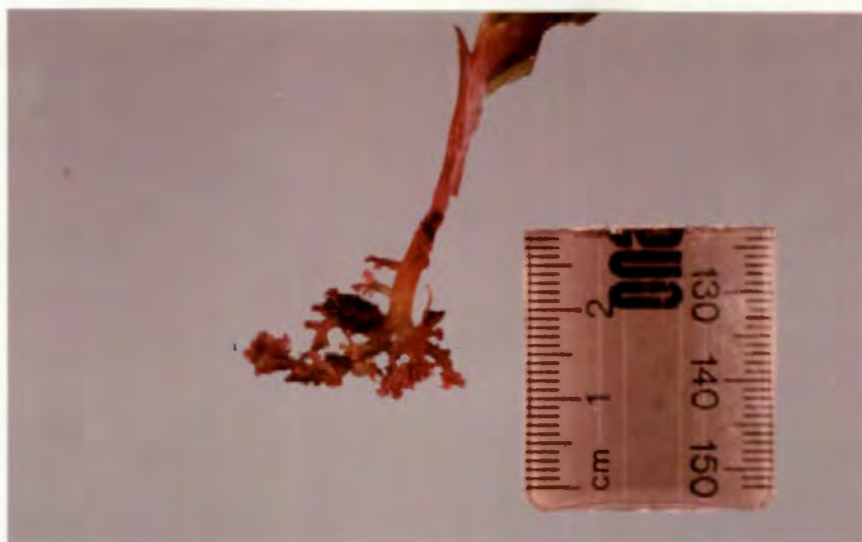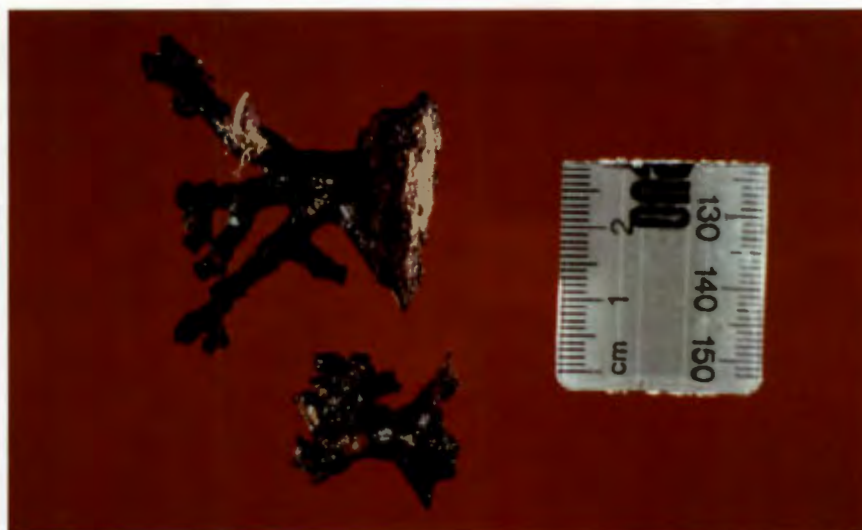
Plates 2a-c. Holdfast morphology. A, spreading holdfast of *Plocamium corallorhiza*. B, rhizome-like holdfast of *C. holmesiana*. C, discoid holdfast of *S. heterophyllum*.

Signs of reproductive development were found in *A. constricta*, *E. obtusa*, *C. holmesiana*, *C. filiformis*, and *Plocamium corallorhiza*. In *A. constricta* receptacles developed, initially only on plants under the low light condition, and later in plants under the medium and high light intensities. Reproductive structures consisting of round dense bundles, like those described in Stegenga *et al.*, (in press) developed on blade surfaces in *E. obtusa*. Reproductive structures of *P. corallorhiza* develop in the axils of lateral branches, as dense clusters of adventitious branching systems typical of this species (Stegenga *et al.*, in press). Reproductive activity was evident in the *Caulerpa* species as the differentiation of the apical portions of blades into gamete production. *B. prolifera* plants also had reproductive structures (small foliaceous proliferation scattered over the blade surface) but these structures had completely developed before plants were been collected from the sea.

Sporeling recruitment did occur on the glass slides laid out under experimental conditions, see Plates 3a,b,c,&d. Sporelings were too small to be identified at the species level, hence it is uncertain whether they originated from study species or not. However due to the seawater filtration system it seems like that at least some them were study species. All macroalgal sporelings found on the glass slides were members of the Rhodophyta. Two types of developing forms could be identified. In the most common form, spores appeared to divide and send out a filament, that would presumably develop into a rhizome of holdfast (Plates 3a,b&c); and less commonly, spores developed as discs (Plate 3d). Sporeling recruitment occurred under all three light intensities, but was more prolific in medium and high light intensities and increased over time.

Although not found on the glass slides, sporelings of kelp and *Ulva* species were found on the tank walls, predominantly under the high light intensities, with less dense stands under medium light intensities and none under low light intensities. *Enteromorpha* species was found growing on the aeration pipe, near the surface of the water, directly under one of the mercury halide lights. The spores of species were possible brought into the tank on the collected material or the marine rock that was stored in the tank.
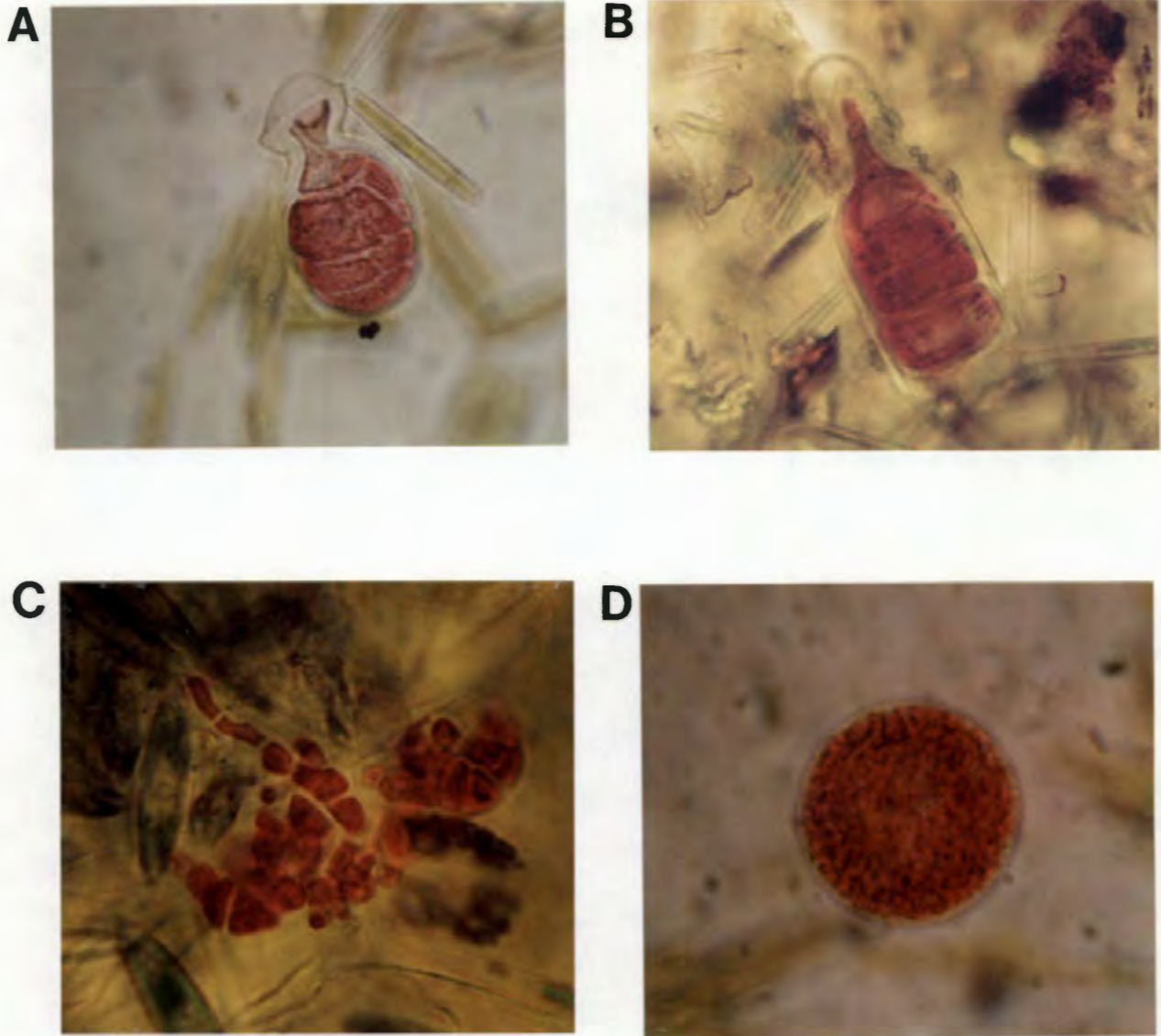
Plates 3a-d. Spore development. 3a-c, Spores dividing and sending out rhizoid-like structures (magnification = 1,25 x 40 x 12.8). 3d, discoid spore development (magnification 2 x 40 x 12.8).

Clear differences in the development of the microalgal communities among light conditions were observed. Microalgal development under high and medium light conditions was prolific, forming a continuous mat (see Plates 4a&b), whereas communities developing under low light conditions were relatively sparse and disconnected (Plate 4c). A succession in community structure over time was apparent. Colonising communities consisted primarily of diatoms (Plate 5a). These were succeeded by Cyanobacteria (blue-greens) which were the dominant communities by week fourteen (Plate 5b). Species diversity increased over time and was greatest in communities developing under the high light condition, and lowest in those under low light.
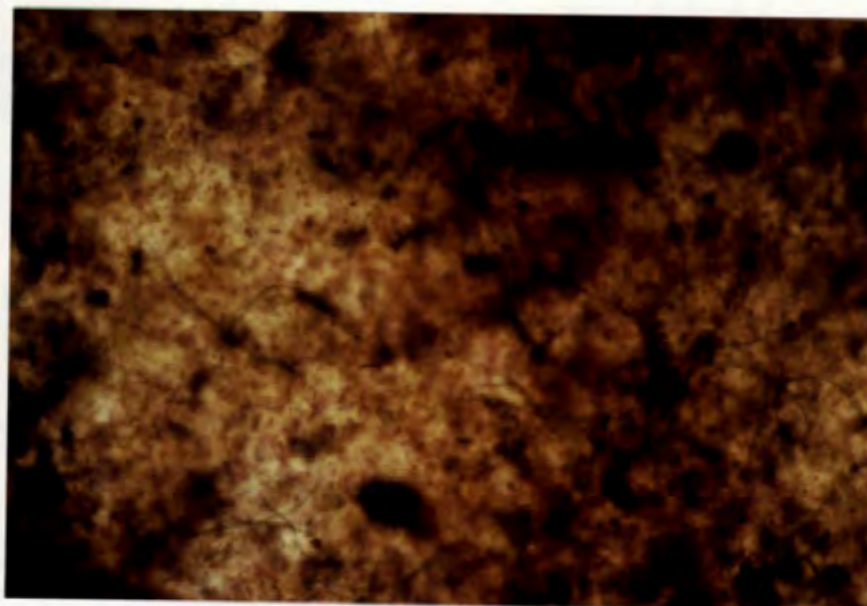
Plates 4a-c. Fourteen week old microalgal communities that established on glass slides place in the experimental tank under three different light intensities. A, high light. B, medium light. C, low light. Magnification = 1.6 x 6.3 x 12.8
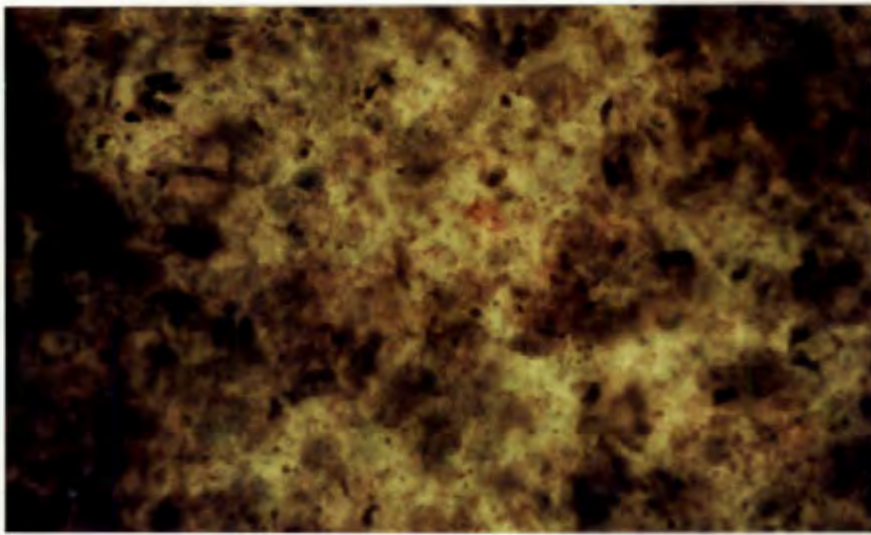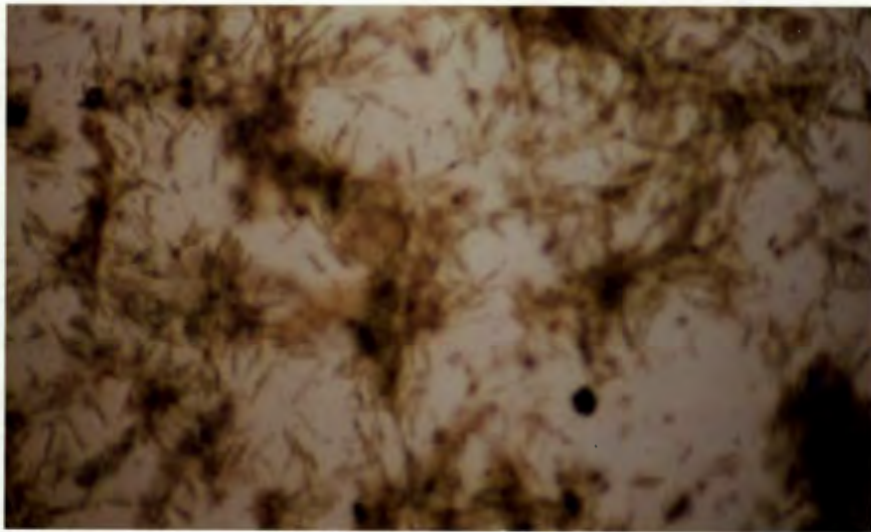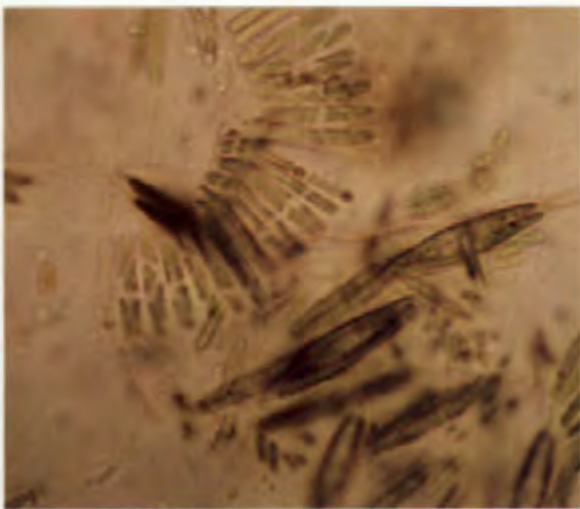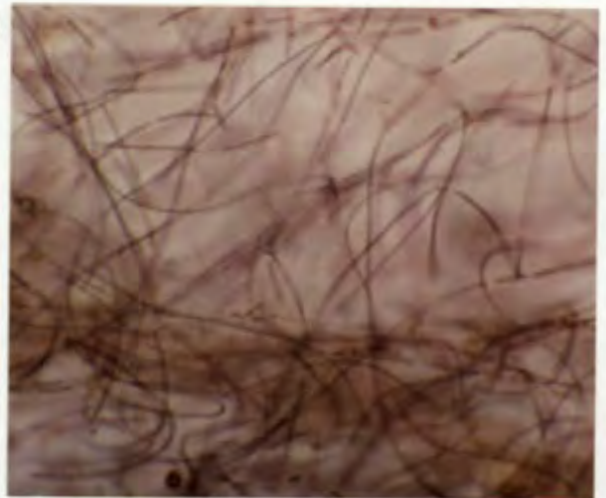
Plates 5a&b. Shifts in microalgal community dominance from diatoms (5a), to cyanobacteria, (5b). Magnification = 1.6 x 40 x 12.8.

Discussion

Irradiance levels in the high light treatment 0.8m (80.9 μmol.m^{-2}.s^{-1}) in the experimental tank were lower than those occurring at 6m in the Kelp Forest Exhibit tank (141.7 μmol.m^{-2}.s^{-1}). The readings taken in the Kelp Forest Exhibit were done at mid day. Hence, irradiance in the Kelp Forest Exhibit may be lower earlier in the morning and in the afternoon compared to the constant eight hours of irradiance that the experimental tank received per day. If the daily irradiance levels in the Kelp tank do not drop below those of the high light intensities in the experimental tanks, seaweeds that did better in the high light conditions of the experimental tank may be expected to do relatively well in the Kelp Forest Exhibit. However, the irradiance levels over a whole day should be determined in order to gain a clearer idea of what may be expected.

The light levels at a depth of 6m in Kelp Forest Exhibit at the Two Oceans Aquarium are similar to those at the bottom of the Kelp Forest Exhibit at the Monterey Bay Aquarium, which measured 49-467 μmol.m^{-2}.s^{-1} on a bright midsummers day. Furthermore, the light levels of the Two Oceans Aquarium Kelp Forest Exhibit compare favourably to those found in the natural environment (Fig. 1). Light levels measured at Saldanha Bay were higher than those of the aquarium from the surface to about 4 m, below which, irradiance levels were similar. Measurements at Saldanha were taken on a clear, sunny summer day, whereas the measurements in the Kelp Forest Exhibit tank were taken on a hazy spring day. Hence it is likely that on sunny days, the light levels in the Kelp Forest Exhibit tank may reach those recorded for Saldanha Bay.

Anderson and Bolton (1985) found that irradiance levels at 6m are much higher during upwelling events (maximum of 600 μmol.m^{-2}.s^{-1}), compared to downwelling event (maximum of 200 μmol.m^{-2}.s^{-1}) during summer at Oudekraal. The average irradiance from three samples taken at 6m in the aquarium was 141.7 μmol.m^{-2}.s^{-1}, which is sightly lower than the levels observed during downwelling at Oudekraal. The value for the downwelling irradiance at Oudekrall was the maximum observed at this depth during downwelling, most other observation found irradiance were in the range of 50-100 μmol.m^{-2}.s^{-1} (Anderson and Bolton, 1985).

The light levels in the Two Oceans Aquarium during winter were not determined. Due to the change in the incident angle that will occur during winter, the ambient irradiance in the Kelp Forest Exhibit may be reduced to levels lower than those found in the natural environment. This is a function of shading due to the containing walls of the tank (these walls extend about 2.5m above the surface of the water). Furthermore, Bolton and Anderson (1995) stress the impact that changes in incident angle between seasons have on light levels. The option of installing lights in the tank, such as those used in the New York Aquarium Kelp Exhibit (Linden and Yarish, 1992), if irradiance levels in the tank prove too low, needs to be explored. Light levels in the North Atlantic Kelp Exhibit at New York Aquarium are supplemented with 1000 Watt metal halide lamps (Linden and Yarish, 1992).

By combining the data on viability (RGR and condition) and re-attachment ability, suitable species for the aquarium can be identified.

H. venosa

Biomass and condition both deteriorated over time and among all light conditions until plants had completely rotted away. The only plant that did not rot away completely died back until only the basal section of the blade and the holdfast remained. This surviving plant did manage to attach its self to the tank floor. Although *H. venosa* would be aesthetically valuable, its poor response to artificial conditions indicated that it is not suitable for establishment in aquaria.

Plocamium corallorhiza

Plant biomass decreased over time. Condition data suggests that although biomass is not significantly affected by light, plant condition is. Plants under low light conditions deteriorated whereas plants under high light conditions were relatively healthy. By the fourteenth week, holdfasts of this species were growing well and were able to attach to the tank floor. New blade growth may have emerged from these plants if left in the tank. Assuming that the new growth is successful, *P. corallorhiza* will be an appropriate choice of understorey species in the Kelp Forest Exhibit.

Pachymenia carnosa

P. carnosa was significantly more productive under high light conditions than under low light conditions. It was observed that this species had been grazed by sea-urchins in the high and medium light conditions. In the absence of such grazers, the positive growth in the high and medium light conditions may have been of a greater magnitude. The condition of the plants remained healthy to relatively healthy thought the experiment. *P. carnosa* would, in these respects, be suitable for the Kelp Forest Exhibit. Unfortunately though, not a single plant re-attached nor was there any sign of holdfast growth. If this species is used in the kelp tank, individuals would have to be collected intact, attached to the rocks they are growing on.

G. capense

G. capense lost less biomass by week fourteen under high light conditions than it did in medium and low light conditions. This pattern was reflected in the condition data. However, by week fourteen the majority of plants in all the light conditions were growing new material, including those in the low light conditions that had earlier been classified as deteriorating. The ability to recover was due to the regeneration of branches which started out as clusters of finely branched material that developed out of the rotting material of secondary and third branches. The newly developing *G. capense* plants attached to the tank floor or false rock.

Similar patterns of regeneration have been reported for *G. sesquipedale*. Santos (1995) found that the recruitment peak of vegetatively developed fronds followed periods of high frond mortality. Furthermore, the standing crop of *G. sesquipedale* is reported to fluctuate greatly with season. It is therefore likely that the pattern of die-back observed for *G. capense*, may, in part, be attributed to seasonal fluctuations in growth, however, this needs further investigation. If newly developing plants are able to grow to maturity in aquaria conditions, this species can be recommended for the Kelp Forest Exhibit.

The light levels in the aquarium will not be limiting to this species, conversely, photoinhibition may occur. Hernández *et al.* (1995) found that there is a common pattern of slight photoinhibition in *G. sesquipedale* in high irradiance levels (above 150 μmol.m^{-2}.s^{-1}), which demonstrates that this species is relatively intolerant to high irradiance, compared to

other species in the same position (low intertidal) on the shore (Hernández *et al.*, 1995). Whether or not similar inhibition may occur in *G. capense* is unknown.

E. obtusa

E. obtusa did well in artificial conditions. New growth and reproductive development occurred on the blades of plants in medium and high light intensities, but little new growth was observed under low light conditions. *E. obtusa* plants were able to successfully re-attach themselves in the majority of cases. The pattern of increased growth toward spring correlates well with seasonal photosynthesis (winter minima; spring maxima) observed in natural populations (Levitt, 1993). This species is highly recommended for establishment in aquaria, if its productivity in the aquarium is not limited by light.

A. constricta

A. constricta plants did very well in artificial conditions. The fluctuating RGR from week to week in indicated that these plants were loosing and gaining mass periodically. This may be explained by two observations made on this species. Firstly, receptacles that were produced would detach from the plant once fertile, causing a decrease in mass. The plant would then gain mass either by producing more receptacles, or new growth. Secondly, this species often shed its epidermal layer of cells, presumably to keep the plants free of epiphytes. The periodic abscission of the epidermal layer has been reported on for a number of species : *Ascophullum nodosum* (Filion-Myklebust and Norton, 1981, cited in Russel and Veldkamp, 1984); *Harlidrys* and other fuicoid genera (Moss, 1982,1984, cited in Russel and Veldkamp, 1984). It is generally agreed that skin shedding "is a defense mechanism against fouling by algal epiphytes" (Russel and Veldkamp, 1984). Shedding may thus have played an important role in maintaining *A. constricta* plants in a consistently healthy state throughout the experiment.

Although *A. constricta* does well in artificial conditions no plants showed any sign of holdfast growth. *A. constricta* is recommended as a suitable species to establish in aquaria conditions. However, plants that are collected for aquaria should not be removed from their substrate, but rather be collected along with the rock they are attached to, as in the case of *P. carnosa*.

B. prolifera

After fourteen weeks the majority of the original blade material had rotted away completely, or was in the process of rotting. Hence, the majority of plants were classified as deteriorating at week fourteen. However, new holdfast growth was observed in six of the plants in the light experiment, and four of the plants in the re-attachment experiment. Although none of the plants had re-attached, it appeared as though, given time they would. Given time, the new hold fast growth may be followed by new blade development (Kain and Norton, 1990). Levitt (1993) found that *B. prolifera* has a seasonal primary productivity, with a winter minimum and spring maximum. The loss of biomass and the deterioration of this species may, in part, have been related to a seasonal reduction in productivity, which was compounded by a poor response to artificial conditions. Whether this species would recover is unknown, hence the suitability of this species for establishment in aquaria remains uncertain.

S. heterophyllum

S. heterophyllum plants in the high light conditions did better than plants under medium and low light intensities. However the accuracy of the biomass data may have been compromised due to handling effects. *S. heterophyllum* plants are relatively brittle, hence leaves or branches were easily broken off when plants were handled. Condition data suggests that plants generally deteriorated, although some recovery was seen by the fourteenth week in plants growing under medium and high light intensities. None of the plants showed any sign of holdfast growth or re-attachment. If this species is used in aquaria, care should be taken in the collection and they would have to be collected attached to rock. This species may do relatively well in aquaria conditions, but can not be highly recommended.

C. holmesiana

Plants deteriorated in condition over time, but this was mainly due to handling damage. Often, the part of the plant that was in the peg deteriorated, and broke off from the rest of the plant. The healthy detached plants grew well, spreading along and attaching to the tank floor. An interesting observation was that plants grown under the low light condition did not attach as readily as plants growing under medium to high light conditions. This phenomenon was observed in other species too, and will be discussed later. This species is highly

recommended for establishment in the understorey of the Kelp Forest Exhibit, and will adjust, and attach relatively quickly.

C. filiformis

Although *C. filiformis* plants lost mass over time, their condition improved significantly in the high light conditions by the fourteenth week, and had plants attached readily. Once again, biomass loss was often the result of damage inflicted be the peg. This species is also recommended for the Kelp Forest Exhibit.

In general, the RGRs of the species investigated here are poor compared to what might be expected in the natural environment. Low and negative RGRs observed in several of the study species may either be related to seasonal fluctuations in productivity; poor responses to artificial conditions (low light levels and minimal water flow) or damage inflicted during collection, and by environmental change. Furthermore, some species may be perennial, and others annual. Very little data is available on the perenniality of South African subtidal species, but reports that do exist indicate that perenniality, with seasonal fluctuations in productivity, may be common (Levitt, 1993). Observations made in this series of experiments may support this. The die back of *B. prolifera*, *G. capense*, *Plocamium corallorhiza*, *S. heterophyllum*, and *H. venosa* to stubby holdfasts, followed by new holdfast (except in *S. heterophyllum*) and blade growth as well as the low productivity of *E. obtusa*, *A. constricta*, and *Pachymenia carnosa* followed by increased RGR in the case of *E. obtusa*, may partially reflect season patterns of productivity of perennial species. Most importantly, the holdfasts of most of these species remained viable, and were able to initiate new growth. This may result in single plants surviving for many years. Seaweeds that cast off parts of their thallus every year are referred to as "pseudoperennial" (Dawers, 1981; Lünning, 1990). Kain and Norton (1990) mention holdfast regeneration as a reasonably common feature in red seaweeds. Perennial species would be advantageous in aquaria. As mentioned earlier, the Kelp Forest Exhibit at the Monterey Bay Aquarium specifically selected local perennial subtidal species to establishment in the tank. Those perennial species in which productivity is merely reduced, eg. *E. obtusa* would be more suitable for aquaria compared to those species which are psuedoperennial, although both may be used.

The lack of water movement is likely to have caused a reduction in the supply of nutrients and gases across the boundary layer, and would have slowed the removal of waste products (Lobban and Harrison, 1990; Kain and Norton, 1990) This would have had an adverse effect on the RGR of the plants. Watanabe and Phillips (1986), referring to the Monterey Bay Kelp Forest Exhibit, suggested that "inadequate water motion may be a chronic problem in the kelp tank". The kelp tank in the Two Oceans Aquarium, as mentioned before, is equipped with a surge generator. The water movement generated should be sufficient to ensure that the plants have a constant nutrient supply, and they will remain "clean". By altering the settings of the surge generator it is possible to simulate "storm" conditions, creating high levels of water movement in the tank approaching those that are experience periodically in the natural environment (Musson, pers. comm.). These wave motion levels have not, however, been quantified.

The species that deteriorated were those with fragile, often thin vegetative tissue, eg *H. venosa*, *Plocamium corallorhiza* and *B. prolifera*. Species such as *Pachymenia carnosa*, *A. constricta* and *E. obtusa*, whose vegetative material is tougher maintained healthier conditions. The reason for this disparity between fragile and tough thallus tissue is unknown. Both *Caulerpa* species, which are delicate, also deteriorated in condition to some extent. This was most likely a function of their susceptibility to handling damage and not seasonal fluctuations in productivity. Both *C. holmesiana* and *C. filiformis* showed good recovery. Notably, those species which did not die back much (*P. carnosa*, *A. constricta* and to a lesser extent *S. heterophyllum*) were the ones with discoid holdfasts.

Out of the species tested for attachment ability on false rock, *C. holmesiana*, *C. filiformis*, *G. capense*, *P. corallorhiza* and *E. capensis* will be able to attach themselves to the false rock in the kelp tank. Unfortunately, the species that coped the best in artificial conditions, namely *A. constricta* and *P. carnosa* showed absolutely no sign of holdfast growth or attachment ability in any of the plants on the false rock, nor any of the plants in the light experiment.

One could pose the question: why could some plants attach and other not? In comparing species that attached with species that did not, it can be said that properties of the holdfast

correlated to attachment ability. All the species that were able to attach themselves have rhizome-like, terete spreading holdfasts, for example *C. holmesiana* (Plate 2b) and *Plocamium corallorhiza* (Plate 2a). Species with discoid holdfasts, for example *S. heterophyllum* (Plate 2c), were the species that could not re-attach. It can therefore be recommended that holdfast structure be noted when collecting species for aquaria. In the case of species with discoid holdfasts, plants that are attached to relatively small rocks can be collected, intact, with the rock.

Several species that attached on false rock under high and medium light conditions did not attach under low light conditions. The cause of poor attachment under low light may be twofold. Firstly, plants under low light are tended to be less productive than those under medium and high light conditions. Low productivity would translate to poor allocation of resources to areas of new growth such as holdfasts or rhizomes. In the case of *C. holmesiana*, plants under low light had very pale fronds, indicating that light levels were too low for efficient photosynthesis.

The second reason for plants not attaching may lie in the composition of the microalgal film on the tank floor. The microalgal film that developed under medium and high light was more prolific than that under the low light. A stable microalgal film may provide a more suitable substrate for plants to attach to than relatively bare painted concrete.

This pattern is reflected in the sporeling recruitment observed on the glass sides that were laid out in the tank. Sporeling recruitment was more prolific under high and medium light conditions. It is known that the ability of cells to stick to surfaces depends on the surface energy, also referred to as surface tension or wettability. Biofilms, here referred to as microalgal films, (made up of bacteria, and "their associated mucilage", and other microbial organisms eg. diatoms), increase surface energy, making the substrate more suitable for macroalgal settlement, (Fletcher *et al.*, 1986; Lobban and Harrison, 1990; Keough and Raimondi, 1995; Weiczorek *et al.*, 1995). These biofilms rapidly colonize exposed marine surfaces (Lobban and Harrison, 1990). The properties or presence of the biofilm may indicate high rates of nutrient supply, a recently disturbed area (or new aquarium) or the presence of allelopathic organisms (Keough and Raimondi, 1995). The relatively prolific

recruitment of sporelings under the high and medium light conditions may also be attributed to light itself.

Keough and Raimondi (1995) investigated the response of settling invertebrate larvae to bioorganic films and found that recruitment increased with film age. Sporeling recruitment in the experimental tank also improved with time (microalgal film age), however this may also be a function of inherent recruitment patterns (South and Whittick, 1987). It is appropriate at this point to point out the composition of the initial community will influence subsequent succession (Kain and Norton, 1990). After three and a half years, the composition of understorey seaweed community in the Monterey Bay Kelp Forest Exhibit was largely function of species that were selected for initially, to supply the tank with spores (Phillips *et al.*, 1988). Sporelings that established in the experimental tank included Rhodophyta species and *Ulva* sp. (most likely from plants in the tank), *Enteromorpha* (undetermined source: either spores in filtered water or from undetected plants on the rocks stored in the tank) and kelp (probably introduced as gametophytes collection material or kelp plants stored in the tank before the experiment). The growth of the *Ulva* species, *Enteromorpha* species and kelp was more advanced than that of the majority of red seaweed sporelings developing on the glass slides. The fact that *Ulva*, *Enteromorpha* and kelp sporelings were found on the upper reaches of the wall and not on the tank floor indicated that these species have a preference or requirement for higher light for initial growth than those of the red seaweed sporelings. Additionally the absence of red seaweed sporelings on the tank walls may be a function of their lack of motility (Drawers, 1981).

The presence and proliferation of the microalgal film in the experimental tank accords with observations made in the Monterey Bay Aquarium Kelp Forest Exhibit (Phillips *et al.*, 1988). The first organisms to colonise the Monterey Kelp Forest Exhibit were benthic diatoms and *Ulva* sp. Observations on the succession of the microalgal film in the experimental tank also found that initial colonising species consisted primarily of diatoms. With time the dominant community changed from diatoms to Cyanobacteria. Diversity also appeared to increased with time, especially under the high light conditions.

The microalgal film in the experimental tank is easily removed manually. It is not known

whether the fouling species will disappear with time as observed in the Monterey Kelp Exhibit (Phillips *et al.*, 1988). Our experiment lasted for just over three months, whereas Monterey Bay Aquaria studies were conducted for over three years. The cover of the microalgal film in the Monterey Bay Kelp Forest Exhibit started to decrease after about five months (Phillips *et al.*, 1988) hence it is possible, and expected, that the microalgal film in the experimental tank would also start to decrease in time. The decrease in microalgal cover observed in the Monterey Bay Kelp Exhibit occurred in autumn. The disappearance of fouling microalgae that are developing in the Two Oceans Aquarium Kelp Exhibit may be influenced by season, but this is speculative.

Sources of experimental error

The relative absence of water movement in the experimental tank was observed to have an adverse effect on the experimental plants. This was due to the fact that plants became covered with organic sediment consisting of diatoms and organic debris. Processes such as photosynthesis, respiration and nutrient uptake may have been hindered by sediment. Furthermore, plants covered by organic sediment lost their aesthetic appeal. The sediment was easily washed off the plants, each time biomass was recorded.

As mentioned earlier, several species were adversely affected by handling. The resultant decrease in biomass may have masked trends of growth that would have been apparent had the plants been left undisturbed.

Plants were grown in winter day length condition throughout the experiment. New growth and sporeling emergence, triggered by longer day lengths typical of summer, would therefore not have been recorded. Furthermore, the duration of the experiment was relatively short, ceasing at the start of spring. The new growth observed on week fourteen could be attributed to circannul rhythms (Lünning, 1990) and productivity fluctuations in perennial species. This can not be clarified unless further observations of spring and summer growth as well as a second autumn and winter are recorded.

The Kelp Forest Exhibit will receive natural sunlight. The light the experimental plants received was artificial. The two different light sources may have different effects on the

seaweed due to the different light qualities. Seaweeds absorb light from a range of wavelengths (see Lünning, 1990). The artificial lights, particularly the mercury halide lights, may not have produced the range of wavelengths necessary for optimal growth of the seaweeds. As mentioned earlier, the light levels in the experimental tank were lower than those recorded in the aquarium at mid day, and those in the natural environment. The relatively poor light conditions are likely to have had a significantly adverse affect on the seaweed growth.

Concluding remarks

Seaweeds that are robust (tough thalli or good recovery abilities), and have spreading holdfasts are highly recommended for use in the Kelp Forest Exhibit at the Two Oceans Aquarium. Suitable plants that have disc holdfasts can be used, provided they are collected already attached to rock substrates, unless some artificial means of attachment is devised. Both perennial species and annual species may be used as long as the alternate life history phase of the annual species establishes. Perennial species that do not die back completely are necessary for the tank in order that an understorey seaweed community is maintained during periods of substantial die-back of the pseudoperennial species, and the senescence of annual seaweeds (not investigates in this study).

Light is an important factor affecting the condition and productivity of seaweeds. The light levels in the Kelp Forest Exhibit at the Two Oceans Aquarium accord reasonably well with those occuring in the natural marine environment and therefore should be conducive to seaweed growth and recruitment. In some shallower areas of the Kelp Forest Exhibit, high light levels may cause photoinhibition in some understorey species, but further investigations will have to be done to establish whether this is the case. The high light levels recorded at these lower depths in the tank will, however, be beneficial to the growth of the kelp, which, in turn, will reduce the possible effects of photoinhibition in understorey, shade adapted species.

A succession in microalgal communities will occur. The cover of this fouling microalgal film can be expected to decrease over time. It is important to remember that marine benthic communities develop over time, and are dynamic. Hence, the community set up in the kelp

forest may take a long time to become reasonably stable. As indicated in the results from this study, most species only start showing positive signs of regeneration some time after being introduced into artificial conditions. The initial species that are established in the Kelp Forest Exhibit may strongly influence the dynamics of the benthic community. Mature, self sustaining communities will take a minimum of two to three years to develop, following observations made by Phillips *et al.* (1988) for the Monterey Bay Kelp Forest Exhibit, and those made on natural community succession (Kain and Norton, 1990). For the initial three years the understorey floral community may be supplemented with the type of species mentioned above. These may not be highly productive but will serve the purpose of seeding the tank with favourable species, and maintaining a reasonable aesthetic component until such time as the community becomes self sustaining.

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