

FORM, FUNCTION AND ENVIRONMENT:
IN SOUTHERN AFRICAN *CODIUM* SPECIES

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ABSTRACT

A variety of species of *Codium*, which occur along the southern African coast were studied ~~to investigate~~ in an attempt to explain the wide interspecific differences in external form in terms of adaptations to different environmental conditions.

For the purpose of this study *Codium* species were divided into two broad morphological groups namely, erect and flattened. The study concentrated more specifically on the consequence of different morphologies on photosynthetic and desiccation rates. This study imparted the following findings:

The *Codium* only two species found exclusively in the subtidal are *C. papenfussii* and *C. megalophysum*. They have flattened morphologies, small surface area to volume ratios and large utricles. The intertidal is inhabited by *Codium* species with both erect and flattened forms.

Net photosynthetic rates of *C. duthieae* (an intertidal species) and *C. stephensiae* (collected from the subtidal) were significantly different especially at lower light intensities. *C. stephensiae* appeared to be better adapted to deeper water which could be attributed to its flattened form.

The subtidal species, *C. papenfussii* was shown to have more chlorophyll per unit area of thallus than the intertidal species, *C. fragile*, *C. stephensiae* and *C. duthieae*. *C. papenfussii*

however, has less chlorophyll per wet weight of thallus than the intertidal species.

The rate of desiccation for the species of *Codium* tested is correlated to surface area to volume ratios. The higher the surface area to volume ratio the more moisture lost. Rehydration following desiccation revealed that the *Codium* species generally occurring in deeper water were unable to reabsorb the moisture lost. There was no correlation between utricle size and desiccation rate.

Codium species found in nutrient rich cooler waters generally had fewer hair-like outgrowths on their thallus than those found in nutrient poor warmer waters.

Introduction:

The coastline of South Africa has 16 *Codium* species, which are siphonaceous multiaxial forms belonging to the family Codiaceae of the Chlorophyta (Silva 1959). There is a wide spectrum of interspecific variation in the external morphology of the different species of *Codium*. The morphologies vary among crustose, spherical, branched erect or blade-like thalli (see Fig. 1). Their internal thallus is spongy and non calcified, consisting of a colourless medulla comprising of dichotomously branched siphons, and a cortex of inflated, club-shaped vesicles (utricles) containing the chloroplasts (South and Whittick 1987). This internal thallus structure is identical in all the different species. Their most important diagnostic feature is the shape of the utricles (Silva 1959). The reproductive structures or gametangia are borne laterally on the utricles.

This study was undertaken in an endeavor to assess, for various *Codium* species, the possible selective pressures responsible for a specific morphology and other adaptations to those environmental pressures, which vary with species distribution. Previous studies have related the functional significance of seaweed growth form to photosynthetic rate (Littler and Arnold 1982), resistance to wave stress (Norton et al 1981), herbivore defense (Littler and Littler 1980), efficiency of light capture (Hay 1986) and desiccation rates (Dromgoole 1980).

It has been suggested that there is a tradeoff between thallus form and photosynthetic rates (Hay 1986). Hay (1986) proposed that algae growing in high light habitats will have a higher surface area to volume ratio, display a multilayered morphology and be highly productive. In contrast algae growing under low light conditions will be monolayered (to avoid self shading), ^{with} a lower surface area to volume, and be slower growing. The multilayered forms, due to their higher surface area to volume ratio, will also have a higher rate of desiccation than the monolayered forms (Dromgoole 1980).

This study will concentrate more specifically on the consequence of the different morphologies on photosynthetic and desiccation rates. Other aspects of the interspecific variation in morphology will also be investigated and an attempt made to relate these variations to contrasting environmental conditions experienced by the different species.

Selected species of *Codium* found along the shore^s of southern Africa and Namibia were used to test the following hypotheses related to light, desiccation and nutrient absorption:-

Codium species found in the intertidal zones will exhibit a more upright and terete morphology with higher surface area to volume ratios, whereas the subtidal species will be flattened prostrate forms with smaller surface area to volume ratios.

Light

Ramus (1978) proposed that stress tolerant shade plants are generally giant-celled, whereas fugitive sun plants tended to be smaller-celled. I therefore hypothesized that the utricles of the subtidal *Codium* will generally be larger than the utricles of the intertidal *Codium* species.

Intertidal *Codium* will exhibit certain attributes which differ from the subtidal species including those occurring in the low intertidal or under ledges in rock pools. These include, higher photosynthetic rates and less chlorophyll per unit area of thallus.

Desiccation

Intertidal terete species with a higher surface area to volume ratio and thinner utricle walls at the utricle apices, will lose water at a more rapid rate than the flatter subtidal species. The intertidal species with their high surface area to volume ratios and their tolerance to periodic desiccation will enable them to recover more successfully than the flatter subtidal species during rehydration.

The spines on the utricles of the intertidal *C. fragile* may act to reduce desiccation in this species despite its high surface area to volume ratio.

Why? How?

Nutrient's

Codium species ~~species~~ found in the cooler nutrient rich West coast waters will have fewer hair-like outgrowths than the warmer South and East coast species. *why?*

METHODS

Distribution and morphology

Most of the data pertaining to the distribution and morphology of the different *Codium* species was obtained from Silva (1959). Personal observations were made regarding the local and geographical distribution of the various *Codium* species at different sites along the Cape coast. These sites included Luderitz (Namibia), Port Nolloth, The Strand, Mossel Bay and Port Elizabeth. Specific conditions were noted such as the particular *Codium* species ability to tolerate sand, and whether the species is found in a more exposed or sheltered habitat.

Laboratory experiments were done to measure photosynthetic, desiccation and rehydration rates and the total pigment content of the various species. The *Codium* species used in the experiments included, *C. duthieae*, *C. stephensiae*, *C. fragile*, *C. papenfussii* and *C. capitatum*. All the species with the exception of *C. capitatum* were collected from the intertidal and subtidal zones at The Strand near Cape Town, Cape Province. *C. capitatum* was collected at N'kambati nature reserve in the Transkei. The

site at The Strand where the *Codium* was collected is a gradually sloping sand - affected rocky shore which is semi-exposed. The rocks offer sheltered crevices and pools in which the *Codium* have established.

Photosynthetic Rates

Various unsuccessful attempts were made in an endeavor to measure the photosynthetic rates of several species of *Codium*. The results obtained showed extreme variation between replicates and were not accurate. Changes were made with respect to the bottles and chemicals used. Care was taken to eliminate any experimental error.

The last attempt provided the data used in this study, was obtained using the following methods:

The photosynthetic rates of three species of *Codium* were measured, *Codium fragile* and *C. stephensiae* (intertidal species) and *Codium stephensiae* collected from the subtidal zone. Winkler titrations (see Dawes 1989) were used to determine the amount of oxygen produced per dry weight of seaweed per hour. The amount of oxygen produced is used as a measure of photosynthetic rate.

Glass bottles (Two liter consol pickling jars) with non-metallic airtight lids were used to incubate the seaweeds. Three replicate portions of algae (\pm 3g each) were cut from the adult plant of the three different species for incubation under a specific light

intensity. Nylon thread was glued to the inside of the bottle lids. The nylon thread was used to suspend the piece of seaweed inside the bottle. The bottles were carefully filled with seawater through which nitrogen gas had been bubbled, to deoxygenate the water. A magnetic stirrer bar was placed inside each of the bottles. The lids were twisted onto the bottles. Care was taken to ensure that no air was trapped inside the bottle once the lid was on. Control jars without seaweed were also filled with seawater in the same manner. *They were close to under water*

All the bottles were placed in a phytotron unit for an incubation time of one hour. The temperature in the phytotron was 15°C.

While in the phytotron the water in each bottle each was stirred slowly by a magnetic stirring bar. This ensured that the seawater continued circulating in the bottle through out the duration of the experiment. Light intensity was measured at intervals throughout the experiment using a light meter. After an hour the bottles were removed from the phytotron unit.

The lids of the bottles were opened carefully. The seaweed was placed on a labelled petridish and put into a 70°C oven to be dried overnight. These were weighed the following morning to determine their dry mass. The seawater in the bottle was carefully siphoned into a BOD bottle. Care was taken to ensure that there was minimal aeration of the water by atmospheric oxygen.

Winkler titrations were done using the seawater from the bottles to measure its oxygen content.

The experiment was repeated at five different light intensities, 377 $\mu\text{E}/\text{m}^2/\text{s}$, 241 $\mu\text{E}/\text{m}^2/\text{s}$, 152 $\mu\text{E}/\text{m}^2/\text{s}$, 61.7 $\mu\text{E}/\text{m}^2/\text{s}$ and 11.3 $\mu\text{E}/\text{m}^2/\text{s}$. Shade cloth was used to decrease the light intensity in the phytotron.

The data collected following the experiment was used in the equation:

$$\text{Photosynthetic rate (mg O}_2\text{ l}^{-1}\text{)} = \frac{Y \times 1}{Y-2} \times f \times V \times 16$$

Where : Y = volume of BOD bottle
f = factor f
V = volume of titre

The photosynthetic rates of the different species of *Codium* were finally expressed as $\text{mg O}_2 \text{gdw}^{-1} \text{hr}^{-1}$

The different rates of photosynthesis of *C. duthieae* and *C. stephensiae* (subtidal) were compared by one-way ANOVA to calculate the F ratio and significant differences between the two data sets. Only these two species were used as the results obtained for the intertidally collected *C. stephensiae* were not accurate. The results obtained are however shown in Appendix II.

Pigment Extraction

The species *Codium fragile*, *Codium duthieae*, *Codium stephensiae* and *Codium papenfussii* were used in this experiment.

Sixty grams of each species was carefully weighed out after it had been patted dry using paper towel. The seaweed was broken up into small pieces. They were then placed in a metal tin. Sufficient liquid nitrogen was poured on top of the seaweed in the tin to ensure that it was frozen solid. The brittle seaweed was then ground finely.

The ground seaweed was left to thaw. Once it had reached room temperature approximately 25ml of acetone (the extraction solvent) was added. The solution was filtered through glass wool into a separation flask mounted on a stand. Fifteen milliliters of petroleum ether was mixed with the contents of the flask.

The flask was left to stand for approximately half an hour to allow the solution in the flask to separate out. If the layers did not separate a few drops of distilled water was added to speed up the separation.

The upper layer contained the pigment extract (petroleum ether). The lower layer was discarded from the flask.

The pigment extract was placed into a vial covered with tin foil to prevent the pigment from fading in the light. This extract was used to measure total pigment content of the seaweed species and for chromatography.

The pigment extracts were diluted 5% extract: 95% petroleum ether. The 'solution' was then scanned over the entire visible spectrum measuring absorbance using a spectrophotometer and plotting the results on a plotter. Total pigment content per unit wet weight of the different *Codium* species was quantified by calculating the total area under the graphs plotted by the spectrophotometer plotter, for the different species. The pigment content per unit area of thallus was calculated by dividing the area under the graph for the different *Codium* species by their surface area to volume ratios (the technique used to calculate the ratio will be described later). The values obtained by this method are meaningless they are merely used to enable an interspecific comparison of the pigment content per unit area of thallus.

Desiccation and Rehydration Rates

Desiccation experiments were done on morphologically different species of *Codium*. The species which were chosen were *Codium fragile*, *Codium duthieae*, *Codium capitatum*, *Codium stephensiae* and *Codium papenfussii*. The former species have a terete upright morphology while the later two have a flattened form. A phytotron unit was used as a desiccation chamber with high light intensity \pm 380 $\mu\text{mol}/\text{m}^2/\text{s}$, controlled temperature (25°C) and air humidity (50%). The seaweeds were weighed prior to being placed in the phototron. Whole plants were used. Three replicates were done for *C. capitatum* and *C. papenfussii*, four replicates were done for *C. fragile* and *C. stephensiae*, and six replicates were done for *C. duthieae*. While inside the phytotron the seaweeds were

positioned in the same way as they would be found on a rock in the intertidal when exposed at low tide. The seaweeds were reweighed hourly for the following 6 hours (the approximate tide time) to monitor the rate of water loss over the time period. Replicates of similar weights were used to calculate the mean water loss for the different species. Desiccation rates of the different species were compared using one-way ANOVA to determine significant differences.

Rehydration of the seaweeds following the 6 hour desiccation period was done by resubmerging the *Codium* species in seawater. The rehydration rate of the different species was determined by weighing the seaweeds at 10 minute time intervals for the first hour of submergence. Before the seaweeds were weighed they were carefully placed on paper towel to remove the excess water. Rehydration rates of the different species were also compared using one-way ANOVA to determine significant differences.

Surface area to volume ratio:-

The surface area to volume ratio of the different species used in the desiccation and rehydration experiments were calculated. This was done by measuring the volume of the piece of seaweed by simple volume displacement technique using a measuring cylinder. The surface area of the same piece of seaweed was determined by coating the entire surface of the damp seaweed with poppy seeds. The seeds were then washed off the seaweed with water, into a funnel lined with filter paper. The excess water was allowed to

drain. The seeds which were trapped on the filter paper were placed into a 40°C oven and weighed after 12 hrs. The surface area of the different species were measured as a function of the weight of the poppy seeds. Three replicates were done for each of the species. The values obtained enabled an interspecific comparison to be made of the varying surface area to volume ratios.

Utricle size:-

Data obtained from the literature will be used to compare utricle sizes between the several *Codium* species being studied. The volume of the utricles was calculated using the formula $2\pi r^2 \times H$ as the volume of the utricle was considered analogous the volume of a cylinder.

Nutrients

Data obtained from the literature was used to investigate whether the species found in the warmer (nutrient poor waters) possess colourless hairs.

RESULTS

Distribution and morphology

Table 1 shows the local distribution of *Codium* on the shore. The different species have been arranged into the various zonation patterns as they would approximately occur along a gradient on the shore. Table 1 also describes the differing morphological

structures of the distinct species in terms of external thallus form and the size of the utricles. No clear patterns regarding these two criteria correlated with location of *Codium* species on the shore can readily be observed.

Representatives of the genus *Codium* can be found along the entire coastline of southern Africa (Table 2). The majority of species can be seen to occur in the 17-19°C temperature range. There are fewer species in the cool West coast waters.

Appendix 1 provides a summary of all the aspects of the different species of *Codium* found along the southern African coastline. Distribution, morphological features and some general aspects on the diverse *Codium* species have been described. It should be noted that the species which have a applanate, flattened form have clusters of utricles, whereas the erect species have individual utricles.

Photosynthetic Rate

The net photosynthetic rates of *C. duthieae* and *C. stephensiae* under different light conditions appear to similar, although $p=0.008$ showing that they are significantly different at the 99% confidence interval (Figure 2). Much of this difference may be attributable to the prominent variation in results obtained for the two species at the lowest light level of 11.3 $\mu\text{E}/\text{m}^2/\text{s}$. At this light level both species appear to have inhibited photosynthesis and have high respiration rates. *C. duthieae* has a

substantially higher respiration rate than *C. stephensiae*. The highest photosynthetic rate for both species is seen to be at 115 $\mu\text{E}/\text{m}^2/\text{s}$.

Pigment content

The pigment content per unit weight of thallus (Table 3) is similar for *C. duthieae*, *C. fragile* and *C. stephensiae*. *C. papenfussii* has a lower chlorophyll content per unit wet weight. The ratio of chlorophyll content per unit area of thallus shows that *C. papenfussii* has a considerably higher chlorophyll content.

Desiccation and Rehydration Rates

The desiccation rates for *C. fragile*, *C. duthieae* and *C. stephensiae* showed a small significant difference of $p=0.018$ with F ratio=3.836. They all had a moisture loss of $\pm 25\%$ after 6 hours. *C. papenfussii* desiccated at a slower rate and lost $\pm 10\%$ of its total moisture content. *C. capitatum* had a total moisture loss of $\pm 45\%$ (Figure 3). There is a significant difference in the rate of desiccation for all the species used, $p=0.0003$ and an F ratio=6.262.

Recovery following desiccation (figure 4), ie. rehydration, showed similar trends for *C. duthieae*, *C. stephensiae* and *C. capitatum*, however the results for these three species are significantly different $p=0.0001$, F ratio=52.33. *C. fragile* showed the greatest results and recovered to almost 100% of the moisture lost during desiccation after just 70 minutes. *C. papenfussii* recovered very

poorly during the rehydration experiments. The rehydration rates for the different species were significantly different $p=0.0002$, F ratio=5.884. It should be remembered that although *C. capitatum* showed a recovery comparable to *C. duthieae* and *C. stephensiae* its overall recovery was not as marked, as its moisture loss during the desiccation experiment was the greatest.

Surface area to volume ratio:-

The surface area to volume ratio was seen to be larger in the upright terete forms, namely *C. fragile*, *C. duthieae* and *C. capitatum*, than in the flattened prostrate species, *C. stephensiae* and *C. papenfussii*. There is a positive correlation between the moisture loss of a particular species and the increase in surface area to volume ratio ($R^2=0.87$). A similar trend is not seen when comparing moisture loss and utricle diameter ($R^2=0.42$) (Figure 5).

Utricle size and utricle wall thickness at the apices:-

In Table 1 it can be seen that the utricles in the subtidal species are substantially larger than those of the intertidal species. There is however, much variation between the different utricle sizes in the intertidal species.

The utricle wall thickness at the apices is $\pm 3u$ in *C. fragile*, $\pm 10u$ in *C. duthieae* and *C. capitatum*, $\pm 30u$ in *C. stephensiae* and $\pm 80u$ in *C. papenfussii*.

Nutrients

In Table 2, the presence or absence of hair-like outgrowths on the utricles, denoted in brackets, indicates that species found in the nutrient poor warmer waters are characterized by a greater number of hair-like outgrowths. *C. fragile* and *C. tenue* are however seen to be exceptions.

DISCUSSION

External morphology of the various *Codium* species

Macroalgae have evolved distinct and predictable patterns of adaptation in response to environmental stresses and disturbance (Littler et al 1983). The productivity of algae in the higher intertidal, per gram dry weight, is greater than in the lower intertidal zones (King and Schramm 1976). Upper shore areas tend to be dominated by opportunistic or fugitive species with rapid growth rates, increased reproductive output, high surface area to volume ratios and high photosynthetic capabilities (Littler and Littler 1981). Thick coarser algae in temporally constant habitats are characterized by a lower surface area to volume ratio and are able to persist at lower photosynthetic and slower growth rates (Ramus 1983). This persistence is gained by differential allocation of resources and energy, decreasing primary productivity by diverting resources away from photosynthetic components and into structural tissue (Littler and Littler 1981,

Littler et al 1983). As light decreases the cost of self-shading in terete species will also outweigh the advantages of an increased thallus area, and flat monolayered species will be favoured (Hay 1986).

This study revealed that the flattened species of *Codium*, *C. papenfussii* and *C. megalophysum*, do in fact occur on the subtidal regions. However, in the intertidal area both species with erect morphologies and those with more prostrate, flattened forms are found (Table 1). At The Strand *C. fragile*, *C. stephensiae* and *C. duthieae* grow in close proximity to each other on the shore (pers. obs.). *C. stephensiae* did however appear to occur deeper than the other two *Codium* species found in the area. At Betty's Bay *C. fragile* is found in the intertidal, up to 0.5m. *C. stephensiae* occurs in the intertidal, 2-4m deep, but may extend down as far as 10m. *C. papenfussii* is found from 2-10m being strictly a subtidal species (Jackelmann pers. comm.).

Careful sampling along shore gradients would need to be done at various sites to determine the exact distribution of the different *Codium* species and their diverse forms related to the species distribution on the shore. The data collected in this study was not detailed enough to observe exact distribution patterns in the intertidal areas. According to this study the hypothesis that *Codium* species found in the intertidal zones will exhibit more upright morphologies, with a corresponding higher surface area to volume ratios, whereas the subtidal species will be flattened

forms with smaller surface area to volume ratios cannot be accepted. I believe that closer inspection of the distribution of *Codium* species in the intertidal zone will reveal a pattern.

may?

There will however be exceptions. For example, *C. capitatum* which is found in the deep intertidal radiating down to the sublittoral zone has a terete, erect morphology with a high surface area to volume ratio of 0.46 (see figure 5). Its thallus has a keratinized tough structure. I feel that this structural toughness could enable the thallus to withstand the drag of the deeper water surge. The high surface area to volume ratio may enables *C. capitatum* to have a greater surface area for photosynthetic capacity at greater depths.

Erect species of *Codium* have gas trapped among the filaments, holding the thallus upright in the water to get increased surface area exposed to light sources and avoid self shading (Dromgoole 1982, Hay 1986). This factor may enable *Codium* species to inhabit deeper water due to this mechanism helping to prevent shading.

Internal structure of the various *Codium* species

Studies have been done on the light utilization capacities of macroalgae in terms of cell size. These studies revealed that stress tolerant shade plants were generally giant-celled, whereas fugitive sun plants tended to be smaller-celled. Ramus (1978) found the internal light trapping abilities of the 'giant-celled'

Codium and the smaller celled *Ulva* to be adapted for low and high light environments respectively. Extremely thin construction and larger cells result in relatively little self-shading of the non-photosynthetic components (Littler and Littler 1981).

It was therefore hypothesized that the utricles of the subtidal *Codium* will generally be larger than the utricles of the intertidal *Codium* species. The intertidal species of *Codium* exhibited wide variation in utricle size (Table 1). *C. papenfussii* and *C. megalophysum*, the two strictly subtidal species have giant utricles, 0.539mm^3 and 29.98mm^3 , respectively. Thus this hypothesis can be accepted. ^{2.578} An interesting observation regarding utricle size is that the flattened forms found in the intertidal generally have smaller utricles than the erect forms. A possible explanation for the is that the species with flattened morphologies have utricles which grow in large clusters whereas the erect species are characterized by having individual utricles. ^(referenza) This phenomenon may therefore be a function of 'design'. *C. prostratum* a species which has a repent (creeps along the substratum), rarely erect thallus with terete branches (see Appendix 1), has individual utricles indicating that the external structure of the thallus may well have an effect on utricle patterns.

Flattened morphologies are important in low light environments as a greater proportion of cells can be orientated perpendicular to the light source (Hay 1986). The disadvantage of having the

smaller cells in terms of light capture, for the prostrate, flattened forms in the intertidal, may be compensated for by their external form.

Air often replaces the water in the medulla in *C. fragile* and produces a reflective surface at the utricles base. Utricles enhance light capture acting as 'integrating spheres'. This is aided by the reflective capacity of the base and the wave guide function of the thin peripheral layer (Ramus 1978). This phenomenon was not examined for any of the *Codium* species in this study.

Light

One of the most important factors influencing patterns of seaweed distribution is light (Vadas and Steneck 1988).

It was proposed that intertidal *Codium* will exhibit certain attributes which differ from the subtidal species including those occurring in the low intertidal or under ledges in rock pools. These include, higher photosynthetic rates and less chlorophyll per unit area of thallus.

Photosynthetic rates

The differences in form affect the efficiency of light capture and influence the light scattering capability within the plant. Algae

manipulate their light capturing antennae so as to optimize photosynthetic rate in order to meet energy requirements for growth. Photosynthetic rates can be optimized by changing pigment ratios, increasing total amount of pigment or increasing the size of their antennae e.g. *Codium fragile*. These factors result in extended vertical distribution (Ramus et al 1976).

Zonation patterns, however appear to correspond more closely to morphology than pigmentation (Ramus 1976 et al, Vadas & Steneck 1988). Algal zonation patterns in the tropical Pacific and Atlantic waters show consistent relationships with morphology. Hillis and Colinvaux (1985) showed that the tropical genus *Halimeda* exhibited morphological zonation of species. The genus varies from erect morphologies in shallow water to low lying morphologies in deep water (Vadas and Steneck 1988). The changes in morphology with an increase in depth may be due to the more efficient light capturing abilities of the flattened forms.

C. duthieae (upright terete form) and *C. stephensiae* (flattened form) would appear to have similar net photosynthetic rates under the different light intensities (see figure 2). This was not expected as terete multilayered species grow much faster than flat monolayered species during periods of adequate light (Hay 1986), thus they would be expected to have a higher photosynthetic rate. Statistical tests indicate that there is a significant difference between the net photosynthetic rates of the two species. As previously mentioned, I believe that the reason for the

significant difference is the variation in photosynthetic performance of *C. duthieae* and *C. stephensiae* at a low light intensity. *C. duthieae* appears to be less well adapted to low light conditions than *C. stephensiae*. Therefore, although *C. stephensiae* was collected from the subtidal it does also occur in the intertidal it may therefore have photosynthetic rates comparative to *C. duthieae*. *C. stephensiae* may be better adapted to survive in the subtidal due to its flattened morphology better orientation for light capture, thus enabling it to increase its depth distribution.

phenotypic or genotypic variation?

During the duration of the experiment the seaweeds were suspended in the seawater in the bottles. The small pieces of *C. stephensiae* may have had a very similar surface area to volume ratio to *C. duthieae*. Experimental error may have accounted for some variation in the results obtained.

Pigment content

The photosynthetic content per unit leaf or thallus area is often higher in shade-plants (those species found in deeper subtidal area) than in sun-plants (those species occurring in the intertidal zone). Under conditions of low light higher pigment content is required to enhance the chance of a photon being absorbed by the antennae molecules of photosystems (Raven 1984). In strong light the lower pigment content avoids photodamage

(irreversible inhibition of photosynthetic apparatus) and photoinhibition (reversible inhibition) (Luning 1990).

Total pigment content per unit area of thallus and per unit weight of thallus was measured for three intertidal species, *C. duthieae*, *C. fragile* and *C. stephensiae* and a subtidal species *C. papenfussii*. In table 3 it can be seen that the three intertidal species have a higher pigment content per unit weight of thallus than *C. papenfussii*. *C. papenfussii* has a far smaller surface area to volume ratio than the other three species (see Appendix 5). However, when the pigment content per unit area of thallus was calculated it was seen that *C. papenfussii* has a total pigment up to 90x higher than the in the intertidal species (Table 3).

Desiccation and Rehydration of different *Codium* species

The primary factor governing the rate of desiccation is the surface area to volume ratio and to a lesser extent water content. Factors such as water content which ranges in species from 80% - 90% of fresh weight, may not be as important for differential desiccation tolerance (Dromgoole 1980). Zaneveld (1937 cited in Dromgoole 1980) found that species with thicker cell wall lose water more slowly. Results obtained by Dromgoole (1980) did not support the hypothesis.

I hypothesized that intertidal terete species with a higher surface area to volume ratio and thinner utricle walls at the

utricle apices, will lose water at a more rapid rate than the flatter subtidal species. They will however, recover more successfully than the flatter subtidal species during rehydration. These hypotheses regarding desiccation and rehydration were both accepted due to the following reasons:-

This study showed that *C. capitatum* a species with a high surface area to volume ratio than *C. papenfussii* which has a far smaller surface area to volume ratio. (figure 3 and figure 5). When the terete erect species are not surrounded by water at low tide the plant lies in a clumped mass on the rock. This may help to trap the water between the terete branches and reduce evaporation from the thallus surface. Despite this, the species with a higher surface area to volume ratio desiccated at a rapid rate.

In *C. papenfussii* there is a positive correlation between utricle diameter and moisture loss. *C. papenfussii* has a relatively high moisture loss relative to its S.A/Vol. ratio. The same correlation is not seen for the other species. It would seem that in species with high surface area (S.A) to volume ratios moisture loss is primarily influenced by the S.A/Vol. ratio.

The wall of the utricles at the utricle apex is considerably thicker in *C. papenfussii* and *C. stephensiae* than in *C. fragile*, *C. duthieae*, and *C. capitatum*. Although the findings of this study support Zaneveld's (1937 cited in Dromgoole 1980) hypothesis that thicker cell wall lose water more slowly, I believe that the

effect of different surface area to volume ratios would be more consequential than the effects of cell wall thickness on desiccation rates of the different *Codium* species.

The rehydration experiments showed that after 70 minutes *C. fragile* was the only species that had recovered almost 100% of the moisture lost during desiccation. Although *C. fragile* did not desiccate at a slower rate than the other species with similar S.A./Vol. ratios, its rehydration was noteworthy in comparison to the other species tested. The spines could in fact act to enhance rapid rehydration rates by increasing the surface area. This may give *C. fragile* a competitive advantage over the other species as it will be able to return to full photosynthesis more quickly than the other species as it is resubmerged with the incoming tide.

C. capitatum and *C. papenfussii*, found in the lower sublittoral and subtidal zones showed poor recovery from desiccation. As previously mentioned, although *C. capitatum* appears to rehydrate at the same rate as *C. stephensiae* and *C. duthieae*, its moisture loss was far greater than the other two species during desiccation. The slow rate of rehydration in *C. capitatum* may be attributable to its inability to tolerate desiccation as the plants are always covered by seawater or its keratinized structure may not be conducive to rapid rehydration. *C. papenfussii* appeared unable to tolerate the desiccation and showed very poor signs of recovery. One could postulate that perhaps there is

utricles damage as *C. papenfussii* is adapted to living in the subtidal.

Nutrient antennae

Colourless hairs enlarge the surface area to volume ratio of algae and serve as possible nutrient antennae. Nutrient shortage is known to cause hair formation on the utricles of *C. fragile* (Benson et al 1983). It was therefore predicted that *Codium* species found in the cooler nutrient rich West coast waters will have fewer hair-like outgrowths than the warmer South and East coast species. In Table 2 it can be seen that the pattern is as predicted. The two exceptions are *C. fragile* and *C. tenue*. *C. fragile* is a fast-growing fugitive species found over a wide distribution range (pers. obs.). Its high productivity may be attributed to many factors one of which may be its ability to absorb plenty of nutrients from the seawater when the plants are covered during high tide. As previously mentioned, the presence of hairs on *C. fragile* are known to be variable. *C. tenue* occurs in lagoons and estuaries, these systems are functionally nutrient poor when compared to the ocean as there is a lack of wave action. The lack of water movement causes a barrier layer to form on the seaweed thallus inhibiting the rapid absorption of nutrients. This factor may attribute to the frequent occurrence of hairs on the utricles of this species as the hairs increase the surface area for nutrient absorption.

Sand and Wave tolerance

This study demonstrates that one morphological form does not appear to be adapted to tolerate sand and wave stress above another. The different species that endure these stresses are significantly diverse in form (Table 1).

Ecological and physiological analysis of factors affecting survival in similar form-groups has the potential to assess selective processes that regulate morphological form (Littler et al 1983). The *Codium* species examined in this study that the two species *C. papenfussii* and *C. megalophysum* are the only two true subtidal species. Their morphology differs markedly from the intertidal species, especially as regards their internal structure e.g. the large utricle size. Erect forms and those species with flattened forms appear to co occur in the intertidal. Some of the species do however appear to have the ability to inhabit deeper water for example, *C. stephensiae* (a flattened species). It is difficult to attribute the variation in morphologies of a different species of *Codium* to a specific set of environmental factors. There do appear to be some patterns, however there are a multitude of selective pressures that could be affecting any particular species. It is therefore difficult to try to clearly predict the exact factors responsible for the selection of a particular form.

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Table 1. Aspects of morphology, distribution and environmental tolerances of the different *Codium* species found in southern Africa. (Modified after Silva 1959)

SPECIES	LOCAL DISTRIBUTION	THALLUS DESCRIPTION	WAVE EXPOSURE	SAND TOLERANCE	UTRICLE SIZE (MM)
<i>Codium tenue</i>	estuaries and lagoons	erect terete		XXX	0.019
<i>Codium isaacii</i>		erect terete			0.046
<i>Codium lucasii</i>	mid-littoral zone	flattened	XX		0.0034
<i>Codium pelliculare</i>	littoral zone	flattened		XXX	0.007
<i>Codium fragile</i>	littoral zone	erect terete	X	XX	0.029
<i>Codium dutbiseae</i>	littoral zone	erect terete	X	XX	0.116
<i>Codium stephensiae</i>	lower littoral zone	flattened		X	0.0048
<i>Codium spongiosum</i>	lower littoral zone	flattened			0.0009
<i>Codium prostratum</i>	lower littoral zone	terete-flattened		XXX	0.012
<i>Codium entricatum</i>	lower littoral zone	erect terete	XXX		0.021
<i>Codium pocockiae</i>	sublittoral fringe	erect terete	X		0.019
<i>Codium capitatum</i>	sublittoral fringe	erect terete			0.0102
<i>Codium platylobium</i>	sublittoral fringe/subtidal	erect flattened blade	X		0.023
<i>Codium papenfussi</i>	Subtidal	Hemispherical-flattened			0.539
<i>Codium megalophyllum</i>	Subtidal	Hemispherical-flattened			25.96

2598?

X = low tolerance; XX = moderate tolerance; XXX = high tolerance

Table 2: Distribution of *Codium* species over varying temperature ranges along the coast of southern Africa

Mean annual surface temperature (°C)				
12-12.5	17-19		> 20	
West coast cold-water	West and south coast cold-water cool-temperate species	South coast cool-temperate to warm-temperate species	South and East coast cool-temperate to warm-temperate and subtropical species	East coast subtropical species
<i>C. isaaci</i> (absent)	<i>C. fragile</i> (Common)	<i>C. stephensiae</i> (scarce) <i>C. incognitum</i> <i>C. papenfussii</i> (absent) <i>C. platylobium</i> (occasional) <i>C. pelliculare</i> (absent) <i>C. tenue</i> (frequent) - estuary <i>C. megalophysum</i> (absent)	<i>C. duthicae</i> (fairly numerous) <i>C. extricatum</i> (common) <i>C. lucasii</i> (common)	<i>C. prostratum</i> (abundant) <i>C. capitatum</i> (present) <i>C. pocockiae</i> (common) <i>C. spongiosum</i> (abundant)

The presence of hairs on the utricles is denoted in the parenthesis

(Modified from Silva 1959)

Table 3. Total pigment content per unit weight and area of thallus for selected subtidal and intertidal *Codium* species

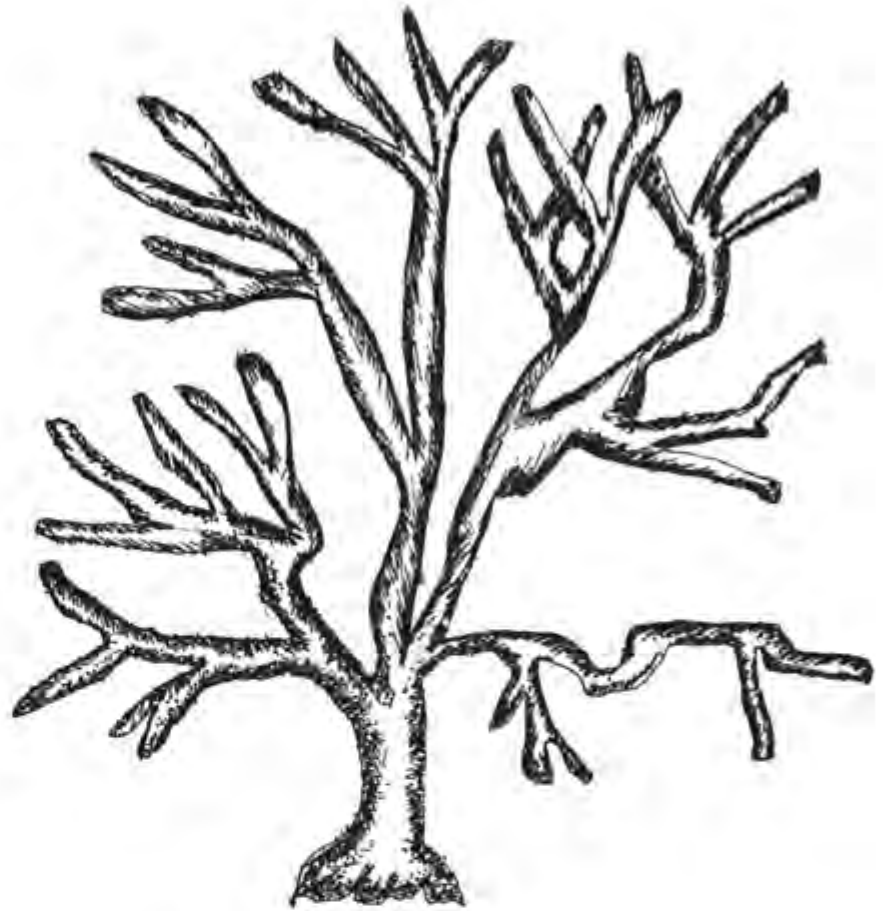
Species	cm ³ ¹	per unit area thallus ²
<i>Codium duthieae</i>	77.8	2
<i>Codium fragile</i>	51.95	1
<i>Codium papenfussii</i>	41.75	92
<i>Codium stephensiae</i>	69.2	3

1) Total pigment content per wet weight, measured as a function of area under the graph drawn by the spectrophotometer plotter.

2) Relative units expressing total pigment content per unit area of thallus



Flattened 'crustose'



Erect terete



Flattened hemispherical

Figure 1. Showing the morphological types of various *Codium* species.

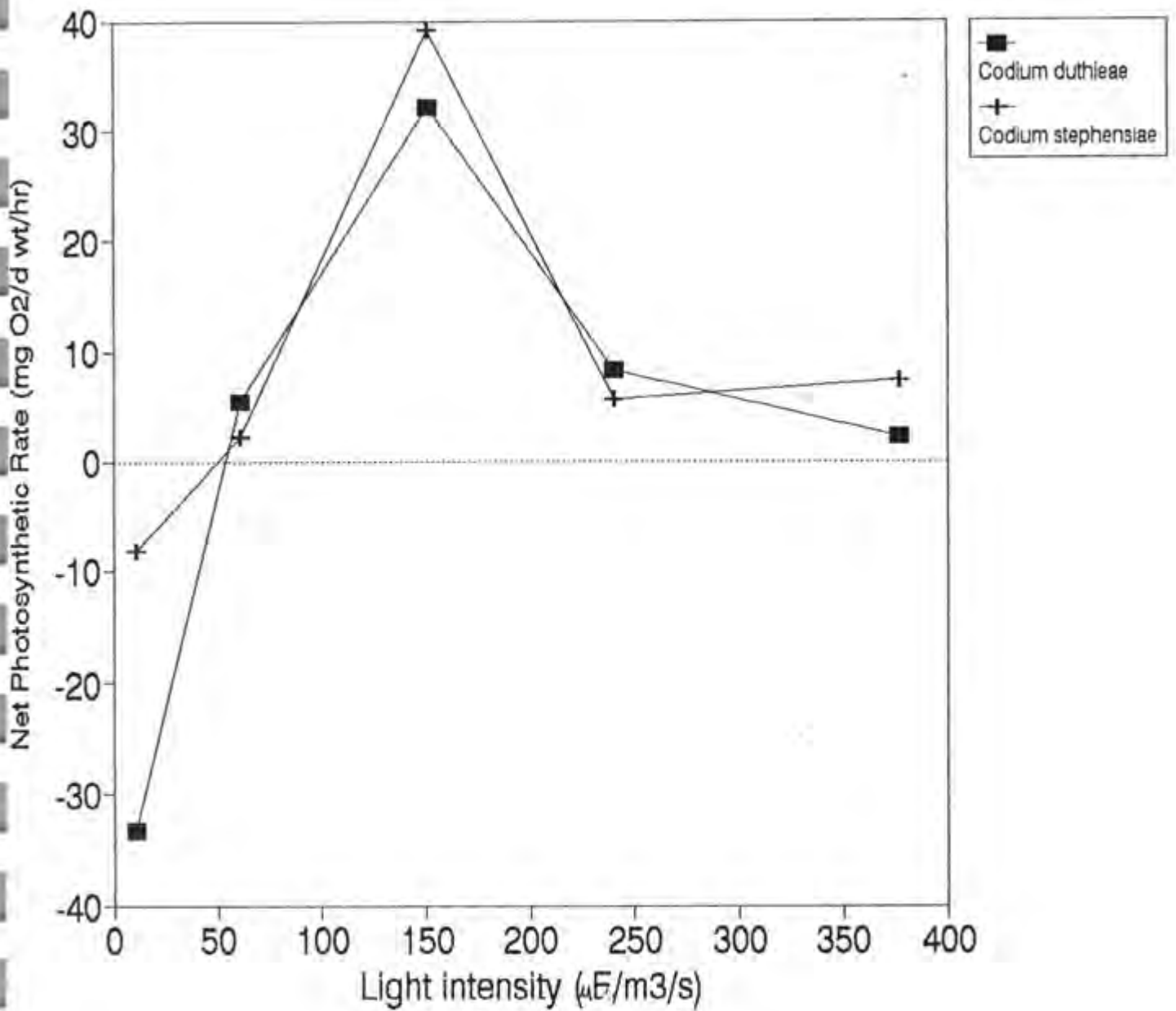


Figure 2: The net photosynthetic rate of *C. duthieae* and *C. stephensiae* under differing light intensities. $p=0.008$ showing a significant difference at the 99% confidence interval.

% original fresh wt?

% Dehydration

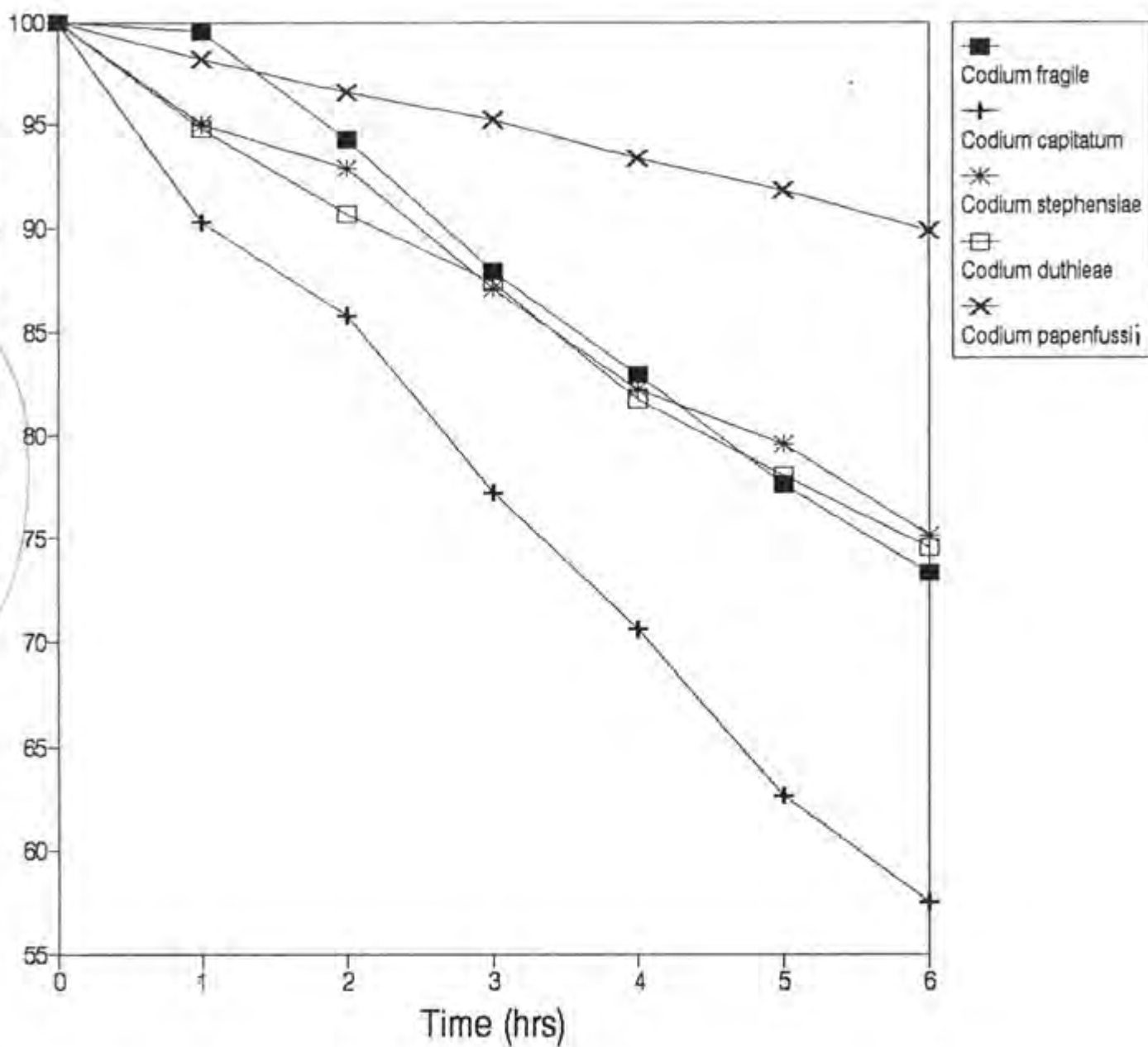


Figure 3: Desiccation rate of selected subtidal and intertidal species of *Codium* over a 6 hr period. $p=0.0003$ showing a significant difference at the 99% confidence interval.

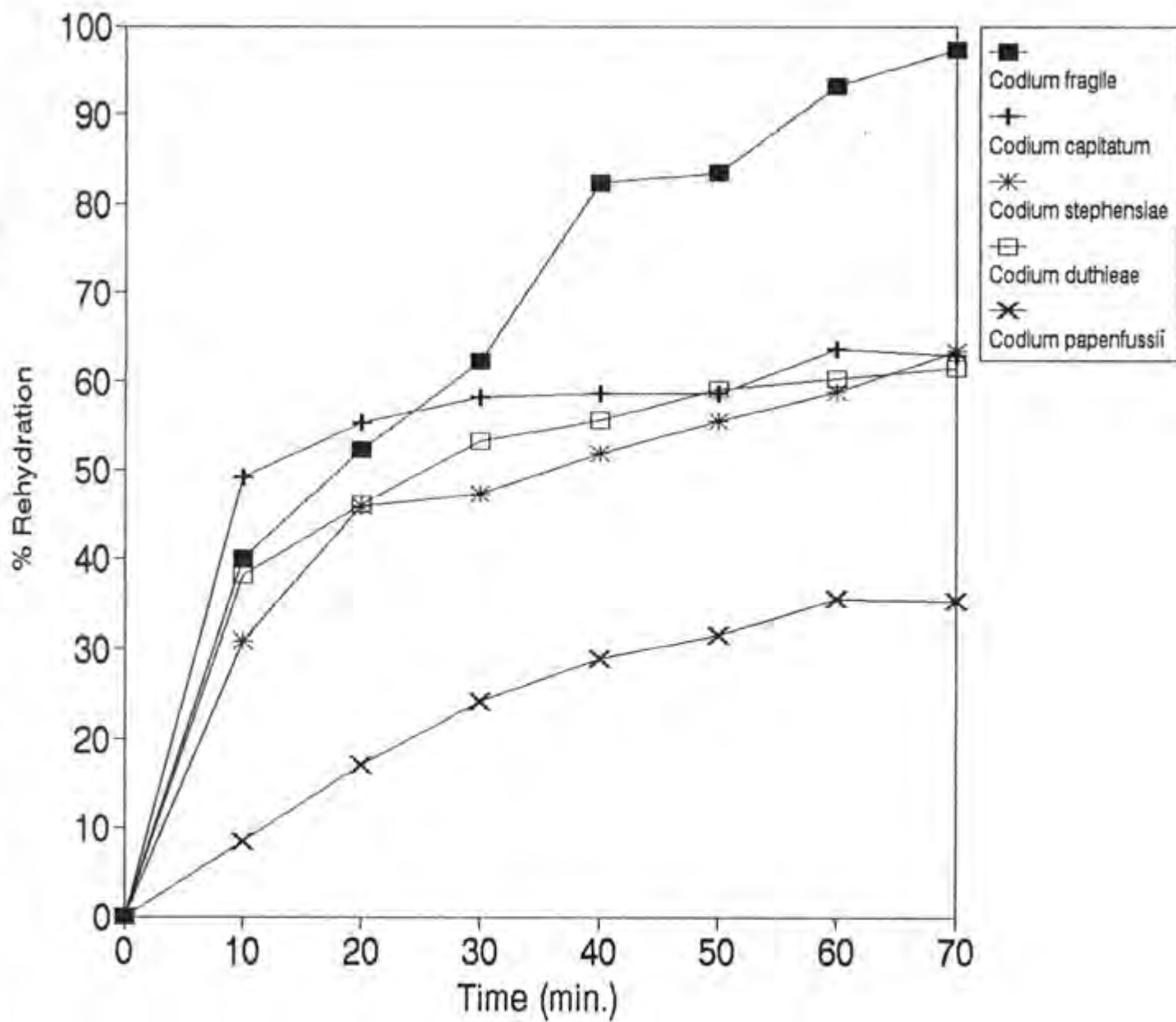


Figure 4: Showing the percentage rehydration of the proportion of water lost during the desiccation experiments of selected subtidal and intertidal *Codium* species over a 70 min. period. $p=0.0002$ showing a significant difference at the 99% confidence interval.

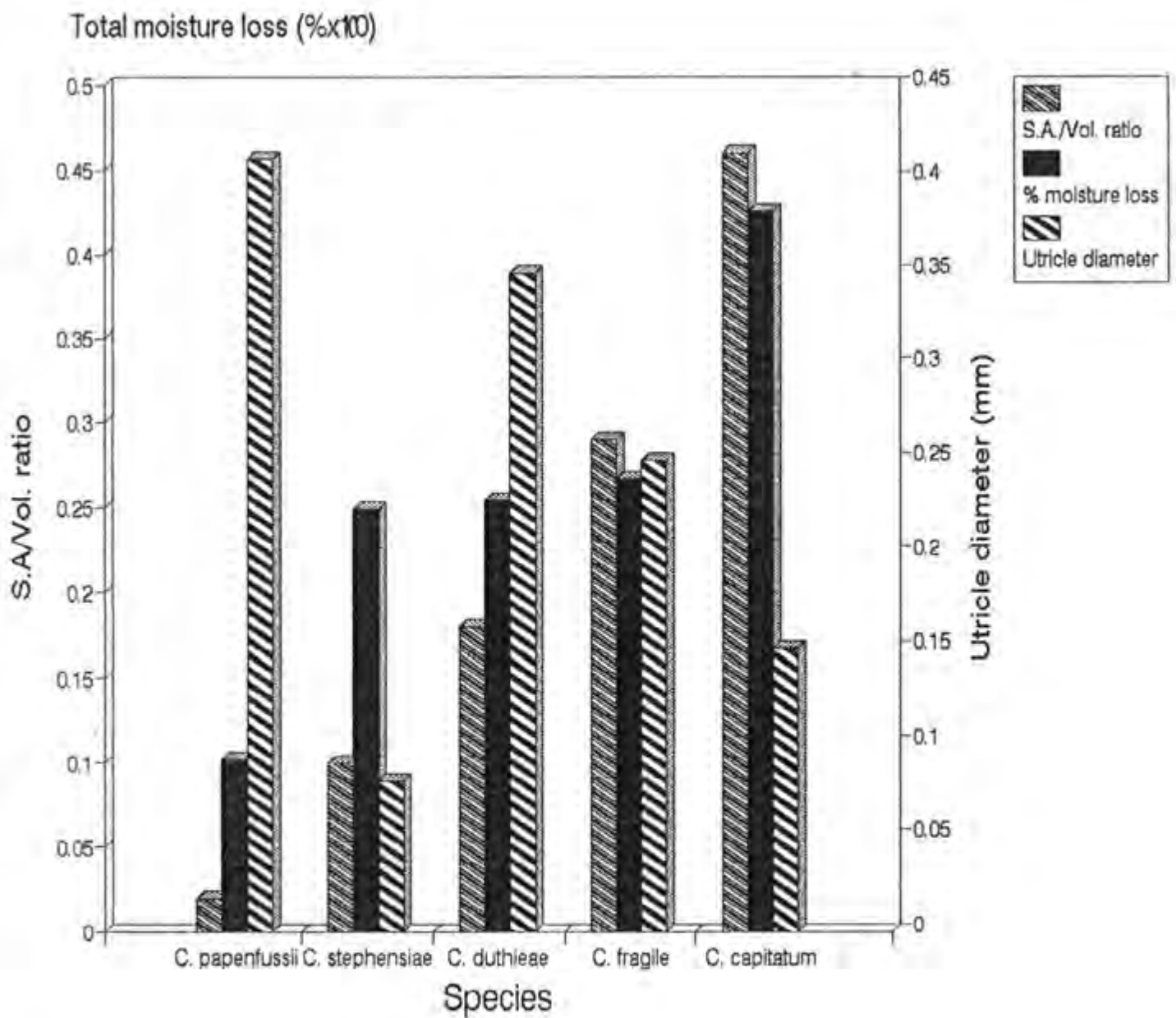


Figure 5: The correlation between percentage a) moisture loss and S.A./Vol. ratios ($R^2=0.87$), b) moisture loss and utricule diameter ($R^2=0.42$), for selected *Codium* species

APPENDIX

Appendix 1: Summary of the distribution, morphology and general characteristics of the *Codium* species found in southern Africa (modified from Silva 1999)

Species Name	Distribution geographical	on the shore	Thallus Description	1) Utricles Description	Diameter	Length	Wall thickness	at apices	Hairs	Medullary filaments (diameter)	Description of apices	General
<i>Codium lucasii</i>	Somerset Strand, False Bay, Simon's Bay, Cape Province to Cape Inhaca, Mozambique	Exposed zone at mid-tide level. Lobes from fully exposed to partially protected.	Applicate, firm, slippery, very dark green. Lobes which form a close flat pattern tightly adherent to the substratum but with free margins.	Utricles with a distinct primary utricle, and branching order on dorsal surface	(80-160)(105-125) ^u	(435-500-800)(1100) ^u	1.5u	3-12u	Common on older utricles.	(1.5)20-35u	truncate, depressed or rounded, approximately cylindrical.	Irregularly sized clusters of utricles without a conspicuous primary utricle
<i>Codium elaphense</i>	Cape Province, Langebaan to Dwesa	Grows in pools in the lower littoral zone on sheltered vertical rock faces	Applicate, procombent, velvety but tough, dark green. Adherent to substratum mainly in central portion by rhizoidal attachments	Clusters with a distinct primary utricle, and branching order on dorsal surface	55-110(-125) ^u	31.5u (final branching order)-1.5mm (1st branching order)	1.5-3u	30u	Scarcely	19-52u	Slightly rounded to truncate or depressed.	Isobilateral
<i>Codium sporopodium</i>	Hibberdene, Natal, to Cabo Inhaca Mozambique	Grows in cracks in flat open bare rock around the rims of small pools in the lower littoral zone.	Applicate or pulvinate, undulate to ceteriform and soft.	In large clusters, those of final order of branching cylindrical or clavate.	130-300(390) ^u	1.4-2mm (final branching order) 2.8-4(-6)mm (lower order of branching)	2-3u	33u	Abundant	30-100u	Finely lamellate and slightly intrusely subovate.	The only strictly Indo-Pacific element in the Codium flora.
<i>Codium papillatense</i>	Camps Bay, Cape Province to Port Edward, Natal.	Inhabits off-shore reefs in deep water under over-hang ledges and in narrow clefts sheltered from the sun.	Hemispherical to subglobose and firm when young becoming hollow with age and slightly depressed on the underside. It is loosely attached to the substratum by tufts of rhizoidal holdfasts.	Mature utricles in small clusters	(300-330-520u)	(2.4-3.4(-5.6)mm)	2-5.5u	12u	Absent	50-110u	truncate or slightly rounded	Mostly collected as drift
<i>Codium megalophyllum</i>	Port Elizabeth, Cape Province to Isipingo, Natal.	Deep water species. Lower littoral zone in recesses or deep potholes protected from sun and air.	Hemispherical or globose, very loose, light green, 9.5cm in diameter, loosely adherent to the substratum by a tuft of rhizoidal holdfasts.	Utricles formed by enlargement of branches of a sympodial system. Secondary utricles bud from primary.	(1-1)5-2.7(-3.9) mm	5-12mm	4-5u	13u	Not observe	21.5-430u	rounded	Secondary sympodial systems often reduced to the degree that utricles are borne directly on parent utricles. Inferior plants are on average smaller.
<i>Codium pellucida</i>	Cape Province: Ariston to Port St. Johns	Sand-covered rocks in the littoral zone.	Applicate, fairly smooth, firm. Attached over its entire lower surface. Dark green, obovate to elongated elliptical.	Primary utricles formed by enlargement of branches of a sympodial system. Secondary utricles bud from primary.	(30-75)(125-165) ^u	700-1100(-1350) ^u	1-1.5u	7u	Absent	12-25u	truncate, depressed or slightly rounded.	
<i>Codium platylochium</i>	Table Bay, Cape Province to Umhlangeni River, Natal.	Eastern range: pools and channels of sublittoral fringe, partial protection. Western: deeper habitat.	Erect, entirely complanate and dichotomously branched above a terete stipe.	Individual utricles cylindrical or slightly clavate, expanded at apex	(65-115-330)(460) ^u	(375-500-700)(840) ^u	1.5u	13u	Occasional	26-60(-85) ^u	truncate, depressed, or slightly rounded	
<i>Codium prostratum</i>	Dwesa, Cape Province, to Cabo Inhaca, Mozambique.	Pools and sand covered terraces of the lower littoral zone.	Repat (rarely erect), subdichotomously branched. Branches terete or somewhat compressed, finger-like overlapping, anastomosing.	Individual utricles subcylindrical or slightly clavate, often tapering towards the base.	65-183u	720-1310u	1.5u	3u	Abundant	20-35u	truncate to slightly rounded.	Its report, subdichotomously branched, overlapping and anastomosing structure is used to distinguish this species from the other members of this genus in southern Africa.
<i>Codium capitatum</i>	Port St. Johns, Cape Province, to Cabo Inhaca, Mozambique.	Deeper pools on the platform of the lower sublittoral zone.	Erect, terete, more or less regularly dichotomously branched immediately above a broad spongy hapetic base.	Individual utricles cylindrical or slightly clavate, often distinctly constricted just below apex, forming a capitulum.	100-21.5u above constriction and 115-260u below.	340-715u	2u	10u	Not common	20-35(-40) ^u	truncate to slightly rounded.	Thallus has a keratinous, tough structure. Highly epiphytized.
<i>Codium poocokate</i>	Port St. Johns, Cape Province, to mouth of Limpopo river.	In pools and on open rock at low tide level.	Thallus erect, 4-10cm high, divaricately branched, the branches of the dichotomy not usually equally developed. Branches uneven width and flattened.	Clavate and slender. Individual utricles	(65-105-235)(300) ^u	(500-650-1050)(1250) ^u	1.5-2u	35u	Common	22-39u	rounded to subovate	The long clavate utricles with markedly and often asymmetrically thickened apices distinguish this species anatomically. In the field this species is recognized by the unequal development of the two branches of the dichotomy, and their uneven width.
<i>Codium terete</i>	Cape Province, Kanyana to Port St. Johns	Occupies a unique habitat, growing on silt covered rocks, shells, concrete or wooden piles in river mouths (estuaries and lagoons).	Thallus erect, light green colour, bushy, edges of the younger branches translucent. Divericate dichotomous branching. Terete interdichotomous, dichotomous flattened and expanded. Regular intra-axillary dilations, and attenuated tips.	Two types: 1. Distal portions of thallus small pinnate or quadrate 2. On the thicker portions of the thallus pyriform or clavate utricles are inter-axillary with the first type.	135-400u 400-700u	330-450u 600-800u	1.5u	2.5u	Frequently present	20-40(-50) ^u	broadly rounded or slightly flattened.	Considerable variation in size, thickness and degree of flattening of the branches, and in the size and degree of thickening of the apical utricular walls.
<i>Codium utricatum</i>	Cape Agulhas, Cape Province, to Umpeigani, Natal.	Sheltered deep tide pools and more luxuriantly, on rocks in exposed areas.	Erect, firm, very dark green, 50cm high, dichotomously branched, branches flattened in the lower part of the thallus, subterete or terete above. Tapering gradually at the apices.	Individual utricles subcylindrical to clavate.	(98-125-280)(325) ^u	450-890u	2u	4.5u	Common	20-40u	truncate, subtruncate, depressed or slightly rounded.	
<i>Codium danthiae</i>	Saldanha Bay, Table Bay, Cape Province, around the mouth of the Limpopo River, Mozambique.	Deeper pools of the sublittoral fringe and lower littoral zone, occasionally in open shallow bays.	Erect, to 60cm high. Dichotomously branched, branches wholly terete, flattened only at the dichotomous, or flattened almost through out.	Individual utricles cylindrical to clavate, notably variable in diameter.	(130-170-500)(720) ^u	800-1800u	2u	10u	Occasional to fairly numerous.	43-72u	broadly rounded or subtruncate.	Wide range of variability in habitat and anatomy. Tendency for the dichotomies to be more flattened in plants growing in protected sites. Difference in utricle size between plants is thought not to be due to environmental differences. May be due to an age difference. Plants along the Natal coast generally the utricles are smaller and stouter with more rounded apices than further west. Strictly a cold water species.
<i>Codium sesseii</i>	Luderitz, Namibia, to Table Bay, Cape Province		Thallus erect, to 20cm, dichotomously branched. Branches terete, tapering at apices.	Individual utricles subcylindrical to clavate or pyriform. Utricles are stout.	185-400(-590) ^u	500-900(-1050) ^u	2u	30-70u	Absent	35-75u	lamellate, roughened by rupturing and etching of outer layers.	
<i>Codium fragile</i>	Swaakopmund, Namibia to Robberg, Cape Province	Pools and channels of the lower littoral zone and sublittoral fringe.	Thallus bushy firm, very dark green. Branches terete may be dichotomously or fastigiatey branched. Broad spongy basal disk.	Individual clavate utricles	(80-130-270)(335) ^u	730-1100u	1.5-2u	thickened	Common	26-40u	thickened and prolonged into a sharp point (micro). Micro chambered, lamellate, sometimes with concentric striations. Become blunt with age.	

GLOSSARY - for Appendix 1

Anastomosing - plants or plant parts intermittently joining and separating to form a web or network.

Apex - growing tip or point. The top.

Applanate - flattened

Axillary - growing in, on or from axil.

Capitulum - A swollen end. A thick cluster of parts.

Cerebriform - brain like form.

Clavate - club-shaped.

Complanate - flattened, level, smooth.

Dichotomy - divided or forked into two equal parts.

Divaricately - widely diverging or speading, forked.

Elliptical - ellipse shape, *ellipse* = a closed conic section shaped like a flattened circle and formed by an inclined plane that does not cut the base of the cone.

Fastigiately - bearing stems or branches in parallel clusters that taper to a point. When the branches are parallel and point upwards.

Floveolate - bearing small pits.

Hapteric - plant part adapted for attachment of support.

Introresly - *intro* = in, into or inward.

Isobilateral - having the same structure on both sides.

Lamellate - made up of layers, joined together.

Obicular - rounded

Procumbent - trailing along the substratum but not secured by rhizoids, haptera, or the like.

Pulvinate - shaped like a cushion.

Pyriiform - pear-shaped, with a broad end towards the base

Repent - creeping along the substratum.

Rhizoidal - pertaining to rhizoids, rootlike.

Subacute - *sub* = less than or imperfectly, *acute* = having a sharp end or point.

Subglobose - *sub* = somewhat or below, *globose* = spherical in form.

Sublittorial - Benthic or bottom region of the ocean, lowest tide level.

Sympodial - A form of development wherein a branch continues growth in the direction of the axis and the axis continues growth as a lateral branch, zig zag fashion. Often there is little size distinction between axis and branch.

Terete - cylindrical, circular in cross-section.

Truncate - Appearing as if cut off at the end, flat at the top, flatly rounded.

Umbonate - with a cone-shaped protrusion.

Undulate - with wavy margins.

APPENDIX II

PHOTOSYNTHESIS EXPERIMENTS

Light intensity: $37.7 \times 10 \text{ E/m}^2/\text{s}$

Species	Vol BOD	Volume of titre	Grams of seaweed	mgO ₂	Initial Correction	Total in BOD	Total in bottle	Change in mgO ₂	in g per dry weight per hour (- = resp)	Mean
C. duthieae	236.9	3.40	0.24	6.52872		5.95203	50.24933	0.44245	1.84352	2.18307
C. duthieae	232.4	3.40	0.30	6.52979		5.95311	51.23158	1.42470	4.74899	
C. duthieae	346.0	3.30	0.27	6.31973		5.74305	49.79519	-0.01169	-0.04331	
C. stephensiae(s)	235.6	3.60	0.33	6.91308		6.33640	53.78947	3.98259	12.06845	7.35512
C. stephensiae(s)	241.9	3.90	0.49	7.48751		6.91082	57.13783	7.33095	14.96112	
C. stephensiae(s)	230.3	3.20	0.29	6.14618		5.56949	48.36726	-1.43962	-4.96421	
C. stephensiae(i)	237.2	3.05	0.34	5.85658		5.27990	44.51852	-5.28837	-15.55402	
C. stephensiae(i)	233.9	2.80	0.18	5.37718		4.80049	41.04740	-8.75948	-48.66379	
C. stephensiae(i)	244.9	2.65	0.40	5.08714		4.51046	36.83511	-12.97177	-32.42942	
Control 1	233.5	3.30		6.33748	-0.38489	5.76080	49.34302	-0.46386		
Control 2	236.8	3.40		6.52874	-0.76848	5.95206	50.27075	0.46386		
Initial O ₂ content 1	237.2	3.10		5.95259						
Initial O ₂ content 1	238.7	3.00		5.76026	-0.57668		49.80688			

Light intensity: 24.07*10 E/m³/s

Species	Vol BOD	Volume of titre	Grams of seaweed	mgO ₂	Initial Correction	Total in BOD	Total in bottle	Change in mgO ₂	in g per dry weight per hour (- = resp)	Mean
C. duthieae	236.9	3.00	0.25	5.76063		5.61610	47.41322	4.13051	16.52206	8.25811
C. duthieae	232.4	2.75	0.26	5.28145		5.13691	44.20752	0.92481	3.55698	
C. duthieae	346.0	2.75	0.24	5.26644		5.12190	44.40957	1.12687	4.69529	
C. stephensiae(s)	235.6	3.00	0.16	5.76090		5.61637	47.67713	4.39443	27.46518	5.67757
C. stephensiae(s)	241.9	3.65	0.29	7.00754		6.86300	56.74245	13.45975	46.41293	
C. stephensiae(s)	230.3	1.75	0.27	3.36119		3.21665	27.93445	-15.34825	-56.84539	
C. stephensiae(i)	237.2	2.50	0.25	4.80048		4.65594	39.25749	-4.02521	-16.10085	-27.196
C. stephensiae(i)	233.9	2.60	0.24	4.99309		4.84856	41.45837	-1.82433	-7.60139	
C. stephensiae(i)	244.9	1.95	0.24	3.74337		3.59883	29.39022	-13.89248	-57.88534	
Control 1	233.5	2.75		5.28124	-0.00071	5.13670	43.99741	0.71471		
Control 2	236.8	2.70		5.18459	-0.28836	5.04005	42.56800	-0.71471		
Initial O2 content 1	237.2	2.75		5.28052						
Initial O2 content 1	238.7	2.55		4.89622						
					-0.14454		43.28270			

Light intensity: 15.17*10 E/m3/s

Species	Vol BOD	Volume of titre	Grams of seaweed	mgO ₂	Initial Correction	Total in BOD	Total in bottle	Change in mgO ₂	in g per dry weight per hour (- = resp)	Mean
C. duthieae	236.9	4.35	0.25	8.35292		7.96813	67.26995	6.03071	24.12286	32.1456
C. duthieae	232.4	4.37	0.18	8.39271		8.00791	68.91492	7.67568	42.64268	
C. duthieae	346.0	4.30	0.23	8.23480		7.85001	68.06365	6.82441	29.67134	
C. stephensiae(s)	235.6	4.90	0.25	9.40948		9.02468	76.61022	15.37098	61.48393	39.1373
C. stephensiae(s)	241.9	4.20	0.16	8.06347		7.67867	63.48636	2.24712	14.04450	
C. stephensiae(s)	230.3	4.60	0.29	8.83513		8.45033	73.38545	12.14621	41.88348	
C. stephensiae(i)	237.2	4.10	0.28	7.87278		7.48799	63.13649	1.89726	6.77592	12.1415
C. stephensiae(i)	233.9	3.90	0.36	7.48964		7.10485	60.75116	-0.48807	-1.35576	
C. stephensiae(i)	244.9	4.70	0.30	9.02248		8.63769	70.54055	9.30131	31.00437	
Control 1	233.5	3.90		7.48975	-0.38505	7.10496	60.85618	-0.38306		
Control 2	236.8	4.00		7.68087	-0.38454	7.29608	61.62229	0.38306		
Initial O ₂ content 1	237.2	3.70		7.10470						
Initial O ₂ content 1	238.7	3.80		7.29633						
					-0.38479		61.23924			

Light intensity: 6.17*10 E/m3/s

Species	Vol BOD	Volume of titre	Grams of seaweed	mgO2	Initial Correction	Total in BOD	Total in bottle	Change in mgO2	in g per dry weight per hour (- = resp)	Mean
C. duthieae	236.9	4.20	0.19	8.06489		7.77612	65.64899	5.22633	27.50701	5.34091
C. duthieae	232.4	3.50	0.18	6.72185		6.43308	55.36216	-5.06050	-28.11386	
C. duthieae	346.0	4.00	0.21	7.66028		7.37152	63.91487	3.49221	16.62959	
C. stephensiae(s)	235.6	3.80	0.21	7.29715		7.00838	59.49390	-0.92876	-4.42266	2.22276
C. stephensiae(s)	241.9	3.95	0.16	7.58350		7.29474	60.31199	-0.11067	-0.69166	
C. stephensiae(s)	230.3	3.90	0.18	7.49065		7.20189	62.54353	2.12087	11.78261	
C. stephensiae(i)	237.2	3.85	0.25	7.39273		7.10397	59.89856	-0.52410	-2.09639	0.7341
C. stephensiae(i)	233.9	3.90	0.25	7.48964		7.20088	61.57228	1.14962	4.59846	
C. stephensiae(i)	244.9	4.00	0.24	7.67871		7.38995	60.35072	-0.07194	-0.29976	
Control 1	233.5	3.80		7.29771	-0.19300	7.00894	60.03378	-0.38888		
Control 2	236.8	3.90		7.48885	-0.38453	7.20009	60.81154	0.38888		
Initial O2 content 1	237.2	3.70		7.10470						
Initial O2 content 1	238.7	3.70		7.10433						
					-0.28876		60.42266			

Light intensity: 1.13×10^5 E/m³/s

Species	Vol BO	Volume titre	Grams seaweed	mgO ₂	Initial Correctio	Total in BOD	Total in bottle	Change in mgO ₂	in g per dry weigh per hour (- = resp	Mean
C. duthieae	236.9	3.90	0.23	7.489		6.912	58.354	-1.252	-5.444	-33.55
C. duthieae	232.4	4.10	0.22	7.874		7.297	62.800	3.194	14.518	
C. duthieae	346.0	4.10	0.16	7.852		7.275	42.052	-17.554	-109.713	
C. stephensiae(235.6	3.80	0.23	7.297		6.720	57.049	-2.557	-11.119	-8.22
C. stephensiae(241.9	4.10	0.20	7.871		7.295	60.311	0.705	3.527	
C. stephensiae(230.3	3.70	0.17	7.107		6.530	56.706	-2.900	-17.058	
C. stephensiae(i	237.2	5.10	0.24	9.793		9.216	77.708	18.102	75.425	30.98
C. stephensiae(i	233.9	4.20	0.25	8.066		7.489	64.036	4.430	17.718	
C. stephensiae(i	244.9	4.10	0.21	7.871		7.294	59.566	-0.040	-0.190	
Control 1	233.5	3.90		7.490	-0.577	6.913	59.212			
Control 2	236.8	4.00		7.681	-0.577	7.104	60.001			
Initial O2 conte	237.2	3.60		6.913						
Initial O2 conte	238.7	3.70		7.104	-0.577		59.606			

APPENDIX III

DESSICATION EXPERIMENTS								
Temperature (°C)	24.6	24.6	24.8	25.4	24.6	24.6	23.5	
Humidity (%)	56.5	56.5	56.6	57	59.3	66.2	68.4	
SPECIES	Mass (g) Initial	1hr	2hrs	3hrs	4hrs	5hrs	6hrs	Total moisture loss (g)
<i>Codium fragile</i>								
1	453.60	432.40	419.30	397.00	381.30	363.50	348.60	105.00
2	114.00	135.70	127.10	119.50	113.10	105.30	99.20	14.80
3	203.60	191.90	184.40	173.90	165.00	156.40	148.20	55.40
4	150.60	138.30	129.90	118.20	110.20	101.60	95.80	54.80
MEAN	156.07	155.30	147.13	137.20	129.43	121.10	114.40	59.90
% moisture loss	100.00	99.51	94.28	87.91	82.93	77.60	73.30	
<i>Codium capitatum</i>								
1	104.20	96.80	93.40	85.40	80.00	74.40	68.50	35.70
2	46.50	43.20	42.30	38.00	34.60	32.00	29.40	17.10
3	33.10	28.70	26.00	23.50	21.60	17.90	16.40	16.70
MEAN	39.80	35.95	34.15	30.75	28.10	24.95	22.90	16.90
% moisture loss	100.00	90.33	85.80	77.26	70.60	62.69	57.54	
<i>Codium stephensiae</i>								
1	13.50	12.90	12.00	10.70	10.30	9.10	8.50	5.00
2	36.00	33.30	32.50	31.10	28.70	27.80	26.80	9.20
3	25.40	24.80	24.30	22.30	21.70	21.20	19.80	5.60
4	24.60	23.60	23.10	21.50	20.30	19.40	18.00	6.60
MEAN	28.67	27.23	26.63	24.97	23.57	22.80	21.53	7.13
% moisture loss	100.00	95.00	92.91	87.09	82.21	79.53	75.12	
<i>Codium duthieae</i>								
1	496.10	482.80	476.50	461.60	450.50	438.60	428.00	68.10
2	73.90	69.40	66.90	63.20	60.60	57.20	54.60	19.30
3	308.30	294.00	285.40	273.20	265.20	255.50	247.60	60.70
4	133.20	123.30	117.80	118.80	105.70	99.80	95.50	37.70
5	144.30	138.20	131.70	124.20	118.10	112.90	107.10	37.20
6	166.50	159.50	153.30	145.00	139.20	133.80	128.50	38.00
MEAN	148.00	140.33	134.27	129.33	121.00	115.50	110.37	43.50
% moisture loss	100.00	94.82	90.72	87.39	81.76	78.04	74.57	
<i>Codium papenfussi</i>								
1	240.80	237.40	233.10	229.30	223.40	217.90	211.10	29.70
2	585.30	570.00	557.30	549.20	537.20	526.40	514.10	71.20
3	637.80	630.70	624.50	615.40	605.40	596.20	585.20	52.60
MEAN	611.55	600.35	590.90	582.30	571.30	561.30	549.65	51.17
% moisture loss	100.00	98.17	96.62	95.22	93.42	91.78	89.88	

APPENDIX IV

REHYDRATION EXPERIMENTS

SPECIES	Mass (g) Initial	10min	20min	30min	40min	50min	60min	70min	Initial mass (g)	Moisture gained (g)
Codium fragile	348.60	400.10	410.00	409.10	412.40	413.90	417.70	417.60	453.60	69.00
	148.20	168.50	171.30	176.60	192.50	193.00	196.90	197.00	203.60	48.80
	99.20	110.90	117.80	121.00	123.90	124.30	128.60	131.10	114.00	31.90
	95.80	113.70	119.30	123.50	129.80	130.20	134.10	136.70	150.60	40.90
MEAN	114.40	131.03	136.13	140.37	148.73	149.17	153.20	154.93	156.07	36.40
Moisture gain (g)	0.00	16.63	21.73	25.97	34.33	34.77	38.80	40.53	41.67	
Moisture gain (%)	0.00	39.92	52.16	62.32	82.40	83.44	93.12	97.28	100.00	
Codium capitatum	68.50	87.50	88.40	91.90	93.60	93.00	94.00	95.60	104.20	27.10
	29.40	37.70	38.80	39.80	39.60	39.80	40.50	40.20	46.50	10.80
	16.40	24.70	25.70	25.70	26.00	25.80	26.80	26.90	33.10	10.50
	22.90	31.20	32.25	32.75	32.80	32.80	33.65	33.55	39.80	10.65
Moisture gain (g)	0.00	8.30	9.35	9.85	9.90	9.90	10.75	10.65	16.90	
Moisture gain (%)	0.00	49.11	55.33	58.28	58.58	58.58	63.61	63.02	100.00	
Codium stephensiae	8.50	10.20	10.30	10.50	10.60	10.90	10.90	11.10	13.50	5.0
	26.80	29.20	30.70	31.20	31.40	31.40	31.70	32.80	36.00	9.20
	19.80	21.80	22.00	22.10	22.40	23.00	23.40	23.50	25.40	5.60
	18.00	20.20	21.70	21.40	21.90	22.10	22.10	21.90	24.60	6.60
MEAN	21.53	23.73	24.80	24.90	25.23	25.50	25.73	26.07	28.67	6.10
Moisture gain (g)	0.00	2.20	3.27	3.37	3.70	3.97	4.20	4.53	7.13	
Moisture gain (%)	0.00	30.84	45.79	47.20	51.87	55.61	58.88	63.55	100.00	

SPECIES	Mass(g) Initial	10min	20min	30min	40min	50min	60min	70min	Initial mass (g)	Moisture gained (g)
<i>Codium duthieae</i>										
1	54.60	62.00	64.20	65.10	66.10	66.00	66.40	65.80	73.90	19.30
2	428.00	445.60	447.10	453.80	458.20	461.80	457.30	459.80	496.10	68.10
3	247.60	266.70	271.40	273.20	275.90	278.30	277.30	276.30	308.30	60.70
4	95.50	110.30	112.60	115.20	116.30	117.40	118.00	118.40	133.20	37.70
5	107.10	120.70	124.90	127.90	128.70	129.90	131.00	131.40	144.30	37.20
6	128.50	143.10	145.50	148.20	148.90	150.60	150.30	150.80	166.50	38.00
MEAN	110.37	124.70	127.67	130.43	131.30	132.63	133.10	133.53	148.00	37.63
Moisture gain (g)	0.00	14.33	17.30	20.07	20.93	22.27	22.73	23.17	37.63	
Moisture gain (%)	0.00	38.09	45.97	53.32	55.62	59.17	60.41	61.56	100.00	
<i>Codium papenfussi</i>										
1	209.80	213.50	215.30	216.10	217.50	218.10	215.50	217.90	240.80	31.00
2	515.70	522.60	528.40	532.60	534.70	537.10	538.80	538.00	585.30	69.60
3	582.70	586.30	591.30	595.90	599.70	600.70	603.80	604.50	637.80	55.10
MEAN	549.20	554.45	559.85	564.25	567.20	568.90	571.30	571.25	611.55	62.35
Moisture gain (g)	0.00	5.25	10.65	15.05	18.00	19.70	22.10	22.05	62.35	
Moisture gain (%)	0.00	8.42	17.08	24.14	28.87	31.60	35.45	35.36	100.00	

APPENDIX V

SURFACE AREA TO VOLUME RATIO OF THE VARIOUS CODIUM SPECIES			
	Volume (ml)	Surface area (g)	SA/Vol Ratio
Codium duthieae	4.50	0.81	
	4.30	0.77	
	4.70	0.85	
Mean	4.50	0.81	0.18
Codium stephensiae	8.00	0.82	
	7.70	0.80	
	8.30	0.84	
Mean	8.00	0.82	0.10
Codium fragile	2.30	0.76	
	2.70	0.70	
	2.50	0.73	
Mean	2.50	0.73	0.29
Codium papenfussi	250.00	5.43	
	237.00	5.00	
	265.00	5.90	
Mean	250.67	5.44	0.02
Codium capitatum	1.80	0.79	
	1.50	0.75	
	1.70	0.77	
Mean	1.67	0.77	0.46