1991

OBSERVED LIFE HISTORY PHASE DISPROPORTIONALITIES

IN ~~SOUTHERN AFRICAN~~ *AEODES ORBITOSA* (SUHR) SCHMITZ

(endemic to Southern Africa)

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Botany Honours Project

ABSTRACT

Three sites were investigated along the coast of Southern Africa (viz.Oudekraal, Sunny Cove and Grossebuct in Luderitz) in order to determine the relative proportions of the various life history phases (viz. tetrasporophyte vs. carposporophyte vs. non-reproductive material). At Oudekraal three different sites of varying wave exposure were sampled to evaluate the effects wave action may have on the expression of life history phase structures. It was found that *Aeodes orbitosa* populations at Oudekraal and Grossebuct were tetrasporophyte dominated, while those at Sunny Cove exhibited similar life history stage proportions. It was established that tetrasporophytes were dominant in the sheltered and exposed sites, but that non-reproductive material was abundant in the semi-sheltered area. Culture experiments were carried out for *A.orbitosa*, and relative spore release as well as percentage survival were investigated. Mature Carposporic material liberated large numbers of clustered carpospores of which approximately 5% had survived into the 3rd week. Released tetraspores were observed to be individually scattered and far fewer in number. Tetraspores displayed a relatively higher mortality rate in that none of them survived into the 2nd week. Germination of both spore types fared better under the 10°C and 15°C temperatures, than those exposed to the higher temperatures (viz. 20°C and 25°C).

INTRODUCTION

Life history diversity and variation in reproductive biology are greater in Rhodophyta than in any other division (Hawkes 1990). Algal reproductive biology has an important effect on the population structures which are observed in nature. The term 'life history' implies the sum of all developmental and reproductive events that occur during the life of individuals, populations or species (Clayton 1988). Most members of the Cryptonemiales are thought to have *Polysiphonia*-type life histories, typified by the occurrence of morphologically identical plants producing tetrasporangia or gametangia and then carposporophytes (Dixon et al 1972). The possible development of this life history is as follows: the plants formed by the germination of carpospores produce tetrasporangia from which tetraspores are released, giving rise to gametangial plants (or plants identified on morphological grounds as the gametangial phase). The tetrasporophyte is diploid and at maturity produce tetraspores by meiotic division. It has also been reported that most red algae combine both sexual and asexual reproductive modes in their life history repertoires (Hawkes 1990). Detailed studies on life history phase development for *A. orbitosa* have not, however, been carried out and for the purpose of this study all possibilities are considered.

what about male gametophytes?

When alternate life history phases are involved, such as tetrasporophytes and carposporophytes, these may be distributed in different proportions in both space and time (De Wreede and Green 1990). It has been suggested that the disproportionality of life history stages indicates that strict alternation of generations is not as important as other regenerative means (Hansen and Doyle 1976).

Is this related to Agoda?

Investigations into life history disproportionalities are unfortunately still meager and relatively new. A fair amount of work has been carried out on *Irideae* (acea) which show varying situations under which one of the life history phases may dominate. May (1986) assigned gametophyte dominance of *I. cordata* to the perennation and differential survival of gametophyte spores or sporelings. Several studies (Hansen 1977; Hansen and Doyle 1976) of the population structure and growth of *I. cordata* in California revealed that tetrasporophytic blades were more abundant than gametophytes at all times of the year except spring. During spring the new year's crop was beginning to develop and mature and at this stage the alternate phases were more or less equal. It was established that the disproportionality of life history stages may arise prior to blade maturation (at the spore level). This was suggested by carrageenan analysis (immature thalli possessed mostly lambda carrageenan characteristic of tetrasporangial thalli), as well as the fact that most blades were derived through the process of perennation and

extensive vegetative growth rather than re-establishing from spores.

The life history dynamics employed by this alga are certainly paradoxical. If the population is usually predominated by mature tetrasporangia this would indicate a high potential for sexual reproduction. Despite this, gametangial thalli consistently made up only a minor part of the populations studied (Hansen 1977).

In 1985 Dyck *et al.* found that *Irideae cordata* showed a gametophytic dominance in July 1982 and April 1983, in the same area that tetrasporophyte dominance was previously recorded by Hansen and Doyle (1976). This suggests that life history stages may form part of a larger cycle, taking some years to move from one stage to another, thus necessitating long term population studies.

It was also observed that fewer gametophytes were occurring in areas of greater wave exposure. Patterns appear to show a general gametophyte dominance in the south (from Oregon to California), giving way to a predominance of tetrasporophytes and finally to sterile blades in the north (Dyck *et al.* 1985).

De Wreede and Green (1990), demontrated that populations of *Irideae splendens* in Vancouver harbour, Canada, showed seasonal changes, with gametophytes dominating in summer

and tetrasporophytes in winter. Several authors have also concluded that the alternation of dominance within generations is governed by seasons (Ang *et al.* 1990; Svedelius 1927 and papers therein). Ang *et al.* (1990) showed, by using matrix models, that differential survival and recruitment rates of the two phases in summer and winter could explain the life history alternations. It was concluded, however, that these seasonal phenomenon are more pronounced at higher latitudes. While alternations occurring at lower latitudes may be changing over periods of several years (De Wreede and Green 1990).

Levitt and Bolton (1989) studied 2 different *Gigartina* species, *G. radula* and *G. stiriata*, on the west coast of Southern Africa. It was established that they were both gametophyte dominated due to high spore and sporeling mortality as the adults were growing vegetatively and out-competing the sporelings. Recruitment favouring of tetraspores may have also been occurring.

Several suggestions have been put forward by Hansen and Doyle (1976), whereby tetrasporophyte dominance could be maintained in a population, these are that:

1) Tetrasporangial crusts are hardier and longer lived than gametangial crusts.
2) Tetraspores have a higher mortality than carpospores (thereby reducing gametophyte establishment).
3) Apomeiosis.

5.

4) Adverse environmental conditions result in the dominance of the "hardier phase", i.e. tetrasporophyte.

In 1986 May monitored the *Irideae cordata* population on San Juan Island, Washington for changes in population structure. Mechanisms were investigated by which the observed dominant life history phase might have been maintained. Over a three year study period she found very little variation in the representative life history phases. She hypothesised that differential recruitment of gametophyte/sporelings in addition to perennation explained long term stability of gametophyte-dominated populations.

Seasonal measurements of growth rates are needed in order to determine if one phase has a faster growth rate and can therefore outcompete the other phases.

Two models have been proposed by May (1986) to explain gametophyte dominance. A *mechanistic model* predicts that both life history phases differ in demographic or physiological responses to their environment, these include differential spore recruitment or sporeling survival and a variation in holdfast turnover rates and growth rates. A *stochastic model* predicts that both phases are equally able to survive and reproduce and that chance events affect the ratios of life history phases.

Joska and Bolton (pers. comm.) observed that populations of *Aeodes orbitosa* studied at Kommetjie show tetrasporophyte dominance. This observation stimulated an interest in the previously unstudied field of life history disproportions of *A. orbitosa* in Southern African. The objective of this project was to investigate different *Aeodes* populations and to assess the proportions of the various life history phases (i.e. tetrasporophyte, carposporophyte and the non-reproductive phase).

This study incorporated two approaches. The first part incorporated field observations and was designed to answer the following questions;

a) Do populations of *A. orbitosa* show dominance of one of the life history phases in different areas?
b) Do environmental conditions, namely wave exposure and temperature, influence the population life history structures observed?
c) Does life history disproportionality in *A. orbitosa* change with latitude, i.e. is there increased dominance by a particular life history phase at Luderitz than on Cape Peninsula?

The second part of the study involves culture experiments and hopes to answer the following questions;

a) Which is the best way to conduct culture experiments

for the tetraspores and carpospores of *A. orbitosa*? ??

b) How does temperature affect spore survival in *A. orbitosa*?

c) Is it possible that the life history disproportionality observed in the field is related to the success of sporeling development? i.e. Does the dominant phase develop from spores with a superior survival rate than that of the inferior phase?

PART ONE

To establish the life history population structure in *A.orbitosa* occurring along the Cape Peninsula of South Africa.

Methods

Collection sites

Aeodes orbitosa was sampled at various sites around the Cape Peninsula and at Luderitz in order to determine the different proportions of life history stages (i.e. gametophyte, tetrasporophyte and non reproductive plants) making up representative populations. The collection sites were chosen to reflect various environmental conditions of the distribution range in which *A. orbitosa* occurs. On the Cape Peninsula, the effects of wave exposure on life history phases were assessed at Oudekraal by sampling sheltered, semi-sheltered and exposed sites. Sunny Cove was chosen as a site in False Bay to assess the effect of relatively higher temperatures on the population structure of the study species . The site at Luderitz was chosen to compare the population structure of this species in its more northerly region of its distribution to those populations occurring in the southerly region.

Sampling procedures

At each site, three 1 X 1m quadrats were sampled in relatively dense stands of *A. orbitosa*. All thalli were removed from the rocks, counted and put into plastic bags.

Sunny Cove and Oudekraal specimens were collected on the 2nd and the 17th of April respectively. Harvesting took place in the morning and the plastic bags were transported to the University of Cape Town. Samples were frozen and stored in a cold room at -20°C until further work was carried out. Specimens were collected from Luderitz on the 14th of May. Samples were preserved in sea water in plastic jars containing 10% formalin which were kept in a box to avoid colour loss with exposure to light during transportation to the University of Cape Town. The samples were left in the formalin and stored in a dark cupboard until further work was carried out.

Determination of life history phases

The determination of the life history phase for individual thalli of *A. orbitosa* was carried out as described by Mrs Joska (pers. comm.). Seaweeds were removed from the cold room, allowed to thaw and completely rinsed in seawater to reduce their thick mucilage coating. Sections of each individual thallus were made, stained with fast green and mounted on a slide for viewing under a compound microscope.

The different life history stages were recognised according to the following morphological structures which were made from personal observations using Chang (1970) as a guide line:

Vegetative/non-reproductive anatomy

The thallus consists of a cellular cortex and a filamentous medulla. The cortex is made up of 7 to 9 cells which are cylindrical to fusiform, and those of the inner layers are slightly larger than those in the outer layers. Lateral processes sometimes link neighbouring cortical cells. The medulla comprises approximately two thirds of the thallus area and is made up of a tangle of simple or branched filaments, which run in all directions. Stellate cells were sometimes observed in the medulla. Between the cortex and the medulla there is an ill-defined transition region consisting of both medullary filaments and cortical cells. See plate 1(a) for internal vegetative structure.

The thalli of *A.orbitosa* are in the form of thick, broad blades which are oval to elliptical in outline. Plants possess a disc-like holdfast and a short, flat stipe, usually less than a centimeter in length. Plant size may vary considerably, being anywhere between a couple of centimeters to over 2m in length.
See plate 1(b & c) for external appearance; as *A.orbitosa* occurs in nature.

Tetrasporophyte internal anatomy

Tetrasporangia occur abundantly on both surfaces of the thallus. The tetrasporangium is formed by the cutting off of a lateral outgrowth from a cortical cell, usually the 4th or 5th cell. The sporangium is ovate in shape and

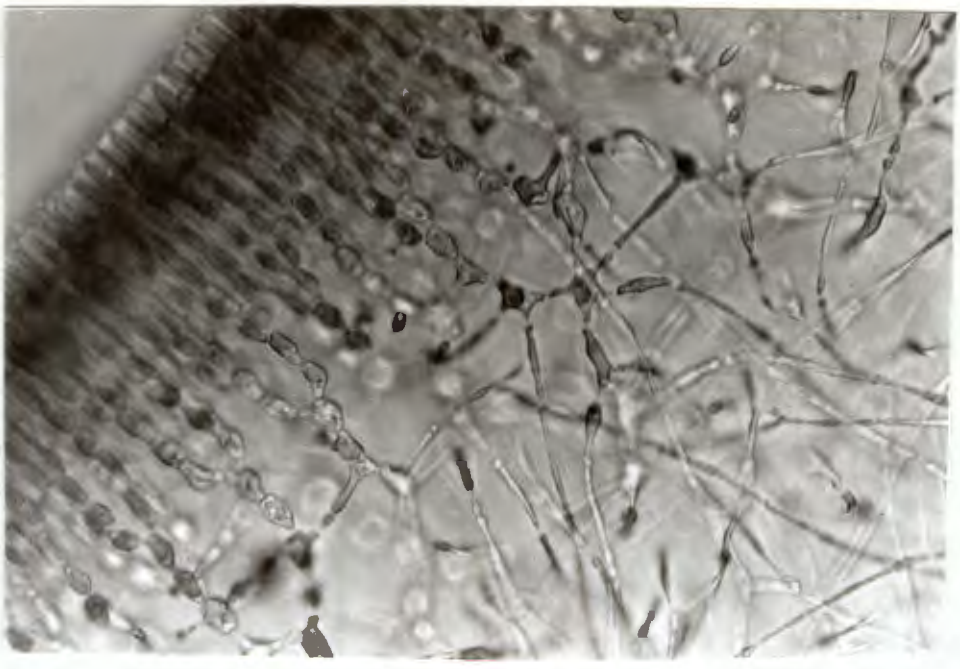

Plate 1A : Internal anatomy of a non-reproductive *A. orbitosa* blade (400x Mag.)

Plate 1B: *A. orbitosa* plant as it occurs in the field.

Plate 1C: An example of the size which an *A. orbitosa* can grow to (specimen found at Platboom-Cape point nature reserve).

Cape of Good Hope

Plate 2: Internal anatomy of tetrasporophyte: showing divided tetraspores embedded in cortical cells of the thallus. (400x Mag.)

Scale?

cruciately divides its contents to form two daughter protoplasts, each of which divides longitudinally forming a total of four spores.
See plates 2, 3, and 4 for tetrasporophyte anatomy.

Carposporophyte internal anatomy

When mature, the cystocarp has a rather thick pericarp surrounding its sporogenous tissue. The pericarp is pear shaped, dark brown and embedded in the thallus. The peripheral cells of the gonimoblast are transformed into the carposporangia.
Chang (1970) claims that in his studies of *Aeodes* no evident ostiole was observed at the top of the cystocarp. In my observations the ostiole appeared as an extension of the pericarp's ampullar filaments, tapering through the cortical cells to the thallus surface.
The carpospores are roughly circular and fill the entire cystocarp. The developing or immature cystocarps are pale in colour. They generally appear as a circular mass of the auxiliary cell ampulla. Auxiliary cell ampullae exhibit four (rarely five) orders of branching.
See plates 5, 6 and 7 for internal anatomy of carposporophyte.

The cystocarps can be seen on blades of carposporophytes if they are held up to a light. They appear as small irregularly distributed aggregations of minute black dots. This was however not used as a visual assessment due to the

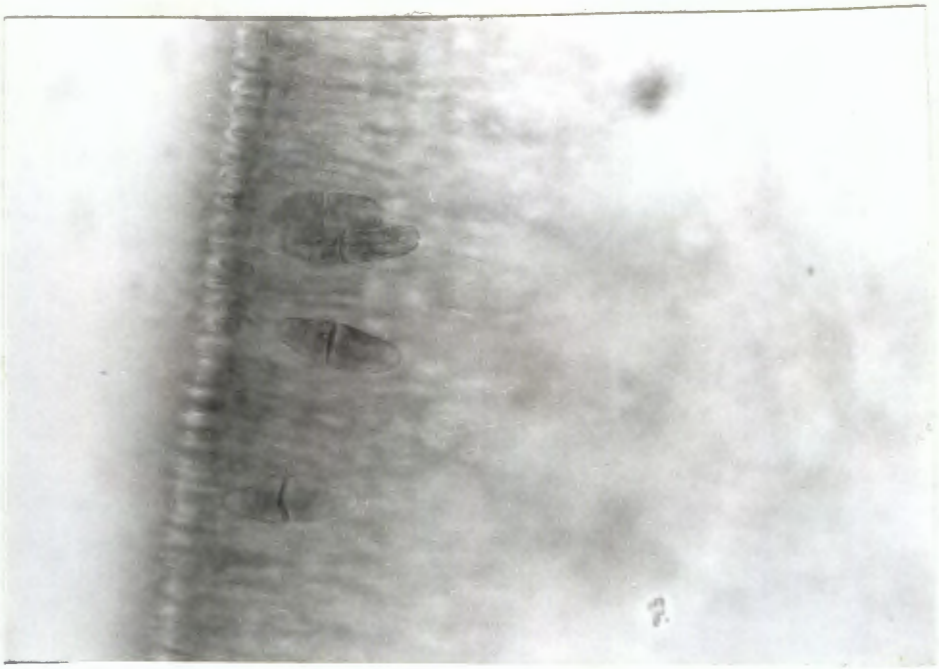

Plate 3: Internal tertasporophyte anatomy emphasizing the tetraspores. (400x Mag.)

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Scale?

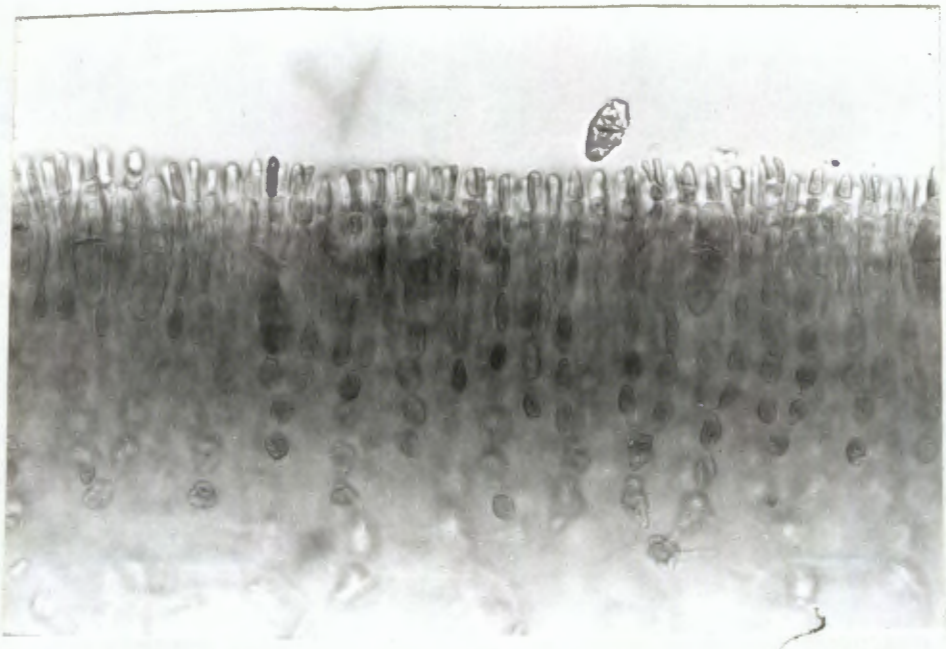

Plate 4: An individual tetraspore, probably released during

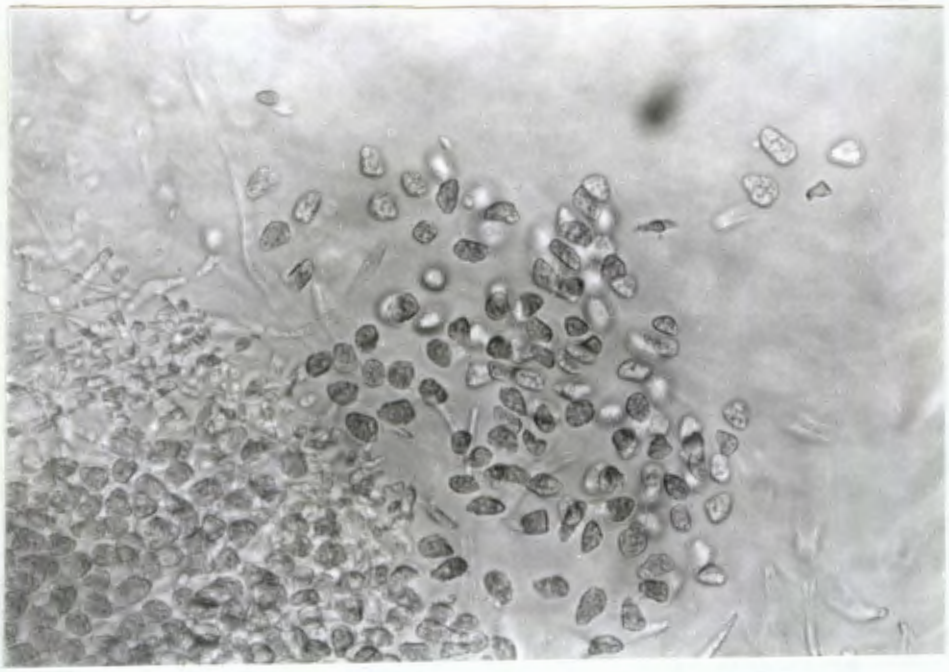

Plate 5: Example of carpospore release from cystocarp, probably during the preparation of the slide. (400x Mag.)

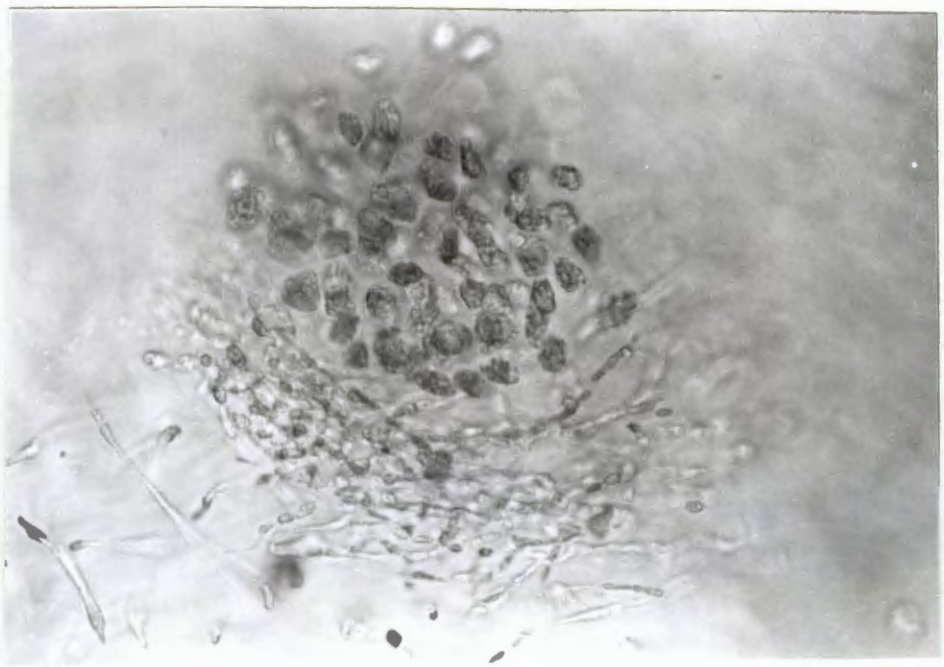

Plate 6: Immature cystocarp. (400x Mag.)

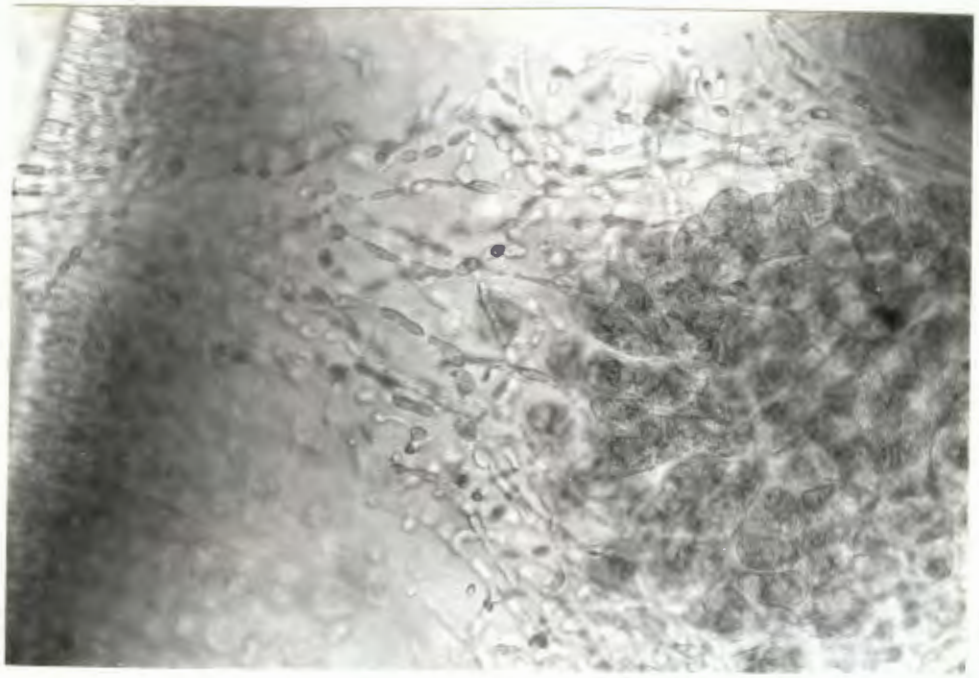

Plate 7: Enlarged view of mature cystocarp embedded in a carposporophyte thallus. Inset: showing ostiole. (400x Mag.)

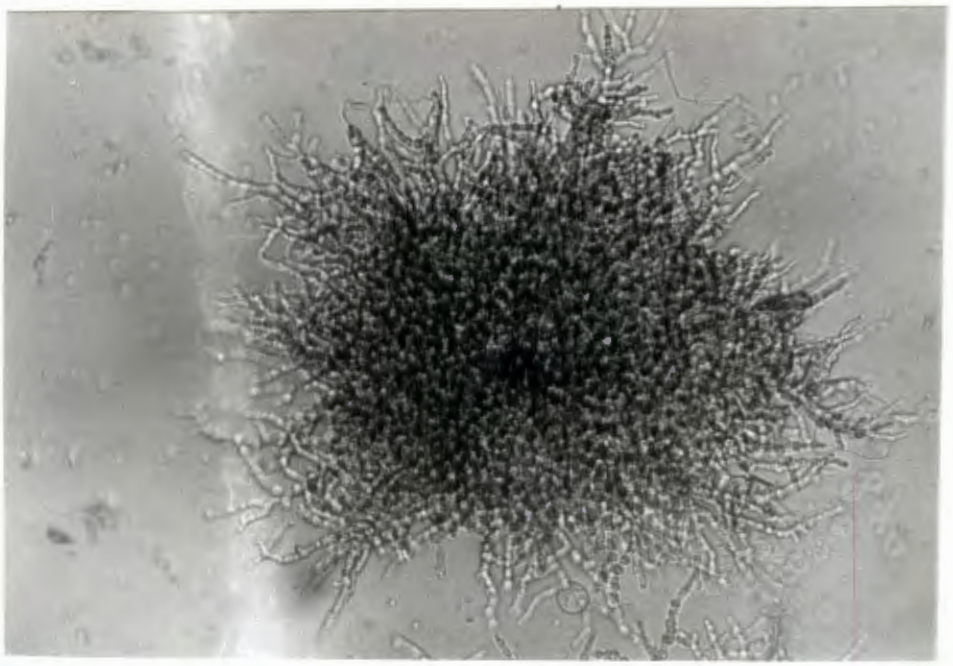

Plate 8: Germination of coalesced carpospores: 3 weeks old. (400x Mag.)

Ectocarpoid contaminant

fact that when looked at microscopically these dots were sometimes found not to be cystocarps but fungi, epiphytes or some other contaminants.

PART TWO

To establish the fecundity of the different life history stages in *A. orbitosa*, in order to assess its importance in determining the population structure observed for *Aeodes* in their natural environments. To also determine the effects of temperature on spore survival.

Germination experiments

Fresh *A. orbitosa* material was collected everytime a germination method was attempted. The life history phases of the plants were determined microscopically as described in the previous section.

All the materials used in the culture experiments were sterilized to avoid the high risk of diatom contamination and subsequent overgrowth (Chapman 1975). Glassware (Slides, petridishes and pipettes) were baked at 100°C for 24 hours and allowed to cool before being used. The sea water was filtered to remove any form of particulate matter and was sterilized by placing them in Erhlenmeyer flasks in a 100°C oven overnight. To alleviate diatom contamination, germanium dioxide (6mg/l) was added to the sterilized sea

water. When not in use, the Erhlenmeyer flasks were sealed with tin foil. All plant material was dipped in a 10% jik solution to disinfect the surface of the blade before being used. Unfortified sea water was used for the experiment as nutrient enriched media was suggested to enhance bacterial infection (Joska and Jackelman pers. comm.)

Experimental equipment and procedure

Twenty four sample petridishes were set up. Each petri dish had a glass slide placed in it and was filled with sea water. Twelve dishes were used for each of the tetraspores and carpospores, respectively. Three dishes of each sex were exposed to three temperatures, namely 10°C, 15°C, 20°C in constant temperature rooms. A fourth temperature exposure of 25°C was achieved by placing the samples in a temperature controlled water bath.

The rooms were fitted with light banks which were fixed to a 16 hour and 8 hour night photoperiod. The number of light tubes and their distance from the samples determined the amount of light energy available. Illuminance was measured in each room using a light meter. The exposure of the experimental material to the light source was standardised to approximately 31 μE by moving the petri dishes to appropriate positions.

Sterilized water was changed every third day.

Scanning for spores:

Glass slides were used as a substratum for spore settlement. A glass cutter was used to scratch grids onto all the slides that were used. Each grid was 20 X 15mm in area and divided into 5 X 5mm blocks. Grids were alphabetically and numerically labelled .

Slides were scanned for spores under low power (100X mag) using the Olympus compound microscope. Light levels were kept as low as possible whilst spore counts were done within 4 minutes to avoid damaging the spores. Three blocks on the grid, where spores appeared relatively dense, were chosen and their location recorded (e.g. B5, A7, C2). Thereafter all the spores within the field of vision were counted under high power (400X mag). Spore counts were made in the same grid areas on a weekly basis to determine percentage survival.

Experimental method one:

June

A. orbitosa thalli were collected from Kommetjie and transported to U.C.T. in plastic bags. On arrival experimental procedures were started immediately as the material had to be as fresh as possible.

Once the sex was determined a plant of each sex (tetrasporophyte and carposporophyte) was cut into 10 small pieces (ca 1 x 2 cm) of material.

The material was then placed in filtered seawater in labelled petridishes (2 pieces per petridish) and left in the 15°C room for 6 hours.(This amount of time was recommended in order to alleviate spore settlement; Jackleman pers,comm.)

After 6 hours the water in the immediate vicinity of the plant was pipetted up and transferred (onto a glass slide in seawater of another petridish) to the previously discussed sterile medium. This was done in the hope of elliminating spore coalescence which is known to occur in germination experiments of this species (Jackelman pers. comm)

Each slide was scanned for spores (on the 3rd day) on the microscope. No spores were found and the experiment was terminated.

Experimental method 2:

A second attempt to induce spore release in A. orbitosa was made in July. Material was again collected at Kommetjie and a method similar to the first was followed.

The following changes were made; plants were put in the sun for 2 hrs and then at 0°C for 2 hrs to try and induce spore release by temperature shock. It was thought that the plants might need more time to drop their spores and therefore the plant material was left overnight in Erlenmeyer flasks. The flasks in turn were placed in a

shaker keeping them in constant motion during this time period.
The shaker was used to reduce the settlement and coalescence of spores that may have been released.

The shaker containing the samples was placed in a dim area (< 10uE). High light intensities are known to affect both release and spore germination (Guiry 1990), although in the previous attempt high light intensity was only 28 uE, light intensity was further reduced to eliminate any possible negative effects.
The water was then pipetted onto slides and checked for spores under the microscope. No spores were found to have been released for either reproductive form.

Experimental Method 3:
Apdes material was collected at Kommetjie in the first week of August and allowed to stand for 48 hours at 15°C (in seawater in glass buckets). All thalli collected were unexpectedly tetrasporophytes so the experiment was dealing only with tetraspores. The plants were given a longer time period in which to release their spores and were subjected to a light intensity of 20 uE.
The water was examined and a few spores were found. The spores were round and red brown in colour and sparsely scattered. Single spores floated around and were few and far between.

Water directly beneath the plant was extracted with a pipette and transferred to the experimental petridishes (sterile sample medium). Three samples were prepared for the 4 different temperature regimes. Spore counts were then made as discussed in a previous section.

Experimental method 4

Spore coalescence was not considered in the following culture experiment carried out in the first week of September. This was decided as the experiments had as yet not been successful and this may have had something to do with the methods employed to alleviate the clumping of spores.

The experimental procedure was similar to that done the first time. Both carposporophytes and tetrasporophytes were sampled. This time however the pieces of blade material were obtained from 5 different plants. The samples were left at 15°C for 2 days at a light intensity of 20uE. Each slide was then transferred to the previously prepared (sterile medium) petridishes in the different temperature rooms. The number of spores were counted up until 30 September (when the lab work for this culture experiment was terminated).

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RESULTS

PART ONE

The proportions of each life history phase (sexes = tetrasporophyte, carposporophyte and non-reproductive) were determined within three different sites of varying wave exposure viz. sheltered, semi-sheltered and exposed (see figure 1). No significant differences were found for any of the sexes between the 3 wave exposure treatments . However within the sheltered sites tetrasporophytes were significantly dominant (52%) over the non-reproductive (38%) and carposporophyte (21%) plants (see figure1; table1) . Wave exposure effects also exhibited significant tetrasporophyte dominance (65%) with similar proportions of carposporophytes (19%) and non-reproductive (22%) plants (see figure 1; table 1). Anovas revealed that the semi-sheltered wave action had no significant effects on life history proportions. T- tests on the other hand showed the non-reproductive dominance to be significant (see figure 1; table1).

I'm not sure what has been analysed here

In summary the individual sexes (tetrasporophyte or carposporophytes or non-reproductive) were similar at each of the sites of varying wave exposures. Wave exposure was however found to effect sex proportions, in that sheltered and exposed populations were tetrasporophyte dominated, while the semi-sheltered sites were dominated by non-reproductive plants.

Now I am very confused.

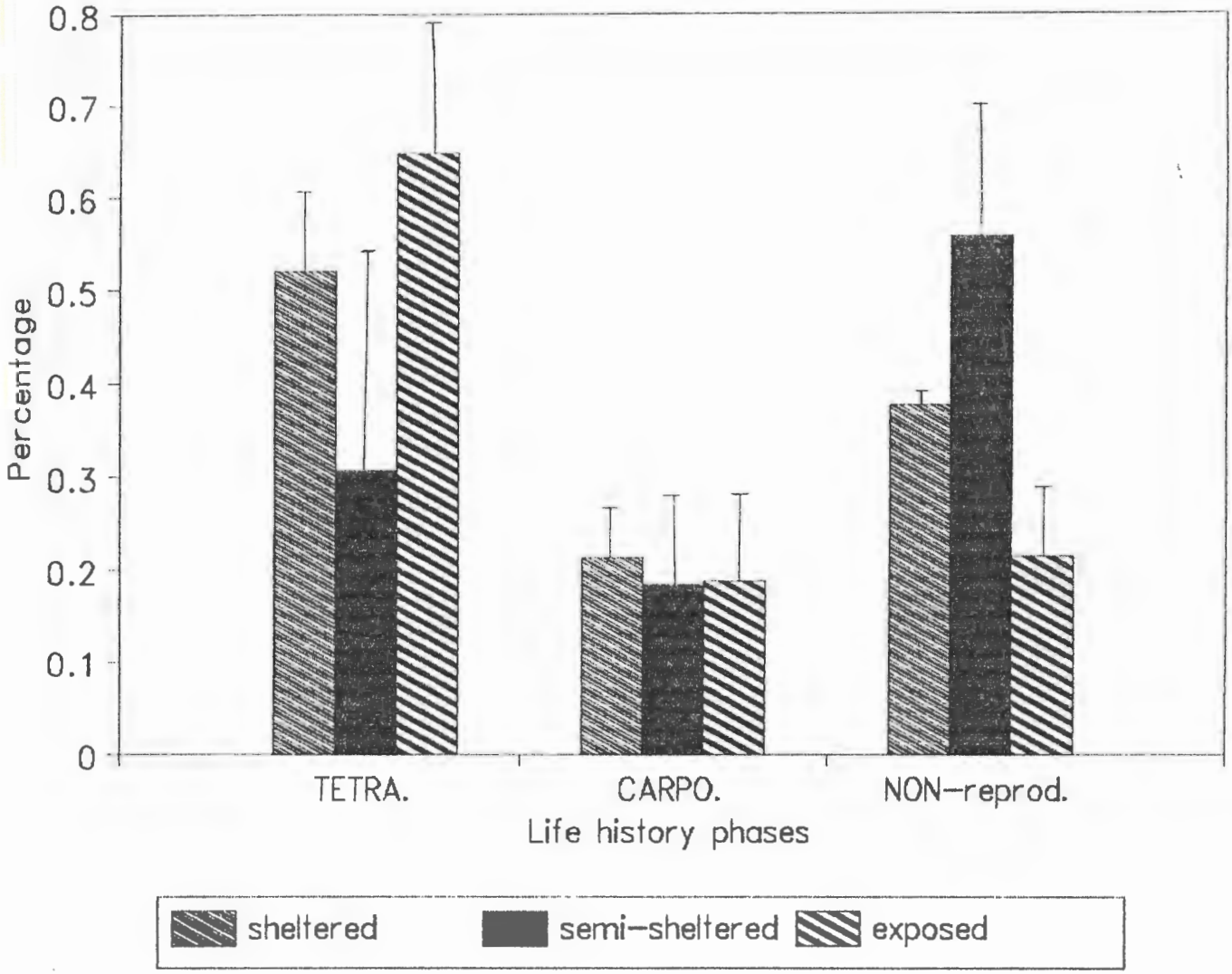

Figure 1: The average percentage (bars) and standard deviation (lines) of tetrasporophytes, carposporophytes and non-reproductive forms of Apdes orbitosa at three sites of varying exposure (boxes). The average was taken from three 1 m^2 samples at each site.

Surely it would have been better to plot the three sexes at each site

Table 1: Life history stage proportions (viz. tetrasporophyte vs.carposporophyte vs. non-reproductive material) in *Aeodes orbitosa* at three sites of varying wave exposure. Proportions are expressed as average percentages derived from three $1m^2$ samples at each site. F ratios derived from one way ANOVA together with significance level. A t-test was done for the semi-sheltered sites as Anovas revealed no significant differences.

	LIFE HISTORY STAGE (SD)		
Wave Exposure	Tetr.	Carp.	Non-rep.
Sheltered	0.52 (0.14)	0.21 (0.01)	0.38 (0.01)
Semi-sheltered	0.31 (0.24)	0.18 (0.08)	0.56 (0.17)
Exposed	0.65 (0.09)	0.19 (0.09)	0.22 (0.06)

	F ratio	Sig. level
Sheltered	13.636	p = 0.0059
Exposed	12.587	p = 0.007

T-test		
Carps. vs non-reps	t =2.86	p = 0.045

The life history stages were determined at three different beaches; namely Oudekraal, Sunny Cove and Grossebuct in Namibia. This was done in order to determine how *A.orbitosa* sex proportions varied along different parts of the coast (see figure 2). The 3 life history phases were found to not differ significantly between Oudekraal, Sunny Cove or Namibia. Within sites however differences between the ~~sexes~~ phases varied significantly at Oudekraal and at Grossebuct (in Luderitz)(see figure 2; table 2). Tetrasporophytes were the dominant ~~sex~~ phase (48%) at Oudekraal followed by the non-reproductive (38%) and carposporophyte (19%) ~~sexes~~. At Luderitz (more northerly distribution of *A.orbitosa*) the tetrasporophytes made up a maximum 60% of the population, while the carposporophytes and non-reproductive plants only made up 9% and 33% respectively.

RESULTS

PART TWO

Carpospore germination experiments

The carpospores were observed to be liberated in large masses, resulting in a clumped distribution, from the reproductive thalli (see table 3). The formation of germ tubes was difficult to determine due to the coalescance of spores. Most of the germinating spores were those which had coalesced, and in the 1st week the germlings/ germ tubes were visible for the spores on the periphery of the clump. The few individual spores which were not clumped usually

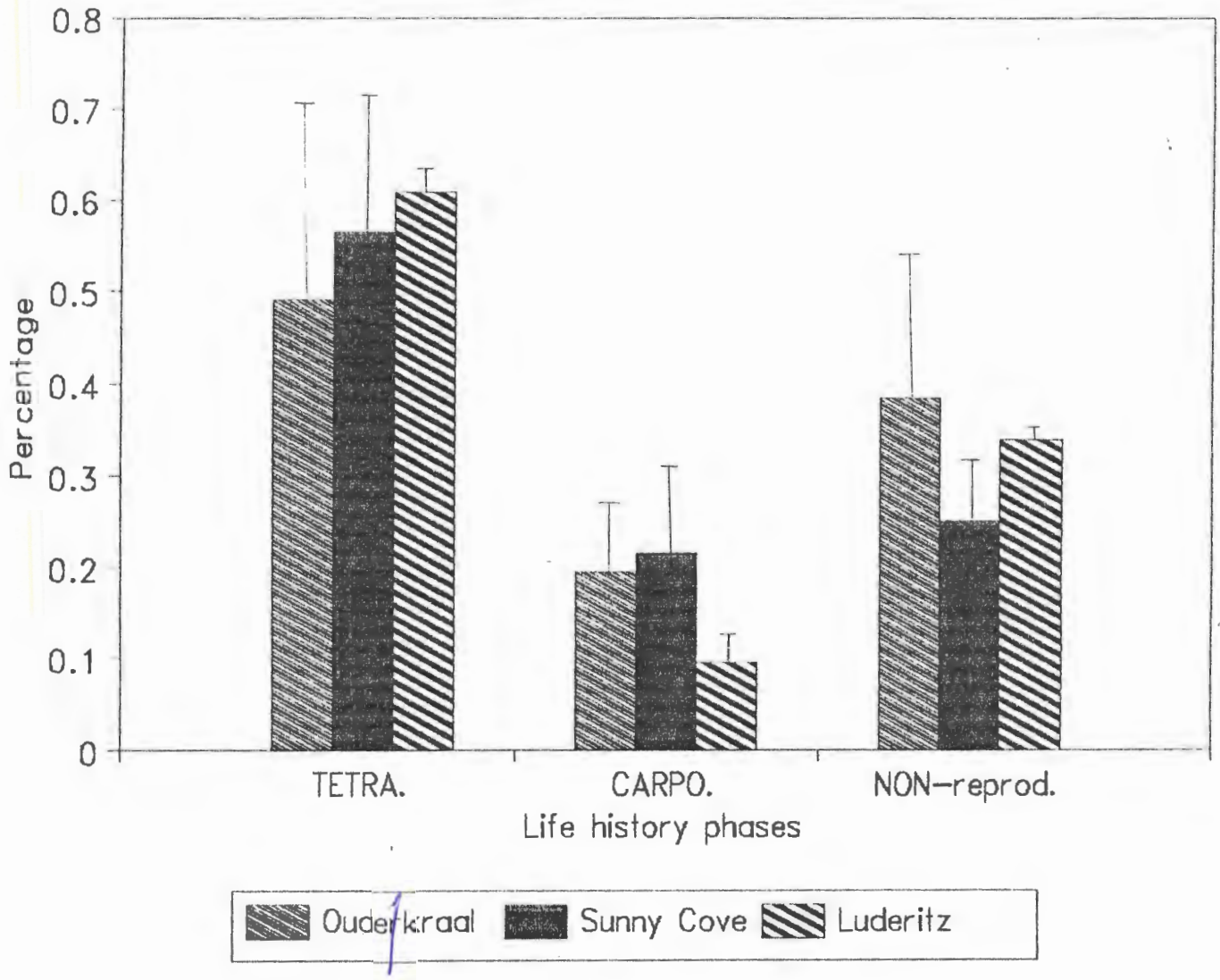

Figure 2: The average percentage (bars) and standard deviation (lines) of tetrasporophytes, carposporophytes and non-reproductive forms of Aodes orbitosa at Oudekraal, Sunny Cove and Luderitz . The average of 9 quadrats was used for Oudekraal and 3 each for Sunny Cove and Luderitz.

Table 2: The average proportions of tetrasporophytes, carposporophytes and non-reproductive forms of *Aeodes orbitosa* at Oudekraal and Luderitz. Proportions are expressed as average percentages derived from 9 quadrats (sheltered, semi-sheltered and wave exposed) at Oudekraal and 3 for the Luderitz. F ratios derived from one way ANOVA shown together with significance levels.

	LIFE HISTORY STAGE (SD)		
Site	Tetr.	Carp.	Non-rep.
Oudekraal	0.49 (0.21)	0.19 (0.07)	0.38 (0.17)
Luderitz	0.6 (0.03)	0.09 (0.02)	0.33 (0.02)
		F ratio	Sig. level
Oudekraal		6.462	p = 0.0057
Luderitz		201.32	p = 0.0000

Table 3: Tetraspore and carpospore numbers released from reproductive material in the 15°C room. Numbers shown are the initial spore counts taken before placing samples under the different temperature regimes (10°C, 15°C, 20°C and 25°C); and are expressed as the average number of spores per 5 X 5mm grid square.

Treatment to be placed under	**Numbers released**	
Temperature (°C)	Tetraspores	Carpospores
10	23	435
15	41	126
20	18	171
25	12	178

didn't survive, the first stages of germination (i.e. formation of germlings with 2 or 3 cells) were observed on the second day. The progression of germination was noted for 3 weeks at which point the developmental stage appeared as in plate 8. - Contaminant: not Ceodes !

Percentage carpospore germination was determined, under different temperature regimes, until the 3rd week (could not be done for longer due to time constraints) and is expressed in figure 3. It was found that carpospore mortality increased with time and that by the third week approximately only 5% had survived. The survival was noted to be greater for those spores grown under the 10°C and 15°C temperatures.Survival rate decreased with higher temperatures, and those spores grown under 25°C all died within the 1st week. This finding is consistant with the temperatures of the natural environments in which *A.orbitosa* usually occur (i.e. where seawater temperatures seldom exceed 20°C).

Tetraspore Germination

Number of tetraspores liberated were far less than that of the carpospores (see table 3). Furthermore the spores were few and far between, no coalescance was observed. The samples exposed to 25°C had all perished within the first week. While those under the 10°C, 15°C and 20°C temperature regimes had low survival rates, but did not survive into the 2nd week (see figure 4).

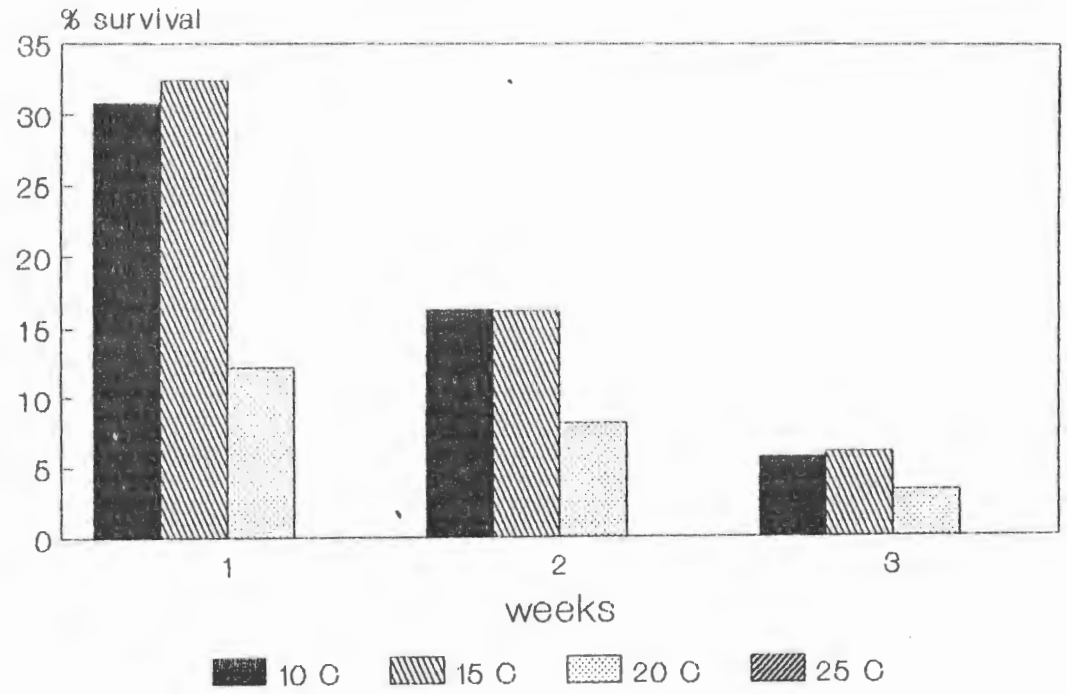

Figure 3: Percentage survival of Carposporophytes spores under different temperatures over a three week period.

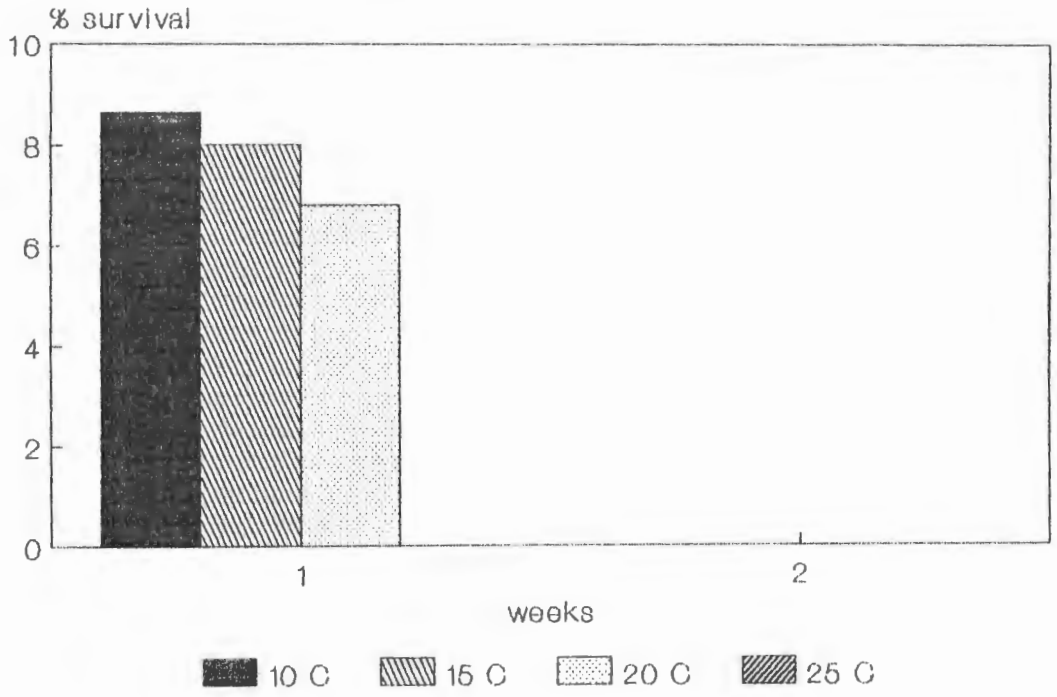

Figure 4: Percentage survival of Tetrasporophyte spores under different temperatures over a three week period.

DISCUSSION

This study established that *A. orbitosa* populations are dominated by tetrasporophytic thalli at each of the areas studied along the coast (viz. Oudekraal, Sunny Cove and Luderitz). Although the tetrasporophyte dominance at Sunny Cove was not found to be statistically valid, this may be due to the fact that too few replicates were sampled. On the other hand, it may be considered that the warmer temperatures of False Bay may have a causal role with respect to the evenning out of the life history population structures. Temperature has been shown to control the morphological expression or alteration of generations in *Irideae laminarioides*, *I.ciliata* (Hannach and Santelices 1985), as well as in several other seaweed species (Luning 1990).

Of all three sites, Luderitz had the greatest tetrasporophyte dominance. This may be associated with its northerly distribution. If one considers that tetrasporophyte dominance may progress in a northward direction (as was found to occur for *I. cordata* by Dyck *et al*. 1985) then this could explain the dominance of tetrasporophyte blades at Luderitz.

In sites of varying wave exposure at Oudekraal, the tetrasporophyte plants were once again observed to dominate in the sheltered areas and in those sites which were

relatively exposed to wave action. It has been proposed that the relative abundance of gametophytes and sporophytes is closely related to the adaptive value of diploidy over haploidy (Hansen and Doyle 1976). The diploid (2n) state is thought to have several advantages over the haploid states e.g. greater structural complexity (Maynard Smith 1986) and heterozygote superiority (Wilson 1981); resulting in the idea that they are more resistant and adaptable than haploids. Thus diploid individuals may be better favoured in variable or unpredictable environments. This notion can be applied to the diploid dominances observed at Oudekraal, if one assumes these two environments to be more severe than the semi-sheltered site.

Differences in water movement are thought to affect the immediate environment in which the plant grows by influencing nutrient availability, waste product removal, rate of gaseous exchange and the extent of light penetration (Jackelman and Bolton 1990). Wave action studies have indicated that environmental stresses occur in both wave exposed and sheltered areas (Cousens 1982; Jackelman and Bolton 1990). The thalli at the exposed sites must contend with the water's mechanical shearing action, while on the other hand, the decreased wave motion in sheltered sites may bring about nutrient depletion and/or desiccation. Perhaps these unfavourable conditions are tolerated more by the "hardier" tetrasporophyte plants in the populations at Oudekraal. In this situation the

semi-sheltered site could be considered the most stable of the three, which may explain the lack of disproportionate life history phases. This supports Dyck *et al.* (1985) suggestions that wave exposure was a contributing factor in their studies on shores where sporophytes of *I. cordata* dominated.

An alternative approach would be to explain the low proportion of sexually reproductive material in the semi-sheltered site. Perhaps these low figures imply that asexual or vegetative reproduction is taking place in these populations. Asexual modes of reproduction are adaptively significant in terms of faster growth rates and it is therefore thought that asexual offspring may be suited in stable environments (Grant 1981). If sexual reproduction is preferential in disturbed sites then the absence thereof is to be expected in this presumably stable site.

Germination experiments revealed a high tetraspore mortality with respect to that of the carpospores. Furthermore the mature carposporophytes were found to liberate a larger number of spores in comparison to the tetrasporophyte reproductive tissue. This may be an important factor in explaining the dominance of tetrasporophytes in nature, as was suggested by Hansen and Doyle (1976). Similar results were found by Guzman-Del Proo et al (1971) in studies on *Gelidium robustom* (Gard), which showed that carposporophytes had superior fecundity as

well as a longer period in which they were active. This, as was asserted by Guzman-Del et al (1971), may partly explain the tetrasporophyte abundance over an entire study area.

The differential survival of spores implies that there is also a difference in recruitment rates, between phases, in nature. Although not tested, it has been observed that crusts of *A.orbitosa* undergo perennation in their natural environment (Levitt pers. comm.) If regenerating crusts do occur then the maintenance of an established life history stage structure is perpetuated.

CONCLUSION

Within a species population structure may depend not only on the life history phases ability to grow and reproduce but on life history variations governed by larger scale environmental changes (Gaines and Lubchenco 1982). On a smaller scale, alternation of generations is dependant on two factors namely, the turnover of older perennating plants and the differential ability of the alternate phases to recruit and reproduce. A study such as this cannot establish the principal factors determining the disproportionate occurrence of life history phases observed in the field. This is due to the fact that the observations being made are only indicative of a limited temporal scale.

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