A phenological study of coalescence in two South African Gigartinales, *Gigartina polycarpa* (Kützing) Setchell *et* Gardner and *Sarcothalia stiriata* (Turner) Leister

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ABSTRACT

Coalescence has been described in a number of coalescing red algae, however the majority of studies are laboratory based. This study examines the phenology of clumping characteristics in *Gigartina polycarpa* and *Sarcothalia stiriata* in the field. Clumps of these two species appear to have a coalesced holdfast from which a number of uprights arise. Clumps of both species display characteristics previously described in coalescing species. This includes size inequality between fertile uprights and juvenile and non-fertile uprights and a loose relationship between basal area and number of uprights. It appears that the phenology of clumps supports previous studies examining phenology without considering coalescence. The distribution of the two species is very different, with a higher proportion of *S. stiriata* conspecifics found next to each other. Conversely *G. polycapra* has a low proportion of near neighbour conspecifics.

INTRODUCTION

Whilst fusion of germinating seeds to form one entity made up of many potentially independent individuals is rare in terrestrial plants, it seems from recent research that it is a widespread phenomenon in crust forming species belonging to numerous orders of red algae, e.g. Ahnfeltiales, Corallinales, Gigartinales, Gracilariales, Halymeniales, Palmaraiales and Rhodymeniales (Santelices *et al.*, 1999). Coalescence among seaweeds is defined as the fusion of individual spores into a coalesced mass that responds as an individual unit.

Evidence for integration of a coalesced mass is both ultrastructural (Santelices *et al.*, 1999) and macroscopic as seen in bicolour individuals (Santelices *et al.*, 1996). Early studies found that spores of red (wild) and green (mutant) type *Gracilaria chilensis* could form a bicolour coalesced holdfast but that uprights corresponded to the parent spore i.e., green portions of the holdfast produced green uprights and red spores produced red uprights (Maggs and Cheney, 1990). This suggests that although spores from different plants have the ability to form a common holdfast, there is no integration between spore derivatives. However later work by Santelices *et al.* (1996) found that in addition to coalescence of the holdfast, fronds within an individual upright may display this bicolour providing evidence for the integration of coalesced spores.

Ultrastructural studies have found two ways in which coalescence may occur. In the first, naked spores fuse and a common cell wall is formed around the coalesced spores. In the second, more common, process individual spores form independent cell walls and integration is facilitated via secondary pit connections in adjoining cell walls (Santelices *et al.*, 1999). This second process was found in members of the Gigartinales (e.g., *Ahnfeltiopsis durvillaei, A. furecellata, Chondrus canaliculatus, Mazaella laminarioides and Sarcothalia crispata*) (Santelices *et al.*, 1999). Coalesced spores show no evidence of scar tissue at the juncture of fusion indicating that fusion is compatible to all coalescing parties (Santelices *et al.*, 1999). Thus the mechanism of coalescence is well understood, however less clear are the implications that growing as a coalesced mass has on the ecology and physiology of species exhibiting this phenomenon.

A number of theories have been proposed concerning the advantages of coalescence. These include increased resistance to grazing and overgrowth by competing species, more resistance to wave action and quicker growth and faster initiation of upright shoots (Maggs and Cheney, 1990). Early studies by Tveter and Mathieson (1976) on *Chondrus crispus* seemed to support these hypothesized advantages as they found that fronds from coalesced spores of *C. crispus* grew faster than fronds from non-coalesced spores. However results from laboratory studies on *G. chilensis* do not support earlier initiation and faster specific growth between coalesced and non-coalesced spores (Muñoz and Santelices, 1994).

The evidence is conflicting and there is no comprehensive analysis on a number and range of species that would provide convincing proof for the hypothesized advantages of coalescence. However in *G. chilensis* the increased genetic potential resulting from coalescence results in increased variation in morphology (Santelices *et al.*, 1996). An increase in variation as a result of coalescence would impact the seaweed industry through the selection of superior strains (Santelices *et al.*, 1995). The assumption is that coalesced spores integrate and act as a single individual cooperating in order to enhance the success of the clump as a whole. However even though one coalesced mass may be made up of a number of genetically different spores, the individual spores do maintain the ability to produce uprights within the coalesced mass (Santelices *et al.*, 1999).

The ecological and physiological processes that apply to unitary organism do not apply for coalescent organisms. For example in coalescing species germination is linearly related to spore density as opposed to non-coalescing species where germination is greatest at intermediate densities (Santelices *et al.*, 1999). The differing traits of a coalescent mass vs a single individual has implications for factors like competition, for some species for example *Sarcothalia crispata* survivorship of sporelings was increased as number of spores in a coalesced mass increased (Santelices *et al.*, 1999). There is also the question of physiological integration, which may be facilitated via pit plugs. If individuals are integrated to some extent what are the dynamics of nutrient acquisition and partitioning? A number of species examined exhibited marked size inequality among individuals within a clump with a few, relatively larger, fertile individuals situated towards the centre of the clump, surrounded by a number of smaller juvenile or infertile individuals. Although these physiological and ecological processes have been studied, the majority of work is laboratory based, working with cultured plants.

Santelices *et al* (1996) highlighted the lack of field observations of coalescing behaviour in red algae and postulated that due to the clumped nature of dispersal and recruitment in *G. chilensis*, coalescence in the field is likely to be more common than described. Two common red algae that occur along the west coat of the Cape Peninsula are *Gigartina polycarpa* (Kützing) Setchell *et* Gardener and *Sarcothalia stiriata* (Turner) Leister. Both species are common in the lower littoral and their distribution extends from Port Nolloth to Cape Agulhas along the west coast of South Africa (Stegenga *et al.*, 1997). *G. polycarpa* and *S. stiriata* grow from disk- like crusts, thought to be an important characteristic feature of coalescing species (Santelices *et al.*, 1999) and occur in mixed beds in the littoral zone (Levitt ,1998).

G. polycarpa and *S. stiriata* have the *Polysiphonia*-type life history. There are two generations, a haploid gametophyte generation with isomorphic males and females and a diploid sporophyte generation (Hawkes, 1990). The phases and sexes can be told apart by gross morphological differences. Female gametophytes of *G. polycarpa* can be differentiated from male gametophytes by abundant cystocarps covering the female gametophyte thallus. Conversely male gametophytes have a relatively smoother thallus. Mature tetrasporophytes can be distinguished from the gametophytes by the tetrasporangial sori which look like small black dots embedded in the thallus.

Female gametophytes of *S. stiriata* are distinguished from male gametophytes by numerous spherical swellings in which the cystocarps are housed. Male gametohpytes have larger fleshy projections. Conversely the tetrasporophytes of *S. stiriata* have a smooth thallus in which tetrasporangial sori are embedded, as with the *G. polycarpa* tetrasporophyte.

The seaweed industry in South Africa is burgeoning with new markets opening for fodder in the abalone industry as well as mariculture prospects of well established agarophytes. Historically a number of red algae, including *Gracilaria* and several species of *Gelidium*, have been collected for their agar. A few kelp species, predominately *Ecklonia maxima* (Osbeck) Papenfuss, are collected as beach cast and used in the fertilizer industry. As yet there is no well established mariculture industry although there are a few preliminary initiatives including the cultivation of *Gracilaria gracilis* (Stackhouse) Steentoft, Irvine *et* Farnham (Stegenga *et al.*, 1997). The seaweed industry is growing and thus there is impetus to identify species that can be potentially exploited. However an integral part of the exploitation of any new species is a clear understanding of the biology of that species to ensure the sustainable management of that species.

To date no carrageenan-producing seaweeds are either collected or cultured in South Africa. In a study by Levitt (1998) a comprehensive analysis was conducted on the population phenology of *G. polycarpa* and *S. stiriata* in order to assess their harvesting potential for carrageenan. Whilst the Levitt study examined similar features that this study will focus on, the study did not examine the population phenology with specific reference to coalescence.

Therefore the aim of this study is to investigate 1) if the features of coalescence described in lab experiments are evident in the field and 2) if clumping characteristics differ between phases within a species and between species and 3) if coalescing characteristics can explain the population phenology previously elucidated by Levitt (1998). This study will also examine the distribution of the population. Tetrasporophytes release both female and male gametophyte spores, therefore it is expected that there would be an even mix of male and female gametophytes of both species. Levitt (1998) described the ratio of male and female gametophytes and tetrasporophytes of *G. polycarpa* as 0.9:0.9:1.1., therefore they are present in roughly equal proportions throughout the year. For *S. stiriata*, the ratio of male and female gametohpytes are relative equal but tetrasporophytes are far less ~~more un~~common, the ratio of the phases is 2.8:2.5:1 (male:female:tetrasporophyte) (Levitt, 1998).

METHODS

The study site at Kommetjie is located along the west coast of the Cape Peninsula (34° 08 1′ S, 18°18 6′ E). A total of 91 clumps were randomly collected during the winter months of August and September 2001. For each species of *Gigartina polycarpa* and *Sarcothalia stiriata* clumps of the three phases were collected i.e., male and female gametophytes and tetrasporophytes. Terminology concerning coalescence varies, in this study the term clump refers to a number of uprights axes that originate from a common holdfast. Although coalescence was not verified by laboratory or ultrastructural studies, it is assumed that the uprights within a clump originate from at least two spores that have coalesced. Considering that clumps of both species typically have at least 15 uprights, it is unlikely that they all would have originated from one spore. However this assumption is taken into consideration when interpreting the results. Clumps of *G. polycarpa* are easy to differentiate from one another as they typically occur as roughly circular patches with few fertile uprights surrounded by a number of small, infertile uprights clearly delineated from other clumps. Clumps of *S. stiriata* are more difficult to distinguish. This species coalesces as a number of uprights that are joined to one another via a spreading horizontal branch, thus there is no common holdfast that all uprights share. In this species distinguishing horizontal joining branches from uprights when they are still small can be difficult as it was observed that an upright often starts off as what looks like an upright but then bends down, forms a holdfast and becomes a connecting element. Also well established uprights may also join onto a nearby upright as so facilitate the spreading of a clump in this manner. Therefore for the purposes of this study an individual upright is defined as having a both an upright axis and a holdfast.

In the field the distance to the first and second nearest neighbour holdfast was measured and recorded as well as the species and phase of the neighbour. For 30 of the 91 samples, dimensions of the common holdfast were measured. Clumps were then collected by carefully removing the whole clump and its coalesced holdfast with a scraper and transported to the laboratory where they were kept at 0 °C until examination.

Although they were not collected and examined, instances where clumps appeared to be multi-phasic (i.e., male and female gametophyte uprights within one clump) were noted to gain some idea of the frequency of coalescence amongst different phases.

Clumps were weighed on a fresh mass basis, in grams. Uprights were divided into mature, fertile individuals; uprights more than 2 cm long but not fertile (termed medium) and uprights less than 2 cm (termed small). Each clump was analysed as follows;

The number of medium and small uprights were counted and the total number in each group weighed. Fertile uprights were weighed as individuals. Each fertile upright was then divided into fertile and sterile portions as follows. For female gametophytes of both species, fertile portions were identified as those portions of the thallus that were covered with spherical swellings. For tetrasporophytes of both species, fertile tissue was identified by the distinctive small black dots that are the tetrasporoangial sori. Fertile tissue for male gametophytes was not estimated as spermatangia are microscopic and are therefore impossible to distinguish with the naked eye. To obtain the fertile tissue those portions that were identified as fertile were then cut with scissors and weighed. Thus this is a relatively crude method of estimating the fertile weight. However aim was to compare between species and not to make any extrapolations of biomass. This is done in order to obtain the proportion of fertile tissue within a clump. This raw data was then analysed as follows:

i) Average weight of a clump of *S. stiriata* male gametophyte (SM) *S. stiriata* female gametophyte (SF), *S. stiriata* tetraporophyte (ST), *G. polycarpa* male gametophyte (PM), *G. polycarpa* female gametophyte (PF) and *G. polycarpa* tetrasporophyte (PT).

ii) Average number of upright individuals in a clump, amount of fertile tissue as a proportion of total clump weight and average size of uprights.

iii) Average basal area of the two species and relationship between number of uprights and basal area.

iv) Near neighbour distribution. This was done in order to examine the randomness of the distribution of clumps. Neighbouring plants are divided into three groups, the same phase, the same species but a different phase and different species. The total in each group is then expressed as a percentage of the total number of clumps of each of the six groups
(PF, PM, PT, SF, SM, ST).

Statistical analysis

Data analysed with ANOVA. Tests specified in results. Significance level $p<0.05$.

RESULTS

Table 1. Number of clumps collected for each of the six groups

	Male gametophytes	Female gametophytes	Tetrasporophytes	Total
G. polycarpa	16	21	17	**54**
S. stiriata	14	14	9	**37**
Total	**30**	**35**	**28**	**91**

Unless otherwise indicated, n values to construct figures and perform statistics are as stated above or as totals of the above.

Average weight of a clump (Fig 1)

For *G. polycarpa* female gametophytes (42.62 ± 6.62g) are on average heavier than both male gametophytes (21.85±4.63g) ($p<0.007$) and tetrasporophytes (26.78 ± 4.42g) ($p<0.03$). Whilst tetrasporophytes are on average heavier than male gametophytes, there is no statistical difference between the two. For *S. stiriata* tetrasporophytes have the heaviest average weight of a clump (30.33 ± 5.6g) followed by female (28.88 ± 5.57g) and then male (25.35 ± 6.19g) gametophytes, however there is no statistical difference between the three phases.

When comparing between the two species *G. polycarpa* females are significantly heavier that *S. stiriata* males ($p<0.03$).

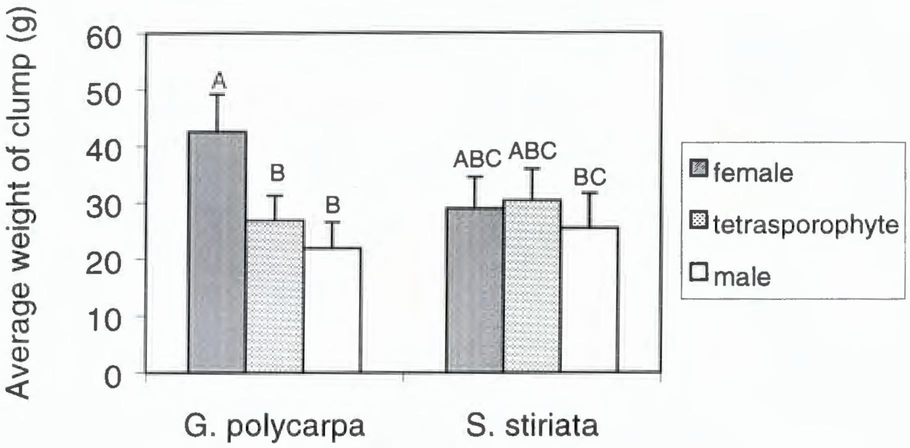

Figure 1. Average weight of clump with S.E bars for male and female gametophytes and tetrasporophytes of *G. polycarpa* and *S. stiriata*. Different letters indicate significant difference (Least-squares difference test).

Fertile weight of a clump (Fig 2)

Female gametophytes of *G. polycarpa* have on average a greater proportion of fertile tissue than tetrasporophytes (72.72 ± 5.19% vs 63.68 ± 3.17%), although not significantly so.

Female gametophytes of *S. stiriata* have on average greater percentage fertile tissue per clump than tetrasporophytes (61.64 ± 3.39% vs 48.51 ± 5.52%), although not significantly so.

Comparing between species, *G polycarpa* females have on average significantly greater proportion of fertile tissue within a clump than both tetrasporophyte and female gametophytes of *S. striiata* ($p<0.001$ and 0.01 respectively)

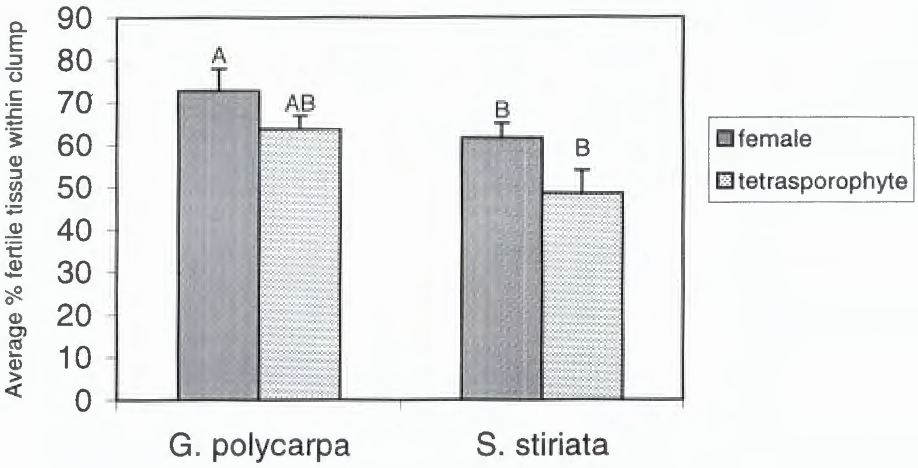

Figure 2. Average percentage of fertile tissue per clump for female gametophytes and tetrasporophytes of *G. polycarpa* and *S stiriata*. Different letters indicate significant difference (Least squares difference test). SE indicated.

Basal area and total number of uprights (Fig 3,4,5)

Clumps of *S. stiriata* have on average a greater basal area of holdfast than *G. polycarpa* (6.39 ± 0.49 cm^2 vs 2.69 ± 1.18 cm^2), although not significantly so (Mann-Whitney U Test, $p< 0.008$). There is a generally positive relationship between the total number of uprights and the basal area for both species (Fig 4 and 5) although for *S. stiriata* the pattern is more clearly defined ($R^2= 0.45$) as it is for *G. ploycarpa* ($R^2= 0.30$).

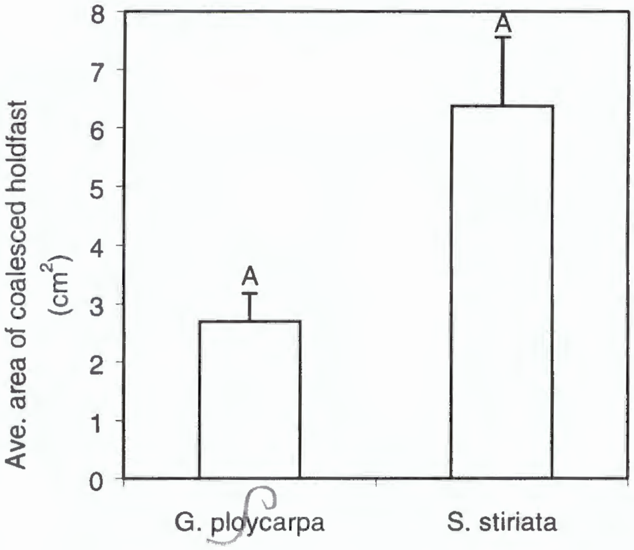

Figure 3. Average area of coalesced holdfasts in clumps of *G. polycarpa* (n= 17) and *S. stiriata* (n=13). There is no statistical difference between the two species (p=0.08). *G. polycarpa* n=17, *S. stiriata* n=13.

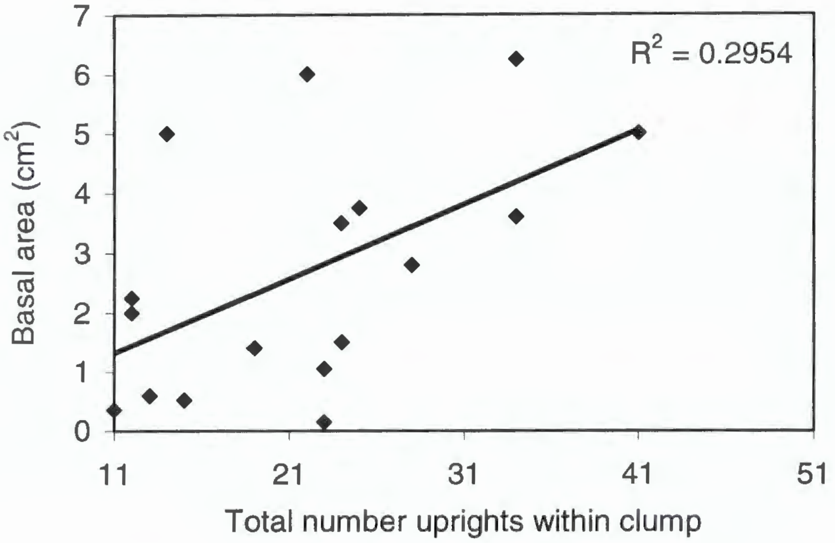

Figure 4. Relationship between total number of uprights (fertile + medium + small) and area of coalesced holdfast for *G. polycarpa* (n=17)

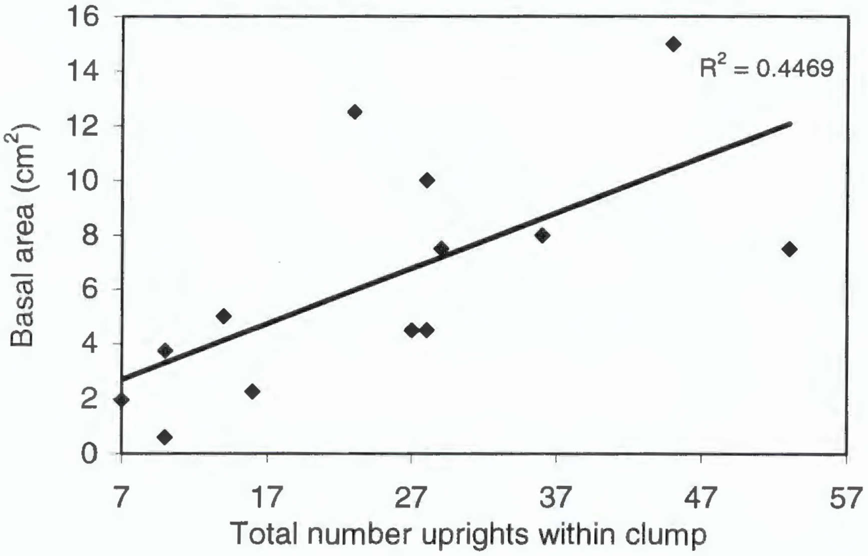

Figure 5. Relationship between total number of uprights (fertile + medium + small) and area of coalesced holdfast for *S. stiriata*. (n=13)

Number of uprights (Fig 6&7)

There is no significant difference in the number of fertile uprights between the phases (male and female gametophyte and tetrasporophyte) for either *G. polycarpa* or *S. stiriata.* There is also no significant difference comparing between species, same phases e.g., tetrasporophytes of *G. polycarpa* and *S. stiriata* (Fig 6). There is no significant difference for average total number of uprights (fertile+medium+small) per clump between *S. stiriata* and *G. polycarpa*, although *S. stiriata* has marginally more total uprights per clump (Fig 7). There is however a significant difference within species between small, medium and fertile uprights ($p<0.0001$) (Fig 7). Within a clump, medium uprights are the most numerous for *S. stiriata.* For *G. polycarpa* small uprights are the most numerous within a clump. There is also a significant interaction between species and number of fertile, medium and small uprights ($p<0.002$) (two factor analysis of variance).

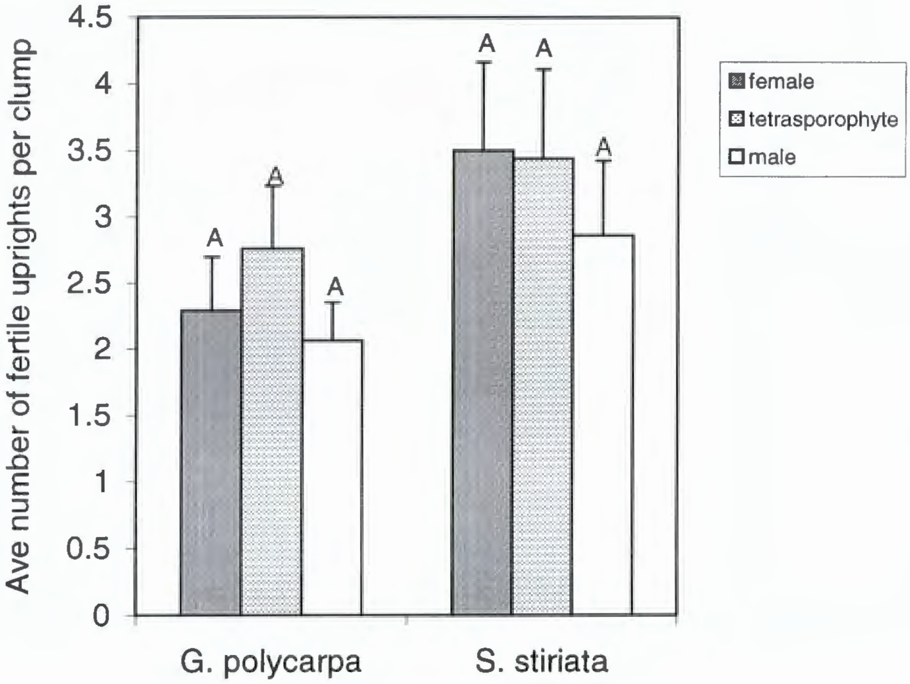

Figure 6. Average number of fertile uprights per clump of female and male gametophyte and tetrasporophytes of *G. polycarpa* and *S. stiriata.* Statistical analysis (Tukeys HSD) show no significant difference within and between species.

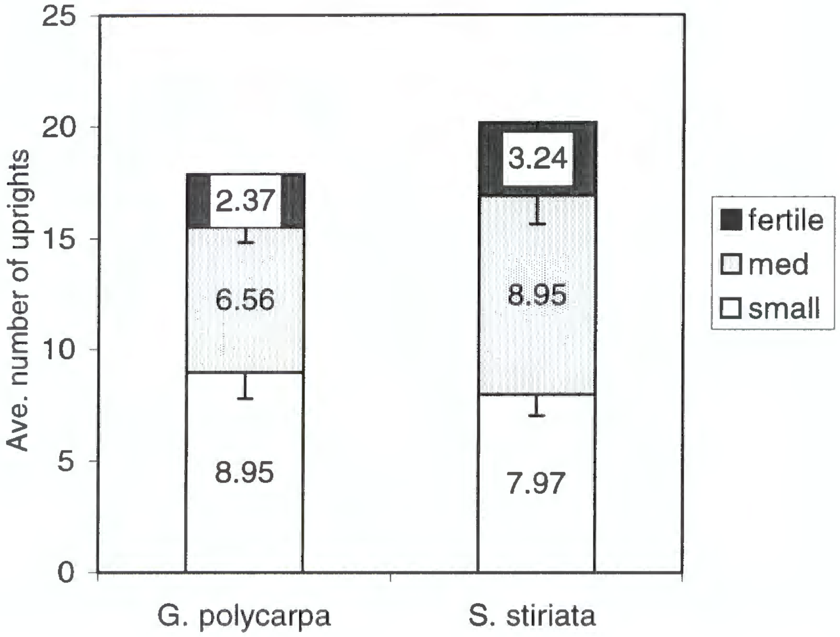

Figure 7. Average number of fertile, medium and small uprights per clump for *G. polycarpa* and *S. stiriata*. For each species the average is a total of male, female and tetrasporophyte clumps together. There is no significant difference in the interaction of species ($p<0.87$). There is a significant difference in the number of uprights ($p<0.00001$). There is a significant interaction between species and number of uprights ($p<0.002$) (Two factor analysis of variance)

Weight of uprights (Fig 8-11)

In *G. polycarpa* there is an exponential relationship between the proportion of fertile tissue and total clump weight ($R^2= 0.7$) (Fig 8). The proportion of fertile tissue of total clump weight is a linear relationship in *S. stiriata*. The R^2 value is low ($R^2=0.1$) (Fig 9).

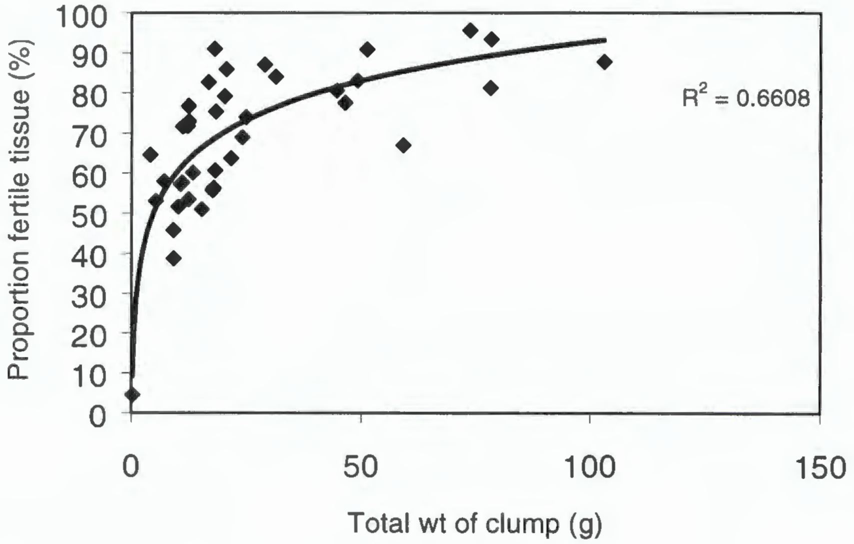

Figure 8. The proportion of fertile tissue of total clump weight of *G. polycarpa* (n=57). There is an exponential relationship between the amount of tissue within a clump that is fertile and the weight of a clump.

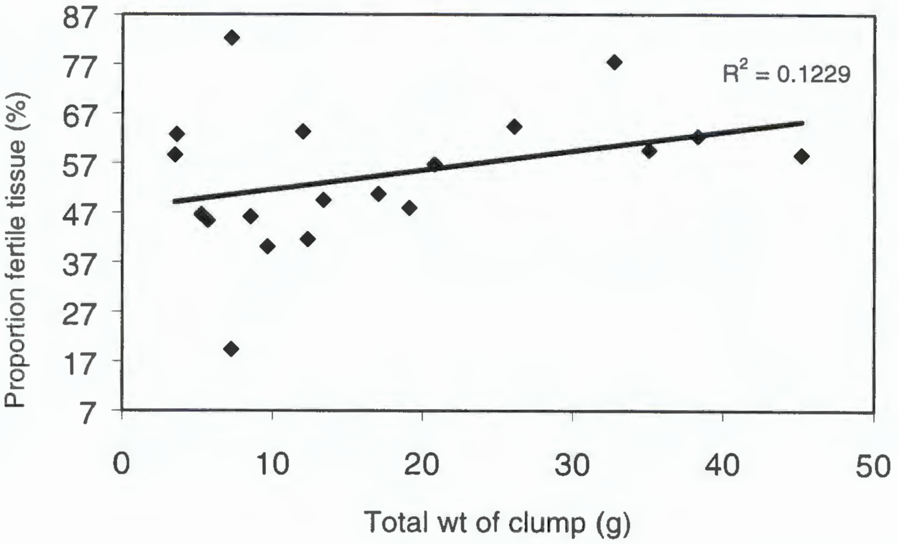

Figure 9. The proportion of fertile tissue of total clump weight of *S. stiriata* (n=34). R^2 =0.12

Fertile uprights may be relatively the least numerous in both species, but they make up significantly the greatest weight of a clump in both species (Fig 10).

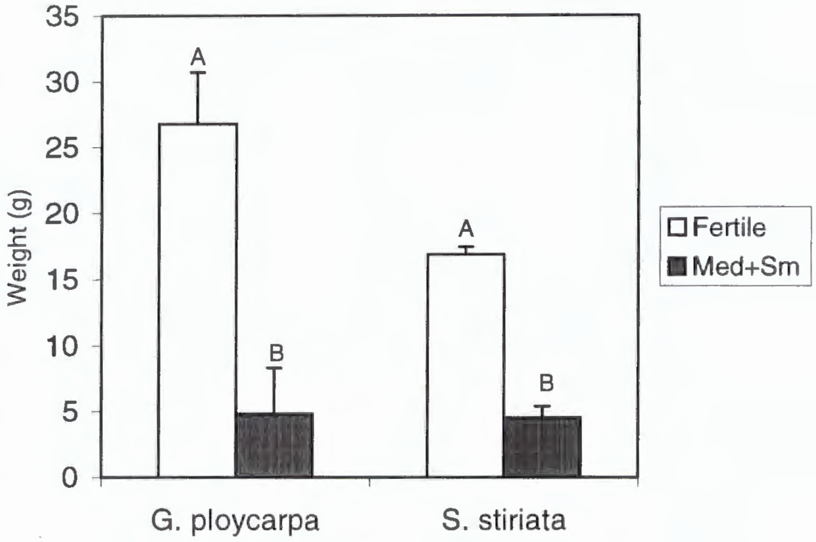

Figure 10. Average weight of fertile and medium+small uprights per clump of *G. polycarpa* and *S. stiriata*. Fertile upright weight is significantly greater than medium+small upright weight for *G. polycarpa* ($p<0.0001$) and *S. stiriata* ($p<0.0001$). There is no significant difference between fertile ($p<0.15$) and med+small weight ($p<0.30$) between species. Note that no tests were done between small+med and fertile between species (e.g. *G. polycarpa* fertile and *S. stiriata* med+small). SE indicated.

The average weight of fertile uprights is significantly greater than the combined average weight of a medium and small upright (Fig 11) for both species. The average weight of a *G. polycarpa* fertile upright 15.12±2.32 g which is significantly greater than the combined average weight of a medium and small upright (0.67±0.09 g) (p<0.0001). The average weight of a *S. stiriata* fertile upright is 8.32±1.17 g which is significantly greater than the combined average weight of a medium and small upright (0.51±0.05 g) (p<0.0001).

Between species, a fertile upright of *G. polycarpa* is on average significantly heavier than a *S. stiriata* fertile upright (p<0.004). However there is no significant difference between the weight of medium+small individuals in the two species (p<0.07). Note that no stastistical tests were done between *G. polycarpa* fertile and *S. stiriata* small+medium, and *vice versa.*

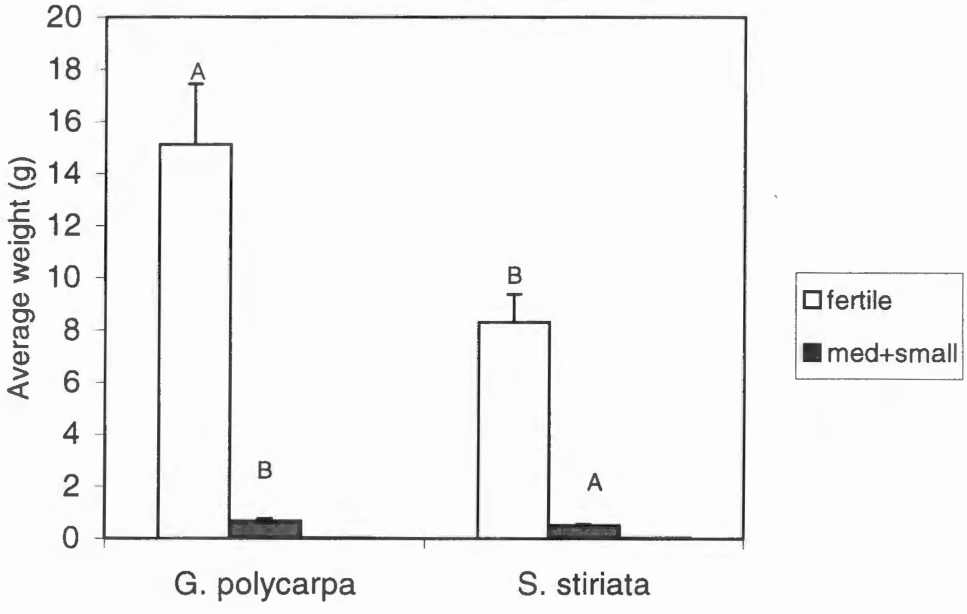

Figure 11. Average weight per upright of fertile, medium + small uprights for *G. polycarpa* and *S. stiriata.*

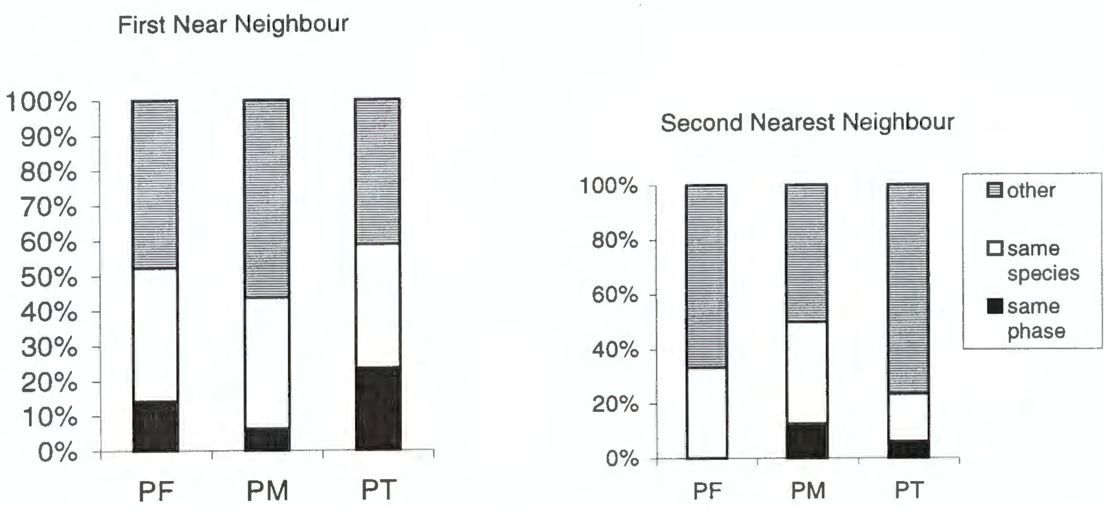

Figure 12. Near neighbour distribution for *G. polycarpa*. PF= female gametophyte, PM= male gametophyte. PT= tetrasporophyte. Data is expressed as a percentage of total number of near neighbours.

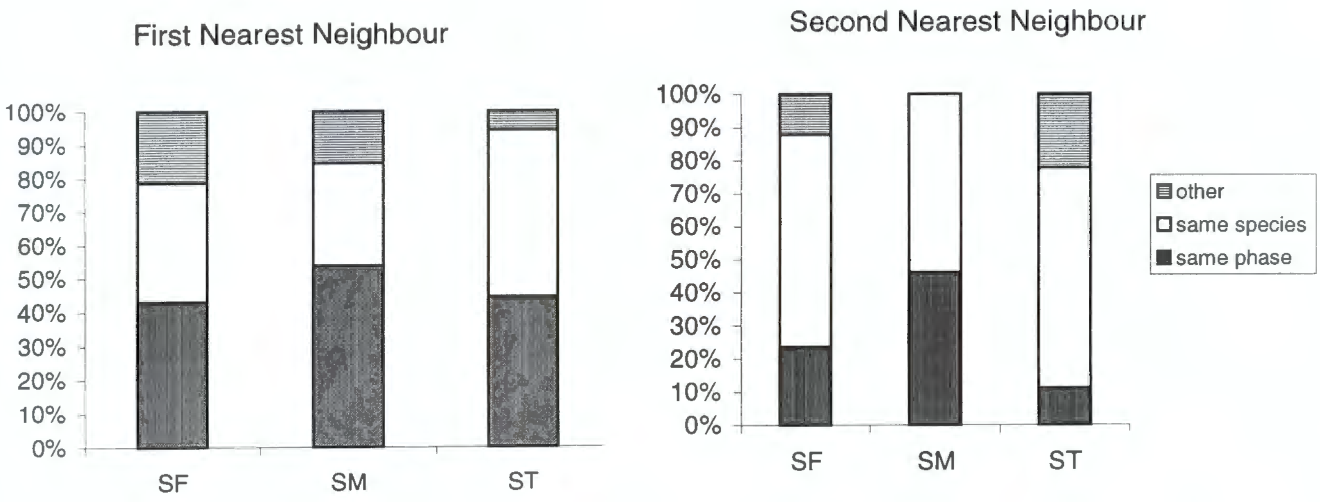

Figure 13. Near Neighbour distribution for *S. stiriata*. SF= female gametophyte, SM= male gametophyte, ST= tetrasporophyte. Data is expressed as a percentage of total number of near neighbours.

DISCUSSION

A number of economically important red algae have been demonstrated to display coalescence, e.g., *Chondrus crispus* in Europe for carrageenan (Guiry and Garbary, 1991), and *Gracilaria chilensis* in South America (Santelices *et al.,* 1995). A key aspect to the continued success of any seaweed industry is an understanding of the ecology of the species exploited, a good illustration of this is the complete failure of the local *Gracilaria* industry in Saldahna Bay in the early 1980's as a result of large-scale construction along the shore (Stegenga *et al.*, 1997).

Average weight of a clump

This study is concerned with the phenology of coalescing behaviour in field populations of two red algae species, the carrageenophytes *G. polycarpa* and *S. stiriata*. The process of coalescence has been well studied in *Gracilaria chilensis* and it is clearly evident that a number red algae species, particularly those with discoid germination, are able to form coalesced masses from individual spores (Santelices *et al.,* 1999).

Clumps were collected during the winter season from August to September with the majority collected during September. A previous study on the population demography of these two species found that for *G. polycarpa* there is on average no difference in the abundance (as a % of the population) of male and female gametophytes and tetrasporophytes (Levitt, 1998), however the abundance ratios vary markedly throughout the year. Since data for the Levitt (1998) study was collected by recording species along a transect it does not take into account the size of the clumps. Therefore it is interesting to see if the phase that is the most abundant is also the heaviest.

In this study clumps of *G. polycarpa* female gametophytes are significantly heavier than tetrasporophytes and male gametophytes. Tetrasporophytes are slightly heavier than male gametophytes but not significantly so. Looking at the monthly abundance ratios of *G. polycarpa* for the month of September male gametophytes and tetrasporophytes are almost equally abundant and female gametophytes are the most abundant. Thus for *G. polycarpa* the abundance ratios follow the pattern of size ratios, and this study supports the results from the Levitt (1998) study, at least for the latter part of winter.

The abundance ratios between the three phases is far more variable for *G. polycarpa* than it is for *S. stiriata* . Throughout the year, tetrasporophytes are the least abundant and male and female gametophytes are on average equally abundant throughout the year. During September male gametophytes are approximately 35% more abundant than female gametophytes (Levitt, 1998). In the results presented here there is no significant difference between the three phases but tetrasporophytes are the heaviest clumps, followed by female and then male gametophytes. Thus it would seem that for *S. stiriata* the winter pattern of abundance ratios between phases and size of clumps is inversely related i.e., the phase that is the least abundant is the heaviest and vice versa.

Fertile weight in a clump

Previous calculations of percentage fertile mass of total thallus weight found comparable results to this study for both species (Fig 2) (Levitt, 1998), even though the methods used in the Levitt study were more precise. As clump size increases with respect to total mass, the proportion of fertile mass increases (Fig 8&9). There is an exponential relationship between the weight of a clump and the proportion of fertile tissue for *G. polycarpa*. (Fig 8). However it must be cautioned that the shape of the exponential curve relies on one point. As clumps were collected randomly, there was no selection for a range of clump sizes. Further collection of data to include a wide range of sizes would further elucidate this relationship. Nevertheless the trend for increasing fertile tissue within a clump as clump size increases illustrates one potential advantage to coalescence if larger clumps are able to allocate more tissue to reproductive effort.

Possible advantages of coalescence

i) *More allocation to reproductive tissue*

If larger clumps are able to allocate more to reproductive tissue, there may be other advantages to coalescing that allow for a larger clump to allocate more resources to reproductive tissue. One is increased desiccation tolerance. The littoral zone, to which *G. polycarpa* and *S. stiriata* are restricted is subject severe desiccation during low tide, as well as wave action, grazing from herbivores and competition for resources such as light and nutrients. Some researchers consider the ability to conserve water as being a primary factor behind the survival of intertidal species (Nienhuis, 1969; Brawley and Johnson, 1991) and importance of growing in a aggregated masses for desiccation tolerance has been demonstrated by other authors (Taylor and Hay, 1994; Levitt and Bolton, 1991). The fact that allocation to reproductive tissue increases as clump weight increases could indicate that growing in a clump confers advantages of individuals growing within the clump, one of which being desiccation tolerance.

Wave action is another factor. A previous study on *G. ploycarpa* at Kommetjie found that plants at exposed sites had less nutritional value and more structural adaptations and gametophytes from sheltered areas had a greater proportion of blades covered in reproductive papillae (Jackelman and Bolton, 1990). The advantage of living in a clump is that peripheral uprights can act as "wave breakers" and as the clump size increases uprights towards the centre are afforded more protection. Whilst protection from wave action has been previously suggested (Maggs and Cheney, 1990), it has not been explicitely demonstrated. In this study there is indirect evidence that coalescence in *G. polycarpa* provides some form of wave protection for fertile uprights, which are typically situated towards the centre of a clump, as proportion of reproductive material increases as clump size increases. However fertile blades of *G. polycarpa* are much larger than medium and smaller blades (Fig 10). Thus it is unlikely that the smaller uprights protect the blades of the fertile uprights. More likely the coalesced holdfast is the area where protection from wave action is the greatest, as thallus tissue can be replaced but an established upright dislodged by wave action cannot reconnect to the substratum. However this remains to be empirically tested and this study did not follow the development of clumps over time.

ii) *Integration and self-thinning*

The proportionate increase in fertile tissue introduces integration. In non-coalescing plants the more dense the population, the greater the demand for resources, hence the self-thinning law was presented to explain how individuals growing in close proximity to each other increase individual performance (in terms of average size) by decreasing density, hence self-thinning. The close proximity of individuals in a clump may reduce the availability of resources (light, nutrients, oxygen) per individual, therefore putting all resources into a few fertile individuals may be a mechanism to reduce the negative effects of crowding.

Working with *Iridaea laminariodes* (Bory) , Martinez and Santelices (1992) established that this coalescing species exhibited none of the characteristics described by density dependant size relations. Size-density interactions can also be described by the Gini coefficient which is a description of size inequality (Weiner and Solbrig, 1984); as density increases size inequality decreases as smaller individuals are outcompeted by larger individuals. However the self-thinning law and density depandant size inequalities do not apply to coalescing red algae. Coalesced clumps of *Iridaea* do not lie along the –3/2 slope of density vs weight, and the density of fronds is greater than would be predicted. Scrosati (1996) found that for clonal plants stand biomass is positively related to frond density (although a clone was defined as the derivatives of a single spore). This provides support for the hypothesis of integration amongst coalesced spores. If spore derivatives within a clump are independent, one would expect that competition between the uprights would result in self-thinning and increasing homogeneity of upright sizes as predicted and described by the self-thinning law and the Gini coefficient. It would be interesting to empirically test if self-thinning occurs in *G. polycarpa* and *S. stiriata*.

Size inequality has been indirectly described in other studies not concerned with coalescence e.g. by Fernández and Menéndez (1991) investigating reproduction In *C. crispus*. However other studies have noticed that coalescing species often display this size inequality of fronds. Clumps of *G. polycarpa* and *S. stiriata* display the marked size inequalities shown for other coalescing species (Martinez and Santelices, 1992; Santelices *et al.*, 1992). Small and medium uprights outnumber fertile uprights for both species ($p<0.0000$) (Fig 7) however fertile uprights are significantly heavier than the combined weight of medium and small uprights for both species (Fig 11). Therefore clumps of *G. polycarpa* and *S. stiriata* display size inequality between fertile uprights and smaller juvenile and infertile uprights. This provides indirect evidence that spores of *G. polycarpa* and *S. stiriata* do coalescence and moreover that there is integration between the coalesced spores.

Further evidence for the inequality of uprights in *G. polycarpa* can be seen in Fig. 4. as the total number of uprights is only slightly correlated to the basal area ($R^2=0.29$), whereas in *S. stiriata* this relationship is stronger ($R^2=0.44$). It could be inferred that the reason for the loose relationship in *G. polycarpa* is due to the fact that uprights are different sized and therefore the relationship between total number of uprights and basal area is not linear.

However it must be noted that a correlation merely shows a pattern and in itself is not an explanation, therefore the suggestions above should be taken as such. Also clumps were collected on a once off basis and the growth patterns of individual clumps was not followed, therefore it is possible that the difference in upright size is merely a function of recruitment, as older uprights senesce, younger ones take their place.

iii) *Near neighbour*

Santelices *et al* suggests (1999) that coalesced in the field is likely to be common due to the clumped nature of spore dispersal. Therefore it is interesting to note that there is a very low occurrence of mixed-phase clumps in the field (data not shown). Out of a sample of 91, there were 6 cases in which phases appeared to coalesce. Although this number is low, it provides further evidence that coalescence does occur in these two species. If tetrasporophytes release both male and female spores then if there are male and females clumps, why is there not a higher percentage of mixed clumps? Although laboratory experiments have managed to coalesce spores from genetically different individuals, it was found that survivorship of the resultant coalesced clump was low (Santelices *et al.*, 1996). It could be that there is some form of control that limits coalescence between the sexes.

From Fig 12 it can be seen that for *G. polycarpa ca* 10% of the first nearest neighbour is the same phase, same species. Overall approximately 50% of the first near neighbour is conspecific, and this decreases for the second nearest neighbour. The data was not collected in quadrats so no assumptions can be made concerning randomness of distribution. It is interesting to note that there is a very low percentage of second nearest neighbour that it the same phase, same species. As the likelihood of the same phase clump being found next to each other is low this suggests that there is some control over which spores coalesce with the other. The percentage of same phase, same species nearest neighbour is higher in *S. stiriata*, more than 40% for the first nearest neighbour and from 10-40% for the second nearest neighbour (Fig 13). One possible explanation may lie in the spreading nature of *S. stiriata* clumps. As mentioned before clumps of *S. stiriata* have horizontal spreading holdfasts and it could be that two clumps next to each other is actually one that has been separated by grazing.

Whatever the case may be for *S. stiriata*, for *G. polycarpa* there is a remarkably low percentage of conspecific first and second near neighbour compared with *S. stiriata*.

One possible reason could be that the spreading holdfast of *S. stiriata* is able to outcompete *G. polycarpa* for substratum space and therefore those clumps of *G. polycarpa* that are able to survive are then distributed amongst *S. stiriata*. It could be that these two species are exploiting different spatial areas. *G. polycarpa* fertile uprights are significantly larger than *S. stiriata* fertile uprights (Fig 11) but S. stiriata has a relatively larger basal area (although not significantly so) (Fig 3). Therefore *S. stiriata* may be exploiting the substratum through a larger, spreading holdfast, and *G. polycarpa* responds by having much larger fertile blades in a smaller area.

If coalescence does occur in *G. polycarpa* and *S. stiriata*, one would have to consider the ecological implications of harvesting. For example, if uprights originating from individual spores integrate within a clump which results in a few fertile individuals surrounded by sterile or juvenile uprights then harvesting, which is commonly done by plucking biomass by hand, is likely to remove the larger fertile uprights. If these uprights are solely responsible for the reproductive effort of the clump, then harvesting is likely to influence fertility. It would be interesting to investigate the impact of harvesting on a clump, i.e., smaller uprights may become fertile if the larger fertile ones are removed.

To conclude *G. polycarpa* and *S. stiriata*, two members of the Gigartinales, appear to demonstrate the characteristics of coalescence that have been described for other species. So called "clumps" of these two species appear to have a coalesced holdfast from which a number of uprights arise. In both species fertile weight is significantly greater than non-fertile weight within a clump (Fig 10). Futhermore fertile uprights are significantly larger than non-fertile and juvenile uprights (Fig 11), this size inequality has been demonstrated for other coalescing species despite the relatively high density of uprights (Martinez and Santelices, 1992). Also the size of the holdfast is loosely correlated to the total number of uprights, there is a better correlation for *S. stiriata* ($R^2 = 0.4$) compared with *G. polycarpa* ($R^2 = 0.3$). This may be due to the morphological structure of *G. polycarpa* which has thin stipes and very broad blades. Lastly, although rare, examples occur where one coalesced holdfast has both male and female uprights, and while this is not evidence of integration between uprights, it does demonstrate that at the least, spore coalescence can result in a coalesced holdfast. Further study lies in laboratory studies which would confirm coalescence in this two species

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