

# Spatial and temporal variation in distribution of *Gelidium canariensis* (Rhodophyta) from natural populations of the Canary Islands

A. Lindgren<sup>1</sup>, N. Bouza<sup>2</sup>, P. Åberg<sup>1</sup> & P. A. Sosa<sup>2\*</sup>

<sup>1</sup> Department of Marine Botany, Göteborg University, Box 461, S-405 30, S-413 19 Göteborg, Sweden
<sup>2</sup> Department of Biology, University of Las Palmas, Campus Universitario Tafira, 35017 Las Palmas de Gran Canaria, Canary Islands, Spain

(\* Author for correspondence: E-mail, pedro.sosa@biologia.ulpgc.es)

Received 12 December 1997; revised 5 June 1998; accepted 7 June 1998

Key words: Canary Islands, Gelidium canariensis, hierarchical sampling, spatial variation, temporal variation

## Abstract

This study was designed to investigate spatial and temporal variation in *Gelidium canariensis* populations at two shores in northern Gran Canaria during two years. Spatial scales ranged from some hundred meters (distance between shores), 10 to 30 m (distance between plots) to less than 3 m (distance between quadrats). *Gelidium* individuals were defined as distinct *Gelidium* clumps. The results show a significant difference in size of clumps between shores, but not on the smaller spatial scales. No significant temporal variation was found. There was no significant temporal or spatial variation in standing crop or density (counts made in quadrats where *Gelidium* was present, rather than counts for the total shore). Sporophytic and gametophytic clumps were also distinguished by identifying reproductive structures in the field. The total proportion of sporophytes was larger than the proportion of gametophytes, but at a smaller scale there could be a shift in dominance. The survival rate of clumps was similar between shores with a mean survival rate of 85%, but there was a significant difference in recruitment between shores. The results indicate a stable population structure.

## Introduction

Gelidium canariensis (Grunow) Seoane Camba is an endemic species of the Canary Islands which grows on wave exposed rocky shores in the lower intertidal. At the lower end of its tidal range it may form smaller beds, but higher on the shore it forms clumps mixed with G. arbuscula and other algae. The tidal range is about 2 m, the part of the G. canariensis population growing higher on the shore being exposed to the air twice a day for about 1 h; wave spray is, however, frequent. Like other Gelidium species, G. canariensis is a perennial with a modular type of construction where erect fronds develop from a basal system of prostate axes that are attached to the substratum by rhizoids. It exhibits the triphasic/polysiphonian life cycle with isomorphic generations, but can also expand vegetatively by growth of new fronds from the prostrate

axes. Also like other *Gelidium* species, sporophytes of *G. canariensis* have been reported as more abundant than female gametophytes based on the presence of reproductive structures (Santelices, 1988; Betancort-Villalba & Gonzalez-Henriquez, 1991; Sosa & Garcia-Reina, 1993). The reproductive structure of male gametophytes is impossible to distinguish in the field.

The aim of this study was to investigate patterns of spatial and temporal variation in populations of *G. canariensis*. The general hypothesis was that variation in population characters of *G. canariensis* should differ at different spatial scales and/or in different years. To distinguish genets (genetic individuals, Kays & Harper, 1974) is often a problem when studying the ecology of algae (e.g. Åberg, 1989; Lazo et al., 1989; Santos, 1994; Lindgren & Åberg, 1996). For plants each genet is usually composed of modules which for *Gelidium* are individual fronds. There is thus two levels of population structure in plant communities, the structure of genets and the structure of modules within genets (Harper, 1977). Whether a specific level or both should be studied depends on the hypotheses tested in the experiment. In the present study, which is part of a larger study of the demography and population genetics of algal populations, we ask questions about genets and to study the frond dynamics alone is thus not relevant here. For that reason it was designed to study genets which have been defined as distinct individual clumps. Whether these clumps are genets or not will be tested in future studies. Two indications that clumps could be genets are that we never found cystocarps and tetrasporangial sori on fronds from the same clump and that no difference in isozyme banding patterns has been found among fronds from the same clump (P.A.Sosa, unpublished results). It is known that sporeling coalescence may occur and that separate genets of the same stage may grow together, but our methods so far have been unable to distinguish this. This study is based on an analysis of the structure of clumps which in many cases porbably are genets; if not, they can be regarded as distinct patches of fronds.

## Materials and methods

## Study area

This study was performed during July 1996 and 1997 at two rocky shores separated by a sandy beach about 450 m long, at Bocabarranco, northern Gran Canaria, Canary Islands. The investigation was performed in the upper part of the *G. canariensis* belt.

## Experimental design

At the two shores, a total of 168 clumps were distinguished, scraped off and put in separate plastic bags and brought back to the laboratory, where maximum circumference (C) and maximum length (L) were measured. Maximum circumference was achieved by laying all fronds from one clump parallel and the maximum circumference will then be at the thickest part of the bundle (cf Åberg, 1990). Dry weight (DW) was measured after drying the clumps to constant weight at 60 °C. To estimate biomass from clump size a regression between  $LC^2$  and DW was done. If there is a strong positive correlation, measuring L and C in the field can be used to estimate the size of clumps (Åberg, 1990).

The spatial variation in clump size and abundance of G. canariensis was investigated on three spatial scales using a hierarchical sampling design. The scales were 2 shores (about 450 m apart), 2 plots within each shore (20-50 m apart) and 5 quadrats within each plot (< 3 m apart). The quadrats  $(0.25 \times 0.25 \text{ m})$  were placed randomly where G. canariensis was present to obtain a large number of clumps rather than an examination of its presence over the whole shore. The study was repeated with a set of new quadrats after one year. All clumps within a quadrat were characterized by maximum length and circumference and, if at least one frond within a clump was reproductive, the life cycle stage (i.e. sporophyte, female gametophyte) was noted. Since quadrats were only placed where G. canariensis was present, the values for standing crop dry weight and density are a measure of biomass and abundance, respectively, in G. canariensis stands, not for a whole shore. To illustrate the size distribution, the clumps were divided into size classes. Since the growth of the genets can be treated as an exponential process (Harper, 1977), the width of the size classes was chosen to be equally large on a logarithmic scale. The survival rate was investigated by monitoring mapped clumps through time and recruitment by noting new clumps within a quadrat.

### Statistical analysis

Spatial and temporal variability were analyzed using analysis of variance (ANOVA). The factor Year was chosen and consequently considered as fixed. The factors Shore, Plot and Quadrats were chosen randomly. In the analysis of the life cycle stages, Stages was also considered as fixed factor. The assumption of homogeneity of variances was tested with Cochran's test (Winer et al., 1991). When variances were heterogeneous, the data were  $\log_e$ - or  $\log_e (x + 1)$  transformed. Post hoc pooling of mean values for quadrats was applied as described in Underwood (1997) and in such cases only the ANOVA table after pooling is given.

## Results

A significant relationship was found between DW and  $LC^2$ , (p < 0.01), (Figure 1) and  $LC^2$  explained 95% of the variation in dry weight. The predictive equation was  $DW = 0.0096LC^2 + 0.45$  (Figure 1).



*Figure 1.* Regression of the relationship between dry weight and  $LC^2$ .

*Table 1.* ANOVA of clumps dry weight after post hoc pooling the factors Plot (Shore), Year \* Plot (Shore) and Year \* Quadrat (Plot, Shore). Data log<sub>e</sub>-transformed to meet assumptions of homogeneity of variances

Source	df	MS	F	Р
Year	1	4.20	2.29	> 0.35
Shore	1	20.01	18.93	< 0.001
Year * Shore	1	1.83	2.62	> 0.10
Quadrat (Plot, Shore)	28	1.06	1.52	> 0.05
Residual	88	0.70		
Cochran's C-test	40,2	0.10		> 0.05

## Dry weight per clump

A significant difference in mean dry weight per clump was found between shores (Table 1), mean clump dry weight being 5.5 g at shore 1 and 2.4 g at shore 2. There was no significant temporal or spatial variation at any of the other scales. Dividing the clumps into size classes showed that a large proportion of the population belonged to size classes 1 and 2 (Figure 2). Within each shore the size distribution is similar in 1996 and 1997.



*Figure 2.* Size frequency distribution of clumps at the two shores in 1996 (white columns) and 1997 (striped columns). Class 1, < 1.16 g; Class 2, < 2.32 g; Class 3, < 3.49 g; Class 4: < 4.66 g; Class 5, > 4.66 g.

*Table 2.* ANOVA of standing crop dry weight within *G. canariensis* stands. Data log<sub>e</sub>-transformed to meet assumptions of homogeneity of variances

Source	df	MS	F	Р
Year	1	1.18	5.76	> 0.25
Shore	1	0.15	1.41	> 0.35
Year * Shore	1	0.20	0.36	> 0.60
Plot (Shore)	2	0.11	0.48	> 0.60
Year * Plot (Shore)	2	0.57	2.63	> 0.05
Residual	32	0.22		
Cochran's C-test	8,4	0.29		> 0.05

*Table 3.* ANOVA of density (clumps  $m^{-2}$ ) within *G. canariensis* stands

Source	df	MS	F	Р
Year	1	2.5	0.21	> 0.70
Shore	1	220.9	4.42	> 0.15
Year * Shore	1	12.1	2.33	> 0.25
Plot (Shore)	2	50.0	1.60	> 0.20
Year * (Plot, Shore)	2	5.2	0.17	> 0.80
Residual	32	31.2		
Cochran's C-test	8,4	0.27		> 0.05



*Figure 3.* Proportion of gametophytes (white columns), sporophytes (black columns) and vegetative clumps (striped columns) in 1996 and 1997. S = shore.

## Standing crop and density

For standing crop dry weight no significant differences were found at any level (Table 2). Mean standing crop at shore 1 was 960 g m<sup>2</sup> and 912 g m<sup>2</sup> at shore 2. There were no significant differences in densities found at any level (Table 3). The mean number of clumps at shore 1 was 136 clumps m<sup>2</sup> and at shore 2 was 211 clumps m<sup>2</sup>.

## Life cycle stages

The proportion of vegetative clumps was much higher in 1997 (Figure 3). This is probably due to the difficult sampling circumstances in 1997, which hindered careful examination of the plants. For that reason we

Table 4. ANOVA of the proportion of female gametophytes and sporophytes in 1996. Data  $log_e$ (x + 1)-transformed to meet assumptions of homogeneity of variances

Source	df	MS	F	Р
Stage	1	0.23	2.7	> 0.30
Shore	1	0.10	0.69	> 0.45
Stage * Shore	1	0.08	0.35	> 0.60
Plot (Shore)	2	0.14	4.35	< 0.05
Stage * Plot (Shore)	2	0.24	7.34	< 0.005
Residual	24	0.03		
Cochran's C-test	8,3	0.42		> 0.05



*Figure 4.* Proportion of gametophytes (white columns) and sporophytes (black columns) in 1996 at plots within shores. S = shore.

only tested the spatial variation in the proportion of life cycle stages for the year 1996. The total proportion of fertile clumps in 1996 was 0. 69 at shore 1 and 0.39 at shore 2 (Figure 3). The significant interaction between Stage and Plot within Shores in Table 4 shows that on a small scale there can be either a dominance of sporophytes or female gametophytes (Table 4, Figure 4). The overall mean for both shores was 37% sporophytes and 15% female gametophytes but this difference was not statistically significant (Table 4).

## Survival and recruitment

There was no significant difference in the survival rate of clumps between the shores (Table 5), and the mean

*Table 5.* ANOVA of survival rate of *G. canariensis* clumps

Source	df	MS	F	Р
Shore Plot (Shore)	1 2 20	0.10 0.04	2.76 1.06	> 0.20 > 0.35
Cochran's C-test	4,5	0.04		> 0.05

value was 85%. There was a significant difference in recruitment between the shores (Table 6) and the mean number of new clumps was 1 at shore 1 and 3 at shore 2.

## Discussion

The strong positive correlation between DW and  $LC^2$ shows that this non-destructive method to estimate the size of clumps in the field works well for G. canariensis. The results indicate that G. canariensis has a stable population structure. There were no significant differences between the years in any of the variables investigated. There was an initial difference between the shores in size structure, the clumps being much larger at shore 1, and this was maintained in the following year. The relatively high survival rate of the clumps also supports this conclusion. However, we do not know anything about the population dynamics within a year, such as the percentage of recruits which fail to survive, frond loss etc. Still, the overall result is that the general population structure remains the same from one year to another. The difference in population structure between the shores could be due to differences in the exposure to wave action. Limpets are harvested at both shores, but to what extent and how often is unknown. Differences in harvesting could give rise to differences in grazing pressure, which in turn could affect the growth of G. canariensis. Since we defined individuals as clumps, it is difficult to compare the individual dry mass and density values with other species of Gelidium, since most studies have been performed on fronds. The standing crop for G. canariensis was about 1000 g m<sup>2</sup> in this study. Standing stock values normally found in commercial beds are reported to range from a some hundred grams to 1.5 kg m<sup>2</sup> (Santelices, 1988). Taking these values into

consideration, *G. canariensis* seems to have quite a high standing crop.

Considering the number of tetrasporangial and carposporangial plants there was a low recruitment of new clumps, mean number of recruits being 1 and 3 for the two shores. However, we have so far no data on temporal variation within or between years. That is, new clumps may have appeared and disappeared without our knowledge within the year we studied and the recruitment may be higher another year. Factors affecting the recruitment and survival of juvenile stages could be the same as those suggested for affecting the growth. Both wave action and grazing have been reported as mortality factors for spores and juvenile stages of Gelidium species (Santelices, 1988). The large number of spores produced in other Gelidium species as well as other perennial red algae seems to be excessive with respect to the amount necessary for maintenance of the population (Bhattacharya, 1985). However, released spores may have a very high mortality. Estimates of the probability of transition from tetraspores to recruits of Gelidium sesquipedale are as low as  $4.7 \times 10^{-5}$  (Santos & Duarte, 1996). Better understanding of the recruitment of G. canariensis requires studies using both larger and smaller temporal scales.

Investigation of the life cycle stages indicates that a large part of the population consisted of vegetative clumps (as have been reported for many red algae e.g. May, 1986; Santelices, 1990; De Wreede & Green, 1990). In 1996 the proportion fertile clumps varied from 0.69 to 0.39 between shores. In 1997 the proportions was about 0.10. The lower proportion in 1997 is probably due to the much more difficult sampling conditions, with high waves and the lowest tide late in the evening and hence decreasing light. In 1996, at the larger spatial scales (500 m) there was a dominance of sporophytes, but at smaller scales (20-50 m) either gametophytes or sporophytes could be dominant (Figure 4). The proportion of gametophytes was in fact even higher, since male gametophytes were not included. These results indicate the importance of including small scales in studies of life cycle ratios of G. canariensis. Factors explaining the pattern may also be ones varying on a small scale; it is known that small-scale variation in light or temperature can be important factors influencing fertility (Santelices, 1988). The relative importance of sexual reproduction could also be different depending on the scale. The opposite situation was found for the other variables, where there was little variation at the smaller spatial scales, which

is usually where the largest variation occurs in marine environments (Lindegardh et al., 1995; Åberg & Pavia, 1997). Additional demographic studies should reveal more about the structure and dynamics of *G. canariensis* populations.

#### Acknowledgements

We thank Per Nilsson at Tjärnö Marine Biological Laboratory for statistical advice. This study is part of the BIOGAP (Biodiversity and Genetics of Algal Populations) project MAS 3-CT 95-0019. European Union, Brussels.

#### References

- Åberg P (1989) Distinguishing between genetic individuals in *As*cophyllum nodosum populations on the Swedish west coast. Br. phycol. J. 24: 183–190.
- Åberg P (1990) Measuring size and choosing category size for a transition matrix study of the seaweed *Ascophyllum nodosum*. Mar. Ecol. Progr. Ser. 63: 281–287.
- Åberg P, Pavia H (1997) Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. Mar. Ecol. Progr. Ser. 158: 111–119.
- Betancort-Villalba MJ, Gonzalez-Henriquez MN (1991) Estudio preliminar sobre la biologia de las poblaciones de *Gelidium canariensis* (Grunow) Seoane en Gran Canaria. Acta Botanica Malacitana 16: 51–58.
- Bhattacharya D (1985) The demography of fronds of *Chondrus* crispus Stackhouse. J. exp. mar. Biol. Ecol. 91: 217–231.
- De Wreede RE, Green LG (1990) Patterns of gemetophyte dominance of *Iridaea splendens* (Rhodophyta) in Vancouver Harbour, Vancouver, British Columbia, Canada. J. appl. Phycol. 2: 27–34.

- Harper JL (1977) Population Biology of Plants. Academic Press, London: 892 pp. Kays S, Harper JL (1974) The regulation of plant and tiller density in a grass sward. J. Ecol. 62: 97–105.
- Kays S, Harper JL (1974) The regulation of plant and tiller density in grass sward. J. Ecol. 62: 97–105.
- Lazo ML, Greenwell M, McLachlan J (1989) Population structure of *Chondrus crispus* Stackhouse (Gigartinaceae, Rhodophyta) along the coast of Prince Edward Island, Canada: distribution of gametophytic and sporophytic fronds. J. exp. mar. Biol. Ecol. 12: 45–58.
- Lindegardh M, André C, Jonsson PR (1995) Analysis of the spatial variability in abundance and age structure of two infaunal bivalves, *Cerastoderma edule* and *C. lamarcki*, using hierarchical sampling programs. Mar. Ecol. Progr. Ser. 116: 85–97.
- Lindgren A, Åberg P (1996) Proportion of life cycle stages of *Chondrus crispus* and its population structure: a comparison between a marine and an estuarine environment. Bot. mar. 39: 263–268.
- May G (1986) Life history variations in a predominantly gametophytic population of *Iridaea cordata* (Gigartinaceae, Rhodophyta). J. Phycol. 22: 448–455.
- Santelices B (1988) Synopsis of biological data on the seaweed genera *Gelidium* and *Pterocladia* (Rhodophyta) FAO Fisheries Synopsis 145.
- Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanogr. Mar. Biol. Annu. Rev. 28: 177–276.
- Santos R (1994) Frond dynamics of the commercial seaweed *Gelid-ium sesquipedale*: effects of size and of frond history. Mar. Ecol. Progr. Ser. 107: 295–305.
- Santos R, Duarte P (1996) Fecundity, spore recruitment and size in *Gelidium sesquipedale* (Gelidiales, Rhodophyta). Hydrobiologia 326/327: 223–228.
- Sosa PA, Garcia-Reina G (1993) Genetic variability of *Gelidium canariensis* (Rhodophyta) determined by isozyme electrophoresis. J. Phycol. 29: 118–124.
- Underwood AJ (1997) Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge, 504 pp.
- Winer BJ, Brown DR, Michels KM (1991) Statistical Principles in Experimental Design. McGraw-Hill, New York, 1057 pp.