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**POPULATION ECOLOGY OF THE COMMERCIAL SEAWEED, GELIDIUM
SESQUIPEDALE: BIOLOGICAL INPUT FOR RESOURCE MANAGEMENT**

by

Rui Orlando Pimenta Santos

Submitted in partial fulfillment of the requirements for the
degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia, Canada

April 1993

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ABSTRACT

Gelidium sesquipedale harvesting for agar along coastal Portugal is managed with little scientific advice, despite decreasing annual yields since the 1970's. This work provides a resource science bases for management of the resource.

Multivariate analyses of the distribution of dominant macrophytes (G. sesquipedale, Saccorhiza polyschides and Laminaria ochroleuca) in relation to local abiotic conditions (depth, sediment loading and substrate topography) in an important commercial bed, suggest that steep slopes and reduced sediment loading favour G. sesquipedale development. By contrast, S. polyschides dominated shallow zones with low slope surfaces and high sediment loading. L. ochroleuca was not significantly correlated to G. sesquipedale distribution, but its interaction with depth suggests that at greater depths (>18 m) it dominates G. sesquipedale.

A tagging experiment along with a 15 month sampling program in a typical, dense, monospecific G. sesquipedale stand, showed that storms and commercial harvesting play a significant role in the regulation of species population dynamics. These disturbances caused high mortality and breakage of larger fronds during summer and fall, thereby keeping intra-specific competition at low levels. During such periods, smaller frond elongation rate was high and mortality low. A pulse in vegetative development of new fronds follows these disturbances, and is probably induced by canopy loss. During spring and early summer, the opposite pattern was found due to faster growth and lower mortality of larger fronds; extensive density-dependent self-thinning was not observed. Annual yields could be enhanced by delaying the season opening.

Demographic simulations using population projection matrix models of machine cutting, recently introduced in Spain, vs. hand-plucking, currently done in Portugal, results in higher population growth rates for cutting than plucking. Assuming the same harvest efficiency, the number of fronds in each size class available the next harvest season will be higher when cut than plucked.

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GENERAL INTRODUCTION

The red alga Gelidium sesquipedale (Clem.) Born. et Thur. occurs along the Northeast Atlantic subtidal (Fig. 1), from England south coast (Dixon and Irvine, 1977) to Senegal (Lawson and John, 1977). Its high quality agar drives its commercial harvest along the coasts of France, Spain, Portugal and Morocco (Santos, R., J. M. Gorostiaga, R. Armisen, J. M. Salinas and J. C. Oliveira, unpublished manuscript; see Appendix 1). Considering its economic importance, insufficient research has been done on both the fishery and the population ecology to provide a sound scientific basis for resource management. In fact, the poor understanding of the intrinsic mechanisms that regulate population dynamics and their interactions with the environment is prevalent in seaweeds (Chapman, 1986a), particularly those occurring in the subtidal (Schiel and Foster, 1986).

As McLachlan (1982), Caddy and Fisher (1984), and Doty et al. (1986) have pointed out, despite numerous scientific articles dealing with the biology and ecology of commercial species, there are few cases of practical information used by managers of natural seaweed resources. Most of resource science has focused on the mapping and evaluation of commercial stands (Michanek, 1975; Naylor, 1976; McHugh and Lanier, 1983). The pioneer work of Baardseth and Grenager (1961) and Baardseth (1970) tackled the methodological problems for seaweed standing stock assessment.

Perhaps the two best examples of seaweed resource management are those of the eastern Canadian fisheries (mainly Chondrus crispus and Ascophyllum nodosum) and of Macrocystis spp off the coast of California. In Canada, regulations has been developed, implemented and amended and both resource development and economic advise have been given based on ecological impact studies of harvest and on the species biology (Pringle and Sharp, 1986, 1990; Sharp, 1986). In this country an ideal situation occurs, where resource science is carried out within a research wing of the agency that has the



Fig. 1. Gelidium sesquipedale geographical distribution

mandate to manage the resource (Pringle, 1986). This is not a common situation. For example in Chile, considerable resource science has been done (Santelices, 1989), but structural and socio-economic constraints limit resource management (Vasquez, 1993).

In California, most Macrocystis spp commercial beds are leased to private entrepreneurs for periods up to 15 years, by a governmental agency that manages the resource (North, 1986). Commercial beds, standing crops and harvest yields have been monitored since 1918 (North, 1986). Many ecological studies of recruitment, survivorship and community interactions have produced results relevant to the ecological effects of harvesting (Barilotti and Zertuche-González, 1990). Much of this work has been funded by harvest companies.

Population modeling is a powerful tool to address specific resource management questions. However, only a few attempts have been made following the pioneer work of Seip (1980), who developed a logistic model to evaluate harvesting strategies of A. nodosum in Norway. Silverthorne (1977) developed a production model of Gelidium robustum harvest, integrating population data and economic parameters of the industry, to establish the optimal production from the resource. Two applications of projection matrix models in the assessment of harvest strategies were by Ang (1987) and Santos (Chapter V). Matrix models to model the demography of seaweed species were first used by De Wreede (1986).

The current work increases our knowledge of the resource science of G. sesquipedale and its application to resource management. It is part of a wider research program on the agar industry, sponsored by the Ministry of Industry, at INETI (National Institute for Engineering and Industrial Technology, formerly LNETI), Lisboa, Portugal. Chapter I (Santos and Duarte, 1991) brings together the scattered information on both the species harvested and the colloid extraction industry in Portugal, which provides the background for the current study. The stock status, the extractors, and the resource management is

discussed. Portugal supports the third largest harvest of agarophytes and is the fifth largest agar producer, but G. sesquipedale annual yields in most beds and total agar production have declined since the early 1970's. Insufficient resource science for management is one limiting factor in the quest for sustainable yields. A resource management structure does exist but management has been done largely without scientific input.

The main G. sesquipedale commercial bed of harvest zone nº 5 (Fig. 1.1), was chosen for this study because of its economic importance [its annual yield represents around one quarter of the total national harvest (Fig. 1.3)], and its proximity to INETL. As there was no information on this subtidal community, a numerical study of the distribution of the dominant macrophytes in relation to local abiotic conditions was done (Chapter II; Santos, 1993a). Two questions were addressed: 1) is the distribution of G. sesquipedale correlated with kelp abundance, depth, sediment loading and/or substrate topography, and 2) what is the strength of the relationship between G. sesquipedale distribution and these factors? Hypotheses on the causal mechanisms for the significant relationships are presented.

Chapter II provides both a general knowledge of the system under study, and the information required to choose an experimental site to investigate the population dynamics of G. sesquipedale. The demographic processes regulating the population dynamics were assessed in Chapter III. The influence of season and frond length on the vital rates of growth (length increase), breakage (length decrease) and mortality were analysed. As well, the effects of frond history on these vital rates, i. e. the effects of frond growth, breakage or the presence of epiphytes on the next time-step's frond growth, breakage and mortality were studied. The influence of an individual's history on its fate is important in the validation of matrix population models such as the one presented in Chapter V, because the model assumes an individual's fate depends only upon its state at time t , and not upon its state at any previous point in time.

The dynamics of a G. sesquipedale commercial stand and the role of physical disturbances such as harvest and storms, were studied in Chapter IV. Seasonal changes of mean frond weight, mean frond length, biomass and density are shown as well as those of frond length and weight structures, quantified by the Gini coefficient (G), the coefficient of variation (CV), and the skewness coefficient (g_1). These are interpreted in relation to the demographic rates (frond growth, breakage, mortality and recruitment) that determine population parameters' variability (Chapter III). The performance of the coefficients was discussed. G. sesquipedale weight/length allometry, "the differential growth of parts or metrics of an organism" (Gould, 1966), was also investigated.

Two empirical relationships quantified by the Gini coefficient, frond density/frond biomass, and mean frond weight/weight distribution inequality were also tested in G. sesquipedale to assess the occurrence and effects of density-dependent processes (Chapter IV). The self-thinning rule or $-3/2$ power law (Yoda et. al, 1963; Weller, 1987) states that the relationship between biomass and density in crowded monospecific plant stands, forms a thinning line beyond which any weight increase is accompanied by a density decrease due to mortality of smaller plants. Similarly, as self-thinning progresses, mean plant weight increases and plant weight inequality (Gini coefficient) decreases (Weiner and Thomas, 1986). A conceptual model for the functioning of the G. sesquipedale populations is proposed.

Chapter V applies the population biology results to a specific resource management question. Cutting machines were recently introduced in Spain to harvest G. sesquipedale (Appendix 1). The impact of this harvest method on population recovery was unknown. A demographic simulation of two alternative harvest techniques using a population projection matrix model is presented. The recovery of a G. sesquipedale population

harvested by plucking, as it is currently done in Portugal (Chapter I), is compared with the new method of machine cutting (Santos, 1993b¹).

Finally, an overview of the G. sesquipedale industry and resource management in the Northeast Atlantic is presented in Appendix 1 (Santos, R., J. M. Gorostiaga, R. Armisén, J. M. Salinas and J. C. Oliveira, unpublished manuscript). This work integrates and updates the industrial and fisheries information in the countries of commercial importance; France, Spain, Portugal and Morocco. We conclude the G. sesquipedale agar industry is in a critical state. We recommend that harvest methods must improve to provide high quality raw material for the extractors. However, research has to be carried out concurrently to prevent overexploitation of populations. Biological data such as those presented here should be integrated with information on harvest yields and effort, to permit development of harvest strategies maximizing sustainable harvest yields. Population models can be a powerful tool to address specific problems such as harvest season, harvesting technology, etc., by projecting population structures. Longer time series of data and more information on density-dependent and historical effects on vital rates are however required.

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CHAPTER I

MARINE PLANT HARVEST IN PORTUGAL

1.1 Introduction

Quantitative information on marine plant harvests has been identified as an important contribution to effective assessment and management of commercial resources (Caddy & Fisher, 1984). Despite its importance, little has been published on the Portuguese industry. However, marine plants have been gathered for fertilizer along the north coast of Portugal since long before the 14th century, when contemporary documents referred to it as an ancient activity (Veiga de Oliveira *et al.*, 1975). These activities continue to the present and can be considered the first phase of resource exploitation. It was followed during this century by a wider scale industrial exploitation for colloid extraction. Palminha (1971) describes the seaweed industry on the Portuguese mainland and the Azores Islands. He records the most important beds and harvest techniques, identifies the extractors and presents designs for harvest impact experiments.

The marine plant harvest in Portugal has never been assessed quantitatively. The present study brings together the available information with the dual objective of both increasing understanding of resource use and laying the foundation for resource management based on resource science. The gathering of marine plants for fertilizer and the seaweed based colloid industry is described and the status of the stocks, the extractors and the resource management is discussed.

1.2 Methods

Industrial data were located in several different sources and were sometimes contradictory or difficult to interpret. Most of the data on production of seaweeds and agar were obtained from two sources: "Junta Central das Casas dos Pescadores" reports which

were published yearly from 1965 to 1974, and "Instituto Nacional de Estatística" reports, published since 1969. Other sources were consulted as well. Manuscripts of the late F. Palminha, who studied the commercial marine plants of Portugal for more than 30 years, were examined, along with several internal reports of the institutions for which he worked. Internal reports from the institution that manages the seaweed resource, "Direcção Geral das Pescas" (DGP), were another important source of information, as were personal communications with DGP staff.

1.3 Results and Discussion

1.3.1 Marine plants for fertilizer

The seaweeds washed ashore along the north coast, mainly Laminaria hyperborea, L. ochroleuca, Saccorhiza polyschides, Fucus vesiculosus, Codium tomentosum, Palmaria palmata, Chondrus crispus and Gelidium sesquipedale, collectively called "sargaço", have been gathered and sold for fertilizer since at least 1308 when their exploitation was first regulated by King D. Dinis (Veiga de Oliveira *et al.*, 1975). A mixture of aquatic vascular plants, mainly Potamogeton pectinatus, Ruppia cirrhosa and Zostera noltii, and algae, including Gracilaria verrucosa, Ulva sp., Enteromorpha sp. and Lola lubrica, collectively called "moliço", has been intensively harvested at Ria de Aveiro. It is collected with handrakes, from boats designed especially for this activity.

Data on both yields and economic importance of both harvests are scarce. The total amount of sargaço collected in 1891 between Rio Minho and Rio Cávado (Zone 1 of Fig. 1.1), was estimated to have a value, corrected for inflation, of 80 million escudos, about US \$500,000 (Baldaque da Silva, 1891 *in* Veiga de Oliveira *et al.*, 1975). The moliço sold in one year from Ria de Aveiro had an estimated value, corrected for inflation, of 480 million escudos, about US \$3,000,000 (Regalla da Fonseca, 1888 *in* Veiga de Oliveira *et al.*, 1975).

Silva (unpublished manuscript) using records of boat number, estimated the yield of molíço for selected years between 1883 and 1967. The yields (always above 150,000 t wet weight) and harvest value were of local importance. Some people harvested full time. The heavy harvest pressure led to early regulation of the activity; harvesters and boats were licensed, an open harvest season identified, and harvest tools and prices specified. The molíço annual crop has decreased since the early 1890's. According to Silva (*in verb.*), the harvesters gradually abandoned the fishery for better paying, and less physically demanding, positions. As well, there has been a shift to increased use of chemical fertilizers. The harvest of molíço and its use as manure is currently being encouraged by municipalities around Ria de Aveiro. In 1985, 1800 t (wet weight) of molíço were harvested. The total amount paid to harvesters was 2.6 million escudos, about US\$17,000. The collection of sargaço, like molíço, lost its economic importance in the last century. Today sargaço is collected on a small scale by some farmers of the north coast, to fertilize poor, sandy soils.

1.3.2 Colloid industry

History and legal regulations

During World War II, the shortage of Asian agar in Europe encouraged the search for colloid producing species in Portugal. Experimental colloid extractions of Portuguese red seaweeds were done by Oliveira (1947). The agarophyte Gelidium sesquipedale was initially collected in the early 1940's at low tide along the continental coast, and then exported. The first Portuguese based agar extraction factory was built in 1947. The high abundance of the agarophyte Pterocladia capillacea on the Azores Islands also indicated commercial potential (Palminha, 1971). By 1971 there were six Portuguese based agar factories, two of these on the Azores. Presently only four are operating, including the two on the Azores.

The export of agarophytes was prohibited in the 1960's when a synthesis on the agar industry was commissioned by the Ministry of Economy, in order to establish a sound basis for the development and regulation of the industry. Regulations were first established in 1964, creating a harvest season and licensing policy. All species could be plucked from the substrate, from March to December, except for members of the Laminariaceae and Gigartinales, which could only be cut. Seaweeds washed ashore could be collected year round. It should be noted that with the recent integration of Portugal into the European Economic Community open market, the export of seaweeds is again possible.

Harvesting by divers was regulated in 1967. Harvest zones were defined to aid in the control of harvest effort. Since then both the number of boats and the number of harvesters have been regulated. There are six harvest zones along the continental coast (Fig. 1.1), nine on the Azores, each representing an island. G. sesquipedale and P. capillacea are hand harvested mainly by boat-based hookah divers. Each boat can have up to five divers working at a time. The divers collect the seaweeds for six to seven hours per day. The harvest is placed in a basket of about 60 kg capacity which is winched into the boat. Each diver can harvest more than one metric ton per day (wet weight).

Small amounts of G. sesquipedale and P. capillacea are gathered by either handraking from small boats or by collecting beached storm toss at low tides. All harvests are sun dried and sold to licensed concentrators who are restricted to buying in a single harvest zone. The concentrators then resell the crop to extractors. Fishermen harvesting beds close to factories sell the wet crop directly to factory representatives. Harvest management is the responsibility of DGP ("Direcção Geral das Pescas"). The start of the harvest season is decided by their personnel together with the harvesters. The decision is based on a subjective assessment of biomass by underwater observers. The harvest generally begins in July and ends in December. Storm toss gathering occurs year round.

Considerable amounts of carrageenophytes, such as C. crispus and Mastocarpus stellatus, are also harvested along the continental coast (Fig. 1.2), mainly from Zones 1 and 2. Fronds are plucked from the intertidal during summer, sun dried, sold to concentrators and then exported. Small amounts of the agarophyte Gracilaria verrucosa are periodically collected in certain estuaries and sheltered bays. However, the extractors recently stopped processing this species.

Gelidium sesquipedale landings

Based on the G. sesquipedale total landings (Fig. 1.3), it appears the harvest was fully developed by the late 1960's. The highest values occurred after 1966, when harvesting by divers was introduced. There was a constant decline in annual landings through the 1970's, followed by an increase in the 1980's. To interpret resource abundance variation based on a time series of annual yields, data on harvest effort, i.e. number of boats, number of divers or diving time, is necessary (Ricker, 1975). Effort data were not formerly recorded with harvest yield. Recently DGP personnel have begun demanding the completion of logbooks for each boat, which will yield daily information on the number of harvesters, diving time, harvest yields and sites harvested. Also, social and economic factors influence harvest effort levels, and therefore must be considered when interpreting variation in landings. Presently, the economic return to harvesters seems adequate to sustain their activity. An average season has 30 to 50 diving days, which will yield a diver/harvester about US \$13,000.

Annual price paid to harvesters per kg of dried seaweed has generally been higher since 1973, due to a change in the economy after the 1974 revolution. The price increase of 1974 was in part an attempt to stimulate effort and halt the trend of decreasing landings.

Figure 1.3 shows the annual landings of G. sesquipedale in each harvest zone. The low yields of Zones 1 and 2 do not necessarily represent low abundances, but instead reflect a low harvest effort. This region has little natural shelter and sea conditions are generally poor. Zones 3 and 6 show increasing yields in recent years (Fig. 1.3). This trend in Zone 6 is due to recent exploitation of virgin beds (in verb. from DGP personnel). The landing decline observed in Zone 4 may be due to recruitment overharvesting. Anecdotal evidence indicates a soft substrate in this zone. It disintegrates when plants are plucked (in verb., DGP), causing high mortalities of prerecruits and holdfasts, and slower bed recovery. The Zone 5 yield curve, shows the common pattern of an exploited resource: a fast increase while the harvest is developing, followed by a strong decrease which is generally a result of overexploitation.

Pterocladia capillacea landings.

The harvest yields of P. capillacea species on the Azores Islands show a steady decrease to the low levels of the 1980's (Fig. 1.4). Except for S. Miguel Island, where they have remained relatively stable, the yields of each island are low through this decade (Fig. 1.4). Flores, Terceira and S. Miguel are the islands where the landings have been consistently higher and presumably where the standing stocks were originally higher.

The present low harvest yields seem to be due to a social rather than an overharvesting phenomena. There has been considerable emigration of young people, thus it is now difficult to get qualified diver harvesters. The S. Miguel yields are more stable because this is the biggest island, and there is more shore based harvesting during low tide periods. Another factor which discourages potential harvesters is the low prices paid for P. capillacea on the islands, which is lower than that paid for G. sesquipedale on the mainland.

Agar extractors

Portuguese agarophyte yields have never exceeded the production capacity of the national agar industry, which Palminha (1971) estimated to be 1,620 t of agar per year. This production potential was incorrectly interpreted as actual production by both Michanek (1975) and Santelices (1988). Each reported Portugal as the second largest producer of agar in the world. In fact, agar production peaked in 1973 at only 806 tons (Fig. 1.5). The decrease in agar production (Fig. 1.5) from the early 1970's to the early 1980's follows the decrease in total catch of agarophytes in Portugal (Figs. 1.3 and 1.4). Even though G. sesquipedale yields recovered in the 1980's, the strong fall in P. capillacea yields prevented a marked increase in total agar production. The importation of raw material was only important for a few years around 1980, to compensate for low a national harvest during that period.

Around 60% of the national agar production is exported to Japan (1985 to 1989 average: 179.0 t), USSR (35.5 t), West Germany (31.1 t), Italy (29.3 t) and Spain (22.7 t). The extractors annual economic return from exportation has decreased in the 1980's in concert with the decline in the crop. Data on the commercial yields of agar per dry weight of plants are not available separately for the two species. However, data on total agar production (Fig. 1.5) and on the use of plants by extractors allow a calculation of the agar yields. The yield varies between 7% and 22%, with an overall average of 15%. This is below the 17% to 25% commercial yields considered normal by Whyte and Englar (1981). According to Ana Lemos (*in verb.*), the G. sesquipedale agar yield obtained by one extractor has been around 20%, but is steadily declining in recent years.

1.4 Conclusions

The requirements for a successful marine plant industry (Pringle *et al.* 1989), are met in Portugal. There are sufficient natural resources, and the harvesting techniques, the labour force, the weather conditions and the harvesters remuneration seem adequate to sustain the activity. There is also a government agency with a mandate to manage the marine plant resource (DGP). With approximately 2500 tons (dry weight) of Gelidium and Pterocladia harvested annually and production of 350 t of agar, Portugal has the third largest annual harvest of these species, after Spain with 4000-5500 t and Japan with 3000-3300 t (Santelices, 1988). Portugal also ranks fifth in the production of agar from Gelidium/Pterocladia after Spain (890 t), Japan (568 t), South Korea (600 t) and Morocco (550 t) (Armisen & Galatas, 1987). Note that the Spanish harvest is largely storm-tossed material, and thus the weight is inflated due to impurities.

Concern about the future of the colloid industry has been expressed by the extractors, particularly with regard to the sustainability of the beds. Also, the integration of Portugal into the EEC common market will make it possible for large multinationals to outcompete the local extractors for national raw material. This study suggests that the concerns of the extractors are well justified. In fact, the total agarophyte landings (Figs. 1.3 and 1.4), the agar production (Fig. 1.5) and the economic income from agar exports have been decreasing and are far from maximum levels attained in the early 1970's. Some recovery of total agarophyte landings has occurred in the last few years. However, this results mainly from the discovery of new, previously unexploited beds in Zone 6. The declining trend in the agar industry indicates the need for scientific studies on the resources. As several authors have pointed out (Silverthorne, 1977, Santelices, 1988 and Pringle and Sharp, 1990), besides knowing the resource distribution and abundance, biological data are also required for management.

Palminha et al. (1982, 1985) assessed the distribution and standing crop of G. sesquipedale along the south coast of Portugal, and Oliveira (1984) presented growth data. Fralick and Andrade (1981) studied some aspects of P. capillacea growth and reproduction and presented management recommendations for this resource, apparently without enough data to support their conclusions (Santelices, 1988).

Most aspects concerning demography, harvest impact on populations and synergistic effects of abiotic factors on growth and on the synthesis of cell-wall polysaccharides have not been studied. The marine plant resources in Portugal have been managed largely without scientific advice; rather, management has been based on the experience and common sense of non-scientific personnel. At present, studies are being carried by the authors on the population biology, productivity and harvest impact on the populations of G. sesquipedale. Production models are being developed so that different harvest strategies can be tested, providing useful indicators to be used to manage the resource.

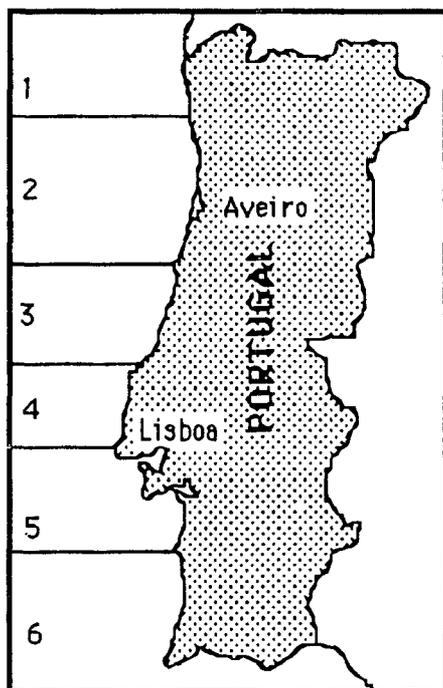


Fig. 1.1. Harvest zones of Portuguese continental coast.

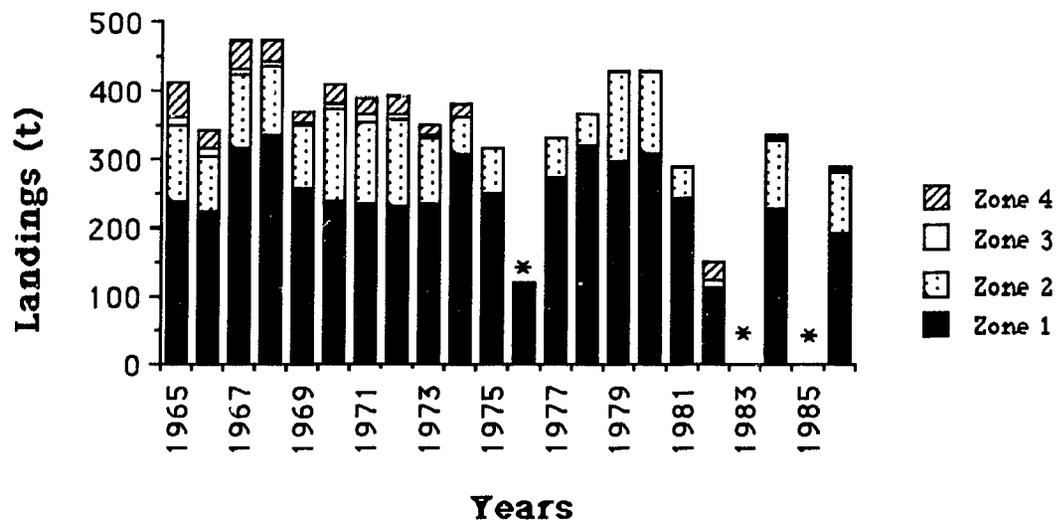


Fig. 1. 2. Annual landings of carrageenophytes (dry weight) along the continental coast. No data are available for years marked with an asterisk.

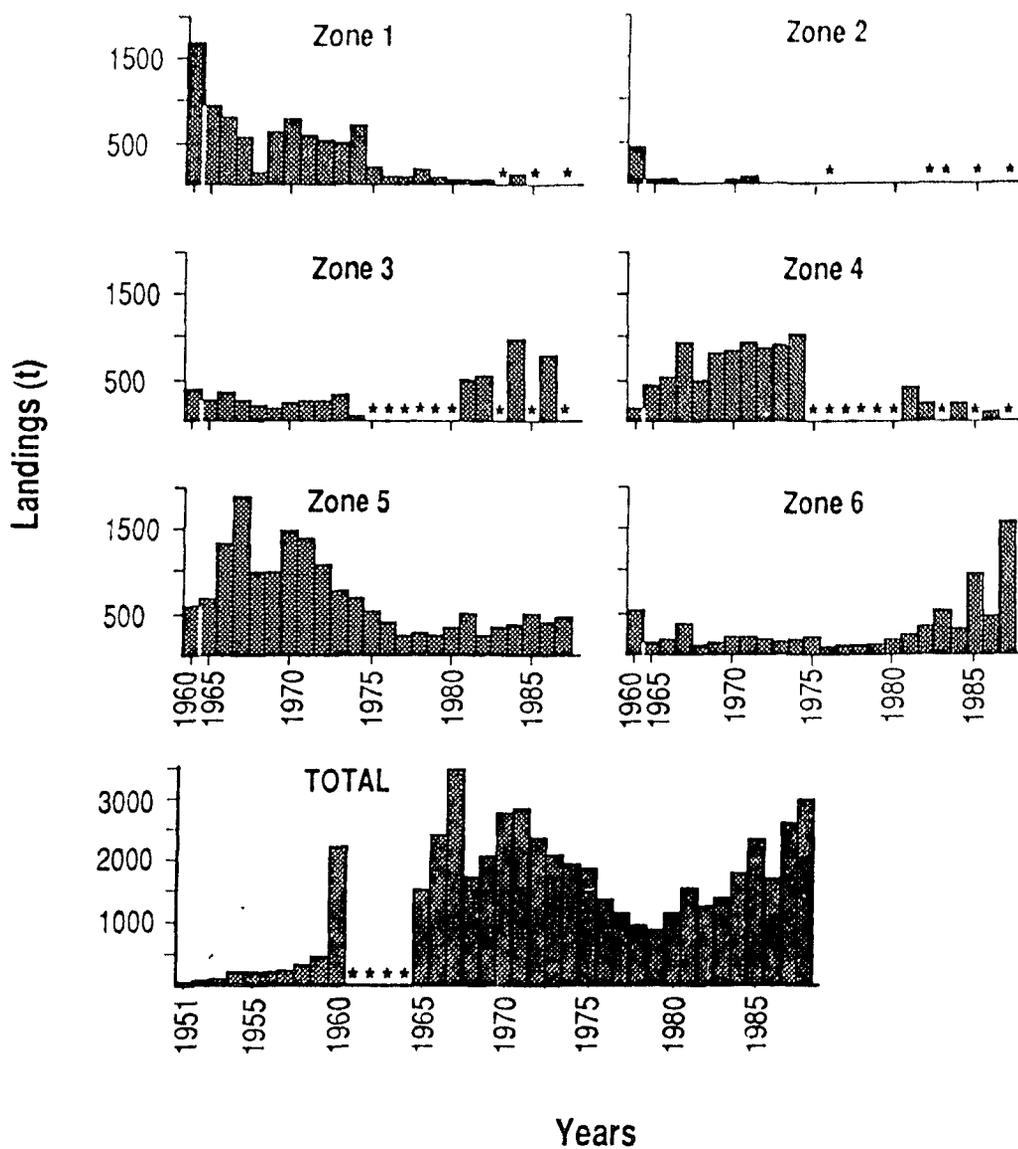


Figure 1.3. Annual landings of *Gelidium sesquipedale* (dry weight) along the continental coast. No data are available for years marked with an asterisk. Data before 1960 were derived from agar production values.

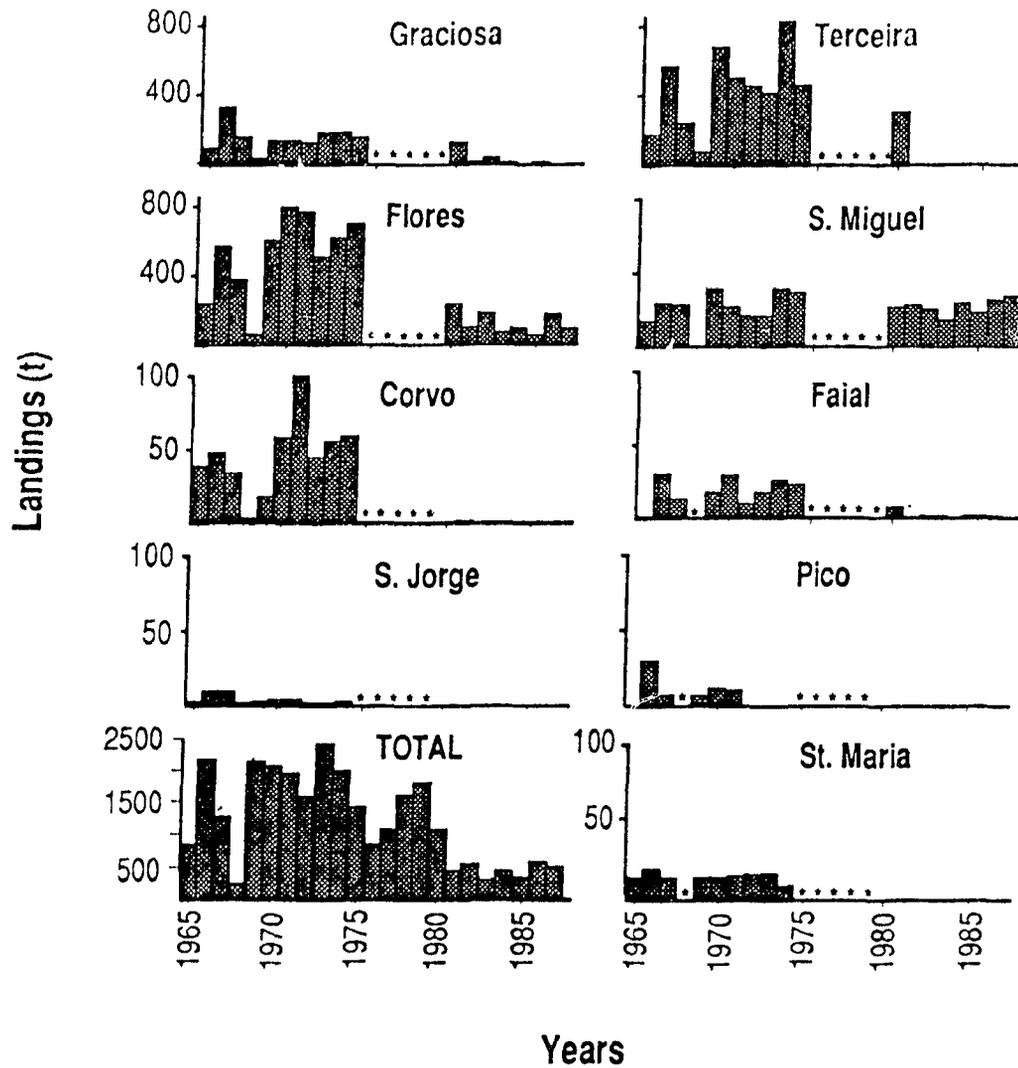


Fig. 1. 4. Annual landings of *Pterocladia capillacea* (dry weight) on the Azores Islands. No data are available for years marked with an asterisk.

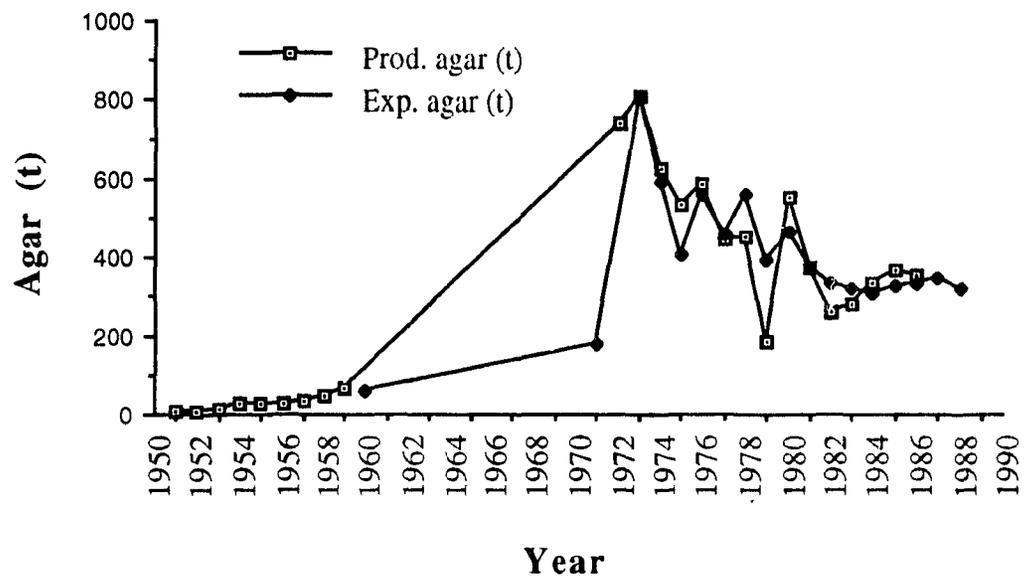


Fig. 1. 5. Portuguese annual production and exportation of agar.

CHAPTER II

A MULTIVARIATE STUDY OF BIOTIC AND ABIOTIC RELATIONSHIPS IN A SUBTIDAL ALGAL STAND

2.1 Introduction

Patterns of species distribution and abundance are determined by a complex interaction of biotic and abiotic factors. The specific processes that structure many macroalgal assemblages are poorly understood, particularly in the subtidal zone. Most studies have been done in the intertidal, on plant-herbivore interactions (Schiel and Foster, 1986). Several abiotic and biotic factors have been proposed to shape the local distribution of seaweeds, with light generally considered as having the most important direct effect (Lobban et al., 1985; Lüning, 1990). The complex fluid dynamics resulting from the interaction of water motion with depth and the topographic characteristics of substratum also have an important effect on the physical stress acting on plants (Vogel, 1981; Koehl, 1986; Denny, 1988), on the assimilation of nutrients and on the settling and development of algal spores (Vadas et al., 1990 and reviews by Lobban et al., 1985 and Lüning, 1990). Other major processes determining the patterns of distribution and abundance of algal species include intra- and interspecific competition (see review in Paine, 1990).

The causal mechanisms that determine the patterns of species distribution can only be detected by experimentation (Underwood, 1986). However, efficient design of experiments will require extensive preliminary analyses of observational data; numerical descriptive studies may play an important role in determining which hypotheses to test experimentally (James and McCulloch, 1990). Multivariate methods have been extensively used in vegetation science to expose trends and patterns of co-distribution of species and environmental factors, and to generate hypothesis of community-environment interactions (Gauch, 1982; Greig-Smith, 1983; Gittins, 1985; Ter Braak, 1987).

Marine ecologists, unlike terrestrial ecologists, have not used numerical methods extensively (see review in Kautsky and Van der Maarel, 1990). Applications of these methods to the study of biotic and environmental relationships in phytobenthic communities were early done by Neushul (1967), who related clusters of similar seaweed species with depth and substrate type along transects. Lindström and Foreman (1978) analysed the seaweed communities of British Columbia to determine major environmental factors related with the species composition. Kautsky and Van der Maarel (1990) recently correlated environmental factors of the Baltic Sea, such as depth, bottom type, slope, wave exposure and amount of sediment on the bottom, with the patterns of species distribution.

Depth (light), substrate topography, sedimentation and competition have all been identified as important factors influencing the local distribution of seaweeds (Lobban et al., 1985; Schiel and Foster, 1986; Lüning, 1990). Field correlations and laboratory studies have provided single factor explanations outlining the general relationships between abiotic and biotic environment and stand abundance, but the effects of interactions are largely unknown. Simple correlations among species distribution and abiotic factors or occurrence of other species have been the most common approach used to identify relationships in the subtidal zone (Schiel and Foster, 1986).

Gelidium sesquipedale (Clem.) Born. et Thur. is a clonal red alga which grows in the subtidal by the continuous production of upright fronds from a small, prostrate system of colorless axes (Dixon, 1958; Fan, 1961). The value of understanding the causes of variation in its abundance is enhanced by its commercial importance. This species is harvested by divers along the Portuguese coast for the extraction of agar. Portugal is the third largest producer of G. sesquipedale and is the fifth in agar production (Chapter I).

The ecological patterns of G. sesquipedale distribution, as in most species of the same genera (Santelices, 1991), indicate that abundant populations occur in habitats of high water motion with steep slopes and low sediment loading. Interspecific competition with

canopy forming kelps is likely to be an important process structuring its distribution and abundance as Montalva and Santelices (1981) have shown for G. chilense. Along the coasts of Spain and Portugal, G. sesquipedale forms high density, nearly monospecific stands, or grows underneath the canopy of the kelps Saccorhiza polyschides (Lightf.) Batt., Laminaria ochroieuca Pyl. and Cystoseira spp. (Saldanha, 1974; Melo and Santos, 1979; Gorostiaga, 1990).

This study addresses two questions concerning the biotic and abiotic relationships in a commercial G. sesquipedale stand: 1) is the distribution of G. sesquipedale, correlated with kelp abundance, depth, sediment loading and substrate topography, and 2) what is the strength of the relationship between G. sesquipedale distribution and the biotic and abiotic factors? I use multivariate and multiple regression techniques to approach respectively the first and the second questions. Two specific objectives are pursued with the second analysis. The first is to investigate the importance of each abiotic and biotic factor in as much as they act independently. The second is to assess the extent to which interactions between abiotic and biotic factors explain variation in G. sesquipedale abundance.

2.2 Methods

The commercial stand of G. sesquipedale studied is located off the north shore of Cape Espichel, Portugal (Fig. 2.1). Sampling was done from 24 of September to 8 of October, 1986. Eighteen transects, averaging 325 m in length, were layed out along 6.6 km of coast, following the point-transect method of Pringle and Semple (1983). The southernmost thirteen transects were 200 m apart in an area of high harvest effort. The northern five transects were 800 m apart, in an area where harvest effort was lower. Quadrats of 50x50 cm were sampled every 10m along the transects. Systematic sampling was used rather than random sampling because it is more effective to describe variability in spatial patterns of communities (see review in Gauch, 1982).

Estimates of subtidal seaweed abundances generally have high variances (Schiel and Foster, 1986). They reflect contagious distributions of species and high sampling errors caused by diving constraints. Consequently, larger samples are required to detect significant relationships. To sample this large area, a fast (and low cost) non-destructive sampling method was selected rather than the more time-consuming biomass sampling. The quadrat density of the two kelp species present in the zone, S. polyschides and L. ochroleuca, was recorded. G. sesquipedale density is very difficult to measure non-destructively because this species occurs in high density mats of algal tufts. Its abundance was assessed by visually estimating its cover (%) inside the quadrats (Pielou, 1981; Dethier, 1984). To assess the reliability of the visual estimates in describing the general abundance of the species, the number of one-meter transect marks in contact with G. sesquipedale tufts was also recorded and compared to visual estimates.

The geological characteristics of the area (Zbyszewski *et al.*, 1965; Ramalho, 1971), define a gradient of bottom topography and sedimentation, that may play an important role in structuring the subtidal algal community. The bed's south edge (Fig. 2.1, transects 1 to 6) topography is characterized by parallel strata oriented WSW-ENE, inclined at 60°. Northward, the strata crop out at 35° and 25° NNE, to almost horizontal (Ramalho, 1971; Rey, 1972). The north edge of the area is characterized by patches of rock and sand. Depth, substratum topography and sediment loading were measured in each quadrat. Substratum inclination and the sediment load were rated using a 1 to 3 scale for slope (1 - horizontal, 2 - sub-vertical and 3 - vertical) and 1 to 4 scale for silt (1 - no sediment to 4 - heavy sediment loading). The number of one-meter transect marks in contact with sand patches was also recorded, to investigate the relationship between the amount of sediment over the rock and transect sand cover. Quadrats that laid on sand were not included in the analysis. A total of 510 quadrats was sampled.

2.2.1 Ordination

Data analyses were done using SYSTAT 5.1 for Macintosh (Wilkinson, 1989). The data's underlying structure was investigated using a principal component analysis (PCA) (see Morrison, 1976 and Hair et al., 1987 for a description and application of the method and James and McCulloch, 1990 for a discussion of its limitations in ecology). To improve the detection of non-linear relationships, *G. sesquipedale* cover data were transformed to $\arcsin\sqrt{x}$, and kelp density was transformed to $\sqrt{x+0.5}$ (Sokal and Rohlf, 1969).

As each of the original variables were measured on different scales, PCA was performed on the correlation matrix rather than on the variance-covariance matrix. Furthermore, this work focuses on the correlation structure of the variables, rather than their variance structure.

Significant principal components were selected by plotting the eigenvalues against the components (Cattell, 1966), to detect when the amount of specific and error variance begins to dominate the shared variance among variables (Hair et al., 1987). The zone where the slope of the curve begins to flatten indicates the maximum number of components to extract. The selected components were then rotated by Varimax rotation, which redistributed variance from earlier to subsequent factors (Hair et al., 1987). This technique is generally used to facilitate the ecological interpretation of the component pattern.

2.2.2 PCA biplots

The original data matrix of all abiotic and biotic variables was transformed by PCA into a rank two matrix, by Varimax rotation on two principal components. This matrix contains the scores of all quadrats for the two principal components. A biplot of variable loading vectors and site scores on the principal components is done, to make the main features of data easier to see (Ter Braak, 1983). Variable vectors with an angle close to 0°

have high positive correlation, angles close to 90° show no correlation and angles toward 180° indicate high negative correlation. Longer vectors show positions of more significance.

2.2.3 Model development

The objective of this regression analysis is to assess the relative statistical importance of variables and their interactions, rather than to select the "best" subset of predictors. Random sampling is necessary to use multiple regression analysis to make predictions (see James and McCulloch, 1990, for a review of the problems in constructing multiple regression models in ecology). The criteria I used to judge the statistical importance are nevertheless the same as those used to select a subset of predictors (cf. Hocking, 1976; Mosteller and Tukey, 1977; Seber, 1977; Draper and Smith, 1981; Henderson and Velleman, 1981). First, a full regression model containing all variables and interactions was built and both the t-values and partial F-values of variables were computed. Reduced models were then constructed, using partial correlations of variables as the selection criteria for the candidates to be included. The significance of partial correlations, t and partial F-values of variables were analysed. The coefficient of determination, R^2 , and the error mean square, MSE, of reduced models were compared with those of full model to assess their prediction ability.

2.2.4 PCA transformation of variables for regression model

PC transformation can be regarded in the same manner as any other transformation that is used to prepare variates for regression. Massy (1965) compared this approach with classical least-squares multiple regressions and concluded that PC regression method is useful in exploratory studies of complex relations between variables. One reason for transforming a set of variables into principal components is that PCA substitutes orthogonal

linear combinations of variables for original variables, removing any multicollinearity among them, while maintaining the original structure of the data (Morrison, 1976). This is particularly important in ecological studies because the original independent variables are often highly correlated with each other. Another advantage resulting from the uncorrelated variables is that the relative importance of predictors in a model is easier to assess, because the order of entering them in the regression does not affect the regression coefficients.

PCA was performed on the original variables excluding G. sesquipedale, using a correlation matrix. The five component axes were rotated using Varimax rotation, so that each component could be mainly identified with one variable. Five component scores for each individual quadrat were then calculated. Component scores associated with each quadrat (each representing one variable) represent a conservative reparameterization of the original data that does not alter the multidimensional geometric relationships among quadrat samples, but allows a more efficient means of describing these relationships in terms of biotic and abiotic factors (Moloney, 1989). A multiple regression model was then constructed, regressing transformed G. sesquipedale cover values against the PC scores associated with each quadrat.

2.3 Results

2.3.1 Distribution patterns of species and abiotic factors

Figure 2.2 shows the distribution patterns of the dominant macrophytes and abiotic factors. Transect averages of biotic and abiotic factors variation along the G. sesquipedale commercial bed are shown. G. sesquipedale transect cover using the point transect method is compared with the eyeball quadrat estimates. Although transect cover absolute values were generally higher than quadrat cover values, the patterns of variation of the species cover along the bed were similar for both methods ($r = 0.89$, $p < 0.0001$). G. sesquipedale cover gradually decreased within the study site from south to north, whereas S.

polyschides density had the opposite distribution pattern. L. ochroleuca density showed no distinct trend. However, the significance of trends can not be assessed from the graphs because with systematic sampling there is no indication of the precision of the mean (standard error) and no possibility of assessing of its difference from the mean in another area (Greig-Smith, 1983).

Besides the natural depth gradient perpendicular to the shore line, an overall depth gradient parallel to the coast was apparent, where average depth decreases northward (Fig. 2.2). Also, the topographic characteristics of the coast determine that quadrat mean slope decreased northward. In contrast, both the amount of sediment over the rock and transect sand cover increase northward. The deposition of sediments over the rock and its effect on the abrasion of fronds is variable with time, and is not considered in the observations. However, transect sand cover is correlated ($r=0.71$, $p=0.001$) with the amount of siltation inside the quadrats (Fig. 2.2); plants near sand patches should be more subjected to the effects of siltation.

2.3.2 Principal Component Analysis

Three PCs were selected for interpretation, based on the analysis of the plot of the eigenvalues against the components (see methods). Table 2.1 shows their loadings, before and after Varimax rotation. They represent the correlation between each original variable and the component. To decide which loadings to interpret, correlation coefficients were tested for significance, using Bonferroni's correction for multiple comparisons. All values of Table 2.1 higher than 0.24 (underlined) are significantly different from zero ($p < 0.001$). However, in PCA the level at which a loading is significant should decrease with the number of variables, and should increase from the first factor to the last (Hair et al., 1987). Based on this, the correlation coefficients higher than 0.40, 0.50 and 0.60 respectively for

the first, second and third principal components, were considered for interpretation (values marked with an asterisk in Table 2.1).

Computation of the first unrotated component extracts a linear combination of variables that accounted for 36% of the total relationship among variables. It is the single best summary of linear relationships among variables, and therefore it represents the gradient structure of data: G. sesquipedale cover, substratum slope and depth were higher where S. polyschides density and siltation were lower (and vice-versa). The second unrotated component explains 18% of total relationship. It suggests that L. ochroleuca density was higher in deeper zones.

Varimax rotation of the three principal components show that the strongest interrelationships of variables were among G. sesquipedale cover, silt and slope. The first rotated component's loadings suggest that this species was more abundant in inclined zones with low siltation. To a lesser degree, data structure suggests that S. polyschides density was lower in such zones. The second principal component suggests that S. polyschides was more abundant in shallow zones.

2.3.3 PCA Biplots

The original data matrix of all abiotic and biotic variables was transformed by PCA into a rank two matrix, by performing a Varimax rotation of the two principal components. The two principal components explained 54.6% of total data relationships. Figure 2.3 shows the biplot of the variable loadings vectors and the quadrat sample scores. G. sesquipedale cover is highly positively correlated with substratum slope, and both are negatively correlated with siltation and, to a lesser degree, with S. polyschides density. L. ochroleuca density and depth are negatively correlated with S. polyschides abundance. To make the graph clearer, only the site scores of the first three transects of the south edge of the area studied and the last six transects (transects 13 to 18) of the north edge are shown.

There is a defined separation of both clusters of samples. The southern cluster is characterized by higher abundance of G. sesquipedale and L. ochroleuca, and higher substratum slopes and depth. The northern cluster shows higher S. polyschides densities and higher siltation (Fig. 2.3).

2.3.4 Full Regression Model

All the original variables except G. sesquipedale were transformed by PCA and varimax-rotated. Each original variable value was replaced by the PC score with which that variable was highly correlated (Table 2.2). A full regression model was then constructed using as predictors all possible main effects and interactions. Table 2.3 shows the predictor coefficients of the full model. Variables with non-significant t and partial F tests are not presented. Non-significant variables do not contribute to the understanding of the regressor variability, when all predictors are included in the model.

Partial F - tests were computed for all predictors to examine their significance and their relative importance in explaining the variance of G. sesquipedale abundance (Table 2.3). At this stage, both the t-values and the partial F-values indicate that the most important variables and interactions may be SLOPE, SAC, SILT, SLOPExLAM, LAMxDEPTH and SLOPExLAMxDEPTHxSILT. However, the partial F-values in the full model also reflect the effects of all factors and interactions that are not significant in the regression, which can distort that judgement.

2.3.5 Reduced model development

A reduced model was constructed in steps. First, correlations between G. sesquipedale and all predictor candidates were computed. The most highly correlated variable, silt ($r = -0.373$), was regressed on G. sesquipedale. Then, partial correlations of

the remaining variables with G. sesquipedale were computed to determine how much of its variation not explained by silt can be accounted for by each of the other predictors.

Variables were entered into the equation one by one, each time choosing the variable with the highest partial correlation after the previous ones had been fixed. The magnitudes of the partial correlations show that after the effect of silt is removed, the most important variable was SLOPE ($r = 0.34$). SAC ($r = -0.35$) and LAMxDEPTH ($r = -0.26$) follow this. The partial correlations of these selected variables are significantly different from zero with a probability $p < 0.001$ (Bonferroni correction for multiple correlations).

After this, there is a marked reduction in the significance of partial correlations. The next highest partial correlations, SACxSILT ($r = 0.15$) and the fourth order interaction SLOPExLAMxDEPTHxSILT ($r = -0.14$), were not significantly different from zero ($p < 0.05$, Bonferroni corrected). This indicates that these variables were not important in explaining the variation of G. sesquipedale distribution, though they significantly contributed to the full model as indicated by their significant t and partial F -values (Table 2.3). Including the next highest partial correlations (SACxSILT, SLOPExLAMxDEPTHxSILT, LAMxSILT and SLOPExDEPTH) in the reduced model, raises the adjusted coefficient of determination to $R^2 = 0.41$ (Table 2.4). The mean-square error of this prediction model is 0.117, not much higher than that of the full model, where $MSE = 0.112$. This shows that the residual variance left after regression is almost the same in both models.

The marked drop in the F -values from the first to the second set of predictors (LAMxDEPTH = 30.5 to SACxSILT = 11.8, Table 2.4) indicates that although the new predictors are useful in explaining additional variance in the dependent variable, their relative importance is much lower. Residual plots of the prediction model do not show any strong deviations from normality. The normal probability plot of the residuals do not

deviate strongly from a straight line, suggesting that the regression does not violate assumptions.

Siltation, S. polyschides and substratum slope are the main variables explaining the variation of G. sesquipedale cover. Their relative importance is not distinguishable because their standardized regression coefficients were not significantly different from each other. Interaction effects were weaker than main effects of SILT, SLOPE and SAC. L. ochroleuca and depth did not significantly explain G. sesquipedale variability when considered separately, but have a negative effect when they act together. Significant relationships were not detected between depth and G. sesquipedale.

2.4 Discussion

The relative importance of the determinants of seaweed distribution vary with scale. On a broad geographical scale, temperature and day length determine the boundaries of species distribution through plant mortality or inhibition of growth or reproduction (Breeman, 1988; Lüning, 1990). On a local scale, light, water motion, substrate topography, sedimentation and competition appear to be the determinants of the zonation observed along the depth gradient (Lobban et al., 1985; Schiel and Foster, 1986; Kain and Norton, 1990).

This study shows that the amount of sediments over the rocky bottom, its slope and S. polyschides density have the strongest relationships with G. sesquipedale cover in the study area. Both PC and multiple regression analyses revealed positive relationships between this species and slope, and negative relationships with silt and S. polyschides (Fig. 2.3 and Table 2.4). Multiple regression analysis indicated the main effects of the three variables were of the same relative magnitude; their standardized regression coefficients were not significantly different (Table 2.4).

High slopes and reduced sediment loading might favour G. sesquipedale development. This species is more abundant than the kelp S. polyschides in such zones. On the other hand, S. polyschides is more abundant than G. sesquipedale on low slope surfaces with high siltation. S. polyschides may tolerate siltation better than G. sesquipedale; in culture studies, Norton (1978) found that spores of this kelp would germinate even when covered with a silt layer.

Within the depth range studied (0 to 18 m), S. polyschides density is the only variable correlated with depth (Fig. 2.3). The density of this kelp drops at depths greater than 10 m (Fig. 2.4). This agrees with other reports of S. polyschides vertical distribution, which found this species confined to the upper zones of the subtidal (John, 1971; Lüning, 1990). In contrast to Cape Espichel, where G. sesquipedale is not correlated with depth, Gorostiaga (1990) reported that along the NE coast of Spain, both biomass and cover decrease with depth. He suggested that this is an effect of siltation which increases with depth. In this area, the depth limit of G. sesquipedale is 9 m.

The density of L. ochroleuca populations is relatively uniform through the study area, overlapping the distribution of S. polyschides (Figs. 2.2 and 2.4). This pattern has not been observed by other authors. John (1971) found distinct, non-overlapping zones of vertical distribution of these species in exposed sites off the NW of Spain and Lüning (1990) reports that through its geographical distribution, L. ochroleuca occupies a deeper zone (down to 25-30 m) than S. polyschides.

The interactions of abiotic and biotic factors affecting subtidal algal stands have seldom been studied (Schiel and Foster, 1986). The only interaction significantly related with G. sesquipedale cover variation was LAMxDEPTH. Although L. ochroleuca by itself does not contribute significant variation, this interaction suggests that at higher depths L. ochroleuca dominates G. sesquipedale. This is supported by the analysis of the correlations between these species in shallow vs deeper zones (Table 2.5). L. ochroleuca

and G. sesquipedale are negatively correlated in deeper zones, which contrasts with their positive correlation in shallow zones. On the other hand, S. polyschides abundance has a negative correlation with G. sesquipedale, of the same magnitude at all depths.

2.4.1 Abiotic factors

Austin (1980), searching for a model of the determinants of plant distribution, recognized three types of environmental factors: indirect factors, which have no direct physiological influence; direct factors, with direct physiological influence; and factors that are an essential resource for plants. Of the environmental gradients considered in this study, sediment is a direct environmental factor. The direct effects of siltation on G. sesquipedale are more likely to influence spore settlement and development, and growth of new vegetative shoots from creeping axes, than adult plants. Devinsky and Vorse (1978) found that even small amounts of sediment would greatly reduce the settlement and development of Macrocystis pyrifera spores. Only in extreme conditions of sand movement may seaweeds be broken by abrasion or killed by prolonged burial (Dahl, 1971; Daly and Mathieson, 1977). In contrast, the topographic shape of rocky bottom, or slope, may not have a direct influence on G. sesquipedale, but rather an indirect one, by affecting the type of water flow. The fluid dynamics resulting from the wave induced water movement and its interactions with the topographic features of the bottom, the presence and shape of plants, and depth are very complex (Vogel, 1981; Denny, 1988). Water movement has both positive and negative direct effects on seaweed development: negative, since the mechanical stress on the plants may increase mortality or breakage (Koehl, 1986); positive, through increasing nutrient availability and spore dispersal (Lobban et al., 1985; Lüning, 1990).

A distinct difference in G. sesquipedale density and frond morphology between horizontal and inclined surfaces is evident in the study site. Frond density on inclined

surfaces decreases with increasing depth (unpublished data). As well, fronds are shorter and bushier on horizontal surfaces than on inclined surfaces where they are longer. The positive relationship between slope and G. sesquipedale cover reflects this. Higher densities on horizontal substrata may be a population response to physical disturbance. Turbulent patterns of water flow are enhanced by the presence of obstacles (Denny, 1988), which are more common on horizontal surfaces. The turbulent flow increases the availability of nutrients as well as the availability of light by increasing frond breakage. This may result in an increase of vegetative growth of new fronds from creeping axes.

Depth (through decreasing light) may also be an important indirect factor influencing the morphology of G. sesquipedale fronds. Macler and West (1987), in culture studies of Gelidium coulteri, showed that plants grown under low light levels were stoloniferous with little branching. When irradiance was increased, plants developed branches. Nevertheless, effects of depth on G. sesquipedale cover were not detected, even as an interaction with slope.

2.4.2 Biotic factors

Competition between kelp and understory species has been described as being for space and for light. Understory species seem adept at monopolizing the substrate, whereas kelps may shade rivals (see review by Kain and Norton, 1990). Many manipulative field experiments have shown that canopy species may reduce the settlement and growth of understory species (e.g. Reed and Foster, 1984; Dean et al., 1989; Kennelly, 1989).

Ojeda and Santelices (1984) did the only competition experiments involving Gelidium species, between Gelidium chilense and the kelp Lessonia nigrescens. If kelp was removed in summer, G. chilense monopolized the substratum and the next year kelp settlement did not occur. By contrast, if kelp was removed in winter, kelp settlement occurred the following year, though G. chilense did extend into the low intertidal levels

previously occupied by the kelp. S. polyschides is an annual species which loses all the fronds during the fall season. If this species does compete with G. sesquipedale their competitive relationship may follow a similar process.

The processes that regulate local patterns in the abundance of G. sesquipedale can only be completely understood when mechanistic causes are revealed. Associations among variables do not imply causation (Hastings, 1987). Three types of information are required to support causality: consistency, responsiveness and a mechanism (Mosteller and Tukey, 1977). There is not sufficient information to assess whether the relationships shown at Cape Espichel occur elsewhere, in other populations or at other times. Palminha et al. (1982), off the south coast of Portugal, and Gorostiaga (1990), off the NE coast of Spain, subjectively observed negative relationships between G. sesquipedale abundance and the amount of sediment. Gorostiaga (1990) also points out the lack of relationship between G. sesquipedale cover and substratum slope, but the range of slopes observed is very low (0 - 40°).

To assess the responsiveness of G. sesquipedale to changes in abiotic and biotic factors, experimental studies must follow this study, manipulating the variables and measure their effects on demographic rates, *in situ*. The mechanism behind the causal relationships can only be revealed through understanding the behavior of the vital rates that regulate population dynamics, when subjected to changes of the background abiotic and biotic factors.

Table 2.1. Variable loadings of first 3 principal components before and after varimax rotation. Underlined correlations are significantly different from zero ($p < 0.001$). Gel, Sac and Lam: Gelidium sesquipedale cover and densities of Saccorhiza polyschides and Laminaria ochroleuca, respectively. Asterisks indicate biologically significant loadings (see text).

Variables	Unrotated			Rotated		
	PC1	PC2	PC3	PC1	PC2	PC3
Gel	<u>0.73*</u>	<u>0.38</u>	0.07	<u>-0.82*</u>	0.11	0.01
Sac	<u>-0.68*</u>	<u>0.24</u>	<u>0.28</u>	<u>0.39</u>	<u>-0.65*</u>	0.14
Lam	<u>0.29</u>	<u>-0.70*</u>	<u>0.57</u>	0.02	0.13	<u>-0.94*</u>
Slope	<u>0.67*</u>	<u>0.35</u>	-0.13	<u>-0.72*</u>	<u>0.24</u>	0.15
Silt	<u>-0.67*</u>	-0.12	<u>-0.48</u>	<u>0.71*</u>	0.06	<u>0.43</u>
Depth	<u>0.44*</u>	<u>-0.52*</u>	<u>-0.58</u>	0.01	<u>0.89*</u>	-0.04
Proportion of relationship explained	0.36	0.18	0.16	0.31	0.22	0.19
Cumulative proportion	0.36	0.54	0.70	0.31	0.53	0.72

Table 2.2. Correlations among principal components (PC) rotated by Varimax and original variables. Each rotated component is highly related with only one variable (bold font). LAM - Laminaria ochroleuca, SAC - Saccorhiza polyschides.

Variables	PC1	PC2	PC3	PC4	PC5
SLOPE(1)	-0.974	0.016	0.084	0.129	0.164
LAM(2)	0.014	-0.989	0.053	0.077	0.110
DEPTH(3)	-0.082	-0.054	0.983	0.154	0.033
SAC(4)	0.130	0.081	-0.160	-0.970	-0.097
SILT(5)	0.164	0.116	-0.034	-0.095	-0.974

Table 2.4. Reduced regression model of *Gelidium sesquipedale* cover (Gel). See Table 2.1 for variables. $N = 496$, $R^2 = 0.418$, adjusted $R^2 = 0.408$, SE of estimate = 0.341

Variable	Coeff.	Std Error	Std coef.	T	P (2 tail)	F	P
CONSTANT	0.600	0.015	0.000	39.034	0.000		
SILT(5)	-0.147	0.016	-0.326	-8.947	0.000	80.041	0.000
SAC(4)	-0.147	0.016	-0.315	-8.931	0.000	79.766	0.000
SLOPE(1)	0.136	0.016	0.300	8.586	0.000	73.719	0.000
LxDE	-0.088	0.016	-0.194	-5.524	0.000	30.515	0.000
SxSI	0.055	0.016	0.122	3.442	0.001	11.847	0.001
LxSI	0.049	0.018	0.098	2.684	0.008	7.202	0.009
SLxLxDExSI	-0.054	0.020	-0.092	-2.618	0.009	6.855	0.008
SLxDE	-0.040	0.016	-0.091	-2.591	0.010	6.711	0.010

ANALYSIS OF VARIANCE

Source	SS	DF	MS	F-ratio	P
Regression	40.709	8	5.089	43.662	0.000
Residual	56.758	487	0.117		

Table 2.5. Pearson correlation matrices of GEL - Gelidium sesquipedale, LAM - Laminaria ochroleuca and SAC - Saccorhiza polyschides in shallow (≤ 9 m) and deeper (≥ 13 m) zones. Underlined values are significant at $p < 0.05$ (Bonferroni corrected probability). See Table 2.1 for variables.

Depth≤ 9m	GEL	LAM	SAC
GEL	1.000		
LAM	<u>0.155</u>	1.000	
SAC	<u>-0.372</u>	<u>-0.225</u>	1.000

n = 390

Depth≥ 13m	GEL	LAM	SAC
GEL	1.000		
LAM	<u>-0.491</u>	1.000	
SAC	<u>-0.315</u>	-0.089	1.000

n = 58

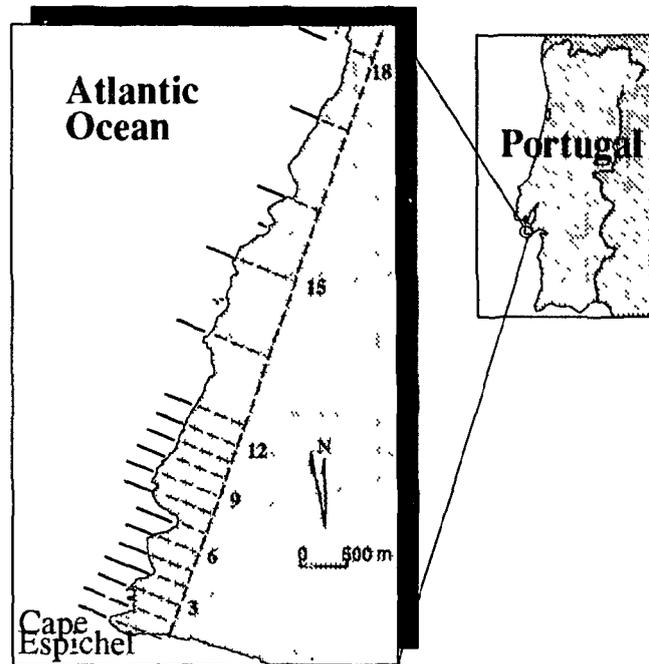


Fig. 2.1. Map of the studied zone, showing location of transects

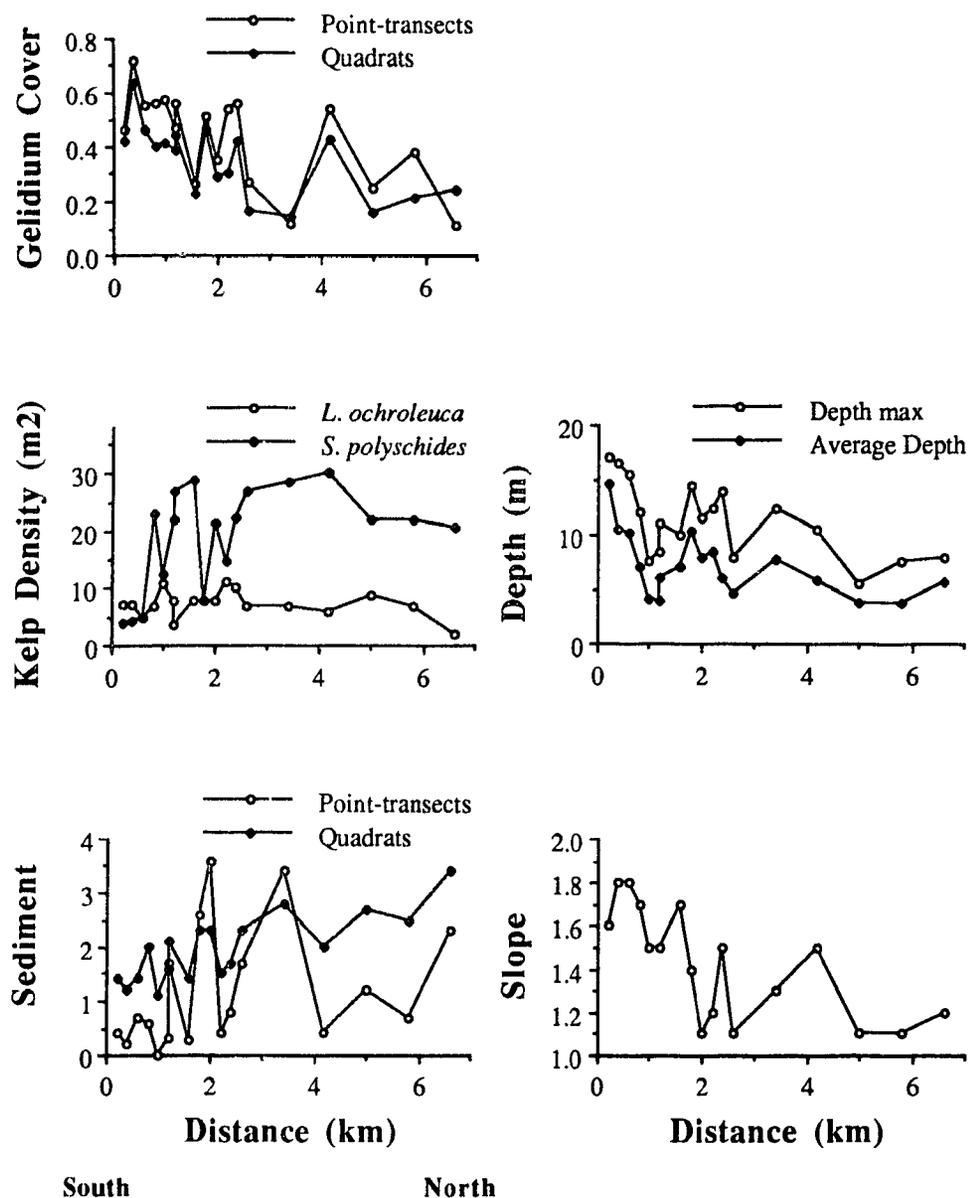


Fig. 2.2. Transect averages of abiotic and biotic factors along the studied area. The distance axis represents transect distances from transect 1 (northward from Cape Espichel). Depth plot shows both average and maximum depth in each transect. Point-transect sediment values are average number of one-meter marks in contact with sand per 10 m of transect. Standard deviations are not represented for convenience of reading. They are of the same magnitude as the mean.

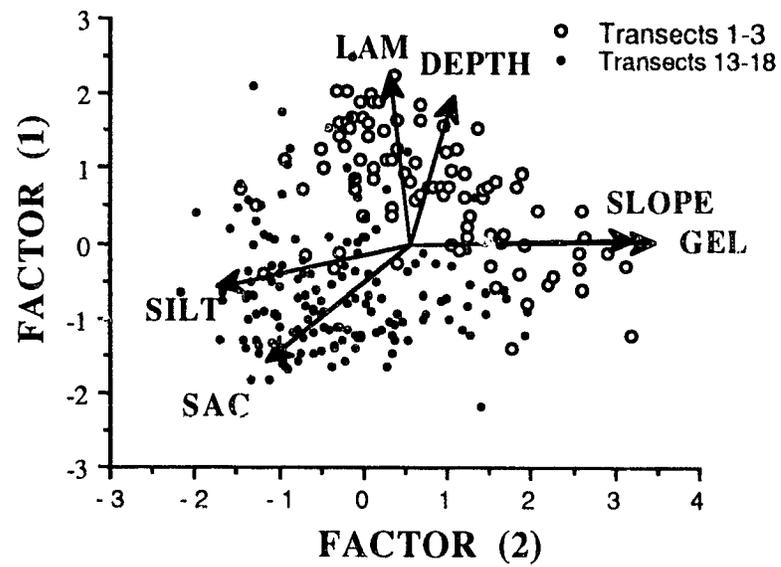


Fig. 2.3. Biplot of the variable loadings vectors and the quadrat sample scores. Only the scores of Transects 1 to 3 and 13 to 18 are shown. GEL - Gelidium sesquipedale, LAM - Laminaria ochroleuca, SAC - Saccorhiza polyschides.

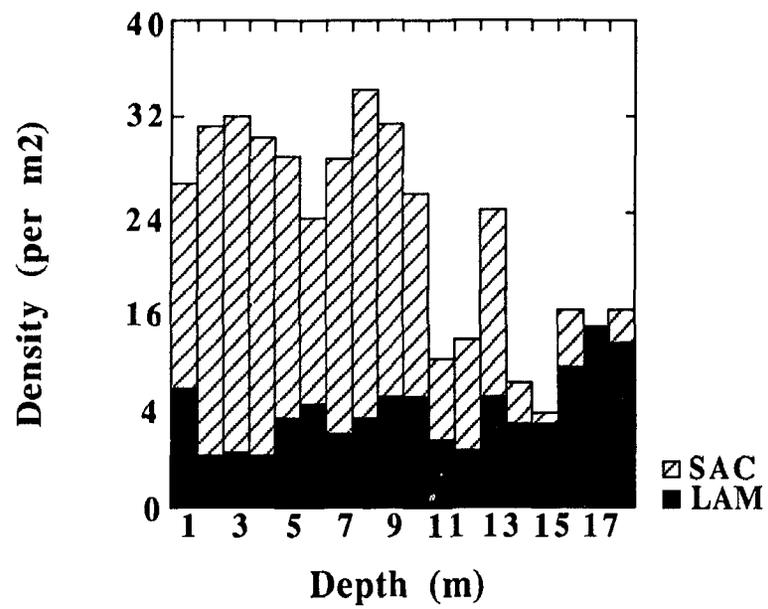


Fig. 4. *Saccorhiza polyschides* (SAC) and *Laminaria ochroleuca* (LAM). Vertical distribution of densities (m⁻²).

CHAPTER III

FROND DYNAMICS OF THE COMMERCIAL SEAWEED GELIDIUM SESQUIPEDALE: EFFECTS OF SIZE, EPIPHYTISM, AND FROND HISTORY.

3.1 Introduction

Gelidium sesquipedale (Clem.) Born. et Thur. is a clonal red alga which grows in the northeast Atlantic subtidal by production of upright fronds from a small, prostrate system of colorless axes, attached to the substrate by rhizoidal protuberances (Dixon, 1958; Fan, 1961). The species typically forms dense stands of clumped fronds, often under a kelp canopy (Ardré, 1970; Lüning, 1990). G. sesquipedale has a triphasic Polysiphonia-type life cycle, the isomorphic tetrasporophyte and gametophyte phases, plus the small carposporophyte developing directly on the female thallus (Kylin, 1923; Dixon, 1959). The tetrasporophyte and female gametophyte can only be distinguished when reproductive. G. sesquipedale is commercially exploited along the coasts of France, Spain, Portugal and Morocco for the production of agar (Appendix 1). More than half of the world's production of Gelidium is obtained from this species (McLachlan, 1985; Armisén and Galatas, 1987).

Growth rates, generally expressed as size changes, have been studied for many seaweed species (Chapman and Craigie, 1977, 1978; De Wreede, 1984; Kain, 1987; Ang, 1991), as has survivorship, usually reported as cohort depletion curves (e. g. Chapman 1984; Schiel, 1985; Dayton et al., 1984; Dean et al. 1989). Growth generally refers to net size variation; influence of thallus breakage component is seldom considered (but see Barilotti and Silverthorne, 1972). Positive and negative changes in frond length are assessed separately in this work and are called growth and breakage, respectively.

The influence of an individual's biological history on its fate has been studied in higher plants, particularly in the development of matrix population models (Bierzychudek,

1982; Meagher and Antonovics, 1982; Huenneke and Marks, 1987; Groenendael and Slim, 1988). These are matrix models of first order Markovian processes, i. e. the transition probabilities from time t to $t+1$ depend only upon the individual's state at time t , and not upon its state at any previous point in time. In some cases, historical effects are likely to influence an individual's fate (Bierzychudek, 1982; Groenendael and Slim, 1988)

Historical effects in seaweed species have been detected in relation to reproduction. In some species individuals stop growing, and in others individuals degenerate when bearing reproductive structures (Santelices, 1978; Dion and D  l  pine, 1983; Klein, 1987). Ang (1992), studying Fucus distichus L., detected a significant negative impact of reproduction on mortality rate in the subsequent time step, but not on longevity of survivors. The relationships between the fate history of individuals in time $t-1$ and their fate in time t appears to have rarely been addressed in seaweed species. This may be particularly important in red seaweeds that grow by apical cell division, as is the case for G. sesquipedale, where breakage of the thallus may affect future elongation rate (L'Hardy-Halos, 1971).

Because it is difficult to distinguish both adjacent clumps and fronds of the different life cycle phases, G. sesquipedale vital rates were studied here at the frond level, independent of the prostrate system or life cycle phase; the module (sensu Harper, 1977) or the metamer (sensu White, 1979), i.e. genetically similar subunits of original genets. The current study assesses the influence of season and frond length, as well as their interaction, on the vital rates growth (length increase), breakage (length decrease) and mortality of G. sesquipedale. The strong dependence of vital rates on an individual's size rather than on age has been widely documented both for higher plants (see review in Caswell, 1989) and for seaweeds (Chapman, 1986; Ang, 1991). To assess the influence of frond history on vital rates, the effects of frond growth and breakage on the next time step frond growth, breakage and mortality, are analysed.

G. sesquipedale fronds off the Portuguese coast are often epiphytized in spring/early summer, by the annuals Dictyota dichotoma (Hudson) Lamouroux, Plocamium cartilagineum (L.) Dixon and Asparagopsis armata Harvey (pers. obs.). The impact of epiphytism was assessed by analyzing the temporal- and size-specific effects of epiphyte presence vs. absence on the next time step growth, breakage, and mortality of G. sesquipedale fronds. Monthly probabilities of growth, breakage and mortality quantified in this study are parameters in a demographic model constructed for resource management (Chapter V), to simulate G. sesquipedale recovery to different harvest strategies.

3.2 Materials and Methods

This study was conducted in a G. sesquipedale commercial bed off Cape Espichel, Portugal (38° 42' N, 9° 22' E). The species occurs in dense stands, particularly in the southern part of the bed, or under the canopy of the kelps Saccorhiza polyschides (Lightfoot) Batters and Laminaria ochroleuca De la Pylaie (see Chapter II). G. sesquipedale cover is positively correlated to substrate slope and negatively correlated to sediment loading and S. polyschides density (Chapter II). The study site was on two inclined strata in the southern part of the bed, where monospecific G. sesquipedale stands spread from 7 m to 14 m in depth (between transects 2 and 3, of Fig. 2.1, Chapter II).

Over 300 fronds dispersed through the study site, and covering most of the size spectrum of the species were haphazardly tagged, using monofilament tags (Sharp and Tremblay, 1985). Lost fronds were continuously replaced, to maintain about 250 observations per sample. Tags were placed on the main axis below the first ramification. The minimum length of a ramified frond was around 4 cm, and those below this length were not studied due to difficulty in manipulating them under the intense wave surge characteristic of this coast. Tagged frond length was measured monthly from August 1989 through September 1990, except in November, December and February, when excessive

wave surge prevented diving. The presence/absence of the epiphytes Dictyota dichotoma, Plocamium cartilagineum and Asparagopsis armata for each tagged frond was recorded.

In this study, a G. sesquipedale frond is considered to have only three possible fates during a given time interval: to be detached (mortality), to decrease or maintain length (breakage) or to increase length (growth). The actual mean length increase per unit of time (30 days) is the elongation rate. It was calculated by grouping all fronds increasing in length in the time interval. Similarly, frond shrinkage rate was calculated for fronds decreasing in length; net elongation rate was calculated by grouping all fronds.

As the absolute time interval (in days) between samples varied, particularly in that period when sea conditions prevented measurement, the percentage fronds that grew, broke or died over each time period were weighted for 30 days, by assuming a linear function for the number of fronds dying in each time interval. Mortality probability per month, M , was calculated as:

$$M = d \times 30 / \Delta t ,$$

where d is number of deaths in time interval Δt (in days). Probabilities for frond breakage and growth per month were then calculated assuming the same ratio between them as observed during the time interval between samples. The number of fronds that grew, broke or died per month was calculated by multiplying the initial number of tags in each time period by the respective corrected probability. G. sesquipedale monthly elongation rate, E (or shrinkage rate), was calculated for all fronds that increased (or decrease) in length as:

$$E = \Delta h \times 30 / \Delta t$$

where Δh is frond length variation.

To assess tag loss rate, thirty fronds were double tagged in August 1989 and followed until March (Fig. 3.1). Loss of only one tag was interpreted as tag decay. Accumulative frond mortality, corrected for tag decay, is close to the uncorrected value,

particularly in the first few months (Fig. 3.1). Thus tag decay was not accounted for when estimating mortality rate. In later months the effect of tag decay on mortality estimates was not important because there were only a few survivors from the initial tagging and most tags were new.

3.2.1 Choice of size (length) classes

When dividing a continuous classification character, such as frond length into categories, the distribution of the observations within categories is affected by the category boundaries chosen. Ideally, all the within-category observations should have the same fate probability, the fate probability of the category center, to minimize the within category error and to increase differences between categories. Differences in the fate of observations within categories, the "distribution error" as well as the "sample error", that occurs when too few observations in each category are available, were first identified by Vandermeer (1978) in the context of choosing category sizes for transition matrix models. He proposed an algorithm to minimize it, later revised and further developed by Moloney (1986). Distribution error is defined by Moloney (1986) as the degree to which the probability that an individual starting in a category will be in the same category in the next time step, deviates from the same probability if all the individuals were aligned in the center of the category. The minimization of the distribution error, as defined by Moloney (1986), selects the distribution of the observations inside a category that will be closest to a central distribution.

Moloney's (1986) algorithm was adapted to derive G. sesquipedale size classes that minimized the distribution error of fronds within length classes (Fig. 3.2). Three length classes were selected (Fig. 3.2). Class I fronds were ≤ 10.1 cm length, class II fronds were > 10.1 cm and ≤ 16.0 cm, and class III fronds were > 16.0 cm. Classes were selected keeping the number of observations of fate (breakage class I - negative or zero

length variation, breakage class II - positive length variation or deaths, growth class I - positive length variation, growth class II - breakage or deaths, mortality class I - deaths, mortality class II - survivors) and elongation rate (class I ≤ 0.5 cm/month, class II > 0.5 cm/month and ≤ 1.0 cm/month, and class III > 1.0 cm/month) equal or higher than 5 in at least 80% of the cases (an assumption of contingency tables) for all time steps.

3.2.2 Data Analysis

Discrete categorical data such as frond breakage/growth, mortality/survival, present/absence of epiphytes, are most appropriately analysed using loglinear models (Bishop et al., 1975; Fienberg, 1979). Caswell (1989) gives a detailed description of how to use these models to choose state variables for demographic models.

Loglinear analysis is based on a linear model relating the logs of the entries of a contingency table to the categorical variables defining the table. This model expresses the log of the count in each cell, $\log m_{ijk}$, as a function of main effects, ν_S and ν_M and interaction parameters, ν_{SM} :

$$\log m_{ijk} = \nu + \nu_{S(i)} + \nu_{M(j)} + \nu_{SM(ij)}$$

for a simple example of a two-way table between initial frond size (S) and frond mortality (M) occurring during a given time period, where ν is the log of the total number of observations in the table, $\nu_{S(i)}$ the effect of the i th size class, $\nu_{M(j)}$ the effect of the j th mortality class (mortality/survival) and $\nu_{SM(ij)}$ the effect of the interaction of the i th size class and the j th mortality class. In a log linear model, an interaction term represents association between categorical variables, i. e. the combined effect of these variables on cell frequency. The statistical significance of an interaction is assessed by comparing the goodness of fit of the model (log likelihood ratio, G) following the addition or deletion of that term from the model (Caswell, 1989). For example, to test if size provides additional information to time about mortality, one examines the change in G of the model

Time \times Size+Time \times Mortality+Size \times Mortality, when compared to the model Time \times Size+Time \times Mortality. The difference among the G values and degrees of freedom between the two models gives the statistical significance of the effect of size on mortality given the contribution of time, S \times M/T.

Loglinear analysis is used in the current study to test statistical interactions of the explanatory variables time and size, with both frond fate and elongation rate, as well as the contribution of each when the other (time or size) is included in the model. The historical effects of frond fate, elongation rate and epiphyte presence on the next time step frond fate and elongation rate are also analysed. In this analysis, breakage and growth are considered the only possible initial frond fates (breakage probability + growth probability = 1), as opposed to the previous analysis where mortality is also a possible fate (breakage probability + growth probability + mortality probability = 1). The impact of epiphytes was tested only for the period April/September 1990, when epiphytism was heavy. All data analyses were done using SYSTAT 5.1 for Macintosh (Wilkinson, 1989).

3.3 Results

3.3.1 *Gelidium sesquipedale* frond dynamics

The temporal variation of *G. sesquipedale* frond fate probability (Fig. 3.3) was highly significant ($p < 0.001$), with or without the inclusion of frond size (S) in the loglinear models (TxM, TxM/S, TxB, TxB/S, TxG, and TxG/S, Table 3.1). Frond mortality was relatively constant throughout the year, with the exception of August/September 1990 (Fig. 3.3), which had a high value (0.56). The tagged fronds may have been removed by professional harvesters as the study site was open to harvesting. The open season begins the middle of July, and continues through summer/fall (Chapter I). High mortality was not observed during the 1989 season because the study site was harvested prior to the tagging experiment (see Chapter IV).

August/September 1990 mortality values may be overestimated because of the tagged fronds not found by divers in September 1990. This occurred every sampling, but was corrected on following samplings when some missing tagged fronds were found. The average percentage missing fronds per sample was 5.5 %. Even considering the maximum percentage missing fronds per sample, 14.9%, the resulting corrected mortality probability, about 0.43, is still higher than the previous month's value, 0.23, supporting the hypothesis of an important harvest mortality during this period.

High probabilities for frond breakage were observed throughout the year (Fig.3.3). Frond breakage attained highest values during late fall and winter months, when severe storms with waves up to 7 m high occurred off Cape Espichel (Fig. 3.4). A smaller breakage peak occurred in June/July 1990 prior to the harvest season (Fig. 3.3). On the other hand, frond growth probability was low in winter. All fronds were probably increasing in length, but breakage was high during this period. Frond growth probability was high through late spring and summer, except from August 1990 to September 1990 due to harvest mortality.

3.3.2 Length variation

The temporal variation of *G. sesquipedale* elongation rate is highly significant, with or without the contribution of size (TxE and TxE/S, Table 3.1). Elongation rate shows a distinct seasonal pattern; high during spring and summer months (about 1 cm/month), while during late fall and winter, it decreased to a minimum of 0.3 ± 0.07 cm (\pm SE) in January/March 1990 (Fig. 3.5). The maximum elongation rate observed was 1.3 ± 0.07 cm/month, in June/July 1990, just before the harvest open season. A sudden decrease was observed in July/August 1990. Elongation recovered to normal summer values during September.

G. sesquipedale frond shrinkage was low during fall/winter, and increased during late spring/summer (Fig. 3.5). Frond net elongation rate was negative during late fall/winter, and positive during spring/summer, except in July/August 1990. The decrease in net elongation rate from May to August 1990 was due to important losses of frond material (shrinkage rate and breakage probability, Figures 3.5 and 3.3).

3.3.3 Effects of size

The effects of G. sesquipedale frond length on breakage and growth probabilities were highly significant ($p < 0.001$), with or without the contribution of time (SxB, SxB/T, SxG and SxG/T, Table 3.1). Shorter fronds (≤ 10.1 cm) were less susceptible to breakage and had a greater chance of increasing in length than longer fronds (Fig. 3.6). The effect of length on mortality was not significant ($p \leq 0.05$, SxM and SxM/T, Table 3.1, and Fig. 3.6).

The effect of frond size on elongation rate was also highly significant ($p < 0.001$, SxE and SxE/T, Table 3.1). Figure 3.7 shows the frequency distribution of elongation rate classes for each frond length class. The frequency of fronds elongating more than 1 cm/month increased with length, in contrast with those elongating less (Fig. 3.7 A). This effect is even more evident during periods of rapid length increase (August to October 1989, April to July 1990 and August to September 1990), when 50% of the fronds longer than 16 cm grew more than 1 cm/month (SxE: $G=21.1$, $df=4$, $p < 0.001$ and SxG/T: $G=19.0$, $df=4$, $p=0.001$), as opposed to shorter fronds which grew significantly less (Fig. 3.7 B).

During periods of slow growth (October/May 1990 and July 1990/August 1990), the effects of frond length on elongation rate do not appear significant (Fig. 3.7 C). High incidence of breakage during these periods resulted in low cell counts, particularly of size class 3 fronds. Loglinear tests of significance are not valid in these cases.

Although the effects of size on frond mortality were not significant when all months were considered in the analysis, for the periods when G. sesquipedale was subjected to strong physical disturbances such as harvesting or storms (August 1989/March 1990 and July/September 1990), frond length did have a significant effect on mortality (SxM: $G=20.2$; $df=2$; $p<0.001$, and SxM/T: $G=20.6$; $df=2$; $p<0.001$). Longer fronds had a greater chance of being detached from the substratum than smaller fronds (Fig. 3.8). Conversely, in March/July 1990 mortality was significantly (SxM: $G=12.0$, $df=2$, $p=0.002$ and SxM/T: $G=10.9$, $df=2$, $p=0.004$) higher for size class 1 fronds than for size class 2 and 3 fronds (Fig. 3.8).

3.3.4 Epiphytes

The epiphytes Dictyota dichotoma, Plocamium cartilagineum and Asparagopsis armata occurred on G. sesquipedale fronds in May and June 1990 (Fig. 3.9), when about 20% of the fronds were epiphytized. In the following month, a sudden increase in epiphyte-bearing fronds was observed, particularly for frond classes 2 and 3. Longer G. sesquipedale fronds were more epiphytized than were shorter fronds (Fig. 3.9); 52% of size class 1 fronds had epiphytes in July, compared with 81% and 88% of the class 2 and 3 fronds, respectively. Epiphytism slowly decreased through to September. Both time and size effects on G. sesquipedale epiphyte load are highly significant, even when effects of the other variable is included in the loglinear models (TxE, TxE/S, SxE and SxE/T, Table 3.1).

3.3.5 Effects of historical events

The recent biological history of a G. sesquipedale frond may play an important role on its fate, and thus on the regulation of its demographics. The fate and elongation rate of a G. sesquipedale frond during the time step t to $t+1$, that broke during the time step $t-1$ to t ,

may be different than had the frond not broken. The significance of these relationships, tested by loglinear analysis, is shown in Table 3.2. Models with or without the contribution of both time and size are presented. In this analysis, only two categories of length (class 1 ≤ 13 cm, class 2 > 13 cm) and elongation rate (class 1 ≤ 0.75 cm/month class 2 > 0.75 cm/month) were considered, so that cells of contingency tables have the maximum number of counts. Unfortunately, some cells are still sparse (frequency < 5 in more than one-fifth of the cells). The significance tests in these cases are suspect. They are marked with one or two asterisks respectively (Table 3.2) if one or both loglinear models used to calculate the interaction have sparse cells.

Significant relationships were detected between breakage and the next time step mortality ($B \times M1$, $p=0.027$), between breakage and next time step breakage ($B \times B1$, $p=0.008$), and between epiphyte presence and next time step mortality ($Ep \times M1$, $p<0.001$), but these were caused by time and size related variability. When time and size contributions are accounted for, these relationships are not significant ($B \times M1/T,S$, $p=0.325$; $B \times B1/T,S$, $p=0.163$; $Ep \times M1/T,S$, $p=0.462$).

On the other hand, G. sesquipedale fronds that break in one time step appear to have lower elongation rates during the next time step than unbroken fronds (Fig. 3.10A). As well, fronds that elongate faster in one time step, have a greater probability of growing than breaking during the next time step (Fig. 3.10B). These effects were significant given the time and size contributions ($B \times E1/T,S$, $p<0.001$, $E \times B1/T,S$, $p<0.001$), but in both cases one of the two loglinear models used to test the effect is based on a small sample size (Table 3.2).

The presence of epiphytic algae on G. sesquipedale did not significantly influence the fate of fronds in the next time step, except for frond mortality probability (Table 3.2). However, this relationship is not significant when both time and size are accounted for ($Ep \times M1/T,S$, $p=0.462$). In order to assess if the attachment and development of epiphytic

spores is enhanced by the increase of damaged zones on G. sesquipedale fronds after breakage, the relationship between frond breakage and the next time step epiphyte presence was also tested. The relationship was not significant given the effects of time and size (BxEp1, $p=0.014$; BxEp1/T,S, $p=0.920$).

3.4 Discussion

3.4.1 Seasonal variation

Both harvest and natural (storm) disturbances play an important role on the seasonal changes of G. sesquipedale frond fate. At Cape Espichel, commercial divers hand-pluck fronds annually, from the middle of July to late fall (Chapter I). It is likely the high frond mortality observed in August/September 1990 was caused by harvest. During the previous harvest season (August to October 1989, Fig. 3.3), mortality and breakage of experimental fronds was low because the study site was harvested prior to the tagging experiment. Mean frond weight, total biomass, and density values dropped from July to August 1989 (Chapter IV).

Storms, in contrast to the harvest, caused more frond breakage than frond mortality. High probabilities of frond breakage and low frond mortality during late fall and winter, periods coincident with strong wave surge suggest that under natural disturbances, G. sesquipedale frond breakage reduces the probability of frond detachment. This appears an adaptation to environments of intense wave-induced physical stress, which is the typical habitat for Gelidiales species (Santelices, 1988). Large quantities of storm-tossed G. sesquipedale fronds occur during fall and winter throughout the species geographical distribution. This phenomenon is well documented because the harvest on shore provides raw material to the agar industry (Seoane-Camba, 1969; Juanes and Borja, 1991; Appendix 1). Of the storm-tossed material, 65% to 92% are broken fronds, lacking the basal portion of the axis (Seoane-Camba, 1966). However, this was not the case for G. robustum

(Gard.) Holl. et Abbott off California, where frond breakage was rare (Silverthorne, 1977).

Frond breakage plays an important role in G. sesquipedale production dynamics. Although fronds grow throughout the year, net elongation rate was negative both during periods of severe sea storms and during July/August 1990 (Fig. 3.5), due to important losses of frond material (Figures 3.3 and 3.5). During late spring and summer, when wave surge is low (Fig. 3.4), frond breakage is probably caused by grazing. Grazing by invertebrates and fishes was not controlled during this experiment, but their activity has been reported as causing extensive trimming of G. sesquipedale axes off Santander, Spain, by weakening axis and making them more susceptible to breakage by wave action (Salinas et al., 1976; Reguera et al., 1978). The later observed more broken fronds were found in spring, coincident with a high abundance of grazers.

The impact of frond breakage is enhanced due to G. sesquipedale's slow elongation rate (see Lüning, 1990, page 364 for examples of maximal growth rates of seaweeds), a feature that has been proposed as characteristic of Gelidiales (Stewart, 1983). At Cape Espichel, elongation rate was low in late fall/winter at about 0.34 cm/month, and peaked at 1.30 cm/month during June/July. Annual average elongation rate was 8.3 cm (0.69 cm/month). These values are similar to elongation rates of intact G. sesquipedale fronds at other localities. Seoane-Camba (1966) reports G. sesquipedale elongation values of 9.0 cm/year, estimated on short fronds (< 10 cm), in the low intertidal zone of Vigo, Spain. The elongation rate of subtidal size class 1 fronds (≤ 10.1 cm) at Cape Espichel was lower (7.8 cm/year). Gorostiaga (1990), reports a length increase variation from 6.1 cm/year to 7.9 cm/year for G. sesquipedale fronds ranging from 5 cm to 15 cm, off Pais Vasco, Spain. Monthly elongation rates varied from a minimum of 0.3 cm/month from November to February, to a maximum of 1.0 cm/month from July to August. Elongation rates at

Cape Espichel for the same size interval were 8.1 cm/year, with a minimum of 0.3 cm/month from October to January and a maximum of 1.1 cm/month from June to July.

Low elongation rates are reported for Gelidium and the closely related Pterocladia species (review in Santelices, 1988), but most authors have not estimated frond breakage, and thus present only net values. This is the case for G. pristoides in South Africa, 8.4 to 9.0 cm/year (Carter and Anderson, 1986); for Gelidium sp., growing in artificial beds in Japan, 9 to 11 cm/year and 6 cm/year (Yamada, 1976); and for G. robustum in Baja California, Mexico, 8.7 cm/year (size class 11-24 cm), 10.2 cm/year (size class 9-13 cm) (Guzmán del Prío and de la Campa Guzmán, 1979). The absolute elongation rates would likely have been higher in those cases had fronds that broke not been included in the calculations.

In most Gelidiales, and particularly for G. sesquipedale (Seane-Camba, 1966, Gorostiaga, 1990), the favorable production seasons are late spring and summer (Fig. 3.5). During this period, even though frond shrinkage was highest, net elongation was positive due to low frond breakage probability (Fig. 3.3). An accurate measure of tissue loss for production estimates cannot be derived based on length decrease because shedding of branches accounting for important biomass losses may occur while the main axis remains intact (Seoane-Camba, 1969).

3.4.2 Effects of size

Longer G. sesquipedale fronds are more vulnerable to detachment during harvesting and storms than shorter fronds (Fig. 3.8). A significant positive effect of frond length on mortality was observed from summer through winter, as opposed to the negative effect observed in spring/early summer. Maximum harvest mortality estimates presented in Chapter V show that longer fronds are particularly vulnerable to harvest. During late fall and winter, longer fronds are more likely to be detached because they are subjected to

higher drag forces caused by wave swell (Denny, 1988). By contrast, during spring and early summer, frond mortality is greater for shorter than for longer fronds. This may be a result of density-dependent self-thinning occurring during this time period (see Chapter IV). In high density monospecific stands, intense competition for light causes mortality of small suppressed plants (Weiner and Thomas, 1986).

Higher mortality and higher breakage of longer fronds over shorter ones have been commonly reported in seaweeds. Populations of G. robustum in California (Barilotti and Silverthorne, 1972; Silverthorne, 1977), of Ascophyllum nodosum (L.) Le Jol. on the west coast of Sweden (Åberg, 1992), and of the kelp Laminaria longicuris Pyle. (Chapman, 1984) and Chondrus crispus Stackh. (Bhattacharya, 1985) off southwestern Nova Scotia, Canada, all show this pattern.

Rarely has higher mortality of smaller fronds over larger ones been observed in seaweeds, which results in most species having a high, positively skewed frond frequency distribution during all seasons. However, there are exceptions (e. g. Schiel, 1985; Chapter IV). Size-specific mortality is highly influenced by the scale at which the study is conducted. For example, studies do not generally include small individuals due to difficulties in monitoring them. Ang (1991) observed higher mortality for size class 1 (<1 cm) Fucus distichus plants off coastal British Columbia, in all seasons but summer, when mortality in larger plants was significantly higher, perhaps due to long exposure at daytime (Ang, 1991). If small individuals are monitored, particularly in high density stands, it is likely that at some point they will have higher mortality than larger ones due to density-dependent self-thinning. Dean et al. (1989) and Reed (1990) interpreted this effect as the result of intra-specific competition for light.

The effect of frond size on elongation rate in Gelidiales has seldom been addressed. At Cape Espichel, G. sesquipedale elongation rate was related to frond length, particularly during periods of high production (Fig 3.5). Longer fronds grew faster than shorter

fronds suggesting a density-dependent mechanism of growth suppression of shorter fronds by longer fronds. G. sesquipedale increases its length by the division of the apical cell (Rodriguez and Santelices, 1987). In crowded conditions, light is more available to the apical portion of longer fronds than to shorter ones. As well, nutrient availability may be lower to shorter fronds due to reduced water movement beneath the canopy. During periods of slow growth (Fig. 3.5), there was no indication of size effect on elongation rate (Fig. 3.7 C).

Gorostiaga's (1990) data on G. sesquipedale elongation rates show significant positive correlations with frond length throughout the year. Guzmán del Prío and de la Campa Guzmán's (1979) indicated the same relationship for G. robustum off Baja California, Mexico, but the elongation rates for the different size classes were measured in different years. The net elongation rates of size class 11-24 cm were consistently higher throughout 1968/1969 than those of size class 9-13 cm during 1970/1971, except in the periods when net elongation rates of longer fronds were negative, while that of the smaller fronds was positive (Tables 3.1 and 3.2 in Guzmán del Prío and de la Campa Guzmán, 1979). However, Barilotti and Silverthorne (1972) reported elongation rates of 9 cm/year for intact G. robustum fronds off California, and no significant correlation between elongation rate and frond length.

3.4.3 Historical effects

There were slight indications that a G. sesquipedale frond's past history influenced its fate. The small number of observations may have affected the experiment. Epiphytes growing on G. sesquipedale were abundant during summer months (Fig. 3.10), particularly on longer fronds, but did not seem to affect frond fate (Table 3.2). However, frond breakage slows growth (Fig. 3.9). Fronds that do not break, grow faster during the following time interval.

This "growth enhancement" of fronds was also observed when testing the impact of elongation rate on frond growth and breakage probabilities. Faster growing fronds have a higher probability of growing than breaking during the next time step (Fig. 3.9). G. sesquipedale fronds under more favorable microenvironmental conditions such as exposure to light, patterns of water flow, neighborhood effects, etc., may have higher growth rates and longer growth periods before breaking or dying.

Reduced growth immediately after breakage may be due to a delay caused by the physiological process of initiating regeneration. Apical regeneration on broken fronds has been reported for several Gelidium species (Johnstone and Feeney, 1944; Barilotti and Silverthorne, 1972; Salinas et al. 1976; Reguera et al., 1978). Gelidium and Pterocladia species have a uniaxial structure and grow by division of the apical cell (Kylin, 1928; Dixon, 1958; Fan, 1961). When the apical cell is lost, cortical cells differentiate into apical cells (Felicini and Arrigoni, 1967; Felicini, 1970) and develop an indeterminate growth axis (Dixon, 1973). One or more axis can develop from the cut surface, probably modifying frond morphology.

The lower elongation rate of broken fronds (Fig. 3.9) explains the unexpected low elongation rate in July/August 1990 during the favorable growing season (Fig. 3.5), because it follows a period of high breakage probability (Fig. 3.3). This effect was not observed by other authors. Seoanne-Camba (1966) did not detect differences between elongation of sheared and intact G. sesquipedale axis along the western coast of Spain. Johnstone and Feeney (1944) observed apical regeneration of cut fronds of G. robustum off California in spring and late fall, following periods of intense surf. The authors speculated that growth was higher as a reaction to frond injuries.

The strong influence of frond breakage on regulating G. sesquipedale frond dynamics during this study may represent an extreme circumstance; the storms that occurred during

late fall/early winter were unusually strong. In less stormy years, frond material lost by breakage may be lower thus increasing annual production. Nevertheless, G. sesquipedale frond breakage is a common event. Salinas et al. (1976) observed that almost all G. sesquipedale fronds longer than 3 cm on the coast of Santander, Spain, showed signs of regrowth from previous axis breakage. Longer time series data of vital rates incorporating annual, stochastic environmental variation are necessary to understand the long term dynamics of this commercial species, and to provide more accurate resource management advice. Studies must also be developed on the long term effects of harvest on frond regeneration and morphology, and on its impact on production rates and agar content.

This work indicates yield overharvesting of Cape Espichel G. sesquipedale bed, as is the case of Chondrus crispus exploitation in Canada's Prince Edward Island (Chopin et al. (1992). Harvesting by divers in the middle of July, as is done in Portugal (Chapter I), reduces yield because the peak summer production is lost. Due to the species slow growth it is not likely that sites harvested once can be re-harvested later in the season. Higher G. sesquipedale yields could be obtained by adjusting the harvest season to that period closest to fall storms, but the sociology of the harvesters and technological problems limiting the rapid completion of harvest must be considered.

Table 3.1. Statistical significance (log likelihood ratio, G) for the interactions of time (first section of table) and size (second section of table) with Gelidium sesquipedale vital rates.

See methods for explanation of log linear models. T = time (10 categories), S = length (SI \leq 10cm, SII $>$ 10.1 and \leq 16.0cm, SIII $>$ 16.0cm), M = mortality/survival, B = breakage/no breakage, G = growth/no growth, E = elongation rate (EI \leq 0.5cm/mo, EII $>$ 0.5 and \leq 1.0cm/mo, EIII $>$ 1.0cm/mo), Ep = epiphytes/no epiphytes.

MODEL	G	df	p
TxM	205.35	9	0.000
TxM/S	207.16	9	0.000
TxB	140.25	9	0.000
TxB/S	196.35	9	0.000
TxG	287.05	9	0.000
TxG/S	294.45	9	0.000
TxE	132.94	9	0.000
TxE/S	294.45	9	0.000
TxEp	314.63	4	0.000
TxEp/S	333.76	4	0.000
SxM	3.96	2	0.138
SxM/T	5.77	2	0.056
SxB	39.49	2	0.000
SxB/T	42.49	2	0.000
SxG	40.26	2	0.000
SxG/T	47.66	2	0.000
SxE	40.26	2	0.000
SxE/T	47.66	2	0.000
SxEp	71.68	2	0.000
SxEp/T	90.81	2	0.000

Table 3.2. Statistical significance (log likelihood ratio, G) of the effects of historical events on Gelidium sesquipedale frond fate. Variables followed by the number 1 are of following time step. T = time (10 categories), S = length (SI \leq 13.0cm, SII $>$ 13.0cm), M = mortality/survival, B = breakage/growth, E = elongation rate (EI \leq 0.75cm/mo, EII $>$ 0.75cm/mo), Ep = epiphytes/no epiphytes. Asterisks show if one or both loglinear models have sparse cells (see text). See methods for explanation of log linear models.

MODEL	G	df	p
BxM1	4.87	1	0.027
BxM1 / T,S	0.97	1	0.325
BxB1	7.13	1	0.008
BxB1 / T,S	1.95	1	0.163
BxE1	24.13	1	0.000*
BxE1 / T,S	20.32	1	0.000*
ExB1	17.56	1	0.000
ExB1 / T,S	25.4	1	0.000*
ExE1	0.19	1	0.663**
ExE1 / T,S	0.21	1	0.647**
ExM1	1.86	1	0.173
ExM1 / T,S	1.00	1	0.317**
EpxB1	0.42	1	0.517
EpxB1 / T,S	1.32	1	0.251
EpxE1	0.02	1	0.888**
EpxE1 / T,S	0.29	1	0.59**
EpxM1	40.48	1	0.000
EpxM1 / T,S	0.54	1	0.462

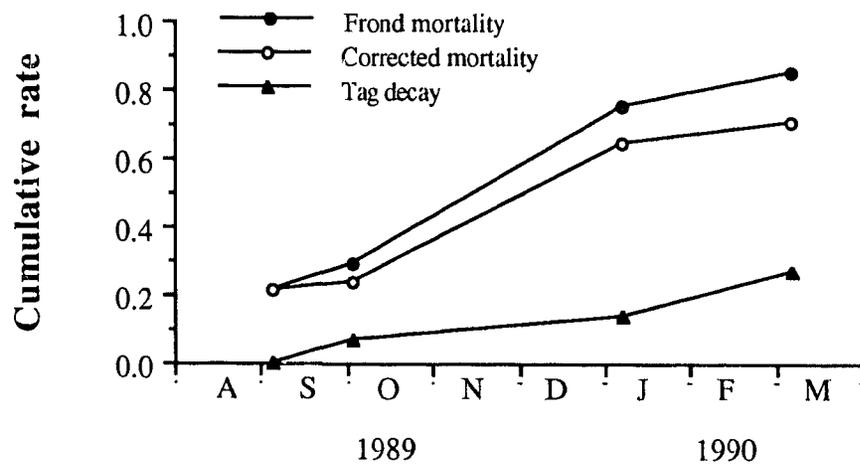


Fig. 3.1. Cumulative mortality and tag decay of *Gelidium sesquipedale* double-tagged fronds. Mortality values corrected for tag losses are plotted as open circles.

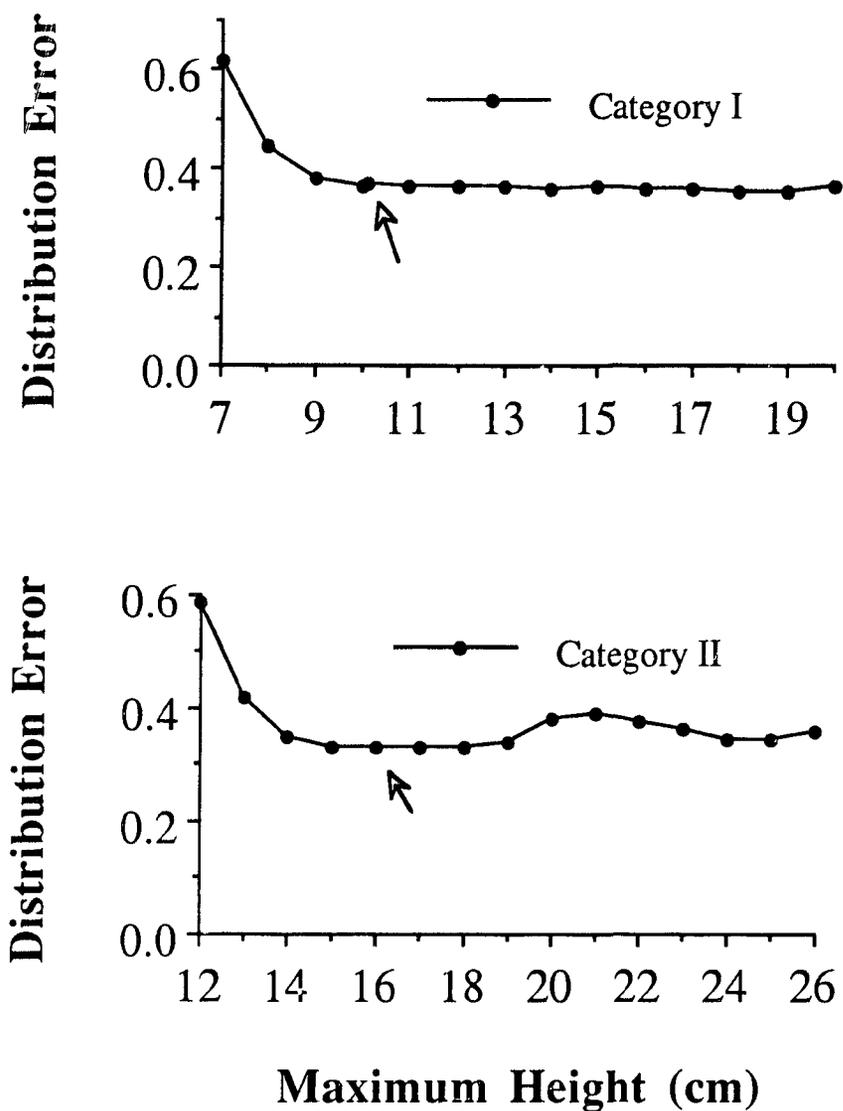


Fig. 3.2. Distribution error for determining *Gelidium sesquipedale* length categories. Arrows show upper limits of categories I and II. Category boundaries were selected so that both the distribution error was low, and the number of observations within categories is significant (see text).

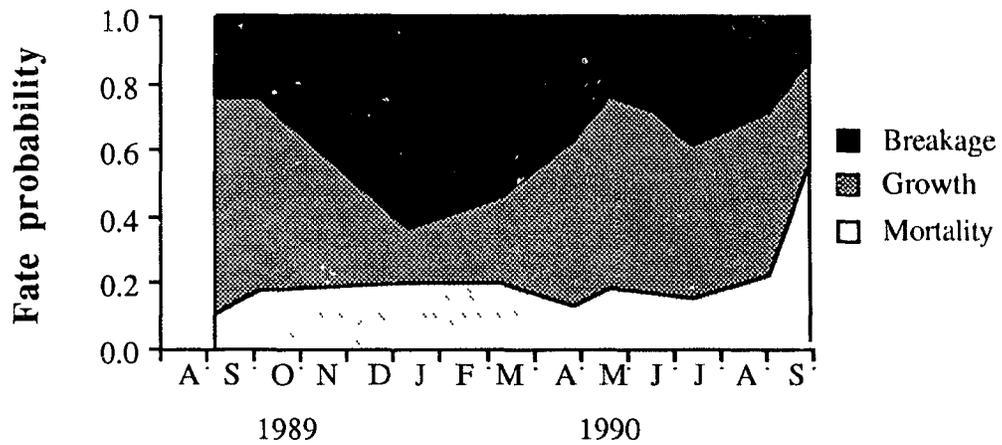


Fig. 3.3. Temporal changes of *Gelidium sesquipedale* frond fate probability: breakage (negative or zero length increase), growth (positive length increase), and mortality.

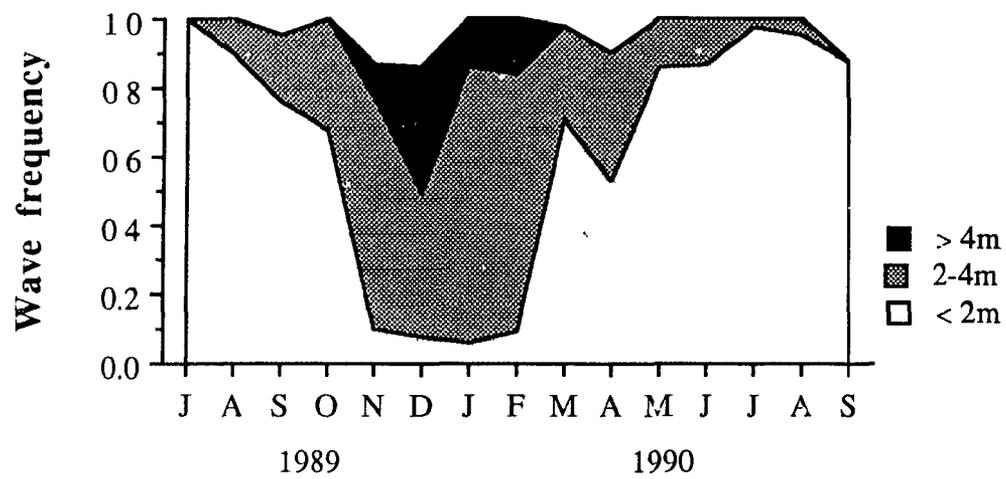


Fig. 3.4. Monthly probabilities for the occurrence of waves of certain heights off Cape Espichel coast. Wave data were obtained with wave simulation model MAR211, from Instituto Nacional de Meteorologia e Geofísica, Lisboa, Portugal.

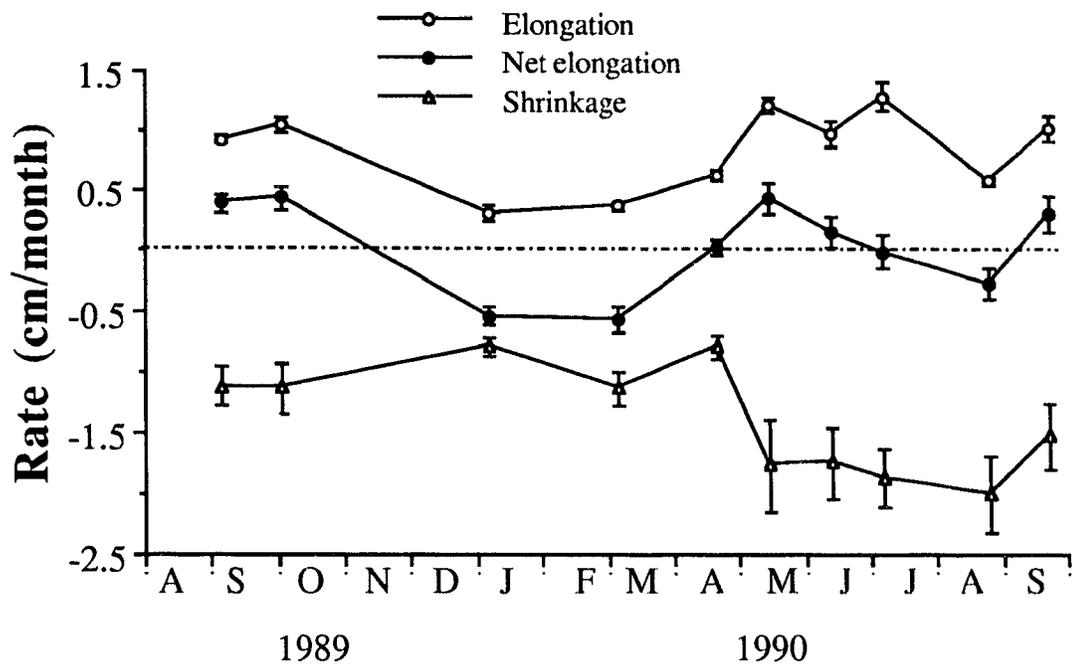


Fig. 3.5. Mean intermonthly variation of *Gelidium sesquipedale* frond length.

Vertical bars are standard errors. Elongation rate was calculated grouping all fronds that increased in length, shrinkage rate grouping all fronds with negative or zero growth and net elongation rate grouping all fronds.

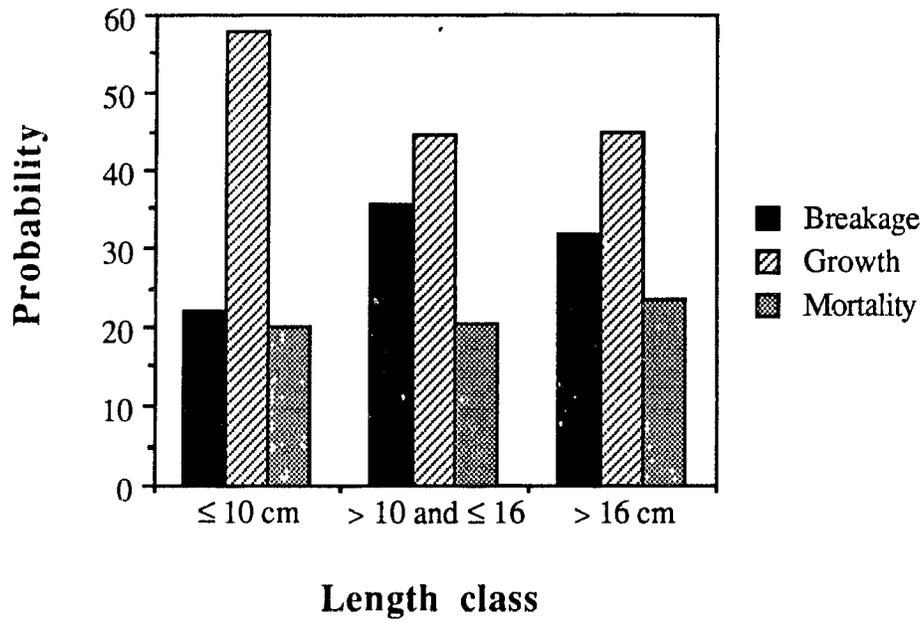


Fig. 3.6. Effect of frond length on frond breakage, growth, and mortality probabilities in *Gelidium sesquipedale*. Size class 1 = fronds ≤ 10.1 cm; size class 2 = fronds >10.1 and ≤ 16 cm; size class 3 = fronds > 16 cm.

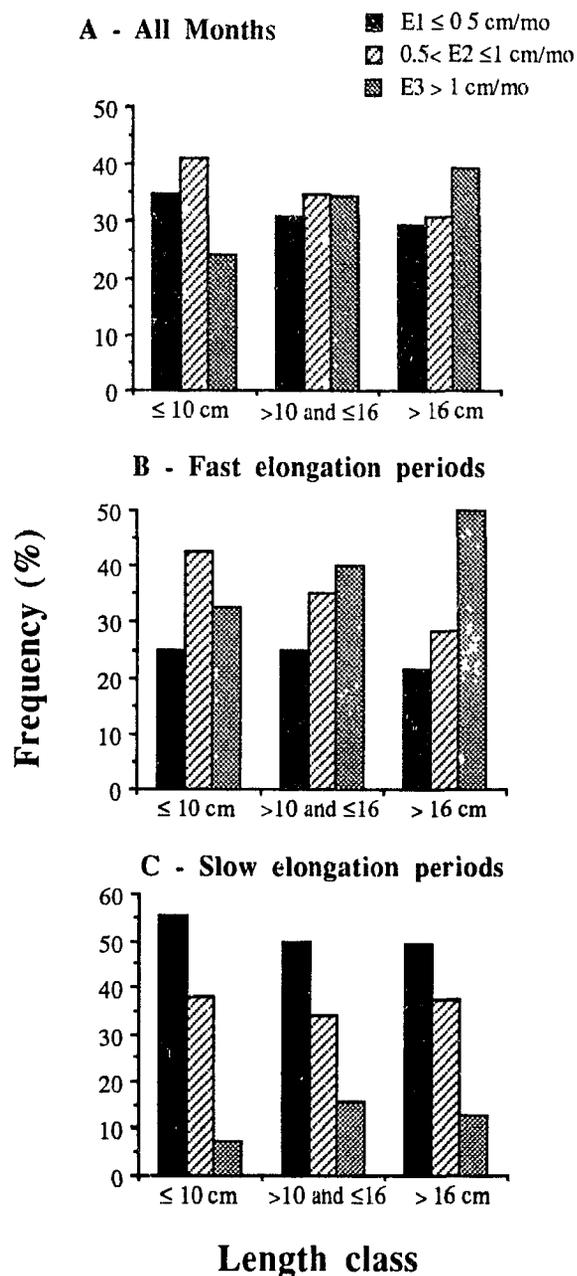


Fig. 3.7. Effect of frond length on frond elongation rate in *Gelidium sesquipedale*. Graph A includes all months, graph B includes only the periods of high elongation rate (August/October 1989, April/July 1990 and August 1990/September 1990), and graph C includes only periods of low elongation rate (October/May 1990 and July 1990/August 1990).

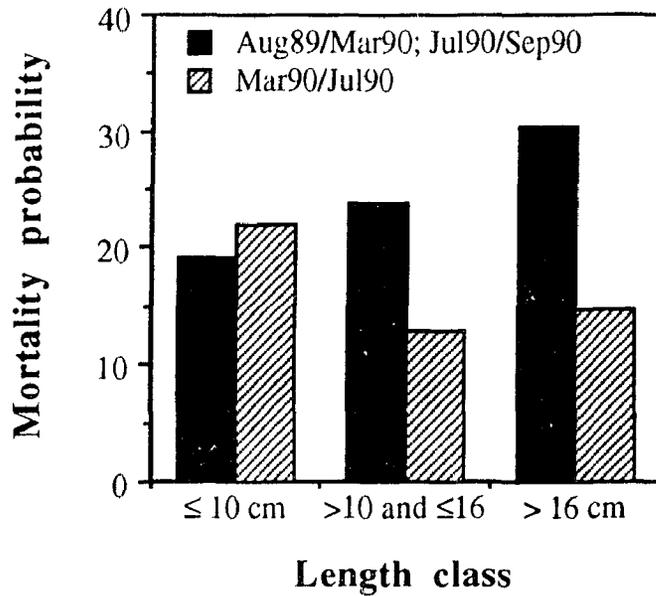


Fig. 3.8. Seasonal effect of frond length on frond mortality in Gelidium sesquipedale. Black bars includes periods of harvest and natural (storms) disturbances: August/March 1990 and July/September 1990. Striped bars shows spring and early summer period (March/July 1990).

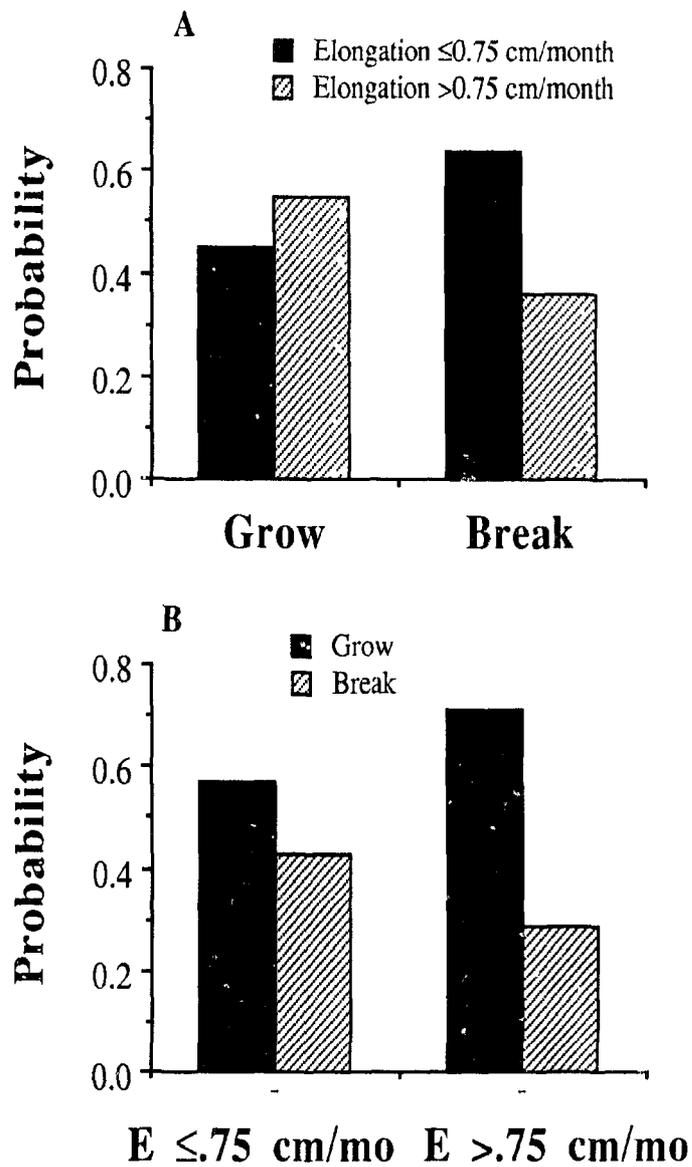


Fig. 3.10. Effects of frond history on vital rates in *Gelidium sesquipedale*. Graph A shows the effect of breakage/growth probability (time t) on elongation rate (time $t+1$). Graph B shows the effects of elongation rate (time t) on breakage/growth probability (time $t+1$).

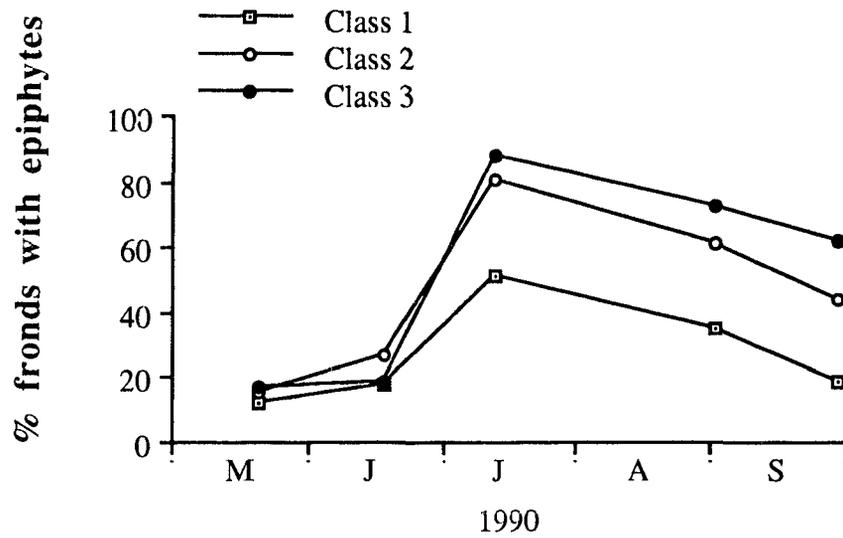


Fig. 3.9. Percentage of Gelidium sesquipedale fronds per length class bearing epiphytes. Size class 1 = fronds ≤ 10.1 cm; size class 2 = fronds > 10.1 and ≤ 16 cm; size class 3 = fronds > 16 cm.

CHAPTER IV
THE ROLE OF PHYSICAL DISTURBANCES AND DENSITY-DEPENDENCE IN THE
POPULATION DYNAMICS OF THE COMMERCIAL SEAWEED GELIDIUM
SESQUIPEDALE

4.1 Introduction

Gelidium sesquipedale (Clem.) Bornet et Thuret (Rhodophyta, Gelidiales), is a clonal red alga that grows in the subtidal off the Northeast Atlantic coast. Upright fronds are produced from a small, prostrate system of axis (Dixon, 1958; Fan, 1961). Dense monospecific stands of clumped fronds develop on exposed shores along the Portuguese coast, covering wide areas of the bottom (Chapter II). The populations are subjected every summer and fall to commercial harvesting by divers, who hand-pluck the seaweed for its agar (Chapter I). As well, natural wave-induced physical stresses likely have an important role on the population dynamics of G. sesquipedale, since local distribution of the Gelidiales are strongly related to wave exposure (Santelices, 1988). Large quantities of G. sesquipedale storm-tossed fronds have been traditionally gathered on shore, providing important quantities of raw material to the agar industry (Appendix 1).

To assess the functioning of populations, plant ecologists have studied the temporal dynamics of frequency distributions of some measure of an individual's size such as plant length, plant mass, stem diameter or leaf area. These frequencies represent a one-time portrayal of the dynamic interaction of the demographic parameters growth, survival and recruitment. Significant changes of size structure through time reflect the combined effect of demographic parameters.

The patterns of difference of size frequency distributions within and among populations have been studied graphically (Mack and Harper, 1977), or mathematically, by considering some statistical measure of distributions. The statistics mean, variance,

skewness and kurtosis describe distributions in considerable detail (Hara, 1988). The fact most plant populations consist of many small individuals and relatively few large ones led to research focused on the skewness of size structures (Koyama and Kira, 1956; Rabinowitz, 1979; Higgins et al., 1984; Schiel, 1985; Higgins and Mack, 1987). Weiner and Solbrig (1984) proposed the use of the Gini coefficient (G) to quantify how individuals of a plant population are ranked in size classes. They claim the Gini coefficient is a better measure of the size differences among individuals in a population (inequality) than the skewness coefficient. There have been several applications of the Gini coefficient (Weiner, 1985; Weiner and Thomas, 1986; Schmitt et al., 1986, 1987; Bonan, 1988; Geber, 1989; Thomas and Weiner, 1989; Martinez and Santelices, 1992). Plant ecologists have also used the coefficient of variation (C.V.=standard deviation/mean) as a statistical measure of inequality among members in a population (Kira et al., 1953; Edmeades and Daynard, 1979; Mack and Pyke, 1983). Bendel et al. (1989) showed that the statistic chosen for the comparison of frequency distributions affects the results. The skewness coefficient, the coefficient of variation and the Gini coefficient have different behaviors, which depend on the underlying distribution of the size metric.

Most work on size distributions of plant populations has been done on greenhouse or on field crops (see reviews by Weiner and Thomas, 1986 and Geber, 1989). However, to understand how demographic processes regulate the structure of natural stands developing in heterogeneous environments, field studies must be conducted (see Schmitt et. al, 1986; Ellison, 1987). In contrast with greenhouse cultures, the structure of natural stands reflects environmental and biotic disturbances in addition to intraspecific competition, which have substantial effects on self-thinning relationships and patterns of size structure change (Thomas and Weiner, 1989).

Intra-specific competition may determine the survival and growth of small fronds within G. sesquipedale's typical crowded stands. Two empirical relationships have been

shown for higher plants under such conditions. The self-thinning rule, or $-3/2$ power law (Yoda et. al, 1963), states that the relationship between biomass and density in crowded monospecific plant stands, forms a thinning line of slope $-3/2$ and an intercept of 4.3, when mean plant weight and density are plotted in log scale; equivalently, a line of slope $-1/2$ and the same intercept, is defined when the logarithm of stand biomass is plotted in place of average plant weight (see review in Westoby, 1984). Weller (1987) concluded that the use of mean frond weight rather than stand biomass is statistically incorrect. If density-independent stresses are absent at the boundary condition defined by the thinning line, mortality or "thinning" of smaller plants is caused by density-dependent competition. This relationship was defined as a general "law" governing any even-aged plant population, and is supported by a wide variety of data from both artificial and natural stands of land plants (White and Harper, 1970; White, 1980; Westoby, 1984), and on seaweeds (Cousens and Hutchings, 1983). Weller (1987) has since shown that the slopes and intercepts of thinning lines are more variable than previously thought.

Although the relationship between density and mean plant weight is much studied, only recently has self-thinning been related to weight inequality (Weiner and Thomas, 1986; Bonan, 1988; Geber, 1989). In a crowded monospecific stand weight inequality generally increases over time until the onset of self-thinning, due to differential growth rates between larger and smaller "suppressed" plants. Then, inequality decreases as self-thinning progresses due to differential size-specific mortality rates. This trend is interpreted as being consistent with the asymmetric competition hypothesis of dominance and suppression of smaller individuals by bigger ones (Begon, 1984; Hara, 1988).

The current study assesses the dynamics of a G. sesquipedale commercial stand and the role played by physical disturbances such as harvest and storms. Seasonal changes of mean frond weight, mean frond length, biomass and density are shown as well as those of frond length and weight structures, quantified by the Gini coefficient (G), the coefficient of

variation (CV), and the skewness coefficient (g_1). These are interpreted in relation to the demographic rates (frond growth, breakage, mortality and recruitment) that determine the population parameters' variability (Chapter III). The performance of the coefficients is discussed. G. sesquipedale weight/length allometry, "the differential growth of parts or metrics of an organism" (Gould, 1966), is also investigated. The two empirical relationships, biomass-density and inequality-mean frond weight, observed in crowded plant stands, are tested to assess density-dependent processes. Based on the information gathered, a conceptual model for the functioning of the population is proposed.

4.2 Methods

It is difficult to match an upright frond with its prostrate system within G. sesquipedale's dense stands, and thus to distinguish fronds that originated from different spores (different genets sensu Harper, 1977). Therefore, G. sesquipedale population dynamics was studied at the frond level, the module (sensu Harper, 1977) or the metamer (sensu White, 1979), i.e. genetically similar subunits of original genets, independently of their prostrate systems.

The field study was conducted in one of the most important G. sesquipedale commercial beds, off Cape Espichel, Portugal (Chapter I). Chapter II described the main biotic and abiotic interactions in this community. The same stand where the species vital rates were investigated (Chapter III), was sampled monthly from July 1989 to September 1990, except for the months of November and December 1989 and February 1990, when sea storms prevented diving. The variation in sampling diving time with biomass sample precision, the ratio of standard error to the mean (Riddle, 1989), had been previously determined for different quadrat sizes (15, 25, 40 and 50 cm) and numbers (Santos, unpublished data); a sample size of five, 40 cm quadrats was selected. All fronds inside the quadrats were removed by carefully handscraping the substrate; the fronds were placed

in a mesh bag. The resultant frond length frequency distribution was similar to that obtained when fronds were scraped and collected with a compressed air device (Santos, unpublished data). All plant material was preserved by freezing.

The variation in both frond morphology and size structure appeared significant between those from the upper and lower portions of the inclined strata upon which the population develops (Santos, pers, obs.). Sampling was thus restricted to the middle zone of the strata, at a constant depth of 9 m. Sampling in July was just prior to the harvest season, which started mid month and extends through the summer and fall (Chapter I).

G. sesquipedale mean frond weight and length were estimated for each monthly quadrat sample by measuring all fronds to the nearest mg and mm, respectively, in three sub-samples. Prior to measuring, the frozen fronds were thawed and surplus water was removed by blotting with paper towel. Allometric relationships between weight and length were analyzed by regression for all monthly samples. The best-fit regression model was achieved by log transformation of weight values, but not length values. A significant second-order polynomial term was considered evidence that the relationship between log weight and length was curvilinear.

4.2.1 Quantifying size structures variability

All data analysis were computed using Systat 5.1 for Macintosh (Wilkinson, 1989), except the Gini coefficient calculations, which were done using a program developed by the author. The skewness coefficient (g_1), the coefficient of variation (C V), and the Gini Coefficient (G), (Sokal and Rohlf, 1969; Kendall and Stuart, 1969), were computed for all samples, to assess the shape and inequality levels of both length and weight structures. Skewness is a shape parameter quantifying deviation in relation to the normal distribution; positive values indicate a long right tail (more small fronds and fewer large fronds) and vice-versa for negative values. In contrast, CV and G are measures of relative precision

that reflect the ratio of a measure of dispersion (respectively the standard deviation and the

coefficient of mean difference, $\sum_i^n \sum_j^n |x_i - x_j| / n^2$, due to Gini, 1912 in Weiner and Solbrig,

1984), to the mean. Unbiased Gini coefficients, G' (Weiner and Solbrig, 1984), were calculated as:

$$G' = \frac{\sum_i^n \sum_j^n |x_i - x_j|}{2\bar{x}n(n-1)}$$

where x_i and x_j are the measures of all possible pairs of individuals. If all observations are the same, representing a minimum inequality, then $G=0$. In an infinite population where all observations are zero except one, then G is maximum and has a value of 1.

Variability of size structure coefficients through time was analyzed using one way ANOVA. May 1990 values were not included in the statistical analysis, because only two quadrats were sampled. Data were log transformed, when necessary, to fulfill the condition of heterodasticity (Sokal and Rohlf, 1981). Post-hoc multiple contrasts analysis was done following Rodger (1974, 1975), to detect significant transitions among contiguous time periods. The critical values for rejecting null contrasts were taken from the F-values tables provided in Rodger (1975).

4.2.2 Density-dependent relationships

To assess density-dependent processes, the time trajectory of the relationship between the logs of both stand biomass and density were analyzed, rather than the more common approach of plotting log mean frond weight and log density (Yoda et al., 1963; White and Harper, 1970; Westoby, 1981, 1984; White 1981). Weller (1987) showed that use of average plant weight is statistically incorrect. The time trajectory of the relationship

between weight inequality, given by the Gini coefficient, and mean frond weight was also analyzed (Weiner and Thomas, 1986; Bonan, 1988; Geber, 1989).

4.3 Results

4.3.1 Variability of population parameters with time

There were significant differences for G. sesquipedale population parameters (mean frond weight, mean frond length, biomass and density) among sampling dates (one-way ANOVA, $p \leq 0.001$). Post-hoc multiple contrast analysis revealed three significant ($p < 0.05$) seasonal transitions (Fig. 4.1) of mean frond weight (Fig. 4.1A) and total biomass per square meter (Fig. 4.1C). High summer pre-harvest conditions in July 1989 were followed by lower levels, coincident with the start of harvesting. Unlike biomass, July 1989 mean frond weight was not significantly different ($p < 0.01$) from summer/early fall. Both parameters troughed in winter, after a period of severe sea conditions (November/December, 1989), when waves up to 7 m height hit the coast of Cape Espichel (Chapter III). In the seasonal transition from winter to spring/summer, mean frond weight and biomass increased, but never recovered the levels of July 1989 (Fig 4.1A, C).

G. sesquipedale mean frond length showed a similar seasonal pattern to mean frond weight and total biomass; a low in winter and incomplete recovery to post-harvest levels of 1989. However, mean frond length did not decrease during harvest seasons (Fig. 4.1B). Frond length increase, observed after the lowest level (January 1990), was faster than frond weight (Fig. 4.1B), indicating that during this period fronds elongate rather than branched. Branching was more intense after April 1990, based on the rapid increase in mean frond weight (Fig. 4.1A).

Seasonal variation of G. sesquipedale frond density was not as important as the other parameters, and in fact significant seasonal periods could not be detected at a significance level of $p = 0.01$. Four seasonal periods are separated at $p < 0.05$ (Fig. 4.1D). Density

decreased from July 1989 to August 1989, and troughed during fall and early winter. In spring/early summer, frond density recovered to July 1989 levels, decreasing again in August 1990. This was the only significant drop in population parameters during the 1990 harvest season (Fig. 4.1 D), but it is likely not related to harvest since the rest of the population parameters did not decrease during this period (Figs. 4.1A,B and C). September 1990 density was not significantly different from August 1990, but when the two months were lumped, density was not significantly different (at $p \leq .05$) from July.

4.3.2 Length-biomass allometry

Regressions between G. sesquipedale frond weight (log) and length are highly significant for all months ($p < .001$). The coefficient of determination, r^2 , (adjusted in the case of second-order regressions) is high in all cases, indicating the good predictive capacity of the models (Table 4.1). Only on three occasions; July 1989, September 1989 and March 1990, were the second-order regressions terms not significant (P^* values of Table 4.1), showing that frond weight increased exponentially with length. Linear models were fitted in these cases. All significant second-order terms have negative signs, indicating that weight increase with length was slower for these cases. Although significant, due to the high number of observations (Table 4.1), the second order-terms only slightly improved the models' performances. The fraction of the total variance explained by the second-order term is small, particularly before April 1990, when the additional variance explained was $\leq 1\%$ (Table 4.1). In May 1990, however, the second-order model explained 11% more variance than a linear model.

The weight-length relationship of G. sesquipedale fronds varied significantly through time (Fig. 4.2). Just prior to the 1989 harvest season, the slope (1st order coefficient) of the relationship was maximum. G. sesquipedale frond weight increased exponentially with length. Following the harvest, the slope of the relationship strongly decreased. A period

of high slope variability with peaks in September 1989, January 1990 and April 1990, followed. During the subsequent spring/summer the slope of the relationship stabilized, progressively increasing with time (Fig. 4.2). G. sesquipedale fronds were then growing faster in weight than in length, perhaps due to the production and growth of lateral branches.

The increasing importance of the second-order coefficient during the summer of 1990 indicates that the shape of the curves is bending (Fig. 4.3). This pattern is more conspicuous when the second-order polynomial regressions were plotted without the observations, and setting the intercepts to zero (Fig. 4.3C). The more pronounced frond branching in intermediate length fronds than in longer fronds is evident from the curvature of the plots. The portion of the frond weight-length cloud below 4 cm (Fig. 4.3A,B), shows a zone where the growth of G. sesquipedale fronds is linear (in absolute values), because small fronds were not branched.

4.3.3 Population structure seasonal variation

The statistical significance of G. sesquipedale weight-inequality change over time is low (p values of Table 4.2), and therefore a clear seasonal pattern was not detected. Temporal variation of CV and g_1 (Fig. 4.4B, C), at significance levels of $p=.06$ and $p=.05$, were due to the reduction of G. sesquipedale fronds, in the small and large weight classes (Fig. 4.5), from August 1989 to August 1990. This causes both a decrease in the variation of frond weights in relation to the mean (CV), and the flattening of the shape of the distribution, reducing the skewness coefficient value (g_1).

In contrast, the time variation of G. sesquipedale frond length distribution inequality is highly significant ($p<.001$, Table 4.2). Three significant seasonal transitions were detected by post-hoc multiple contrast analysis ($p<.05$), when using G and CV statistics (horizontal bars, Figs. 4.6A, B). The two periods, August/October 1989 and

June/September 1990, are not significantly different from each other. When analyzing the length distributions with the skewness coefficient (g_1), only two significant transitions are revealed (Fig. 4.6C). Length distribution skewness in July 1989 was not significantly different from that of August/September 1990.

Significant transitions in size distribution inequalities represent periods when the combined effect of frond growth, breakage and mortality, and recruitment of new fronds, was significant. To investigate these, all length data in each time period were pooled and frequency distributions plotted (1 cm size class density per square meter, Fig. 4.7). There was a general reduction in frond density between July 1989 and the period of August/October 1989 (Fig. 4.7A). Also, the right tail of the distribution increased, reflecting elongation of shorter fronds.

The next significant seasonal transition was between August/October 1989 and January/April 1990, characterized by an increase in density of fronds < 4 cm, and a decrease in density for fronds > 6 cm. (Fig. 4.7B). During the last seasonal transition, to the period June/September 1990, a reverse pattern was observed (Fig. 4.7C). The density of smaller fronds decreased, while the density of larger fronds increased due to the growth of the winter recruits.

4.3.4 Density-dependent relationships

Additional data of seven quadrat samples obtained at the same site in July 1988 are included in the log biomass and log density plots (Fig. 4.8A). Data points lay mostly above the theoretical boundary line for self-thinning populations shown in the graph, $\log_{10} B = 4.3 - 1/2 \log_{10} N$, where B is the stand biomass density (per m^2) and N is frond density (per m^2) (Fig. 4.8A). The highest values for *G. sesquipedale* weight and density were in July 1988 and July 1989, while the lowest values occurred the following winter

(January 1990/March 1990). The time trajectory of the relationship increased from winter of 1989 to July 1990, but did not reach the values of July 1988 and 1989 (Fig. 4.8A).

G. sesquipedale weight inequalities (Gini coefficient) during 1989/1990, increased significantly ($R^2=.29$, $p<.001$) with mean frond weight. The time trajectory of this relationship shows a similar pattern to the biomass-density relationship (Fig. 4.8B). Values increased from winter to summer, decreasing afterwards. The maximum values of 1990, attained in August, were lower than those of 1989. *G. sesquipedale* mean frond weight was low (Fig. 4.1A), and there were fewer heavier fronds than in August 1989 (Fig. 4.5), when weight inequality peaked. The regression line showed in the graph includes July 1988 values ($R^2=.45$, $p<.001$).

4.4 Discussion

4.4.1 Population dynamics

G. sesquipedale population dynamics, not unexpectedly, showed a marked seasonality; frond weight, length, density and total biomass peaked in summer and troughed in winter (Fig. 4.1). Population parameter changes were related to both environmental and human induced disturbances (storms and harvest). The sharp drop in all populations parameters, except mean frond length after July 1989, reflected in the first significant transition of frond length distribution (Fig. 4.7A), is coincident with the start of harvest season. During this season, 12 boats carrying an average of four divers, collected about 1700 t of wet seaweed (J. Oliveira, pers. com.). That mean frond length does not decrease with the 1989 harvest, suggests that some fronds may have lost their branches while their main axis remained intact, or that heavier fronds (more branched with more surface) are more likely to be detached than longer, less branched fronds. A similar situation was observed in *Chondrus crispus* commercial beds off Prince Edward Island,

Canada, where the dragrake appears to select for the branched fronds (Pringle and Semple, 1988).

Winter low values for the measured population parameters followed a period of unusually strong storms (Chapter III, Fig. 3.4). The dynamics of frond survival, growth and recruitment during this period, derived from the analysis of the seasonal transitions of length structures (Fig. 4.7), are supported by Santos' (Chapter III) tagging study of G. sesquipedale frond dynamics. Summer to winter transitions are caused by the longer fronds' higher mortality during harvest and higher frond breakage during storms.

The pulse of short fronds (≤ 4 cm), observed in winter/early spring (Fig. 4.7), reflects recruitment of new fronds rather than breakage of longer fronds, because density increased during this period (Fig. 4.1). Chapter V showed that the number of size class 1 fronds (4 to 10 cm) is high even after discounting both frond breakage and growth, respectively, into and out of the class. The pulse of size class 1 fronds was detected in March/April (Chapter V), indicating that new fronds developed some months earlier, probably in reaction to the reduction of the canopy due to late fall storms.

Frond recruitment appears to originate by vegetative growth of the prostrate system (Dixon, 1958; Fan, 1961), rather than through the development of new fronds from spores. Vegetative growth is the most important process for the recovery of populations of Gelidium species (Santelices, 1988). This was supported by the lack of frond recruitment of G. sesquipedale on ceramic tiles placed in the study site (Santos, unpublished data). A similar dynamic has been suggested for the highly disturbed commercial stands of G. crispus off Prince Edward Island, which have higher densities of small fronds than do non-harvested beds (Chopin et al, 1988).

G. sesquipedale fronds recruited in winter, grew to longer size classes during spring/summer of 1990 (Fig. 4.7C). Yet, the stand did not recover to the maximum values of July 1989. Frond length distribution change from summer 1989 to 1990 reflects this

(Fig. 4.7). The same trend is shown in demographic simulations of the population and was supported by the large decrease in harvest landings between 1989 and 1990 (Chapter V). The effects of harvesting on the G. sesquipedale population parameters was not detected in 1990, likely due to reduced effort, probably because of poor catch per unit effort.

4.4.2 Performance of size-distribution coefficients

The behavior of the three statistics used to quantify the temporal variability of the size-distributions of a natural stand of G. sesquipedale generally agrees with Bendel et al.'s (1989) conclusions, derived from both artificial and empirical greenhouse experiments. The Gini and the coefficient of variation had similar performances, whereas skewness was more related to the latter. G and CV were highly correlated to one another for both weight and length ($r=0.84$ and $r=0.98$, respectively), while g_1 was, in both cases, more correlated to CV ($r=0.78$ and $r=0.68$, respectively) than to G ($r=0.36$ and $r=0.57$, respectively). Gini is a more robust inequality measure than CV and g_1 ; it has lower values of sum of squares within groups (Table 4.2), because it is less sensitive to variation in the distribution tails (Bendel et al., 1989).

The performance of the coefficients when applied to weight vs length distributions was different, particularly for G and CV (Figs. 4.4 and 4.6). G. sesquipedale population inequality can not be studied using weight or length differently as measures of size. Frond length might be preferred to weight. It was not possible to detect seasonal variations of the species weight structure, because the statistics are sensitive to variations of the right tail of these highly skewed distributions (Fig. 4.4). The presence of a few heavy fronds has an important effect on weight statistics; a larger sample size was thus needed. Also, weight variation for small changes in length is low, particularly in small fronds, and thus more difficult to detect. CV and g_1 coefficients might be more appropriate than G to study

weight distributions. G failed to detect any temporal variability of G. sesquipedale weight inequality (Table 4.2).

4.4.3 Allometric relationships

G. sesquipedale frond weight-length relationships were highly variable through time (Fig. 4.2), supporting Weiner and Thomas' (1992) suggestion that size is not a unified concept in those plant species showing great plasticity in growth form. Inferences from one size metric to another in G. sesquipedale are not accurate, unless the time variability of the relationship is considered. Plant allometric changes can be explained in terms of intra-specific competition and size-dependent growth after the onset of competition (White, 1981; Weller, 1987; Weiner and Thomas, 1992). Yet, in natural populations of G. sesquipedale, physical disturbances are likely to play a fundamental role on allometry variability. The loss of branches due to commercial harvest and storms, reduces the slope of the weight-length relationship to a low in winter (Fig. 4.2). During spring and summer the opposite pattern was observed, probably due to the production and growth of lateral branches (Fig. 4.2). The peaks of first-order coefficients observed in September 1989, January 1990 and April 1990, followed periods when high frond breakage (Chapter III) reduced the slope values to low levels (Fig. 4.2). This may be explained by an increase in frond weight without elongation, due to the concentration of storage substances in broken fronds to induce regeneration. The lowest elongation rates of fronds immediately after breakage compared with intact fronds support this hypothesis (Chapter III).

The storage of photosynthates for later growth is common in seaweeds. This process may increase substantially the weight of individuals, particularly in kelp species of the genus Laminaria where laminarin may account for 36% of the total dry matter (review in Mann, 1973). The nitrate and ammonium uptake rates of immature L. groenlandica plants was higher than in larger plants, preparing them for growth (Harrison et al., 1986).

Kaliaperumal and Kalimuthu (1976) observed that manitol content of Turbinaria decurrens Bory increased prior to reproduction.

G. sesquipedale weight-length allometry indicate that in spring/summer frond branching is high, particularly for intermediate length fronds (4 to 14 cm, Fig. 4.3C). Branching was evident from the increase in mean frond weight from April to May, after a period when weight was constant despite the increase of frond mean length (Fig. 4.1A, B). Higher increase in weight through branching of intermediate length fronds may be due to different growth patterns, or simply the loss of lower lateral branches in longer fronds (Dixon, 1958; Seoane-Camba, 1969). Other explanations may lie in the fronds' past condition. Those having lost the apical tip through breakage of the main axis may become bushier and heavier through the development of several axes from the cut surface (Felicini and Arrigoni, 1967; Felicini, 1970), compared with intact fronds. Aspects of Gelidium regeneration capacity by differentiation of one or more cortical cells of the injured zone into new apical cells has been studied (Dixon, 1958; Felicini and Arrigoni, 1967; Felicini, 1970; Reguera et al., 1978), but subsequent morphological changes have never been addressed.

4.4.4 Density-dependent relationships

The time trajectory of G. sesquipedale inequality-mean frond weight relationship (Fig. 4.8B) is consistent with the asymmetric competition theory (Begon, 1984; Hara, 1988), where, in crowded stands, weight inequality is predicted to increase with increased mean plant weight until the onset of self-thinning. At this point, inequality decreases as mortality of smaller plants progresses (Weiner and Thomas, 1986). The G. sesquipedale population studied here never reached a distinct self-thinning situation.

G. sesquipedale weight inequality/mean frond weight relationships increased from a low in winter to a maximum in summer (Fig. 4.8B), suggesting a differential biomass increase between heavier and lighter fronds during this period. A similar pattern was also

observed for frond elongation rate (Chapter III). Differential growth may be due to density-dependent suppression of smaller fronds by larger ones or by a density-independent difference in growth patterns. Although G. sesquipedale axis elongates by division of one apical cell (Rodriguez and Santelices, 1987), the rate of elongation of subsequent cells may be higher in larger fronds, independent of crowding. Further studies are needed to clarify this point.

During this period, although frond mortality was higher for shorter than longer fronds (Chapter III), its effect was not strong enough to decrease size inequality or to be detected in the biomass-density relationship (Fig. 4.8A). The time trajectory of this relationship did not bend along a self-thinning line, the dynamic self-thinning line of the stand (Weller, 1990), as predicted. The decrease of both relationships from summer to winter (Fig. 4.8A, B) was induced by physical disturbances (commercial harvest and storms) that caused higher mortality and breakage of larger fronds (Chapter III).

Thomas and Weiner (1989) noted that the ability of small, suppressed plants of the annual, Impatiens pallida Nutt., to survive was critical in determining the relationship between mean plant weight and size inequality. They report a slope of 0.41 before the onset of self-thinning, which is similar to the slope of 0.45, found for G. sesquipedale (Fig 4.8B). In plant populations where self-thinning is important, slopes of -0.20 and -0.10 were reported, respectively for two conifer species (Weiner and Thomas, 1986) and for the annual wild-rice Zizania aquatica (Weiner and Whigham, 1988).

The onset of natural self-thinning in G. sesquipedale populations is probably precluded by the thinning and frond breakage caused by harvest during early summer. Gelidium spp. generally occurs in habitats exposed to strong wave surge (Santelices, 1988), hence they likely rarely reach a self-thinning situation. Following summer production peaks, large biomass losses occur during fall/winter storms, which are

harvested along the shores in different parts of the world, and constitute the basis of important agar industries (Michanek, 1975; Santelices, 1988; Appendix 1).

A general trend towards increasing weight inequality with increased mean plant weight through time has been observed in greenhouse studies (see review by Weiner and Thomas, 1986) and in natural land plant stands (Schmitt et al., 1987; Thomas and Weiner, 1989). In seaweeds, there are insufficient data to determine whether density-dependent thinning is common. Possibly, the only published work analyzing this relationship is Martinez and Santelices (1992), who found no significant relationship between G and mean frond weight in a Chilean population of the red alga Iridaea laminarioides. The authors suggest this might be common in seaweed species, resulting from a lack of self-thinning, as Pitelka (1984) reported for physiologically integrated clonal ramets. Martinez and Santelices (1992) studied this relationship at only one point in time, it is thus not possible to understand the time trajectory of the relationship. Ang and De Wreede (1993) observed a general increase in size inequality in the development of seeded blocks and cleared plots of Fucus distichus (L.) Powell from winter to spring, probably due to a greater mortality of smaller plants (Ang and De Wreede, 1993). This trend became less distinct in summer due to increased mortality of larger plants.

In seaweeds, the more appropriate competition model might be the one-sided, as opposed to two-sided model, in which resource depletion will have an effect proportional to the size of the plant (see review of plant competition models in Weiner and Thomas, 1986). The one-sided competition model predicts that small plants will be more suppressed than bigger ones when resources are not evenly distributed, i. e. when larger plants can have more resources than the smaller ones, because of size. This is the generally accepted model in higher plants when competition is for light, but when it is for nutrients, the two sided model may be more appropriate. In subtidal seaweeds, not only is light more readily available for larger plants, but so are nutrients due to the fluid mechanics of this

environment. Under the canopy, water movement is reduced and the boundary layers of small fronds can be more easily nutrient depleted (Koehl, 1986; Denny, 1988). Larger plants are more exposed to both light and water movement, at least in the upper parts of the thallus. This is particularly important in species such as Gelidium spp where growth is apical.

This work shows the importance of disturbances, both natural (stochastically occurring storms) and human (predictable harvest) on the regulation of G. sesquipedale population dynamics. The following conceptual model of the species population dynamics is suggested (Fig. 4.9). Both the relationships, biomass-density and inequality-mean frond weight, decrease from summer to winter (Fig. 4.9) due to physical disturbances. Disturbances cause high large frond mortality and breakage during summer and fall (Chapter III), keeping intra-specific competition at low levels. During such periods, smaller frond elongation rate is high and their mortality is low (Chapter III). The recruitment peak of vegetatively developed fronds follows these disturbances (Fig. 4.7), and is probably induced by biomass loss. During spring and early summer, the opposite pattern was observed (Fig. 4.9) due to faster growth and lower mortality of larger fronds (Chapter III). The G. sesquipedale stand studied never reached the level where extensive self-thinning caused the time trajectory of these relationships to bend in opposite directions (Fig. 4.9), as Weiner and Thomas (1986) and Weller (1987, 1990) reported for higher plants. The dynamic-thinning line (Weller, 1990) of this G. sesquipedale stand may be well above the interspecific self-thinning line (Yoda et al., 1963; Weller, 1987). To assess if density-dependent self-thinning occurs in natural stands of G. sesquipedale or other subtidal clonal algae, similar studies should be done in non-harvested populations or in years when wave surge is less extreme.

Table 4.1. Significance tests for allometric relationships between Gelidium sesquipedale log frond weight and frond length.

Date	N	r ²	Sign	P*	% Change in r ²
4-Jul-1989	462	0.73		0.568	0.00
2-Aug-1989	706	0.75	-	0.001	0.00
6-Sep-1989	494	0.76		0.206	0.00
4-Oct-1989	556	0.79	-	0.005	0.00
8-Jan-1990	1970	0.69	-	<0.001	0.01
9-Mar-1990	1186	0.81		0.811	0.00
24-Apr-1990	1113	0.78	-	<0.001	0.05
18-May-1990	357	0.82	-	<0.001	0.11
16-Jun-1990	825	0.84	-	<0.001	0.07
10-Jul-1990	865	0.80	-	<0.001	0.04
29-Aug-1990	789	0.84	-	<0.001	0.05
25-Sep-1990	910	0.80	-	<0.001	0.06

N: n^o of observations; r²: adjusted coefficient of determination of best fitted model (simple or second order); Sign: sign of significant second-order term; P*: significance of second order term in regression; % Change in r²: Fraction of sample variation that is explained by second-order term = 1-(r² linear/r² 2nd-order)

Table 4.2. ANOVA summary statistics for time variance of Gelidium sesquipedale weight and length distribution inequality. G = Gini coefficient, CV = coefficient of variation, g_1 = skewness coefficient.

Coefficient	Sum of Squares		F	Probability
	between groups (df=10)	within groups (df=44)		
G' (weight)	0.034	0.097	1.532	0.160
log CV (weight)	0.491	1.074	2.014	0.055
log g_1 (weight)	1.454	3.074	2.081	0.047
G (length)	0.075	0.025	13.409	0.000
log CV (length)	0.745	0.283	11.562	0.000
g_1 (length)	3.219	3.405	4.159	0.000

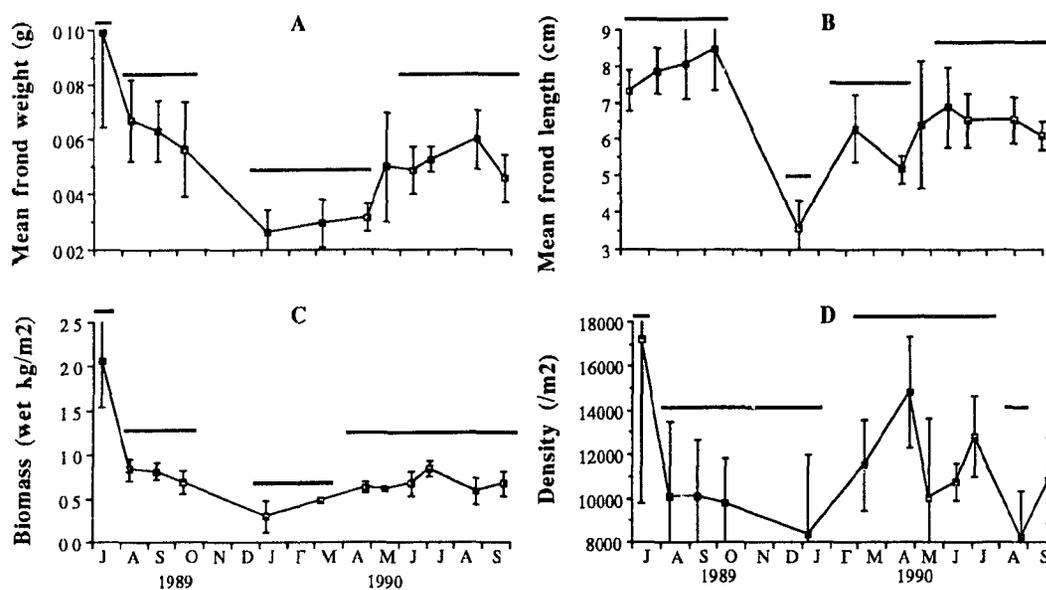


Fig. 4.1. Time variation of *Gelidium sesquipedale* population parameters, frond weight (A), mean frond length (B), biomass per square meter (C) and density per square meter (D). Vertical bars indicate one standard deviation from the mean (n=5). Horizontal lines show significant seasonal transitions (at p<.05). Bars at the same level are not significantly different. May sample (n=2) was not included in statistical analysis.

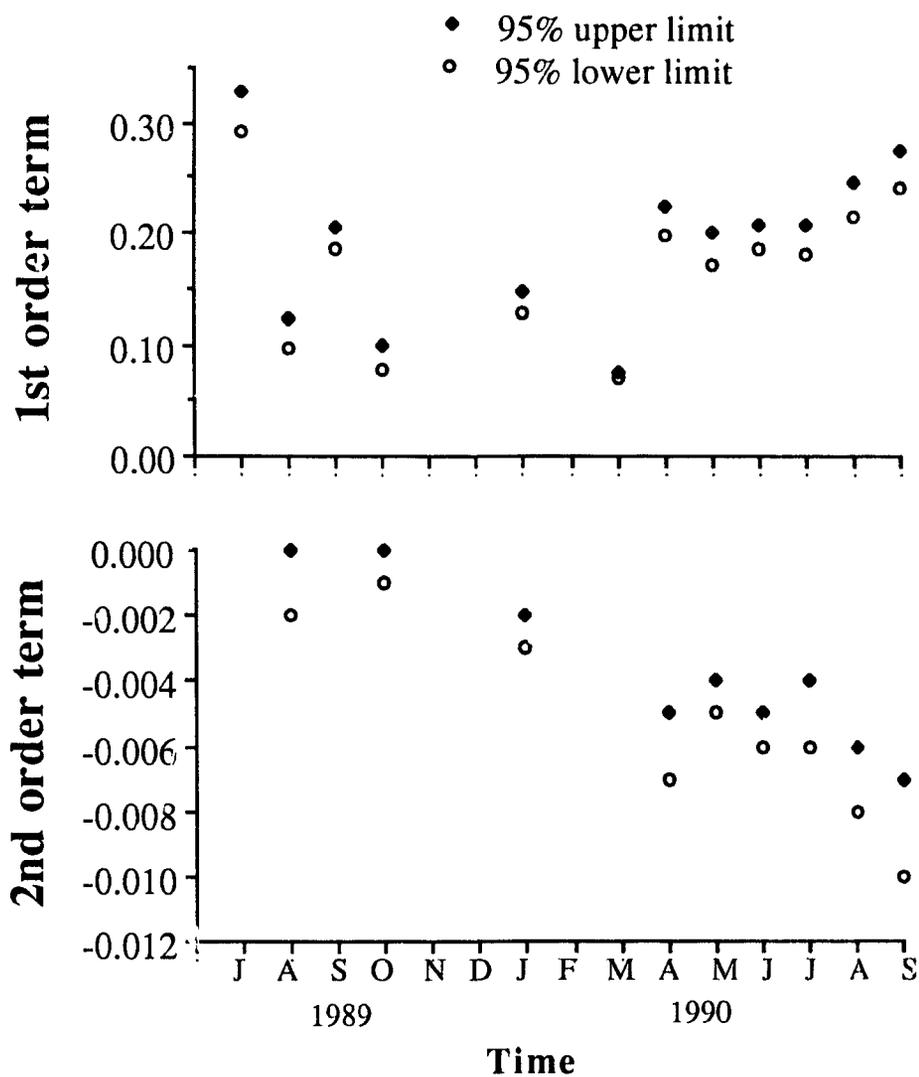


Fig. 4.2. Time variation of second-order polynomial regression coefficients between *Gelidium sesquipedale* log mean frond weight and mean frond length. Upper and lower 95 % confidence limits are plotted. Linear models were fitted in the months of July 1989, August 1989 and March 1990 because second-order terms were not significant.

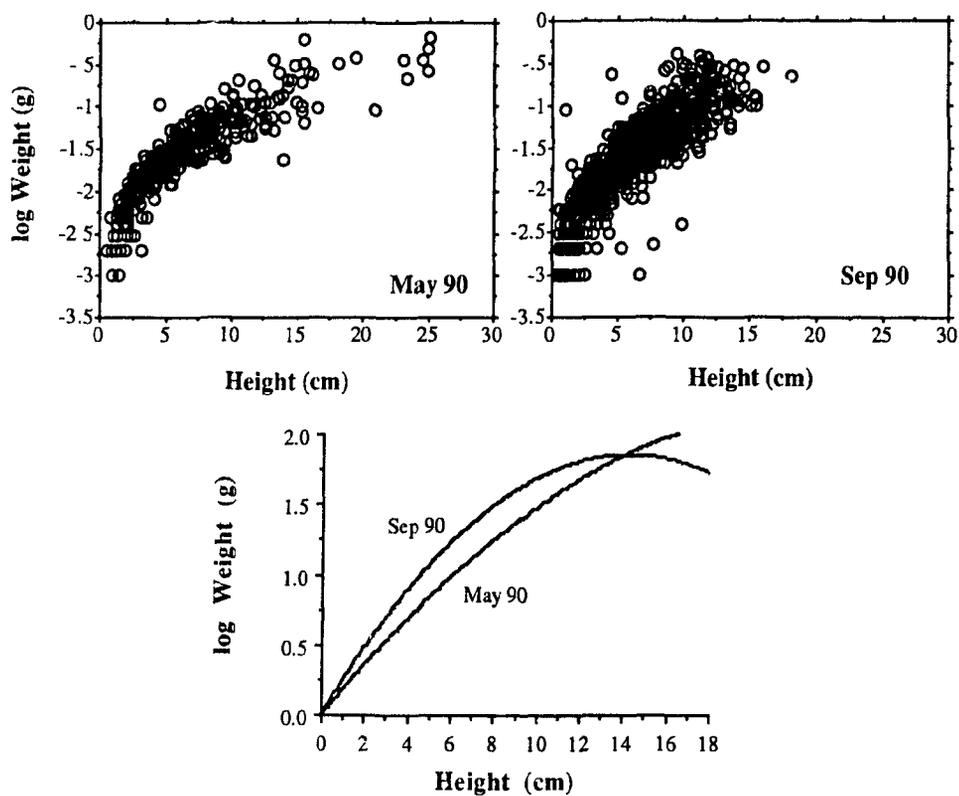


Fig. 4.3. Change in shape of the Gelidium sesquipedale log weight-length relationships during summer, 1990. For clarity, only May 1990 (A) and September 1990 (B) months are presented. Line graph shows second-order polynomial regression curves without plotting data points (C).

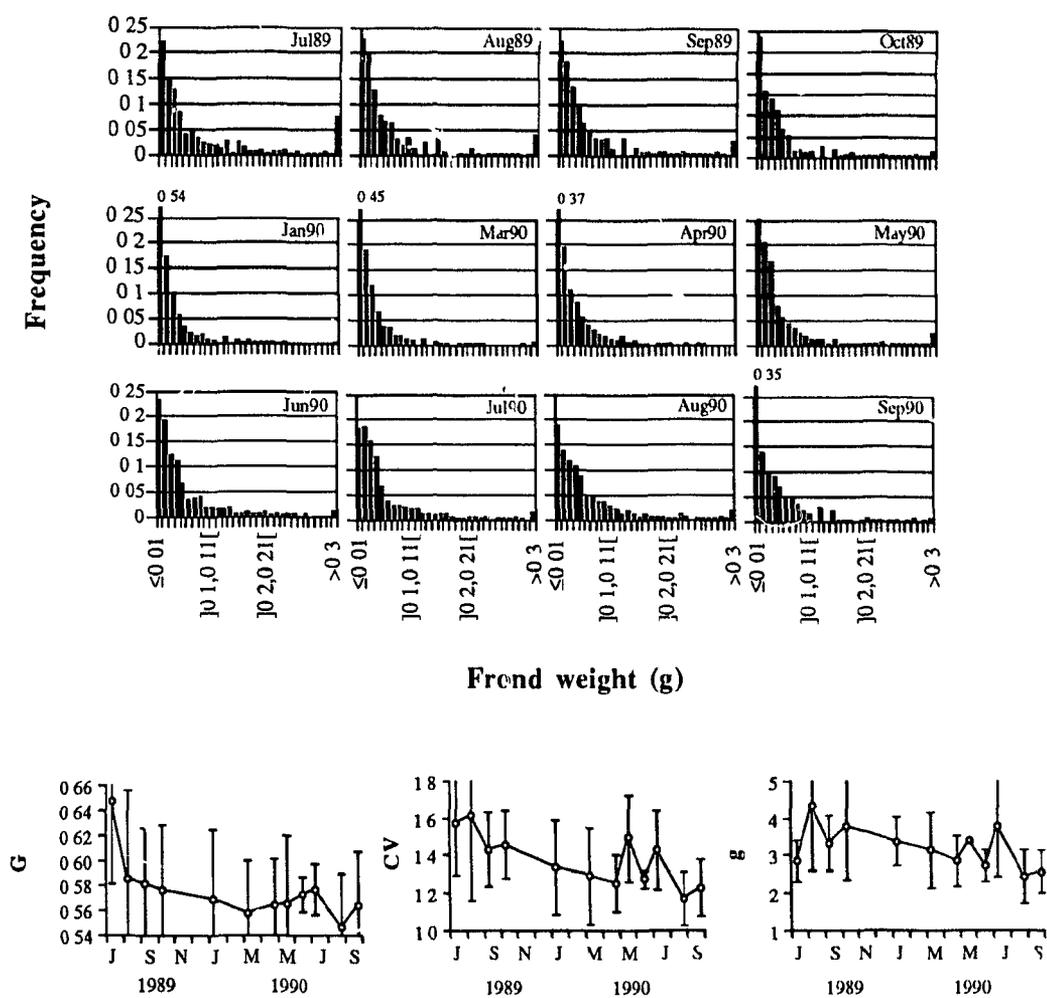


Fig. 4.4. Annual variation of *Gelidium sesquipedale* weight structures (bar graphs) and weight distribution inequalities (line graphs), measured by (A) the Gini coefficient (G), (B) the coefficient of variation (CV) and (C) the skewness coefficient (g_1). Vertical bars of inequality graphs indicate one standard deviation from the mean (n=5). May sample (n=2) was not included in statistical analysis.

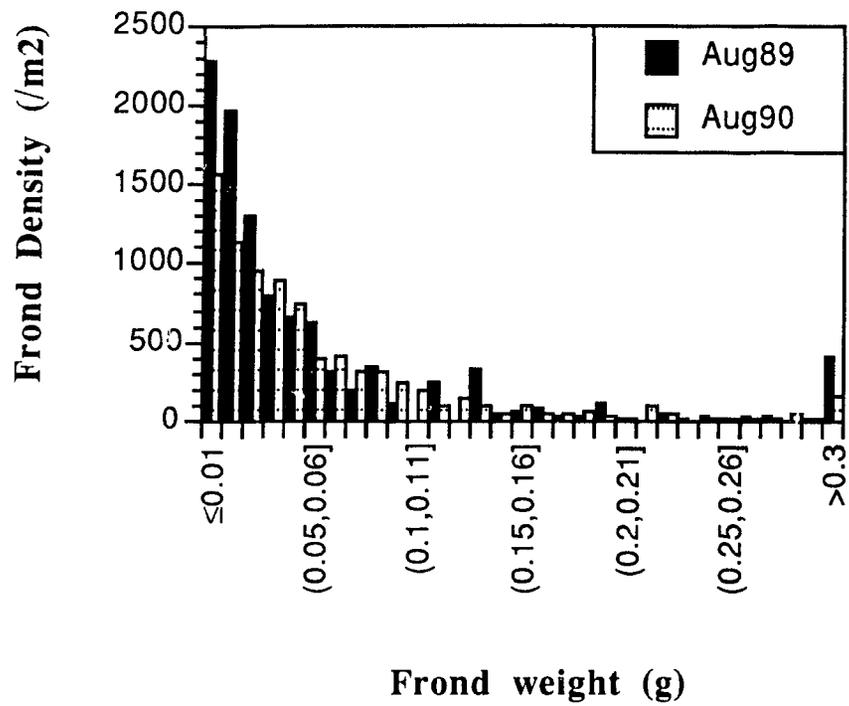


Fig. 4.5. Comparison of the significant changes for the inequality of *Gelidium sesquipedale* weight distributions: August 1989 to August 1990.

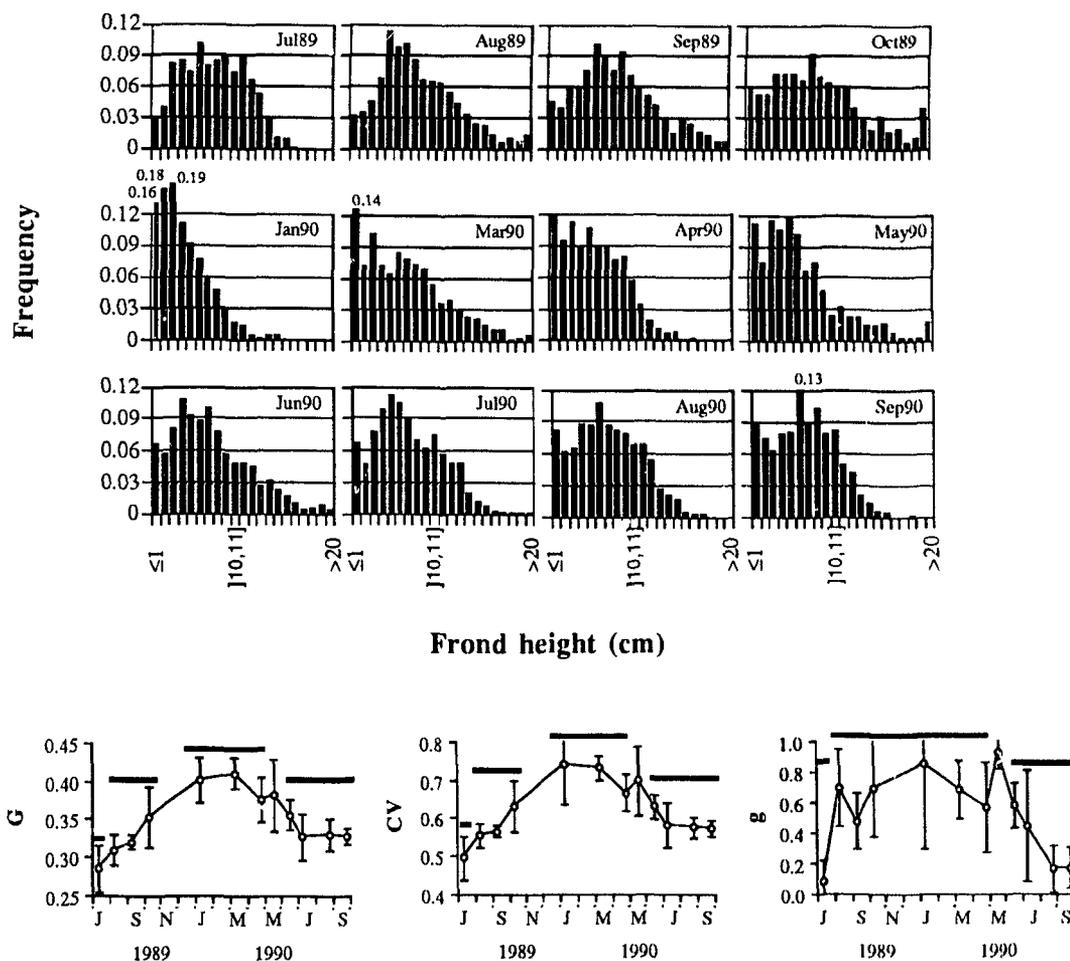


Fig. 4.6. Annual variation of *Gelidium sesquipedale* length structures (bar graphs) and length distribution inequalities (line graphs), measured by (A) the Gini coefficient (G), (B) the coefficient of variation (CV) and (C) the skewness coefficient (g_1). Vertical bars of inequality graphs indicate one standard deviation from the mean ($n=5$). Horizontal lines show significant seasonal transitions (at $p < 0.05$). May sample ($n=2$) was not included in statistical analysis.

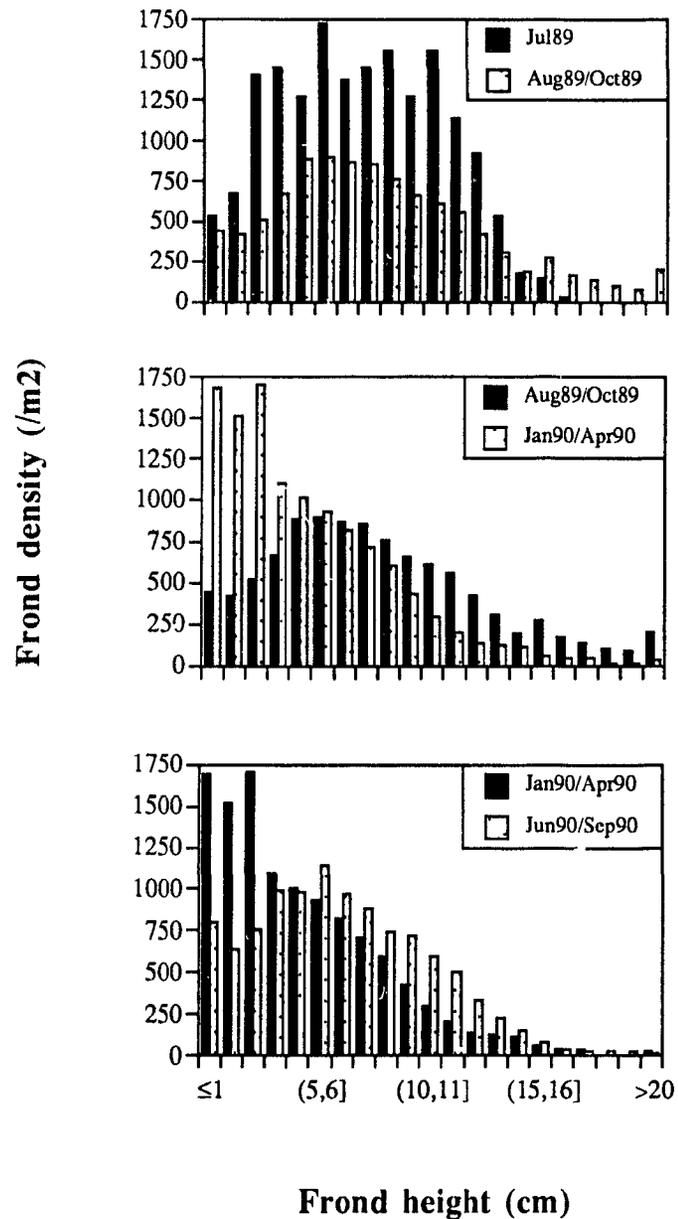


Fig. 4.7. Comparison of the three significant changes on the inequality of *Gelidium sesquipedale* length distributions; from July 1989 to August/October 1989 (A), from August/October 1989 to January/April 1990 (B) and from January/April 1990 to June/September 1990 (C).

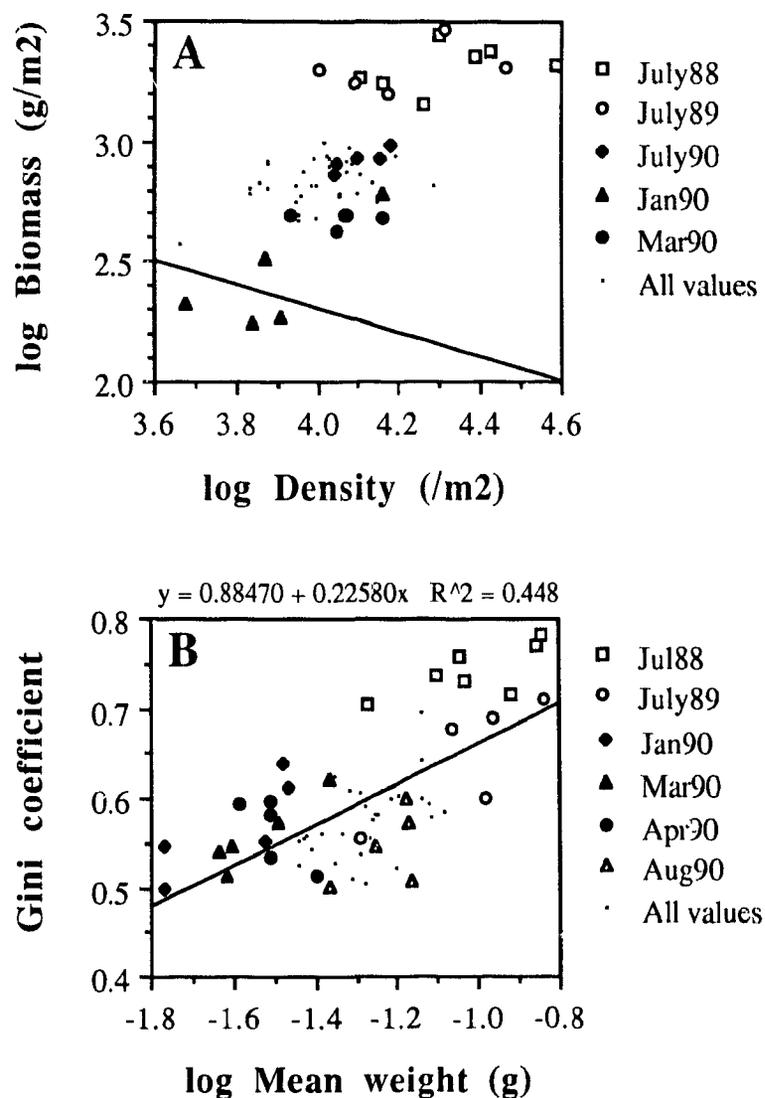


Fig. 4.8. (A) Time trajectory of the relationships between *Gelidium sesquipedale* log biomass (per m²) and log density (per m²) and (B) between frond weight inequality (Gini coefficient) and log mean frond weight. Line presented in A is the self-thinning line (see text). Regression between the Gini coefficient and log mean weight includes July 1988 values.

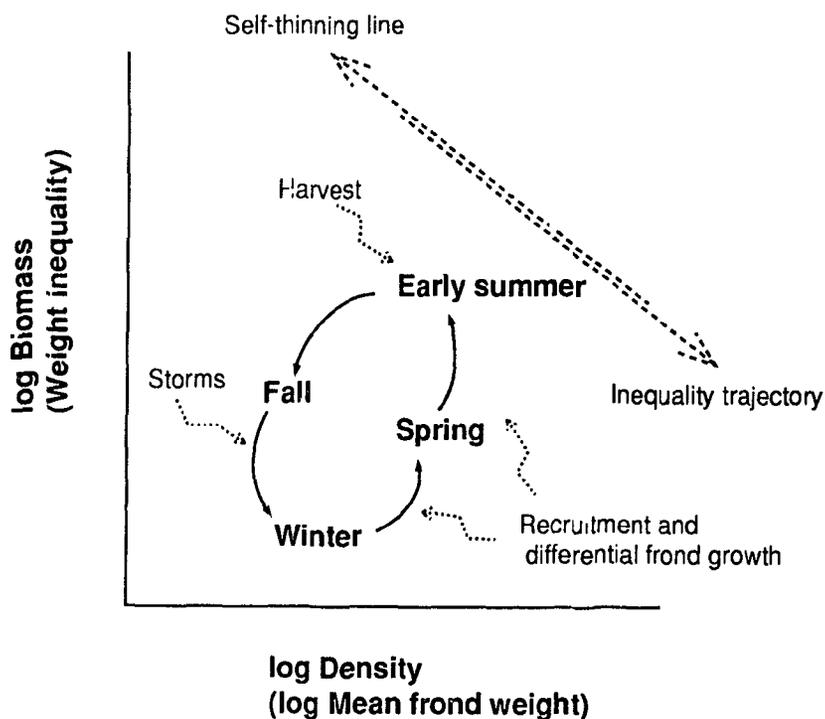


Fig. 4.9. Conceptual model of *Gelidium sesquipedale* population dynamics. The relationships between both log biomass and log density and between inequality (Gini coefficient) and log mean frond weight increased from winter to summer. This was due to the suppressed growth of smaller fronds during this period of high elongation rates. The population studied did not attain a self-thinning condition when the time trajectory of the relationships should bend along opposite directions (dashed arrows). Physical disturbances (harvest and storms, dotted lines) caused high mortality and breakage particularly of larger fronds, reducing intra-specific competition pressure to low levels where self-thinning does not occur. Both relationships decreased during this period to a low in winter.

CHAPTER V

PLUCKING OR CUTTING GELIDIUM SESQUIPEDALE? A DEMOGRAPHIC SIMULATION OF HARVEST IMPACT USING A POPULATION PROJECTION MATRIX MODEL.

5.1 Introduction

The subtidal agarophyte Gelidium sesquipedale has been commercially harvested along the coasts of Spain, Portugal and Morocco mainly by two methods; gathering storm tossed fronds, and by directly hand-plucking fronds (Palminha, 1971; De Craene, 1971; Juanes & Borja, 1991). In Spain, most of the harvest yield is storm tossed. This technique has no direct impact on the population dynamics, but is very inefficient. Only 18 to 35% of the cast off is recovered (Borja 1987). Other disadvantage of this method is the low and unpredictable quality of the harvest. G. sesquipedale is mixed with sand and other seaweed species, which greatly reduces the agar yield of the harvest (Appendix 1).

Hand-plucking by divers has been the main source of raw material in Portugal since the 1960's. Overharvesting of some beds has been observed (Chapter I). Since 1990, mechanical devices are being used to harvest the seaweed from boats along Spain's Asturias and Cantabria coasts (Appendix 1). The machines apparently leave a 4 cm to 8 cm stump and do not decrease frond density (Gorostiaga, pers. comm.). The relative impact of the two direct harvest methods on the recovery of populations is controversial, as evidenced in a recent meeting on Gelidium, among harvesters, managers, scientists and representatives from industry (Juanes et al., 1991).

Experiments on recovery of G. sesquipedale after plucking or cutting have yielded inconclusive results. Questions essential to choosing the best harvest strategy have not been adequately addressed. Seoane-Camba (1966) reported that the average annual growth of fronds in Vigo, Spain, cut to 1.5 to 3.2 cm was similar to the fronds tagged after

experimental plucking. Yet, he gives no information on the size of the later fronds, on the effect of frond size on growth, or on the population structures prior to and after the experiments. Gorostiaga (1990), studying G. sesquipedale on the Basque coast of Spain, tested two levels of each harvest strategy, measuring the biomass and population structure of the harvest after one, two and three years. He concluded that moderate cutting (8 cm) every two years was the harvest strategy that would maximize the harvest yield, but his experimental design was weak. The treatment effects were confounded by the annual biomass variation, which was not controlled, no replicates were used, and the experimental blocks were not randomly distributed.

In this study I attempt to discern which harvest strategy, plucking or cutting, will result in a better recovery of G. sesquipedale populations to the next harvest season. A size-based matrix model is constructed (Caswell, 1989; Ang and De Wreede, 1990; Åberg, 1992). It contains the empirically derived vital rates of a G. sesquipedale population commercially exploited by hand-plucking (Chapter V). The cutting vital rates of the population were derived from these data. The magnitude of the population's recovery to the next harvest season is determined comparing predicted population structures. This approach allows the rapid assessment of the intrinsic mechanisms regulating the population recovery, rather than the longer time required by an empirical study.

5.2 Methods

The study was conducted in the south edge of an important G. sesquipedale commercial bed off Cape Espichel, Sesimbra, Portugal, where the species is most abundant (Chapter II). Two inclined surfaces of high G. sesquipedale cover (8 m to 12m depth) that are characteristic of this zone, were sampled monthly from September 1989 to September 1990, except in the months of November, December and February, when sea conditions did not permit diving.

As the species habit (Dixon, 1958 and Fan, 1961) makes difficult the identification of physiologically separated individuals (the genets sensu Harper 1977), the population demography was studied at the frond level (erect axis), independently of their origin. Moreover, it is difficult to distinguish plants of the different life cycle phases as the tetrasporophytes and gametophytes are isomorphic. A size-based matrix model was developed, rather than an age-based one, because the harvest effort is selective for size rather than age. Furthermore, there is strong support for a stage-based rather than age-based classification in plants, because size is often a better predictor of population vital rates (Caswell, 1989).

FronD mortality, growth and breakage were quantified by monitoring the number and length of 300 tagged (Sharp and Tremblay, 1985) fronds haphazardly selected through the study site, and covering the size spectrum of the species. Fronds with less than 4 cm could not be tagged. Lost fronds were continuously replaced to maintain a statistically sound number of cases. The population was also sampled over the same period, by scraping five 40 cm quadrats. Total recruitment (both from vegetative growth and from spore germination) was evaluated by combining data on growth, mortality, breakage and density variation of the first size class through time. Density increase of the first size class from one sample to another, after discounting all possible transitions due to mortality, growth to higher classes and frond breakage to the first size class, was interpreted as recruitment. In terms of the model, recruitment is the number of new fronds per old frond in size class x that will survive to the next time step and enter size class y . The details of demographic data are presented in Chapter III.

Six size classes were selected following Moloney's (1986) algorithm: I) 4 to 10 cm, II) 11 to 12 cm, III) 13 to 14 cm, IV) 15 to 22 cm, V) 23 to 25 cm and VI) > 25 cm. Transition probabilities among these size classes were calculated and nine matrices covering one year, were constructed. A periodic matrix product of these matrices was calculated

(Caswell, 1989). In the monthly matrices it was assumed that a frond will not grow more than 6 cm in one time step (cf. Chapter III), and therefore recruits will only enter the first size class (4 to 10 cm). In the case of the annual product matrix, recruits may enter other size classes than the first one.

High frond mortalities were observed during harvest season (July /August and August/September), and interpreted as commercial harvest of tagged fronds. The harvest season survivorship reflects both natural and harvest mortality. Therefore, the periodic matrix product describes the population annual dynamics under harvest by plucking. To simulate the cutting strategy, the two population projection matrices corresponding to the harvest season were replaced by hypothetical values derived as follows, and the corresponding product matrix was calculated for the cutting situation.

5.2.1 Transition probabilities to higher size classes.

The transition probabilities from the size class j to the size class i in the plucking case, $P_p(i,j)$, can be expressed as:

$$P_p(i,j) = (1-M(j)) * G(i,j) \quad \text{for } i>j \quad (1)$$

where $M(j)$ is the total mortality (natural plus harvest) of class j and $G(i,j)$ is the probability of growing to the next size class in the time step of one month.

Similarly in the cutting matrix $M(j)$ is the total mortality, but here it is assumed there are no plucked fronds and thus $M(j)$ is equal to the natural mortality, $M_n(j)$. In fact, the percentage of plucked plants by the Spanish mechanical devices is less than 2%, (Gorostiaga, pers. comm.). Because estimates of size class-specific natural mortality for the harvest season are unavailable (tagged fronds were exposed to the harvest), I have assumed it to be equal to the mortalities observed immediately before the harvest (June/July 1990). This may be a reasonable assumption as environmental conditions are similar to those of the harvest season.

The transition probability to a higher size class in the cutting case, $P(i,j)$, can then be derived as follows:

$$P(i,j) = (1 - M_n(j)) * G(i,j)$$

from (1)

$$G(i,j) = P_p(i,j) / (1 - M(j))$$

$$P(i,j) = (1 - M_n(j)) * [P_p(i,j) / (1 - M(j))]$$

5.2.2 Transition probabilities to smaller size classes.

Assuming the harvest occurs at the beginning of each time period, the transition probabilities from size class j to size class i can be expressed as:

$$P(i,j) = B_h(i,j) + B_n(i,j) * (1 - B_h(i,j)) \quad \text{for } i < j$$

where $B_h(i,j)$ is breakage caused by the harvest and $B_n(i,j)$ is natural breakage, which will only act on fronds not broken by the harvest $(1 - B_h(i,j))$.

Values of $B_h(i,j)$ for cutting will depend on the mechanical device used. The cutters of Asturias and Cantabria, Spain, are height regulated at class 1 fronds. The transition probabilities of any class j to class 1 can thus be expressed by:

$$P(1,j) = H_e(j) + B_n(1,j) * (1 - H_e(j)) \quad \text{for } j > 1$$

where $H_e(j)$ is the harvest efficiency, i. e., the harvest percentage of the harvestable population. For purposes of comparison between the two harvest strategies, the same harvest efficiency value was considered. This variable was estimated as:

$$H_e(j) = M_p(j) / M_{pmax}(j)$$

where $M_p(j)$ is the plucking mortality that actually occurred in the two time periods (July/August and August/September) and $M_{pmax}(j)$ is the maximum plucking mortality of each size class. The maximum plucking mortality per size class was experimentally assessed by Santos (unpublished data): it is 0.54 for class I, 0.78 for class II, 0.89 for class III, 0.95 for class IV, 0.99 for class V and 1.0 for class VI. The plucking mortality,

$M_p(j)$ is calculated as follows (assuming that the harvest occurs at the beginning of each time period):

$$M(j) = M_p(j) + M_n(j) * (1 - M_p(j))$$

$$M_p(j) = (M(j) - M_n(j)) / (1 - M_n(j))$$

Assuming all cut fronds will now be in class 1, the transition probabilities of any class j to a lower class i different than one, are equal to the natural breakage $B_n(i,j)$:

$$P(i,j) = B_n(i,j) \quad \text{for } 1 < i < j$$

As in the case of natural mortality, there is no independent estimate of class specific natural breakage during the harvest season. Thus it will be considered equal to that prior the harvest season (June/July).

5.2.3 Probability of staying in the same size class.

Since the total mortality of a size class j is the difference from unity of the sum of all the possible transitions from that class to another (including itself):

$$M(j) = 1 - \sum P(i,j)$$

the probability of a frond staying in the same class in the time step, can be calculated as

$$P(j,j) = 1 - \sum P(i,j) - M(j) \quad \text{and } i \neq j$$

since it was assumed that cutting harvest does not pluck the plants, $M(j) = M_n(j)$, and thus:

$$P(j,j) = 1 - \sum P(i,j) - M_n(j)$$

5.3 Results and Discussion

Table 5.1 shows the annual product matrices used to project the *G. sesquipedale* population under different harvest strategies. The projection matrix A is the observed plucking situation, and it describes the annual dynamics of the population. Matrix cell

values represent both the survivorship and recruitment contributions. The transition probabilities among size classes without considering recruitment are shown inside parenthesis. Values in the diagonal represent the probabilities of a frond surviving and staying in the same size class, the values above it represent the probabilities of surviving and breaking to a lower class and the values below it represent the probabilities of surviving and growing to a higher class. Annual survivorships are very low compared to values of the projection matrix including recruitment, showing the important effect of recruitment on the population dynamics. The total survivorship of size classes decreases with size; in the plucking case, a first size class frond (4 to 10 cm) has about seven times more chances of surviving one year ($p=0.078$) than a sixth size class frond (>25 cm, $p=0.011$).

The principal eigenvalue of matrix A (Table 5.1) is the asymptotic population growth rate, λ (Caswell, 1989). Its value is lower than unity ($\lambda=0.85$), indicating that if the vital rates remain constant, the population will decrease to extinction. In fact, the population did not recover in 1990 to the maximum pre-harvest levels of summer 1989 (Chapter IV) due to the unusually adverse sea conditions during late fall/early winter (Chapter III).

The hypothetical cutting situation where recruitment is assumed to be the same as in A (matrix B of Table 5.1) shows a much higher population growth rate ($\lambda=1.35$) than the plucking case ($\lambda=0.85$). This suggests a population harvested by cutting will recover much faster. However, the recruitment values of matrix B may be overestimated. Harvest by cutting does not cause frond mortality, hence recruitment may be low due to space constraints for the growth of new erect fronds from the prostrate axes.

Another estimate of recruitment in the cutting situation should reflect spring/summer environmental conditions. Both recruitment probabilities estimated prior to the harvest season, from May to June (0.19) and June to July (0.35), seem adequate (Fig. 5.1). Even selecting the lower of these values, the cutting simulation (matrix C of Table 5.1) indicates

that this strategy will result in a higher population growth rate ($\lambda=1.08$) than the plucking strategy ($\lambda=0.85$).

Table 5.2 shows the September 1989 population structure, and the observed vs projected population structures after 12 months. At this point, the alternative strategy of harvest by cutting (both B and C recruitment rates) was also simulated. The population structures prior to the start of the next harvest season, resulting from 10 more months of projection, are also presented. In this second simulation period it is assumed that the vital rates are the same as those of the previous one.

Although the objective of this model is not to predict the absolute densities of G. sesquipedale size classes, because of its density independence (see Caswell, 1989), its accuracy in describing the annual dynamics of this population was assessed by comparing the observed and projected size class structures after 12 months of simulation (Sep/90, Table 5.2). Projected structures underestimate size classes I to III, and overestimate size classes IV to VI. Nevertheless, the model predicts a marked decrease of G. sesquipedale standing stock, suggested both by the value of population growth rate ($\lambda < 1$) and by the decrease of projected frond numbers, particularly of higher classes, after 12 months (Sep/90, Table 5.2), and after 22 months (July /91-Plucking vector, Table 5.2). This projection is validated both by the population structure observed in Sep/90 (Table 5.2), and by the low harvest landings in 1990 and 1991 compared with 1989, respectively 817 t, 231 t and 1683 t (J. Oliveira pers. comm.).

The population structures projected to July/91 suggest the population will recover better after cutting than after plucking. Both cutting B and C population vectors show that higher densities of all size classes would be available to the harvest than in the plucking case (Table 5.2).

5.4 Conclusions

A general conclusion of this work is that the G. sesquipedale population studied would recover faster if the fronds were harvested by cutting to a length of about 7 cm (the middle of the first size class) rather than it actually does after being harvested by plucking. For all size classes, the number of fronds available in the next harvest season would be higher, and therefore better yields could be obtained. This supports the conclusions of the experimental study done by Gorostiaga (1990) on the Basque Coast, Spain. The model developed here, can also be used to estimate the optimum time to start G. sesquipedale harvest season, and the optimum length to which the fronds should be cut in order to maximize a sustainable harvest yield.

Based on the model assumptions, the development and use of mechanical harvesters may increase G. sesquipedale yields. Nevertheless, to decide if the harvest by plucking currently practiced in Portugal, should be replaced by a cutting strategy, other factors must be considered. A cost analysis of the investment (in time and money) necessary to harvest the same yield should be done for both methods. Social and economic factors should also be considered. Studies on the harvest efficiency of both methods and its impact on G. sesquipedale populations are needed. In this study, the harvest efficiency of plucking and cutting was simply assumed to be the same, but they are likely to be different. Also, different cutting devices have different harvest efficiencies. For example, the cutting of the fronds by divers using shears does not seem an alternative to cutting machines as it is most likely very inefficient in time.

It is my belief that the approach taken in this study should be further developed. Much work has to be done, as data on the population biology of G. sesquipedale are very poor. Longer time series of the species vital rates must be collected, so that the time variance of population parameters can be assessed. The relationship of these parameters, particularly the recruitment rates, to stand density must also be understood for purposes of

prediction. In order to generalize the conclusions of these studies models must be calibrated for different geographical areas.

Table 5.1. Projection matrices used in the simulation of harvest strategies. A. Annual vital rates of plucking case. Values inside parenthesis are the transition probabilities of survivors among size classes (without recruitment). B. Annual vital rates of cutting case (recruitment assumed to be the same as previous matrix). C. Cutting matrix considering June/July recruitment (see text). λ values are the asymptotic population growth rates. $n(t)$ is the population structure vector.

$$A = \begin{bmatrix} (0198) 7119 & (0163) 6621 & (0089) 4636 & (0040) 3578 & (0029) 3277 & (0014) 2857 \\ (0093) 0929 & (0086) 0839 & (0051) 0582 & (0025) 0439 & (0019) 0400 & (0010) 0343 \\ (0049) 0340 & (0054) 0315 & (0037) 0222 & (0024) 0167 & (0020) 0152 & (0012) 0128 \\ (0043) 0198 & (0061) 0199 & (0058) 0156 & (0061) 0138 & (0057) 0128 & (0045) 0107 \\ (0006) 0023 & (0010) 0025 & (0013) 0024 & (0020) 0028 & (0021) 0028 & (0016) 0029 \\ (0000) 0001 & (0001) 0002 & (0003) 0004 & (0008) 0008 & (0010) 0010 & (0016) 0017 \end{bmatrix}$$

$$\lambda = 0.8485$$

$$B = \begin{bmatrix} 1.2227 & 1.1129 & 0.7852 & 0.6140 & 0.5647 & 0.4971 \\ 0.0946 & 0.0856 & 0.0599 & 0.0462 & 0.0423 & 0.0369 \\ 0.0486 & 0.0442 & 0.0310 & 0.0236 & 0.0215 & 0.0185 \\ 0.0223 & 0.0218 & 0.0166 & 0.0143 & 0.0133 & 0.0115 \\ 0.0039 & 0.0042 & 0.0036 & 0.0038 & 0.0038 & 0.0041 \\ 0.0003 & 0.0003 & 0.0003 & 0.0004 & 0.0004 & 0.0004 \end{bmatrix} \quad n(t) = \begin{bmatrix} \text{Size Class 1} \\ 2 \\ 3 \\ 4 \\ 5 \\ 6 \end{bmatrix}$$

$$\lambda = 1.353$$

$$C = \begin{bmatrix} 0.9262 & 0.8426 & 0.5943 & 0.4644 & 0.4271 & 0.3760 \\ 0.1152 & 0.1043 & 0.0731 & 0.0565 & 0.0518 & 0.0452 \\ 0.0516 & 0.0469 & 0.0328 & 0.0251 & 0.0229 & 0.0197 \\ 0.0223 & 0.0218 & 0.0166 & 0.0143 & 0.0133 & 0.0115 \\ 0.0039 & 0.0042 & 0.0036 & 0.0038 & 0.0038 & 0.0041 \\ 0.0003 & 0.0003 & 0.0003 & 0.0004 & 0.0004 & 0.0004 \end{bmatrix}$$

$$\lambda = 1.0773$$

Table 5.2. Column vectors of population structures (fronds per m²) before and after 12 and 22 months of simulation. Projected population structures of September 90 and July/91-Plucking were derived from matrix A. Cutting B and Cutting C were derived from matrices B and C (Table 5.1).

Population Structures					
Sep/89	Sep/90		July/91		
Initial	Observed	Projected	Plucking	Cutting B	Cutting C
$\begin{bmatrix} 5268 \\ 1130 \\ 697 \\ 1038 \\ 32 \\ 16 \end{bmatrix}$	$\begin{bmatrix} 6193 \\ 1004 \\ 348 \\ 110 \\ 0 \\ 0 \end{bmatrix}$	$\begin{bmatrix} 5313 \\ 672 \\ 248 \\ 152 \\ 20 \\ 2 \end{bmatrix}$	$\begin{bmatrix} 4906 \\ 686 \\ 377 \\ 209 \\ 12 \\ 1 \end{bmatrix}$	$\begin{bmatrix} 7849 \\ 1097 \\ 600 \\ 329 \\ 17 \\ 2 \end{bmatrix}$	$\begin{bmatrix} 6241 \\ 872 \\ 479 \\ 266 \\ 15 \\ 2 \end{bmatrix}$

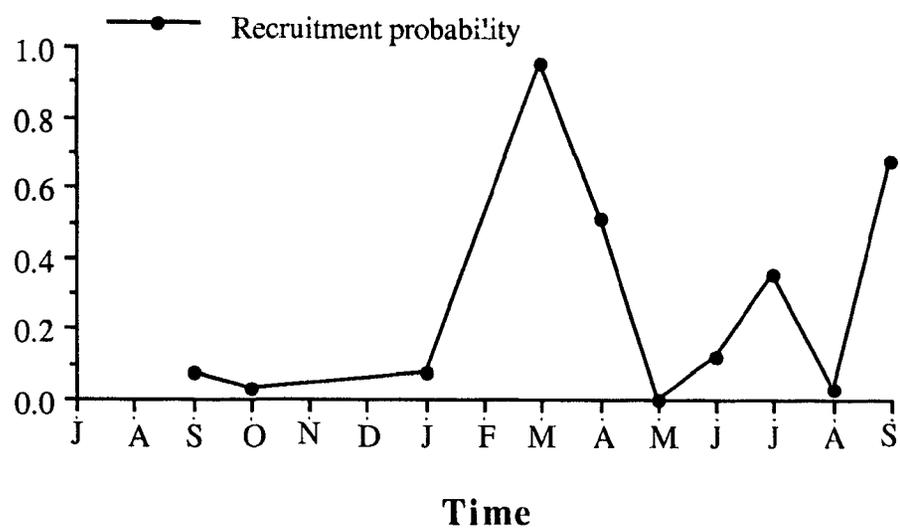


Fig. 5.1. Time variation of frond recruitment (per old frond) to size class 1 (4 to 10 cm fronds).

APPENDIX 1

GELIDIUM SESQUIPEDALE INDUSTRY AND RESOURCE MANAGEMENT IN THE NORTHEAST ATLANTIC^a .

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A1.1 Introduction

Gelidium sesquipedale is an economically important subtidal agarophyte of the Northeast Atlantic. Commercial quantities are harvested along the Atlantic coasts of Spain, Portugal and Morocco. Spain has both the largest world crop of G. sesquipedale, with annual yields of 4 000 to 5 500 t of dry seaweed (Santelices, 1988), and the largest annual agar production, at 890 t (Armisen and Galatas, 1987). The landings may be overestimated due to impurities, as the crop is largely from storm tossed. Morocco ranks fourth in agar

^a Paper presented at XIVth International Seaweed Symposium, Mini-Symposium I. Management of seaweed resources.

production at 550 t (Armisen and Galatas, 1987). Santelices (1988) reports harvest yields from 1000 to 1500 t for Morocco, but are more likely to range between 3000 t to 3500 t (T. Lebbar, per. comm.¹). Portugal ranks fifth in annual agar production with 350 t, extracted from a harvest of about 2500 t (Santos and Duarte, 1991). In France, 350 t to 500 t are harvested with an agar production of 80 t (Mabeau, 1989).

This work briefly describes the various sectors of the agar industry in those countries, with a focus on the resource science and resource management. We conclude that the industry is in critical situation and point out the limiting factors to obtaining optimal yield from the wild harvest.

A1.2 Development of agar industry

Storm cast seaweed was harvested for fertilizer along the coasts of Portugal (Santos and Duarte, 1991) and Spain for centuries, but it was not until the 1940's that the marine colloid industry was initiated, due to an European shortage of Japanese agar during World War II. Initially, farmers harvested the storm tossed fronds of G. sesquipedale or plucked the fronds by hand at low tide. G. sesquipedale harvest spread through the Atlantic coasts of Spain (mostly along Cantabria and Asturias shores), Portugal, and Spanish Sahara (now under Morocco's control). The increased value of this resource prompted the direct exploitation of the species subtidal stands. Two to five divers equipped with compressed air systems (hookah), operating from small boats, plucked fronds by hand. This harvest technique began in 1952, 1966 and 1964 in Spain, Portugal and Morocco respectively.

The agar industry experienced rapid development. By the late 1960's early 1970's, there were twelve factories in Spain (Albertos, 1968), four in Portugal, including two in

¹ T. Lebbar, SETEXAM, Morocco (agar extractor).

the Açores islands extracting agar from Pterocladia capillacea (Palminha, 1971), and four in Morocco (De Craene, 1971); agar production capacity now outstripped harvest yields. Albertos (1968) estimated Spanish factories were working at 42% capacity. Annual agar production capacity in Portugal was 1 620 t (Palminha, 1971), about twice peak agar production of 806 t in 1973 (Santos and Duarte, 1991). Overcapitalization in extraction was probably due to overestimates of resource production capacity. For example, Fonseca (1966) estimated an annual Portuguese agarophyte harvest yield of 8 000 t (dry) (6000 t of G. sesquipedale and 2000 t P. capillacea), which would correspond to 1 300 t of agar. In fact, the maximum harvest yields (dry) of both species combined never exceeded 4 500 t (Santos and Duarte, 1991).

Commercial G. sesquipedale harvesting was regulated by harvest season and licensing policy in 1956 and 1964 in Spain and Portugal respectively. Diver harvest was regulated in Portugal in 1967. In Spain, the resource was allocated to agar companies by the Ministry of Commerce. Personnel from the Instituto Español de Oceanografía were to provide biological advice for resource management. In 1970, an association of agar companies was created to share the crop and to avoid competition for resources. A percentage of raw material was assigned to each company in relation to the agar exported the previous year. Divers were limited to an annual harvest of 3 000 t (wet) of G. sesquipedale. The company allocated beds became common property in 1988. The hand-plucked harvest is gradually being replaced by diver operated cutting machines, who have received new concessions. Conflicts have since arisen from storm toss harvesters fearing reduced cast offs.

In Morocco, G. sesquipedale has been harvested by hand-plucking at low tide or by collecting storm cast plants since 1957. In the past, up to 3 000 harvesters gathered seaweed. More recently, the Ministry of Fisheries granted harvest companies diver exploitation rights. These companies own several boats carrying up to twelve divers.

A1.3 Resource Management Plan

The Northwest Atlantic G. sesquipedale resource is managed by controlling harvest zones, harvest season and harvest effort. In Spain, the fisheries department of each autonomous region, Pais Vasco, Cantabria, Asturias and Galicia have the resource management mandate while in Portugal and Morocco this responsibility lies with the Ministries of the Sea and of Fisheries, respectively. New legislation is being proposed in Portugal to give the fisheries research institute, "Instituto Nacional de Investigação das Pescas", a more active role in fisheries management.

A1.3.1 Harvest zones and season

Along the Spanish Atlantic coast the four harvest zones correspond to each autonomous regions' boundaries (Fig. A.1); Portugal has six harvest zones, defined by legislation in 1967 and modified in 1977 and 1981. Harvest zones are not used in Morocco. The most heavily harvested beds of Spain, Portugal and Morocco are also shown in Figure A.1.

The hand-plucking season starts in July in all countries. Precise dates may be established locally each year, depending on factors such as weather, standing stock and occasionally social factors. Although the plucking season legally extends to year's end, the season's end is usually dictated by weather. The fall deterioration of sea conditions restricts the diver harvest. Storm tossed plants can be gathered year round, but only during fall and early winter is there enough G. sesquipedale drift to permit gathering. Several tools such as modified nets and rakes, are used in Spain to collect near shore drift weed. Seaweeds accumulated on the bottom are collected from boats by net dragging or by divers using suction devices (see description of harvest methods in Palminha, 1971 and Juanes and Borja, 1991).

A1.3.2 Harvest effort and yields

Storm toss harvesters numbers are not limited, but frond cropping effort is limited by the number of licenced boat and divers per boat. To manage harvest impact on the resource, catch rates are determined per zone. Unfortunately, plucked and storm toss data are lumped in Spain and Morocco.

To provide diver harvest data each boat must log the sites harvested each day, the number of divers, the diving hours and yields. This information, although only recently collected in Spain and Portugal, is incomplete, unpublished, and thus not easily accessible. Yield data have been collected in each Portuguese harvest zone by official concentrators who receive and weight the harvester's crop.

Spanish diver harvest yield is a small percentage of the total harvest. Currently, 90% of the annual harvest yield is storm toss gathered. Seaweed transport to factories is done under permit from local authorities who then log the shipment's weight. Unfortunately, seaweeds are often transported without permit.

During 1966 to 1978, about 50 boats were used to harvest G. sesquipedale in Spain, but unfortunately landings data are unavailable (Fig. A.2 A). At present, only 10 boats in Asturias, 3 in Cantabria and 2 in Pais Vasco are operating. Spanish landings of recent years have been high, but unstable (Fig. A.2 A). This production instability together with the low quality of storm toss material due to debris (sand and other seaweeds), poses serious problems to the industry, which requires a steady input of high quality raw material.

In Spain the diver harvest was never very important and thus there has been little risk of overexploitation. The recently introduced cutting machines in Spain, will change this unless well managed. Yields of 2000 kg(wet)/day/diver (2800 kg maximum) have been

obtained in Cantabria by Algatecsa company, whereas a yield of 900-1000 kg/day/diver was obtained by a harvester cooperative in Gijón, Asturias.

Portuguese landings peaked during the late 1960's early 1970's, decreased throughout the 1970's and recovered during the 80's (Fig. A.2); the recent trend is downward. Before diver harvest started in 1966, there was up to 10,000 G. sesquipedale shore collectors. Hereafter, the number of harvesters decreased drastically. Harvest by divers takes place in Zones III to VI only, as zone I and II (Fig. A.1) do not have harbours and sea conditions are poor.

Annual yields are not available for Morocco. Currently, G. sesquipedale is harvested intensively by divers mainly in the zones of Cap d'El Jadida, Sidi Bouzid and Moulay Abdellah. The first area (Fig. A.1) is 20 km long and supplies about 75% of total annual yield.

An essential parameter to manage G. sesquipedale populations is the rigorous control of the catch and of the harvest effort in each commercial bed. Statistical indicators of resource abundance such as CPUE (catch per unit of effort) and sustainable yields can then be derived for each bed (Ricker, 1975; Getz and Haight, 1989). But attaining good effort data is difficult. Boat number alone is not a good measure. The number of days of good weather varies from year to year and amongst harvest zones. In Spain and Portugal, it ranges between 13 and 50, the number of divers per boat varies between 2 and 5, as does the number of dive hours spent harvesting (up to 8 h/day).

The best indicator of harvest effort is the total number of dive hours per bed, easily calculated from logbooks, but unfortunately not readily available. Oliveira (unpublished data), since 1986 has calculated annual harvest effort as the product of diver number and days harvested (men x days) for each Portuguese harvest zone. TACs (total allowable catch) were derived to limit the harvest.

A1.3.3 Agar extractors

There is one French factory extracting agar from G. sesquipedale, five in Spain, one in Portugal, and two in Morocco. The agar industry peaked in the early 1970's, coincidental with the harvest peak. Since then, seven factories in Spain, three in Portugal and two in Morocco have closed.

Dried seaweeds can be stored for a long period of time. Before selling, the crop is sundried to a maximum of 20% humidity. In Spain, a company was recently created to machine dry the crop. Wet seaweed is bought and immediately processed in certain Spanish and Portuguese locations.

Dried seaweed price is generally dictated by the purity of the crop. Storm tossed seaweed value may be less than 20% of the diver harvested crop. One kilogram of dry, top quality Spanish G. sesquipedale ranged between US \$1.7 and \$2.7 between 1988 and 1991. In Portugal, price paid to harvesters is about \$1.4 while in Morocco it recently increased from \$0.6 (price in 1988/89) to \$1.2. The storm tossed Spanish prices recently dropped to a value of \$0.5. This reflects both poor crop quality and industrial difficulties.

Spanish agar production was maintained at the high levels of the early 1970's by importing G. sesquipedale from Morocco and France. Portuguese production decreased (Fig. A.2B). Commercial agar yield obtained per dry kilogram varies between 8% and 25%, depending on the extraction process and raw material quality.

Most agar produced in Spain, Portugal and Morocco is exported. Three grades are produced: unpurified food grade (\$10 to \$15 per kg), and purified pharmacological and bacteriological grades (\$25 to \$40 per kg). Highly priced agarose (up to \$300 to \$1500 per kg) is also produced (see Armisén and Galatas, 1987 and Armisén, 1991). Bacteriological grade agar and agarose are processed in Spain only. The 1983 income for Spanish agar exports was about \$14 million; in Morocco in 1985 it was \$10 million. The annual export value from Portugal, from 1985 to 1988, was \$5 million .

A1.4 Scientific assessment

The main thrust of G. sesquipedale researchers has been both to map the main beds and to evaluate standing stocks. Table A.1 shows assessments made along Spanish and Portuguese coasts. There are no data for Morocco. Standing stocks are difficult to compare because errors of estimates are not available. Estimates are generally based on systematic sampling rather than on random sampling. The total Spanish standing stock is about 9 times that of Portugal.

In contrast with standing stock estimates, which alone are not very useful for resource management, much less effort has been directed to the study of the biology and ecology of G. sesquipedale. Data on the demographic parameters that regulate the species population dynamics, such as growth, breakage, mortality and recruitment are scarce. Until recently, few data were available on frond growth and production (Seoane-Camba, 1965, 1966; Oliveira, 1989; Anadón and Fernández, 1986). Consequently, population structure changes representing dynamic interactions among demographic parameters cannot be adequately interpreted. This problem emerges from the work of Salinas et al. (1976) and Reguera et al. (1978) who studied frond height structure of five populations located off the coast of Cantabria, Spain.

Currently, more aspects of the specie's biology and ecology are being assessed (Juanes et al., 1991). G. sesquipedale population biology off the coast of Pais Vasco, Spain was investigated by Gorostiaga, 1990). Torres et al. (1991) presented the first ecophysiological study of G. sesquipedale, on the effects of temperature and light on pigment concentration, C/N ratio and cell-wall polysaccharides. Salinas (1991) studied the reattachment of fronds by emission of rhizoidal clusters from apical portions of thalli, showing its importance to the natural recovery of populations and its potential use to cultivate the species. Santos (Chapters II, III, IV) studied the strenght of the relationship

between G. sesquipedale local distribution and biotic and abiotic factors, the species vital rates and its population dynamics, in a commercial bed off Cape Espichel, Portugal.

Studies applied to the specific problem of testing different harvest strategies such as hand-plucking vs shear-cutting were done by Seoane-Camba (1966) and Gorostiaga (1990). Santos (Chapter V) constructed a demographic matrix model of G. sesquipedale, and assessed two alternative harvest strategies: hand-plucking and machine-cutting. Simulations of the population structure recovery after both methods, assuming the same harvest efficiency, support the conclusions of previous workers that G. sesquipedale populations may recover better following cutting than plucking.

A1.5 Conclusions and recommendations

In summary, during and after the World War II the high demand of the international agar market together with the discovery of abundant G. sesquipedale stands along the Atlantic coasts of Spain, Portugal and Morocco, provided the necessary favorable conditions for the industry to establish. About twenty factories in total were operating in the early 1970's in Spain, Portugal and Morocco. Demand for raw material outgrew resource availability during the 1980's. High prices paid for raw material outstripped agar values, thus extractor profits decreased and less competitive factories closed. G. sesquipedale inflated price caused less expensive Gracilaria to be used. Also, traditional uses of agar were partially replaced with lower priced carrageenans. The last decade brought a steady decline in the G. sesquipedale industry; the number of factories is now only nine. The recent political instability of Russia and eastern Europe caused markets to decline by 500 t of agar and may force a reassessment of the industry.

The future of the agar industry will depend first on industrial technical renovation to produce high quality agar products efficiently, and to expand markets. The annual world

demand of bacteriological grade agar is about 250 t and of agarose is about 15 t. Secondly, there must be a sustainable annual yield of high quality raw material.

A major problem of the storm toss harvest and thus of the seaweed supply to the Spanish factories is its low quality; price should be scaled to reflect quality. This harvest method has the advantage of not adversely impacting the attached populations; the disadvantage is its inefficiency as only 18% to 35% of the cast is recovered (Borja, 1987). The alternative method of cropping fronds prior to cast is more efficient, but overharvesting is then a concern. To assess the sustainability of harvest, the commercial beds must be monitored by rigorously controlling both captures and harvest effort. Logbook regulations should be enforced. This information must also be analyzed and published yearly, so that it will be readily available.

In the last few years, the pressure of storm toss harvesters on the resource managers, have discouraged the concession of new licences to harvest G. sesquipedale with cutting machines in Spain. Apart from social factors, there is some indication that this method may be more adequate to harvest the resource than hand-plucking. In fact, Santos (in press b) show that it may improve yields, assuming the same harvest efficiency for both methods. If the cutting method is going to be used extensively, it is most important to the sustainability of G. sesquipedale stocks that studies will be conducted on its harvest impact on the populations and on their recovery to harvest.

The recovery of the populations to the next harvest season depends both on the rate of exploitation and on the environmental conditions of the transition period, which determine the rates of frond mortality, growth, breakage and recruitment. More studies should thus be initiated on the biology and on ecology of the species, particularly on the relationships of the environmental factors with the demographic parameters and productivity. Also, the harvest season opening should be manipulated to maximize yields. Matrix population models, such as Santos (in press b) developed, are a powerful tool to determine the best

harvest timing by predicting the development of the population structure. Finally, a wider communication and interdisciplinary work between the scientific community, the managers, and the industrials would significantly improve the identification and the search for solutions to the factors that limit harvest yields.

Table A.1. Gelidium sesquipedale standing stocks (wet weight) in Spain and in Portugal.

Harvest Zone	Bed	Standing Stock (wet t)	Author
Pais Vasco	Eastern	16000	Borja (1987,1988)
	Western	5000	Borja (1987,1988)
	Total	21000	
Cantabria	Eastern	6290	Juanes & Gutiérrez (1992)
	Western	18143	Juanes (pers. comm.)
	Total	24433	
Asturias	Eastern	7270	Llera et al. (1990)
	Western	4650	Vizcaíno (pers. comm.)
	Total	11920	
Total Spain		57353	
Portugal 3	S. Martinho	3214* - 2370**	J. Oliveira (unpub. data)
Portugal 5	Sesimbra	910***	J. Oliveira (unpub. data)
Portugal 6	Odeceixe	550* - 620***	J. Oliveira (unpub. data)
	Alvor	1350* - 490***	J. Oliveira (unpub. data)
	South coast	232	Palminha et al. (1985)
	(excluding Alvor)		
Total Portugal		6200	J. Oliveira (unpub. data)

Pais Vasco and Cantabria estimates refer to the whole coast line while Asturias estimates refer only to the commercial beds. *, **, *** are values estimated in 1989, 1990 and 1991, respectively.



Fig. A.1. Map of *Gelidium sesquipedale* harvest zones and most important commercial beds in Spain, Portugal and Morocco. Beds are numbered as: 1 - Pasajes, 2 - Orio, 3 - Noja, 4 - Requejada, 5 - San Vicente/Llanes, 6 - Lastres, 7 - Luanco, 8 - S. Martinho, 9 - Peniche, 10 - Sesimbra/C. Espichel, 11 - Odeceixe, 12 - Alvor, 13 - Cap d'El Jadida. Portuguese harvest zones are in Roman numbers.

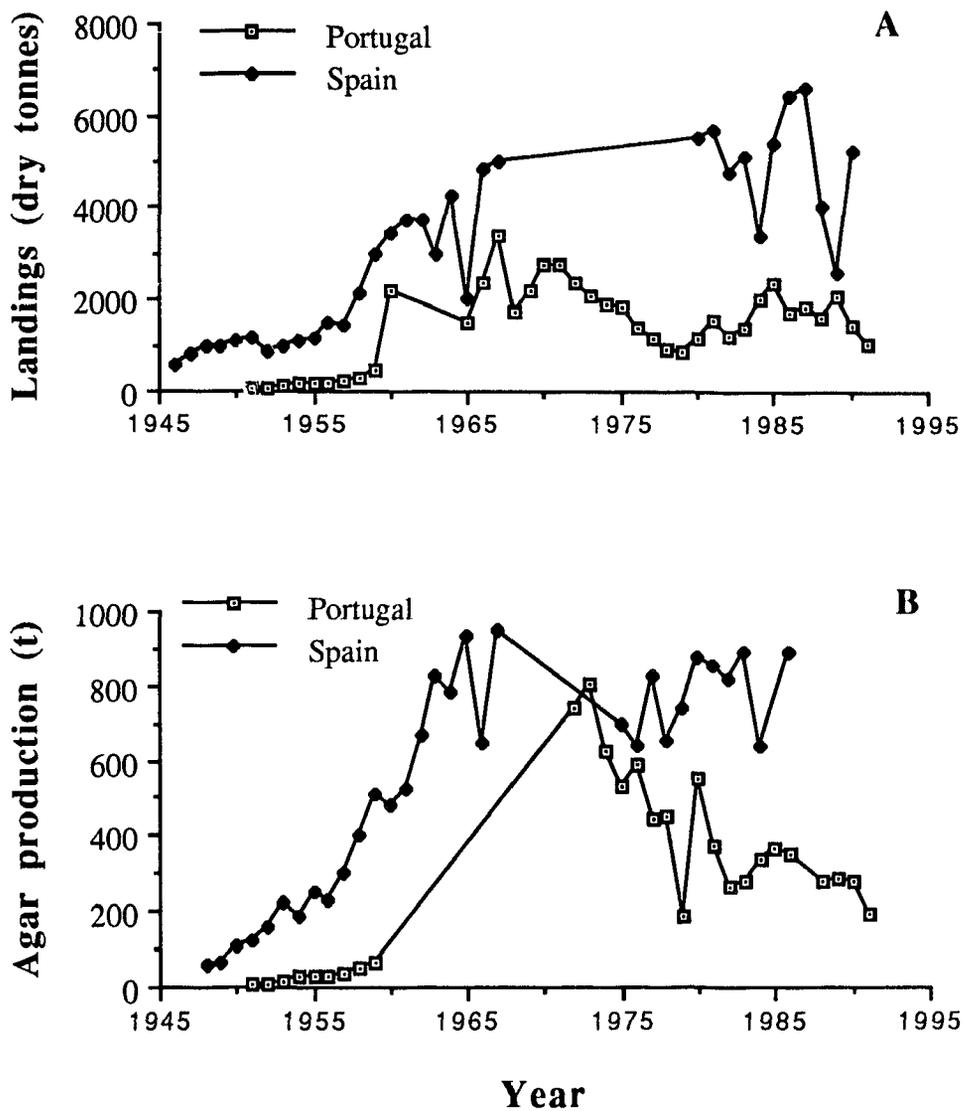


Fig. A.2. Annual *Gelidium sesquipedale* landings (A) and agar production (B) in Spain and Portugal. Spanish landings include debris from storm toss harvest, and Portuguese landings include a maximum of 2% of *Gracilaria* spp.

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