

## The relationship between stand biomass and frond density in the clonal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinaceae)

Ricardo Scrosati

The University of British Columbia, Department of Botany, Vancouver, BC V6T 1Z4, Canada; e-mail:

scrosati@unixg.ubc.ca, Fax: 1-604-822-6089

**Key words:** biomass-density relationship, Gigartinaceae, *Mazzaella cornucopiae*, seaweed, self-thinning

### Abstract

The negative relationship between stand biomass and plant density observed in terrestrial plants was tested among fronds of a clonal red alga, *Mazzaella cornucopiae*. Stand biomass and frond density were estimated bimonthly for 1 year on 7 permanent quadrats. A positive linear correlation was found between biomass and density for the whole data set, suggesting the lack of self-thinning among fronds of this intertidal alga at natural densities. Higher frond densities could favor increased water retention among fronds, thus minimizing desiccation during low tides. In this way, stands could maintain higher production of biomass. Fronds may also be cushioned better against wave action at higher frond densities, thus decreasing the detachment of larger fronds. The temporal variation of the relationship between biomass and density was plotted separately for these 7 quadrats. Four quadrats showed positive linear correlation between both variables (the other three quadrats showed non-significant positive linear correlation). Their four slopes are statistically similar to that found for the entire data set. It is possible, then, that there is only one positive slope for the biomass-density relationship in this population. If this is true, standing biomass could be estimated from the density of fronds.

### Introduction

For species of terrestrial plants occurring in monospecific, even-aged, and crowded stands, a bilogarithmic plot of stand biomass versus plant density results in a negative correlation (Weller, 1987, 1989). This relationship, hereafter referred to as the Biomass-Density relationship, must not be confused with the self-thinning lines. The self-thinning lines describe the temporal variation of the relationship between stand biomass and plant density of different plant stands plotted separately. As plant stands age, they reach a point where density-dependent mortality results in a decrease in plant density while stand biomass increases, resulting in a negative slope in the biomass-density plot. All data points used to describe the self-thinning lines for different species define the Biomass-Density relationship for the plant kingdom (Weller, 1987, 1989).

The population ecology of clonal plants can be studied from two points of view: the ecology of genet and the ecology of ramets, which are the actually or potentially independent members of a genet (Jackson *et al.*, 1985). In clonal red seaweeds such as those of the family Gigartinaceae, the genet is the entire thallus originated by a single spore, and it is composed by several foliose fronds produced by a crustose holdfast. Fronds can be considered as ramets, because of their potential capacity of independent life, together with an associated portion of holdfast. There have been few studies of the Biomass-Density relationship in marine algae at genet or ramet levels (Schiel & Choat, 1980; Cousens & Hutchings, 1983; Martínez & Santelices, 1992; Santos, 1995), which present somehow different conclusions (see Discussion for more details). The objective of this research was to study the Biomass-Density relationship at the frond level in a clonal red alga of the family Gigartinaceae, *Mazzaella cornucopiae* (Postels *et* Ruprecht) Hommersand (= *Iridaea*



*cornucopiae*), and to relate these results to those of previous studies on both algae and terrestrial plants. *M. cornucopiae* grows along the Pacific coast of North America, from Alaska to California (Abbott, 1971). As many clonal algae grow, holdfasts of different genets may coalesce (Maggs & Cheney, 1990), sometimes forming dense aggregations of fronds which cover high percentages of the available space. Under those conditions, it can be virtually impossible to distinguish individual genets in the field. The Biomass-Density relationship was studied here in stands where most of the genets could not be differentiated, i.e., fronds were counted and measured regardless whether they belonged to the same genet or not. In other words, the Biomass-Density relationship was analyzed in the population of fronds. It is also of interest that, if any correlation is found between stand biomass and frond density, it would be possible to estimate biomass from the density of fronds.

The temporal variation of the relationship between biomass and density in land plants (self-thinning line) has different slopes depending on site conditions (Weller, 1987). It is important, then, to determine the variability of the temporal variation of this relationship at the frond level in these clonal seaweeds. The second objective of this study was to investigate the possible existence of different slopes that describe the temporal variation of the relationship between stand biomass and frond density for *M. cornucopiae* from different sites.

### Materials and methods

The study site is located on Prasiola Point (48°49' N, 125°10' W), Barkley Sound, in the vicinity of Bamfield Marine Station, on the West coast of Vancouver Island, British Columbia, Canada. There, dense stands of *Mazzaella cornucopiae* occur in the high rocky intertidal zone, with occasional patches of the brown algae *Fucus gardneri* Silva and *Pelvetiopsis limitata* Gardner. In this area, 7 transects were placed over stands with high cover of *M. cornucopiae*, and one 10 × 10 cm quadrat was randomly located on each transect. Frond density and stand biomass were estimated on each quadrat at bimonthly intervals, from June 1993 until June 1994. There were 7 sampling dates: 2–6 June 93, 16–20 August 93, 15–18 October 93, 10–12 December 93, 24–27 February 94, 25–29 April 94, and 21–25 June 94. Given the limited time available for fieldwork on each date, data were estimated from six 2 × 2 cm

randomly chosen subquadrats on each quadrat (total area of 6 subquadrats = 24 cm<sup>2</sup>). All fronds present in subquadrats were counted, and frond length was measured using a stick divided in 0.5 cm long size-classes. Fresh weight of fronds was estimated using the relationship between length and fresh weight, which was calculated from 167 haphazardly collected fronds on 29 April 1994 in the same study area. This relationship is  $\text{Weight} = 0.011 \times \text{Length}^{1.698}$ , with weight in g, and length in cm (Figure 1).

For the study of biomass-density relationships, Weller (1987) recommended the use of stand biomass instead of mean plant weight as usually measured previously by other authors, for statistical reasons. Mean plant weight should not be correlated to plant density, since it is a derived variable which comes from dividing stand biomass by number of plants (which is contained in plant density), thus becoming a case of spurious correlation (Weller, 1987). For this reason, stand biomass was used in this paper instead of mean frond weight. Recently, Petraitis (1995) criticized Weller's approach, but Petraitis' analysis only applies to situations where mean plant weight is calculated from samples with a constant number of plants taken from the experimental quadrats, a very uncommon situation (Petraitis, 1995). In general, then, number of plants is a random variable, so mean plant weight constitutes a ratio, and its use is not recommended (see Jackson & Somers, 1991, and Albrecht *et al.*, 1993 for a deeper discussion on ratio utilization).

The linear relationship between the log<sub>10</sub> of frond density and the log<sub>10</sub> of stand biomass for the whole data set was calculated using principal components analysis (PCA). This is one of the appropriate techniques which can be used when the model I regression can not be applied such as in this case, because the measurement of both variables is subject to error which is not experimentally controlled (Sokal & Rohlf, 1981, Weller, 1987). The temporal variation of the relationship between biomass and density was also plotted for each quadrat separately, and the linear relationship between both variables was obtained by PCA. The Pearson correlation coefficient was calculated in every case, and its significance was assessed using the appropriate table given by Fisher & Yates (1963). Slopes of relationships which had a significant correlation between biomass and density were compared by calculating confidence limits on slopes (Sokal & Rohlf, 1981). Statistical analyses were conducted using SYSTAT 5.2.1 for Macintosh (Wilkinson *et al.*, 1992).



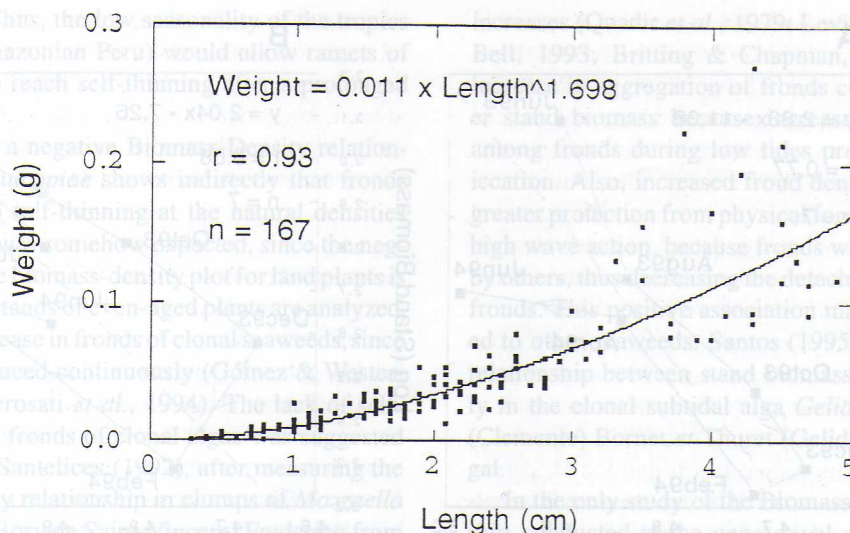


Figure 1. Relationship between frond height (cm) and fresh weight (g) in *Mazzaella cornucopiae*.

## Results

During the entire study period, frond density oscillated between 4–17 fronds  $\text{cm}^{-2}$  ( $8 \pm 0.5$ ; mean  $\pm$  s.e.;  $n=49$ ), whereas stand biomass ranged between 17–167  $\text{mg cm}^{-2}$  ( $72 \pm 5$ ). Maximum values were usually observed in summer, and minimum values generally in winter.

The relationship between log stand biomass and log frond density for the whole data set is shown in Figure 2. These variables are significantly positively correlated ( $p < 0.01$ ). Biomass is expressed in  $\text{g m}^{-2}$  and frond density expressed as fronds  $\text{m}^{-2}$  in order to allow the reader to compare these results with those reported by previous researchers.

The temporal variation of the relationship between biomass and density in quadrats 2, 3, 5, and 7 is shown in Figure 3, where a significant linear correlation between both variables was found ( $p < 0.05$  for quadrats 2, 3, and 5, and  $p < 0.01$  for quadrat 7). The five slopes shown here (Figures 2 and 3) are statistically similar ( $p < 0.05$ ). The correlation between biomass and density found for the time-series of this relationship for quadrats 1, 4, and 6 was not significantly different from zero ( $p > 0.05$ ), but correlation values were nonetheless positive (0.42, 0.30, and 0.50, respectively).

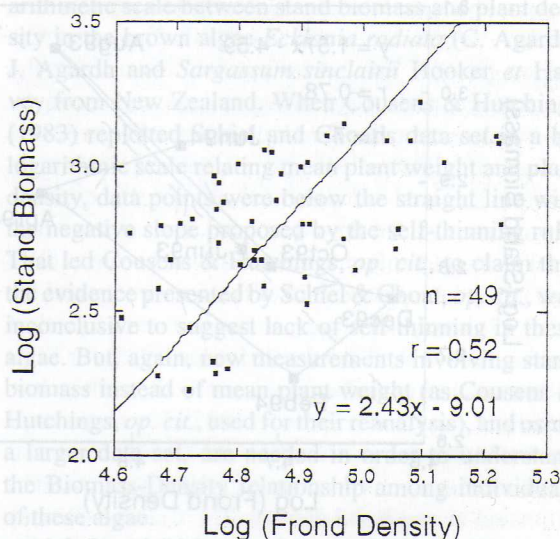


Figure 2. Relationship between log stand biomass ( $\text{g m}^{-2}$ ) and log frond density (fronds  $\text{m}^{-2}$ ) using the whole data set. The functional relationship between both variables was obtained by PCA.

## Discussion

Stands of crowded land plants which are self-thinning exhibit a negative slope when the time-series of the relationship between stand biomass and plant density is plotted on a bi-logarithmic scale. The plant self-thinning rule (Yoda *et al.*, 1963) predicts a single ideal slope of  $-1/2$  for this relationship, but this has been rejected as a quantitative rule, since the thinning slopes change systematically with species, age, shade toler-



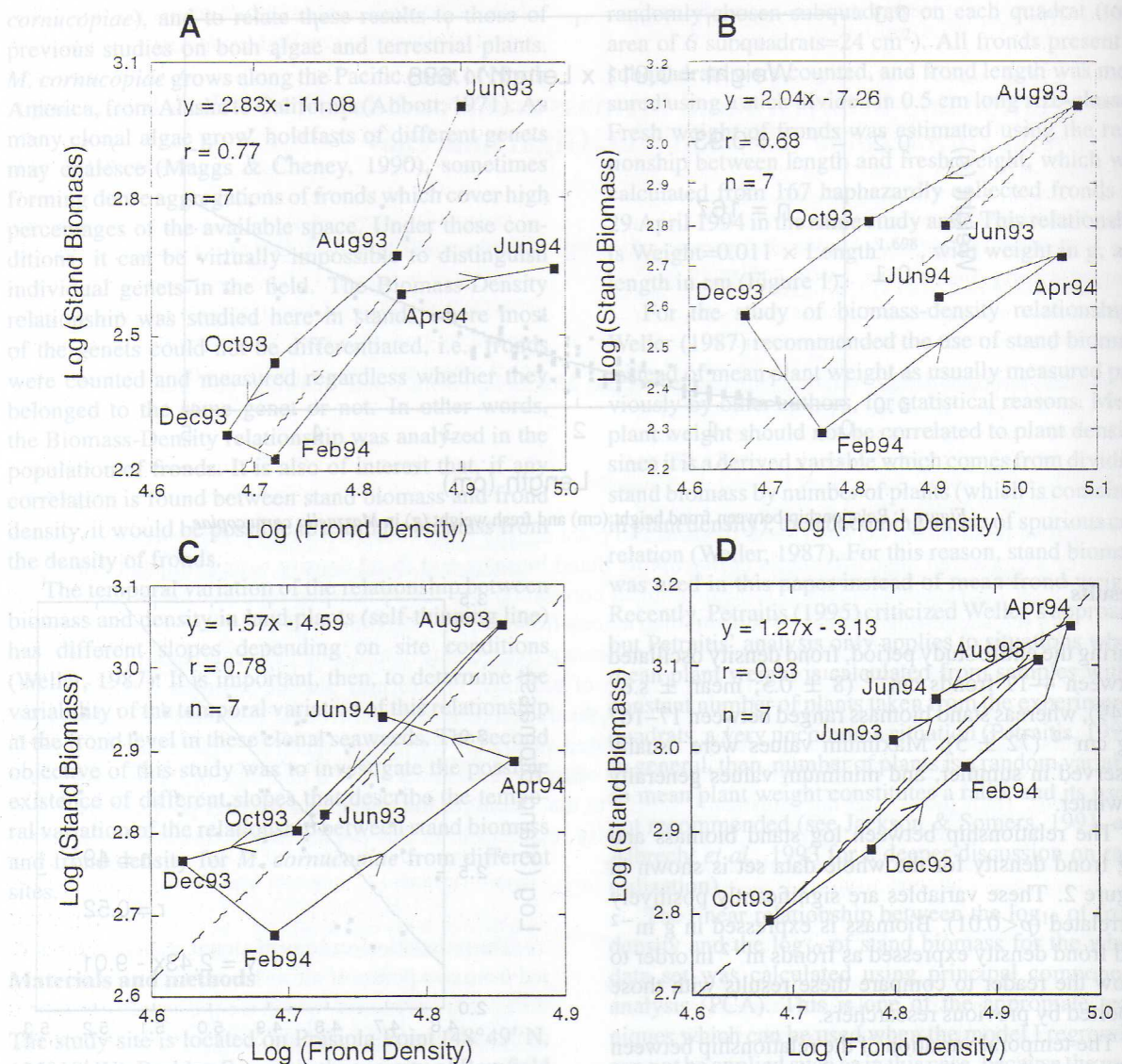


Figure 3. Temporal variation of the relationship between log stand biomass ( $\text{g m}^{-2}$ ) and log frond density ( $\text{fronds m}^{-2}$ ). A: quadrat 2; B: quadrat 3; C: quadrat 5; D: quadrat 7. The month in which each data point was recorded is noted. The functional relationships between both variables (dashed lines) were obtained by PCA.

ance, and site conditions (Weller, 1987; Zeide, 1987). The terrestrial Biomass-Density relationship comprises all data points used to describe the self-thinning lines, so this negative relationship indirectly indicates the existence of competition among plants in the stand, through density-dependent mortality as the stand ages.

Until recently, self-thinning was not believed to occur among ramets of clonal terrestrial plants (Hutchings, 1979; Pitelka, 1984) or even clonal aquatic ferns (Room & Julien, 1994), probably because ramets are physiologically integrated. This would apply to clon-

al seaweeds as well, where there is a certain degree of physiological integration among fronds (Maggs & Cheney, 1990). However, self-thinning was found recently to occur among shoots of the perennial clonal grass *Gynerium sagittatum* (Aublet) Palisot de Beauvois (Poaceae) from tropical Peruvian floodplains (de Kroon & Kalliolia, 1995). They suggested that the seasonality of shoot growth is a major influence on the expression of self-thinning in clonal plants: periodic density-independent mortality and density-dependent shoot natality in spring would not allow shoots to reach



self-thinning. Thus, the low seasonality of the tropics (such as in Amazonian Peru) would allow ramets of clonal plants to reach self-thinning after a prolonged period.

The lack of a negative Biomass-Density relationship in *M. cornucopiae* shows indirectly that fronds do not undergo self-thinning at the natural densities observed. This was somehow expected, since the negative slope in the biomass-density plot for land plants is obtained when stands of even-aged plants are analyzed, which is not the case in fronds of clonal seaweeds, since fronds are produced continuously (Gómez & Westemeier, 1991; Scrosati *et al.*, 1994). The lack of self-thinning among fronds of clonal algae was suggested by Martínez & Santelices (1992), after measuring the Biomass-Density relationship in clumps of *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq from Chile. In this alga, there was no significant correlation between mean frond weight and frond density within individual clumps. However, mean frond weight in each clump was used instead of clump biomass, following the choice of previous authors working with terrestrial plants, who used mean plant weight instead of the preferable choice stand biomass. It would be very interesting to analyze the relationship between stand biomass and frond density in *M. laminarioides*, since its growth form is similar to that of *M. cornucopiae* (pers. obs.).

The evidence presented here for *Mazzaella cornucopiae* and that obtained from *M. laminarioides* by Martínez & Santelices (1992) leads to the conclusion that there may not be self-thinning among fronds of clonal algae of this genus at natural densities. Moreover, the observations presented here for *M. cornucopiae* indicate that higher frond densities would actually favor a higher stand biomass. It is important to note that the data points recorded for the Biomass-Density relationship for *M. cornucopiae* lay above the lines proposed for the terrestrial Biomass-Density relationship (Weller, 1989). The explanation for this positive association can be related to environmental conditions. In other intertidal seaweeds, a denser aggregation of fronds increases the resistance to desiccation and/or herbivory (Hay, 1981; Padilla, 1984; Taylor & Hay, 1984). In intertidal populations of seaweeds such as *M. cornucopiae*, desiccation is an important ecological factor determining physiological performance, especially during the high temperatures at low tides in the summer (Levitt & Bolton, 1991; Kübler & Davison, 1993; Bell, 1993). Emerged photosynthetic rates are generally lower when thallus desiccation

increases (Quadir *et al.*, 1979; Levitt & Bolton, 1991; Bell, 1993; Britting & Chapman, 1993). Thus, an increase in aggregation of fronds could favor a higher stand biomass because increased water retention among fronds during low tides prevents strong desiccation. Also, increased frond density could provide greater protection from physical forces imposed by the high wave action, because fronds would be cushioned by others, thus decreasing the detachment rate of larger fronds. This positive association may also be extended to other seaweeds. Santos (1995) found a positive relationship between stand biomass and frond density in the clonal subtidal alga *Gelidium sesquipedale* (Clemente) Bornet *et* Thuret (Gelidiales) from Portugal.

In the only study of the Biomass-Density relationship conducted at the genet level on seaweeds (i.e., measuring individuals and not ramets), Schiel & Choat (1980) found a significant positive correlation on an arithmetic scale between stand biomass and plant density in the brown algae *Ecklonia radiata* (C. Agardh) J. Agardh and *Sargassum sinclairii* Hooker *et* Harvey from New Zealand. When Cousens & Hutchings (1983) replotted Schiel and Choat's data set in a bi-logarithmic scale relating mean plant weight and plant density, data points were below the straight line with the negative slope proposed by the self-thinning rule. That led Cousens & Hutchings, *op. cit.*, to claim that the evidence presented by Schiel & Choat, *op. cit.*, was inconclusive to suggest lack of self-thinning in these algae. But, again, new measurements involving stand biomass instead of mean plant weight (as Cousens & Hutchings, *op. cit.*, used for their reanalysis), and using a larger data set, are needed in order to understand the Biomass-Density relationship among individuals of these algae.

As shown in Results, a significant positive correlation between biomass and density was found in quadrats 2, 3, 5, and 7, when the temporal variation of this relationship was plotted. Data points 'moved' back and forth along fitted lines accordingly with seasons. Similar patterns of cyclical seasonal movements in the biomass-density plot were observed in stands of ramets of clonal perennial herbs by Hutchings (1979), although there was no correlation between biomass and density (using mean shoot weight instead of stand biomass). The four slopes found here are not significantly different, and, indeed, they are statistically similar to the slope found for the whole data set. This evidence suggests that there is only one slope for the relationship between biomass and density in this pop-



ulation. The other three quadrats (numbers 1, 4, and 6) did not show a significant linear correlation between stand biomass and frond density. However, correlation coefficients were still positive, and it has to be noticed that 7 sampling dates were taken into account for this analysis. It is logical to expect that a significant correlation for these three quadrats may come with increased sample size (=more sampling dates), because the critical correlation decreases accordingly (Fisher & Yates, 1963). Thus, the full acceptance of the existence of one or more than one slopes awaits more observations on this population. In any case, positive or no correlation between biomass and density indicates lack of self-thinning.

The highest natural densities found for *M. cornucopiae* in this study occurred in the summer. Normally, sea conditions become more harsh after the warm season, which may contribute to the detachment of larger fronds. It is not clear what would happen in the hypothetical situation of constant good growth conditions: would stands show self-thinning after prolonged growth? This seems unlikely considering the possibility of physiological interactions among ramets. Nonetheless, constant good growth conditions would be very difficult to achieve in these intertidal sites with a strong seasonal component to answer this question experimentally. On the other hand, the estimation of algal biomass is often time-consuming because: (1) it may require a measurement of the size structure of the stand, (2) it may not be very accurate if certain plotless techniques are used (Littler & Littler, 1985), or (3) it sometimes involves destructive methods, such as harvesting of parcels (De Wreede, 1985). If a single slope for the Biomass-Density relationship holds for different sites, that means that an average biomass could be estimated at any frond density. The Biomass-Density relationship could be a quicker, non-destructive tool to estimate standing biomass just from counting fronds in a given area.

It is important to notice again that the Biomass-Density relationship has been focused in *M. cornucopiae* at the frond (ramet) level, not at the genet level. What might happen if we studied this relationship among different genets? The coalescence of holdfasts and frequent conditions of high frond densities and percent cover make it almost impossible to identify separate genets in the field. However, the negative relationship observed in terrestrial plant stands probably would not occur in clonal algae, because neighbor genets may coalesce instead of competitively exclude one another, thus presenting different patterns of growth and mor-

tality than terrestrial plants. With respect to the temporal variation of the relationship between biomass and density, any study at the genet level should require, at least, mapping the position of different genets from early stages in order to describe correctly their patterns of growth, coalescence, and mortality.

### Acknowledgments

Sincere thanks are extended to Dr Robert De Wreede, for his general supervision, Dr Frank Shaughnessy, Dr Rui Santos, and an anonymous reviewer, for their useful comments, Dr Alfred Brülisauer and Dr Robert Schutz, for their statistical advice, and the personnel of Bamfield Marine Station. Financial support was provided by an operating grant of the Natural Sciences and Engineering Research Council of Canada (NSERC) to Dr Robert De Wreede. Travel funds to attend the ISS-Valdivia were mainly provided by the Faculty of Graduate Studies of UBC and from the XIII ISS-Vancouver Organizing Committee (through Dr Ron Foreman), whom I also acknowledge with gratitude.

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## Introduction

Since the beginning of this century, numerous Antarctic expeditions have greatly increased our knowledge of the benthic flora of both Antarctic and circumantarctic areas (Papenfuss, 1964; Arnaud et al., 1967). Studies done during most recent expeditions have increased our floristic knowledge (Zaneveld, 1966a; Zaneveld & Sanford, 1980; Cormaci et al., 1992a) and have also provided a significant contribution to our knowledge of the geographical distribution and of the zonation of algal communities, especially for the Ross Sea (Zaneveld, 1966b; Arnaud, 1974; Miller & Pearse, 1991; Cormaci et al., 1992b).

In contrast, quantitative observations on the density and biomass of algal populations in both Antarctic and subantarctic regions are very rare, and they primarily regard *Macrocystis* and *Diavillea* populations (Dalepine et al., 1985; Tussenbroek, 1993). Only a few data refer to the algal biomass of the Ross Sea (Miller & Pearse, 1991; Gambi et al., 1994).

In this paper we present quantitative data on the summer biomass of a population of *Iridaea cordata* (Turner) Bory occurring at Terra Nova Bay (Ross Sea, Antarctica). This species, distributed throughout the circumantarctic area (Dalepine et al., 1985), is distributed in Terra Nova Bay throughout the infralittoral zone (according to the Genoa system terminology, Luning, 1990), but it is more frequent and abundant in the upper infralittoral (Miller & Pearse, 1991; Cormaci et al., 1992b).

## Description of sites studied

Terra Nova Bay (Ross Sea) is located between Cape Washington (74°30.90' S, 165°42.00' E) and Cape Russel (74°54.00' S, 163°54.70' E). Sampling was done at two stations (Figure 1). The first, named 'Wharf IB', is near the Italian Base (74°41.58' S, 164°07.05' E). It is located at the promontory that delimits Gerlache Inlet to the south. The second, named