Studies on the Ecology and Production of Seaweeds of Economic and Potential Economic Importance on the Namibian Coast.

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ABSTRACT

The seaweeds of the Namibian coast have received little attention from researchers despite the fact that there is a successful industry based on seaweed exploitation. Beach cast *Gracilaria verrucosa* (Hudson) Papenfuss is collected (9000-15000 t (wet) y^{-1}) in the Luderitz area for the production of agar, *Laminaria schinzii* Foslie was harvested for a short period from April 1987 to March 1989 and there is an increasing interest in utilizing other seaweed species on the coast.

The natural beds of *Gracilaria verrucosa* in the Luderitz area were mapped and biomass estimated in summer (August 1991) and winter (January1992) and beach cast collections were analyzed to ascertain patterns. The distribution of *G. verrucosa* was influenced by sediment type with most occurring on firm (constituting at least 60% 106-212 um) sediments. The largest surface area and biomass of the beds occurred in the northern portion of the Lagoon/Bay system, where the largest biomass of beach cast occurs. Most of the beds occur between 4-8m depth.

Beach cast follows a distinct pattern at most sites in the northern, more wave exposed portion of the Bay/ Lagoon system, being highest in autumn/winter when swell is generally highest. In the southern half of the Bay/Lagoon system beach cast did not follow an annual pattern. Though the southern portion of the system is more wave protected, strong wind driven currents operate which were recorded at 0.44 m s^{-1} during 40 km h^{-1} south winds. The northern portion of the system is deeper than the southern and thus most of the beds in the northern portion occur deeper than in the southern portion. It is postulated that the deeper beds are less susceptible to wave and wind chop action and can attain a large biomass before the plant reaches a size that the point of attachment can no longer hold (usually during large winter swell).

Gracilaria fragments were grown on ropes to investigate various aspects of growth. The optimal depth for growth was found to be 0.5-2.5m and the highest (specific growth rate 11-12% d^{-1}) growth rate occurred in summer and extended throughout autumn in years where high temperatures occurred in autumn. Low growth rates occurred in winter (8% d^{-1}). Growth rate varied with different seeding weights; large seeding weights had lower growth rates over 11 days, 12.1% d^{-1} and 5.7% d^{-1} for 10g and 70g seeding weights respectively. The reduction was attributed to self shading and fragmentation of the plants. Seasonal agar yield was highest in autumn/winter and lowest in summer/autumn and correlated negatively with daylength. In plants grown at various depths the agar yield correlated negatively with growth rate.

Using growth rate (incorporating the factors that effect it) and swell as variables, the beach cast of *Gracilaria verrucosa* from 1988 to 1991 was simulated using a matrix model. The model accounted for over 57% of the variation. By using the model as an investigative tool it was found that the timing of swell as well as its size were very important to the total annual beach cast. Largest simulated annual beach cast occurred during the absence of large swell and the smallest annual beach cast occurred during a year with large autumn swell. Warm water events increased growth rate and as a result beach cast was higher. Given the temperatures for the first few months of a year the beach cast for that year can be predicted for a range of different swell scenarios using the model.

Seasonal growth rate of *Laminaria schinzii* varied from 5-13mm d^{-1}, the period of highest growth was in autumn/summer and lowest in winter and growth in the more exposed site tended to be lower. Photoperiod was hypothesized to be the most important controlling factor. Plants in more wave exposed sites had a lower frond surface area, narrower and thicker fronds, and longer and heavier stipes than those growing in sheltered sites; these differences were more marked in deep water. The attachment strength of the plants did not vary with degree of exposure indicating that a reduction in the surface area offered to wave action was the adaptive route chosen to cope with wave exposure. In the presence of *Ecklonia maxima* (Osbeck) Papenfuss the stipes of *L. schinzii* tended to be shorter and to have a more solid stipe, approaching that of *L. pallida* Greville ex J. Ag.

Percentage cover of *Porphyra capensis* Kutzing, *Aeodes orbitosa* (Suhr) Schmitz, *Gigartina radula* (Esper) J. Ag. *Gigartina stiriata* (Turner) J. Ag. and other dominant intertidal seaweeds showed a marked seasonal growth pattern with a maximum in summer/autumn and minimum in winter. Peak cover of *Aeodes* and *Gigartina* tended to occur later on the more sheltered shore (Halifax) and throughout the year *Aeodes* was more abundant on the more sheltered shore and *Gigartina* was more abundant on the more exposed shore (Grossebucht). Sea temperature and light were the most important factors influencing the seasonal pattern of percentage cover.

CHAPTER 1

GENERAL INTRODUCTION

1.1 The need for seaweed research in Namibia.

Situated on the south west coast of Africa, Namibia is, for the most part, arid and as such, terrestrially, is relatively infertile. Most agricultural activities are confined to the north of the country where subsistence farming is the usual practice. Most of the wealth of the country is generated through the various mining and fishing industries. Many people are employed in recovering the rich deposits of, amongst other minerals, diamonds, uranium, lead and zinc and in catching the abundant fish in the country's rich coastal waters. Despite these mining and fishing activities, unemployment is high and this is particularly a problem in the coastal areas where farming of any description is impossible due to the desert conditions and lack of access to coastal areas due to national parks, diamond mining areas and absence of road or rail infrastructure (Molloy, 1990).

Since Namibia gained independence from South Africa in March 1990, the various governmental bodies have been actively involved in identifying the country's resources and the potential of each. Through research, the country wishes to utilize its marine resources optimally. The policy is to utilize the resource to its full potential without detriment and so create jobs and revenue. A seaweed industry which started prior to independence in Luderitz has created badly needed jobs in the area. These jobs need to be secured and the industry expanded. This study aims to go some way to identifying the seaweed resources and investigating avenues for expanding the industry.

Most of the study is devoted to *Gracilaria verrucosa* because the present industry is based on this resource and it is desirable to expand this industry. *Laminaria schinzii* Foslie was experimentally harvested for a brief period as a small market had opened up for the dried product so this is regarded as the second most important utilizable seaweed. The rest of the study concentrates on other seaweeds which may have economic potential.

1.2 The marine climate

The most prominent feature of the circulation in the eastern half of the South Atlantic ocean is the Benguela current (Stander, 1964). The Benguela system created by this current lies between Cape Point (34° 10' S) and Cape Frio (18° 40' S) and includes the west coast of South Africa and most of the coast of Namibia (Shannon, 1985). The marine climate of the 1500 km coast of Namibia, which stretches from the Kunene river (17° 30' S) to the Orange river (28° 20' S) is dictated by this cold current.

The occurrence of upwelling cells in the system (Stander, 1964) contributes to the lowering of sea temperature and increase in nutrient enrichment. Physical stress exerted by long shore winds causes mass seaward transport of waters due to the Ekman spiral. Movement in the northern hemisphere is deflected to the right and in the southern hemisphere to the left by the Coriolis effect (which is caused by the rotation of the earth). Surface water moves in the same direction as the wind and each layer of water drags on the one below it, and in each layer the coriolis effect works. The flow turns progressively farther away from the wind direction until it ultimately is in the opposite direction. The net direction of mass transport is at 90° to the direction of the wind (right in the northern and left in the southern hemispheres). This transported water is replaced by cold water with relatively low salinity, low dissolved oxygen but high nutrient content (Calvert and Price, 1971) which upwells to the surface to replace the mass balance (Bailey, unpubl.). Of the eight localized upwelling cells of the Benguela system (Lutjeharms and Meeuwis, 1987), the Luderitz cell has been identified as the principal upwelling center, where offshore winds are strongest and hence temperatures lowest. Temperatures increase slightly north and south of this cell (Bailey, unpubl; Shannon, 1985; Lutjeharms and Meeuwis, 1987; Agenbag and Shannon, 1988).

The marine climate and the corresponding biota of Namibia and the west coast of South Africa has been described as cold temperate (Stephenson, 1948). Luning (1990) described the region as warm temperate with a cool temperate south western province and Bolton (1986) argued for the term warm temperate as the gametophytes of the kelps, *Ecklonia maxima* (Osbeck) Papenfuss and *Laminaria pallida* Greville ex J. Ag. which grow in the area grew best at higher temperatures, under laboratory conditions, than most kelps and as such cannot be used to indicate a cold temperate environment (an argument which had been used by Stephenson, 1948). Further, Luning (1990) pointed out that *Durvillaea antarctica* (Cham.) Hariot which is a typical cold-water species does not occur in the area. Other publications simply use temperate (Bolton and Levitt, 1987). The average temperature range for Luderitz is 12-14.8 °C (using a 23 day running average, to smooth the data over 10 years, Molloy, 1990). This places Luderitz in an intermediate temperate position as 12° C is above the winter maximum for cold temperate and 14.8° C is below the summer minimum for warm temperateas understood in the North Atlantic (van den Hoek, 1975). Intrusions of warm water occur at approximately 10 year intervals, and this El Nino-like phenomenon raises temperatures 2-5 °C higher than normal (Brundrit, 1984).

The relatively straight and unindented coast of Namibia offers no protection from the large Atlantic swells which generally approach from a south-westerly direction except in the few bays along the coast at Luderitz, Hottentots Bay, Sandwich Harbour and Walvis Bay (fig. 1.1). Tides are semi-diurnal and amplitude is small with an absolute minimum of 0.42 m and an absolute maximum of 1.88 m (Molloy, 1990).

1.2.1 Coastal Topography (see fig. 1.1)

The only predominantly rocky area on the Namibian coast occurs from Luderitz (26° 39' S) to Bogenfels (27° 25' S) 80 km south of Luderitz, the rest of the 1500 km coast is sandy with scattered rocky outcrops. In the north, from Swakopmund (22° 55' S) to the Angolan border there are a few rocky outcrops along the predominantly sandy coast. Most of the rock in this area occurs in the low intertidal or subtidal and is often inundated with sand. South of Swakopmund is the South African owned Walvis Bay enclave and immediately south of that is the Namib Naukluft park with sand dunes reaching down to the waters edge. Closer to Luderitz the rocky outcrops become larger and more frequent (Molloy, 1990). The only sheltered areas are; Luderitz Bay, Hottentots Bay, Spencer Bay, Sandwich Harbour and Walvis Bay. Luderitz is alone in having substantial rocky areas. The continental shelf is typically ca. 140 kms wide along the coast but there are some narrow points, most notably just south of Luderitz (Birch and Rodgers, 1973). The sea floor on the shelf is predominantly rocky with patches of thin sedimentation south of Luderitz, while between Luderitz and Cape Frio deposits of diatomaceous muds exist. (Shannon, 1985). These anoxic muds frequently give rise to sulphur eruptions in the Walvis Bay region.

1.3 Seaweed studies to date:

Luning (1990) gave the northern and southern boundaries of the "southwestern African province" as, Mossamedes in Angola south to Cape Agulhas in South Africa, which includes the entire coast of Namibia. Hommersand (1986), in a study of southern African red algae, stated that the Namibian seaweed flora belongs with that of the west coast of South Africa, though species richness decreases as one proceeds north. Hommersand (1986) states further that "the comparative poverty of the flora is due, in part, to a lack collections and published records". Based on available data he estimated that 60% of the red algal species of Namibia have their closest relationships with those of southern Australia, Tasmania, New Zealand or South America, which he attributed to dispersal events in the Oligocene and Miocene, rather than continental drift.

The seaweed flora of South Africa is relatively well known (Lawson *et al.* 1990) and the seaweeds of Angola have been investigated by Lawson *et al.* (1975). However, the Namibian coast which links the two has been poorly studied. The inaccessibility of the coast due to the Namib desert and absence of a road infrastructure are probably responsible for the lack of attention.

Initial published records of the seaweeds of the Namibian coast were incidentally included in faunal studies of the intertidal shores by Penrith and Kensley (1970 a and b) and Kensley and Penrith (1980). Wynne (1986) made a once-off collection at Swakopmund including 63 species, and Lawson *et al.* (1990) published a survey of parts of the coast (Luderitz, Elizabeth Bay and Swakopmund) conducted in 1957 and updated the species list to 196 records a number of which are doubtful (Engledow *et al.*, in prep). A study of the utilized and potentially utilizable seaweeds was carried out by Molloy (1990). Single species distributions have been reported into Namibia (e.g. Simons, 1966, 1968 and 1976; Simons and Jarman, 1981; Price *et al,* 1978 and 1988; Bolton and Anderson, 1987).

1.4 Exploitation:

Gracilaroid algae grow in the mud and sand of the Luderitz Lagoon and Bay and attached to rock in the Swakopmund and Walvis Bay areas (Molloy, 1990). Material collected from Swakopmund and further north was identified as *Gracilariopsis* (Engledow and Stegenga, pers. comm..). Since 1981 a Gracilarioid alga has been collected at Luderitz as beach cast (Rotmann, 1987; Molloy, 1990; Critchley *et al.* 1991). From 1986 onwards all material that washed up (10-15,000 wet tonnes year^{-1}) was collected (Molloy, in press). Until 1991 one third of the collected seaweed was used for agar extraction at the plant at Luderitz and the remainder was exported. The extraction plant was built in 1986 and went into production in early 1987. Presently, no agar is extracted, rather the seaweed is alkali treated, dried and exported to Ireland for further processing.

Laminaria schinzii is the only other seaweed that has been utilized commercially in Namibia (Molloy, 1990 and in press). Between August 1987 and March 1989, 137 tonnes (wet) were harvested. Only blades were harvested. The blades were cut by hand 2 cm above the meristem, air dried and exported to Taiwan for human consumption.

Molloy (1990) identified other seaweeds of possible economic importance on the Namibian coast. These were; *Porphyra capensis* Kutzing, *Aeodes orbitosa* (Suhr) Schmitz, *Iridaea capensis* J. Ag., *Gigartina radula* (Esper) J. Ag. and *G. stiriata* (Turner) J. Ag. and *Suhria vittata* (L.) J. Ag. In South Africa, all of the species identified by Molloy (1990) as being of commercial or possible commercial importance, with the exception of *Aeodes orbitosa* and *Iridaea capensis*, have been utilized at one time or another (Anderson *et al.*, 1989) *Gracilaria verrucosa* (Huds.) Papenfuss has been harvested sporadically since World War II for agar production, *Suhria vittata* has also been collected for agar but supplies are very small. Beach casts of *Ecklonia maxima* and *Laminaria schinzii* have been collected since 1953, dried and, for the most part, exported for alginate extraction. *Gigartina radula* and *G. stiriata* were sporadically harvested between 1956 and 1978, most being exported for carrageenan extraction. Small collections of *Porphyra capensis* were made between 1965 and 1978, with an unknown quantity exported to Japan (Anderson *et al.*, 1989).

1.5 *Gracilariaceae:*

The genus *Gracilaria* has been a taxonomic headache to phycologists since its inception by Greville in 1830 (Fredericq and Hommersand, 1989). *Gracilaria verrucosa* is probably the most controversial species in the genus. The type specimen of *G. verrucosa* is from the south coast of England (*G. confervoides* (L.) Grev. = *G. verrucosa*) and since the description, reports of seaweeds from all over the world have been ascribed to *Gracilaria verrucosa*, particularly exploited seaweeds that have a *Gracilaria verrucosa*-type terete thallus (Mclachlan and Bird, 1986). The holotype having been lost, the description of Hudson (1762) has been designated the lectotype (Dixon and Irvine 1977). Morphological variability and the lack of tangible morphological features (Bird *et al.* 1982) contribute to the taxonomic confusion. Investigators have turned to fine structure (Fredericq and Hommersand 1989), hybridisation (Plastino and Oliveira, 1988) and genetic studies (Bird *et al.* 1982, Bird and Rice 1990 and Rice and Bird, 1990) to distinguish between seaweeds in the *"G. verrucosa"* group. Bird *et al.* (1982) reported British Isles *G. verrucosa* to have a chromosome number of n=32 but Bird and Rice (1990) point out that the specimen investigated by Bird *et al.* (1982) was *Gracilariopsis* and that the typical chromosome number for *Gracilaria verrucosa* is n=24. Fredericq and Hommersand (1989) proposed a new order, the *Gracilariales,* based on the reproductive development of *G. verrucosa.* Santelices and Doty (1989) suggest that the names *G. verrucosa, G. confervoides, G, edulis* (Gmel.) Silva and *G. foliifera* (Forssk.) Borg may rarely be correctly applied. Rice and Bird (1990) suggest the possibility that Hudson's *G. verrucosa* may have been *Gracilariopsis,* which is extremely difficult to distinguish from *G. verrucosa*-type seaweeds and Steentoft (1991) has confirmed their suspicions, traditionally proposing, however, that the genus *Gracilaria* should be conserved as circumscribed. Commercial exploiters prefer to refer to seaweed stocks by locality rather than scientific name (Stancioff, 1981).

One of the main distinguishing factors between *Gracilaria* and *Gracilariopsis* is the presence (*Gracilaria*) or absence (*Gracilariopsis*) of nutritive filaments issuing from the gonimoblast cells of the cystocarp (Fredericq and Hommersand, 1989). In South Africa the *Gracilaria* growing in Langebaan Lagoon on the west Cape coast has been identified as *Gracilaria verrucosa* (Isaac, 1956 as *G. conferviodes* and Stegenga pers. comm..) and at Simonstown near Cape Town and Swakopmund in Namibia the terete Gracilarioid species growing on the open coast is *Gracilariopsis* (Stegenga and Engledow pers. comm.., genus identification based on the presence or absence of nutritive filaments in the cystocarp). As no fertile material from Luderitz has ever been reported, and none was found in this study, the name *Gracilaria verrucosa* is retained pending further investigation. The Luderitz material is similar in morphology and habitat to the Saldanha Bay *G. verrucosa.*

1.5.1 Commercial Gracilariaceae: Natural Stocks, Growth and Cultivation.

The Gracilariaceae is one of the most economically important famalies of seaweeds. In 1986 it was estimated (Mclachlan and Bird, 1986) that about 5000 tonnes of agar was processed from 25,000 to 30,000 tonnes (dry) of *Gracilaria* and *Gracilariopsis*. Other uses for *Gracilaria* include human consumption (Abbott, 1988), energy production (Hanisak, 1987) and feed for abalone (Santelices and Doty, 1989).

This commercial importance, and the 100 or so described species in the genera *Gracilaria* and *Gracilariopsis* (Mclachlan and Bird, 1986), has led to the group being very intensively studied worldwide. The natural stocks of greatest importance occur in Chile, Argentina, Brazil, South Africa and Namibia (Santelices and Doty, 1989; Anderson, 1989; Rotmann 1987). Until 1984 the Chilean beds, which account for one third to one half of the world supply, could keep up with demand. Demand, however, steadily increased with the result that the Chilean beds were over-harvested (Santelices and Ugarte, 1987; Pizarro and Barrales, 1986). This sent out a warning to other exploiters of natural beds and so methods of farming the various species were investigated.

Chile leads the field in large scale open water cultivation of *Gracilaria*. Between 1984 and 1988 the harvest of natural beds decreased from 110,000 to 36,500 tonnes (wet) per year and at the same time yields from farmed *Gracilaria* increased from 680 to 23,109 tonnes (wet) (Santelices and Ugarte, 1990). In Chile, bottom planting (Pizarro and Barrales, 1986) to duplicate and extend the natural beds is preferred.

Other commercial cultivation of *Gracilaria* includes brackish pond cultivation in Taiwan (Liu et al., 1981; Yang, *et al.* 1981; Chiang, 1981; van der Meer, 1983) and raft cultivation in the West Indies (Smith, 1989). Preliminary studies towards commercial cultivation have been reported from Venezuela (Rincones-Leon, 1989), China (Li *et al.*, 1984; Ren *et al.* 1984), Kenya (Coppejans, 1989), Namibia (Rotmann, 1987), the Philippines (Trono *et al.*, 1981), the USA (Hansen, 1984; Hanisak, 1987) and Israel (Friedlander *et al.*, 1987).

Though *Gracilaria* was known to contain agar for many years, it was considered to be poor quality until the Japanese developed the strong alkaline pretreatment which improved the quality and aroused major commercial interest (Armisen and Galates, 1987). Presently, species of *Gracilaria* are collected from South America, southern Africa, India, Indonesia and the Far East.

Agar is a complex polysaccharide which forms the matrix of cell walls of *Gracilaria* species and other "agarophytes" (Lahaye and Yaphe, 1988). This complex polysaccharide is made up of two fractions viz. agarose (relatively neutral and usually unsubstituted) and agarobiose (usually substituted with methoxyl, sulphate esters and pyruvate ketal groups; Lahaye and Yaphe, 1988). Yaphe (1984) identified three groups of *Gracilaria* agars: 1) high gel strength with neutral unsubstituted agarose, 2) lower gel strength with agarose substituted with sulphate and pyruvate groups and 3) lowest gel strength, highly substituted with sulphate and methoxyl groups present.

Laboratory and ecological studies on members of the Gracilariaceae tend to have three main aims viz. A) biomass production, B) agar yield and C) agar quality (Table 1.1).

SEAWEED ORIGIN AND REFERENCE	EMPHASIS	PARAMETERS TESTED
G. verrucosa, Norway (Stokke, 1957)	A	Temperature and salinity
G. verrucosa, U.K. (Jones, 1959b)	A	Season
G. verrucosa, U.K. (Jones, 1959a)	A	Water motion, irradiance
G. dentata J. Ag., Ghana (John and Asare, 1975)	A,B,C	Season
G. bursa-pastoris (Gmel.) Silva and *G. coronopifolia*, Hawaii (Hoyle, 1978a)	B, C	Season
G. bursa-pastoris and *G. coronopifolia*, Hawaii (Hoyle, 1978b)	B, C	Reproductive phase
G. tikvahiae McLachlan, U.S.A. (Asare, 1980)	C	Season
G. tikvahiae, U.S.A. (Bird and Hanisak, 1981)	C	Methane digestion
G. verrucosa, *G. salicornia* and *G. coronopifolia*, Philippines (Trono, 1981)	A	Season
G. (6 species) Caribbean (Hay and Norris, 1984)	A	Season
G. verrucosa, U.S.A. (Bird, 1984)	A	Season
G. tikvahiae, Canada (Craigie and Wen, 1984)	B, C	Temperature, tissue age
Various *Gracilaria* species, Canada (Craigie *et al.* 1984)	C	Nitrogen, different species
G. cf. *conferta*, Israel, (Friedlander and Zelikovitch, 1984)	A, B, C	Season

contd.

SEAWEED ORIGIN AND REFERENCE	**EMPHASIS**	**PARAMETERS TESTED**
G. sjoestedtii, U.S.A. (Hansen, 1984)	A, B, C	
Various *Gracilaria* sp., Canada (Yaphe, 1984)	C	
G. tikvahiae, U.S.A. (Fujita and Goldman, 1985)	A	Nutrients, water motion
G. tikvahiae, U.S.A. (Lapointe, 1985)	A	Nutrients
G. sp., Chile (Edding *et al.*, 1987)	A, B	Season
G. cf. *conferta*, (Schousboe) J. et G. Feldmann Israel (Friedlander *et al.*, 1987)	A, B, C	Season
G. verrucosa, Norway (Rueness *et al.*, 1987)	A	Nitrogen, season, depth
Various *Gracilaria* sp., Brazil (Silva *et al.* 1987)	A	Season
G. verrucosa (G-16), U.S.A. (Breden and Bird, 1988)	A	Contaminating algae
G. verrucosa (G-16), U.S.A. (Daugherty and Bird, 1988)	A, B, C	Salinity, temperature
G. pseudoverrucosa, Canada (Lahaye and Yaphe, 1988)	C	Season
G. verrucosa, Argentina (Boraso de Zaixso, 1989)	A	Season, environmental factors substratum
G. sordida W.A. Nelson, New Zealand (Christeller and Laing, (1989)	B, C	Irradiance, temperature, nitrogen
G. secundata Harv. and *G. verrucosa*, (Lignell and Pedersen, 1989)	C	Growth rate

contd.

SEAWEED ORIGIN AND REFERENCE	EMPHASIS	PARAMETERS TESTED
G. sp., Chile (Macchiavello, 1989)	A, B	Season
G. sordida, New Zealand (Nelson, 1989)	A	Season
G. verrucosa (G-16), U.S.A. (Bird and Ryther, 1990)	B, C	Temperature, salinity, irradiance
G. verrucosa and *G. tikvahiae*, U.S.A. (Dawes and Koch, 1990)	A	Nutrients
G. domingensis Sonder ex Kutz., Brazil (Duairatnam *et al.*, 1990)	B, C	Season, calcium addition
G. sordida and *G. verrucosa*, New Zealand and U.S.A (Eckman and Pedersen 1990)	A, B, C	Irradiance, daylength, temperature
G. truncata Kraft. and *G. eucheumoides* Harvey, New Zealand (Furneaux, *et al.* 1990)	C	
G. sordida, New Zealand (Pickering *et al.*, 1990)	A, B, C	Season, density, reproductive phase
G. sordida, New Zealand (Eckman *et al.* 1991)	B	Salinity, nutrients, darkness
G. foliifera, U.S.A (DeBoer, 1978)	C	Nitrogen

Table 1.1 Laboratory and ecological studies on members of the Gracilariaceae showing parameters tested and emphasis: A = biomass production, B = agar yield and C = agar quality.

The results of these investigations give clues as to the optimal site and strain for farming as these are the two most important factors the commercial farmer must consider (Boraso de Zaixso, 1989). Most early studies concentrated on the growth of the plants and the role played by environmental factors. Later, attention turned to agar yield and agar quality. This presumably reflects the market trends and demands. It is interesting to note that most of the above studies, apart from those involving *G. verrucosa*, *G. foliifera* and *G. secundata,* were performed on species that are not major commercial sources of agar.

1.6 *Laminaria*

Laminaria schinzii, the only hollow stiped digitate species, is one of only four *Laminaria* species in the southern hemisphere the others being *L. pallida* (South Africa), *L. brasiliensis* Joly *et* Oliveira Filho and *L. abyssalis* Joly et Oliveira Filho, the last two occurring in deep water off the coast of Brazil (Joly and Oliveira Filho, 1967; Kain, 1979; Dieckmann, 1980; Luning, 1990; Bolton, 1987). The two Brazilian species grow in the tropics at 22° S (Kain, 1979) but *L. schinzii*, reported at 18° 59' S (Penrith and Kensley, 1970b), grows closer to the equator than any other *Laminaria*. In both cases ambient seawater temperature regimes are temperate, because of upwelling in Namibia, and water depth in Brazil.

The *Laminariales* are not free from taxonomic chaos. Over 100 species have been described for the genus but most of these have been discounted (Kain, 1979). Kain (1979) further states that much of the taxonomic confusion is caused by the morphological variability of the genus. Species delimitation is generally based on relatively few morphological characters many of which show considerable genetic and phenotypic variation.

Most of the modern investigations of *Laminaria* taxonomy at the species level have involved the Simplices section, which are the plants with undivided (non-digitate) blades. The work of Chapman (1973 and 1974) indicated that *L. saccharina* (L.)

Lamour and *L. longicruris* la Pyl. are interfertile. and can be considered conspecific (see Luning, 1990). Bolton *et al.* (1983) crossed north Atlantic *L. saccharina, L. longicruris* with Japanese *L. ochotensis* and demonstrating a degree of interfertility.

The difference between *L. schinzii* and *L. pallida* is in the morphology of the stipe. The stipe of *L. pallida* grows to a maximum of 3m is solid and conical tapering slightly towards the junction of the stipe and blade. The stipe of *L. schinzii*, on the other hand, grows to a maximum of 5m is hollow and tapers distally and proximally from the widest mid region (pers. obs.)

The most intensively studied *Laminaria* species are *L. hyperborea* (Gunn.) Fosl., *L. saccharina, L. longicruris, L. japonica* Aresch. and *L. digitata* (Huds.) Lamour. Most aspects of the ecology, growth and reproduction of *L. hyperborea* were investigated by Kain (1963, 1964, 1969, 1971, 1975, 1976a, 1976b and 1977). Luning (1969) investigated the seasonal growth of fronds of *L. hyperborea* and later demonstrated (Luning, 1986) that the initiation of a new frond is a photoperiodic response. Luning (1970) also manipulated the growth rate and size of *L. hyperborea in situ*. Hopkin and Kain (1978) investigated the effects of pollutants on *L. hyperborea*, while near shore cultivation was investigated by Dion and Gloven (1989).

The uptake and storage of nutrients and their effects on growth in *L. longicruris* has been reported by Chapman and Craigie (1977) and Gagne *et al.* (1982). Accumulation of nitrate coincided with the winter maximum of dissolved nitrogen in the seawater. Rapid growth was reached after depletion of ambient nitrate levels due to explosions in phytoplankton populations suggesting that accumulated reserves of nitrogen were being tapped (Chapman and Craigie, 1977). In populations where ambient nitrate concentrations are relatively constant there was little storage (Gagne *et al.*, 1982). Luning, (1971) was the first to demonstrate nutrient translocation in *Laminaria*, the new fronds of *L. hyperborea* assimilated nutrients from the old frond. Translocation has been demonstrated for many other species of *Laminaria* including *L. digitata* where nutrients were transported from the mature blade to the meristematic region. Morphological variation with season, exposure and depth was studied by Chapman (1973). He found stipes of the non-digitate complex of *Laminaria* in Nova Scotia to increase in length in early summer and to decrease in autumn to winter due to loss of larger plants. Stipes tended to be longer and hollow in sheltered conditions and there was a significant difference in stipe length (longer in deeper water) only in sheltered water. Laminarian stipes may be short or long in exposed sites and fronds are often narrower, thicker and longer in exposed sites (Norton *et al.*, 1981; Sundene, 1962; Gerard and Mann, 1979). Population dynamics (Chapman, 1984) have been studied for *Laminaria longicruris* and *L. digitata* from Nova Scotia. The two species produced 8.9×10^9 and 20.02×10^9 spores m^{-2} y^{-1} respectively and recruitment from these spores was increased if the red algal understory was removed. Gametogenesis of L. longicruris was reduced at 5 and 20° C, this inhibition was greater with higher nitrogrn concentration, production of sporophytes was totally inhibited at 20° C (Yarish *et al.*, 1990). The structure and biomass of *L. longicruris* beds were investigated by Sharp and Carter (1986) with a view to harvesting and Smith (1985) reported on regrowth after trial harvesting.

Druehl (1967a) reported on the effect of water temperature, salinity and motion on distribution of *L. groenlandica*Rosenv. A long stiped form was restricted to high wave energy areas and both long and short stipe forms were absent from areas of high temperature and low salinity. Luning and Freshwater (1980) determined the upper and lower survival limits of *L. groenlandica* and *L. saccharina* from the north east Pacific as -1.5 to 18° C. Seasonal growth of *L. groenlandica* was most closely related to temperature and first year plants had the most prolonged growth season (Druehl *et al.*, 1987). Seasonal growth of *L. longicruris* and *L. digitata* was most rapid in January to April and slow in July to October on the Atlantic coast of Canada (Mann, 1972) while Egan and Yarish (1990) found linear growth rate and production of *L. longicruris* growing in Long Island Sound to be maximal in May and minimal in August-September. The southern most limit of *Laminaria* in the west Atlantic was found by Egan and Yarish (1988) to be off the coast of New Jersey where a population of *L. saccharina* was found growing at a depth of 28-36m. Boden (1979) investigated the effect of depth on growth, and the effect of seasonal light and temperature on the development of gametophytes and young sporophytes was described by Lee and Brinkhuis (1988).

The ecology and growth of *L. digitata* has been reported on by Sundene (1962 and 1964). Of the southern hemisphere species the ecology and cultivation of *L. brasiliensis* and *L. abyssalis* were described by Oliveira (1981) and Yoneshigue and Oliveira (1987). Dieckmann (1980) has investigated the growth of *L. pallida* on the Cape Peninsula of South Africa. He found the blades of this digitate species to grow throughout the year with a seasonal low from May to July, accelerating to a maximum growth rate in October to November. The seasonal increase in growth rate was more rapid than the seasonal decrease and plants growing at 8 m and 14 m followed a similar seasonal pattern except that the peaks were lower at the 14 m station and the onset of rapid growth occurred 1 month later at the deeper site. Photoperiod was hypothesized to be the most important seasonal regulatory factor.

Wild stocks of *Laminaria* are harvested for alginate production in Scotland, Ireland, Norway, France, China, Japan and Korea and for food in the Far East (McHugh, 1987). Cultivation of *Laminaria* is expanding particularly in the Far East where *L. japonica, L. angustata,* Kjellm *L. ochotensis* Miyabe and *L. religosa* Miyabe are extensively grown (Druehl, 1988). Minor cultivation of *L. saccharina* takes place in Canada, the U.K. and the U.S.A. and *L. groenlandica* has also been cultivated in Canada (Druehl, 1988)

There are no biological reports on *L. schinzii* except for a preliminary investigation carried out by Molloy (1990).

1.7 Other seaweeds of potential economic importance.

The seaweed flora of Namibia forms a biogeographic continuum with that of the west coast of South Africa (Hommersand, 1986; Lawson *et al.*, 1990). The seaweeds of possible economic importance are *Porphyra capensis,* and *Aeodes orbitosa,* which occur intertidally (and subtidally in the case of *Aeodes*) throughout the region and *Gigartina radula* and *Gigartina stiriata* which occur intertidally on the southern half of the coast (Molloy, 1990).

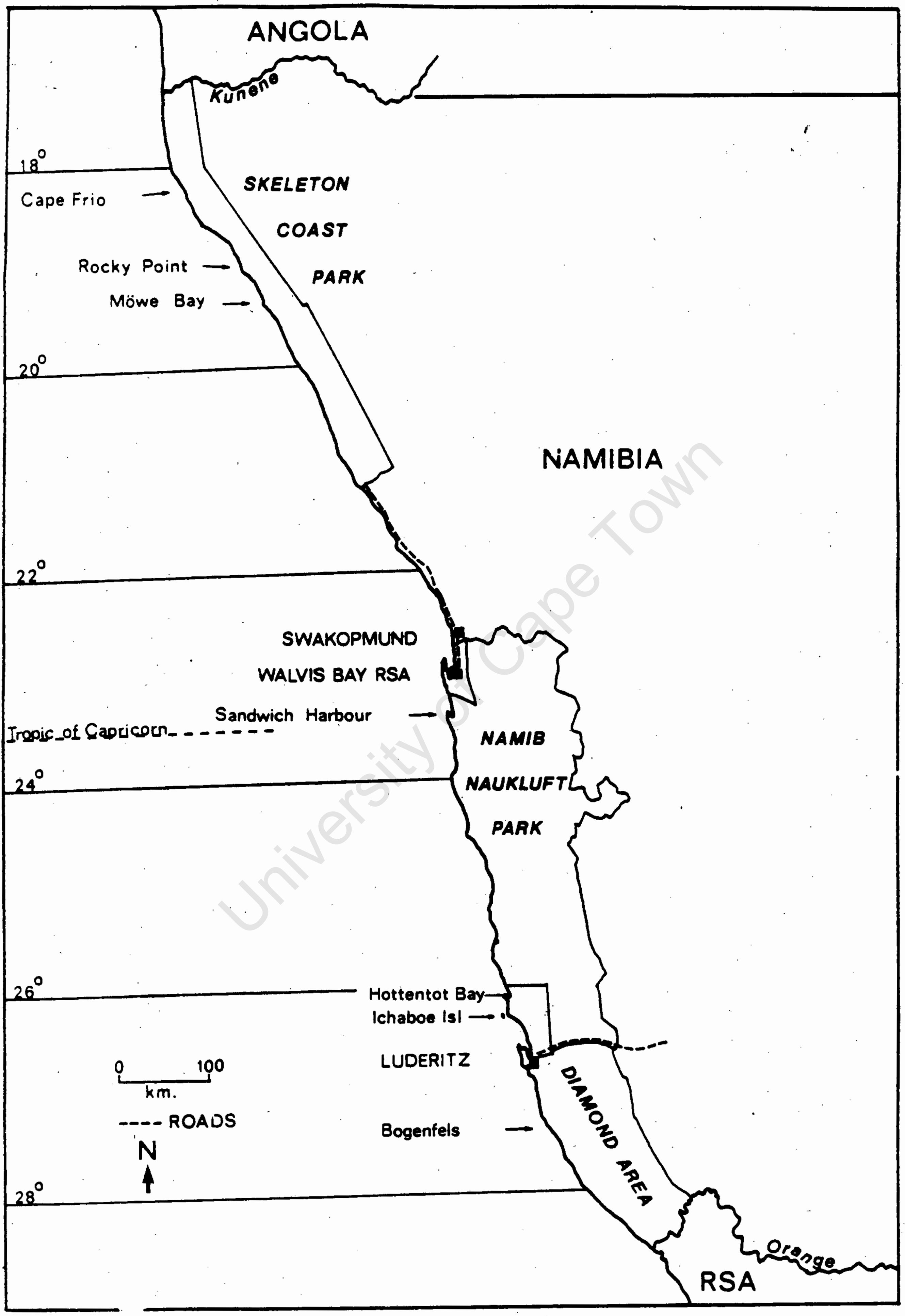
Gigartina radula and *G. stiriata* produce a carrageenan (Anderson *et al.*, 1989) which has similar properties to that of *Chondrus crispus* (Moltino *et al.* 1953) . Furneaux and Miller (1986) extracted the polysaccharide from *Gigartina stiriata* and found it to be a 3:1:1 mixture of *k*-, *l*-, and *u* + *v*- carrageenans. The viscosity of the polysaccharide extracted from *Aeodes orbitosa* was found by Moltino *et al.* (1953) to be considerably more viscous than that from *Gigartina radula.* The polysaccharide of *Aeodes orbitosa* has been named "aeodan" (Nunn and Parolis, 1968) and is composed of highly sulphated D-galactose. *Porphyra capensis* probably refers to more than one species (Isaac, 1957) but as yet their taxonomy has not been clarified. On the South African west coast 5 species of *Porphyra* have been identified (Stegenga, *et al.*, in prep), although the bulk of the biomass is *P. capensis.*

None of these seaweeds of potential economic importance is currently being utilized but studies (Levitt and Bolton unpubl.) are underway in South Africa to assess standing stocks, growth rates etc. of *Gigartina radula* and *G. stiriata* as the local industry in South Africa has shown interest in carrageenan production.

1.8 Plan of Thesis

This study is the first to scientifically investigate aspects of the Namibian seaweed resources. Most attention is given to the species that are, or have been utilized, but the species with potential for utilization are also included.

Figure 1.2 The coast of Namibia.


ANGOLA
Kunene
18°
Cape Frio
SKELETON
COAST
PARK
Rocky Point
Möwe Bay
20°
NAMIBIA
22°
SWAKOPMUND
WALVIS BAY RSA
Sandwich Harbour
Tropic of Capricorn
NAMIB
NAUKLUFT
PARK
24°
26°
Hottentot Bay
Ichaboe Isl
LUDERITZ
0
100
km.
---- ROADS
N
DIAMOND AREA
Bogenfels
28°
Orange
RSA

CHAPTER 2

Distribution, biomass and production of *Gracilaria* at Luderitz.

2.1 Introduction

The only *Gracilaria* population of commercial size on the Namibian coast occurs in the Bay and Lagoon at Luderitz. Though specimens of terete gracilarioid plants have been recorded further north, at Swakopmund, these were isolated plants found attached (Wynne, 1986; Lawson *et al.*, 1990) or in the drift (Molloy, 1990).

The *Gracilaria* population at Luderitz has been commercially exploited since 1981 (Rotmann, 1987; Critchley *et al.*, 1991). It is fortunate that only beach cast material has been collected as no ecological study of any nature has been carried out. The population at Luderitz has been called *Gracilaria verrucosa* (Hudson) Papenfuss (Rotmann, unpubl., 1987; Lawson *et al.*, 1990; Molloy, 1990, in press; Critchley *et al.* 1991) though the application of this name is not based on any taxonomic study. The confusion regarding the classification of the Luderitz population is caused firstly by the general confusion in the Gracilariaceae, secondly the lack of attention the flora of the area has received (see Chapter 1.), but more importantly, fertile material has never been found in the area. This third fact renders a taxonomic classification of the seaweed virtually impossible as so many of the tools of red algal taxonomy are based on reproductive anatomy, particularly of the female. It was pointed out by Santelices and Ugarte (1990) that the commercial *Gracilaria* in Chile is often infertile.

These taxonomic difficulties cause problems when one wishes to draw comparisons between various populations (McLachlan and Bird, 1986) but results from similar seaweeds growing in similar habitats can offer useful comparison.

The most economically important *Gracilaria* beds frequently occur as free living, monospecific stands on mud or sand (Mclachlan and Bird, 1986; Kautsky, 1989).

Stokke (1957) found the Norwegian *Gracilaria verrucosa* beds to be restricted to "semi-closed bays". A muddy substratum from 1-4 meters was found to be the most favorable for the unattached population. Culture under various temperatures revealed that at 10° C and below no growth occurred. Stokke (1957) suggested that the virtually monospecific stands of the *G. verrucosa* population may be accounted for by the relatively high tolerance of H_2S the seaweed was shown to have, both experimentally and apparently in nature. Water with high H_2S levels invades the beds annually. Rueness *et al.* (1987) found the Norwegian *G. verrucosa* restricted to bays with summer temperatures in excess of 20° C in Oslofjiord.

Gracilaria lemaniformis (now, *Gracilariopsis lemaniformis* (Bory) Dawson, Acleto *et* Feldvik (Fredericq and Hommersand, 1989) in Chile was found to grow on muddy substrata in which an underground thallus system gave rise to erect thalli (Santelices and Ugarte, 1987). The seaweed grew between 2-9 meters at Bahia la Herradura and 1-6 meters at Bahia Tongoy on the Chilean coast (Santelices *et al.*, 1984). In these beds spatial biomass was found to be very variable but the underground thallus system was found to be relatively constant (Santelices and Doty, 1989).

Gracilaria chilensis Bird, McLachlan *et* Oliveira and an unidentified *Gracilaria* species were found growing in three sheltered bays in Chile between 2-9 meters on a sandy bottom. The temperature range for the bays was 10-20° C and salinity was constant at 35%o (Santelices and Ugarte, 1990).

In Argentina, Boraso de Zaixso (1989) reported *Gracilaria verrucosa* populations associated with mud at Bahia Melo and Bustamante and mud, small pebbles and shells at Gulfo Nuevo and Bahia Arredondo. At B. Melo *Gracilaria verrucosa* was found associated with ascidians and polychaetes - the animals attach to the thalli and this combination anchors the community (Boraso de Zaixso, 1989). As in Chile the standing biomass was found to be very variable spatially and some of the temporal variation was found to correlate reasonably with temperature.

In South Africa *Gracilaria verrucosa* grows extensively in the shallow Langebaan Lagoon part of the Saldanha Bay complex (Isaac, 1956, as *G. conferviodes*; Simons, 1977; Christie, 1981 and Rotmann, 1990). Both Isaac (1956) and Simons (1977) discuss the distribution, whereas Christie (1981) studied the production and distribution of (among other taxa) *Gracilaria* and correlated the low biomass and production in the southern end of the lagoon with low nutrient availability due to decreased water movement.

Anderson *et al.* (1989) and Rotmann (1990) reported on the commercial collections of the seaweed from Saldanha Bay, which in the three years previous to 1974 were over 1000 t (dry) annually (record high was 2013.5 t in 1967). After 1974 the stocks collapsed, apparently due to dredging and the construction of a ore loading jetty in the bay. Rotmann (1990) then reported on the recovery of the resource which has subsequently collapsed and re-appeared again (Anderson, pers. comm.).

Densities were higher on sandy rather than muddy substrata in Langebaan Lagoon (Isaac, 1956) whereas Simons (1977) reported that *Gracilaria* grew as drift near the bottom of Saldanha Bay. Fox and Stephens (1942) found the *Gracilaria* at Langebaan Lagoon to grow on sandy or sand/rock substrata and that large beach cast occurred during winter storms. Beach cast was most abundant between November to March in Saldanha Bay (Isaac, 1956) but Rotmann (1990) reported that beach cast in Saldanha Bay was irregular and depended on swells and wind driven currents.

Rotmann (1987) briefly described the collection of beach cast *Gracilaria verrucosa* at Luderitz and gave an outline of the seaweed industry. This was updated by Critchley et al., (1991).

The state of the *Gracilaria* resource *in situ* has never been investigated. Thus, the industry, which in Luderitz offers much needed employment, finds it very difficult to budget in advance and there is the constant fear that the stocks may collapse as they did in Saldanha Bay.

2.2 Study Area.

For the purposes of this study the LUDERITZ BAY system is divided into Luderitz bay, Luderitz Lagoon and Shearwater Bay (fig. 2.1). These entities were valleys formed by wind erosion and subsequent flooding when sea levels rose in the Holocene; no rivers flow into the area. Average annual rainfall is a mere 20 mm. and this usually falls between March and August. These valleys are orientated in a north/south direction and the prevailing wind direction is southerly. Spot depths for the area were obtained from nautical maps and these, coupled with depth readings taken with a "Lowrance X-16" echosounder, gave an accurate picture of the bathymetry.

The seaweed washes up in large quantities at certain points in the area (fig. 2.1). In the Luderitz Lagoon these are, Griffith Bays 1, 2, 3 and 4 a series of small bays on the western shore of the Lagoon, Radford Bay a small bay on the eastern side, and Angola and Leibies, two rocky shores on the eastern side of the Lagoon. In the Bay system the washup sites are Aeroplane Bay, a small bay, and Angra Pequena an adjacent 1 km rocky shore in the southern portion of the system, LBC 1, 2 and 3, a 2 km stretch of rocky shore in the mid portion of the Bay, Agate Beach a 2 km sandy beach in the northern portion of the Bay and Flamingo Bay a bay with a sandy shore in the northern end of the Bay. Shearwater Bay is a large bay to the west of the Luderitz Lagoon/Bay system.

2.3 Materials and Methods.

Two surveys of the Lagoon and Bay were carried out in August 1991 and January 1992; other spot samples were taken at other times of the year. Sampling was done using SCUBA and a shark cage (as the Bay and Lagoon are infested with sharks) lowered from a boat. Fixed to the open bottom of the cage was a 1x1 m quadrat. This system of sampling was random in practice as the samples were taken wherever the cage landed. For each survey 45 sites, to cover the study area, were dived and one 1 m^2 quadrat per site was taken. The attached seaweed, in the quadrat, both above and below the substratum was collected and placed in numbered plastic bags for later weighing. Position, depth and associated flora and fauna (if any) were noted and a sample of the substratum was taken for analysis. Before ascent, a circuit of the cage within a 10 m radius was swum to subjectively judge the uniformity of the bed density.

Shearwater Bay was not included in the surveys as it is a large Bay and contributes a small percentage (1.3-8.3%, table 2.1) to the total washup.

To construct density distribution maps of the surveys, biomass class intervals were chosen depending on the range of biomass per m^2 for each survey. The biomass/m^2 at each site then fell into a size class. If a neighbouring site had a different biomass, say one size class difference, then the mid-point between the neighbouring sites was taken to represent the transition. Neighbouring sites that differed by more than one biomass class had the intermediate size classes entered between them so that the transition from high to low density and vice versa was uniform. Biomass size class contours were then drawn by hand to link up all the areas of equal biomass.

Total area of the *Gracilaria* beds and % biomass and surface area at depth intervals were worked out using transparent film on which a calibrated grid with squares representing 200X200 m (4 hectares) laid over the distribution map which in turn was laid over the bathymetric map. Number of squares or portions thereof were counted, and from this surface area was calculated.

Data on seaweed beach casts (washup) were obtained from Taurus Atlantic Seaweeds, Namibia. Though collection began in 1981, only from 1986 onwards was all beach cast collected. Monthly collection totals from 1981 onwards and daily collection figures per site from March 1987 onwards were obtained. It is stipulated in the concession granted to the industry, by the Government, that in addition to collecting *Gracilaria*, they must keep the beaches clean consequently all washed up *Gracilaria* was collected. The beach cast was loaded into trucks that, when fully loaded, held 4 tonnes of *Gracilaria* so that the number of truck loads multiplied by 4 gave the tonnage collected. All the shores were inspected for *Gracilaria* every morning so that beach cast was generally collected the day after it was washed up.

Sea temperature, at 1 meter, was taken every working day at the harbour jetty by personnel at the Sea Fisheries Lab, every day at Dias Point Lighthouse by the Lighthouse keepers and by myself at various times in the Lagoon and Bay. All temperatures were taken using thermometers accurate to 0.1° C and a series of temperatures were taken in the Lagoon using a "Thermoscript" model 8380oo Goerz Metrawatt, sealed in a water tight container. Swell, wind direction and wind strength were taken 7 times per day, everyday, by the Dias Point Lighthouse keepers. Current readings in the Bay and Lagoon were taken with a Marsh and McBirney model 201D portable water current meter.

Analysis of the sediments were carried out at the Geological Survey of Namibia. A wet sieving technique (see Buchanan, 1984) was employed with sieve mesh sizes of 300 um, 212 um, 180 um, 106 um and 63 um. The sediments were oven dried to constant weight and then rehydrated overnight. Each sediment was washed through the sieve with the largest mesh size, the portion which passed through was then washed through the sieve with the next largest mesh size and so on. The portion of each sediment remaining in each sieve was then oven dried to constant weight. Each fraction was expressed as a % of the total. The sediments were then categorized into 3 main groups; A > 212 um, B 106-212 um and C < 106 um based on 60% or more of the sediment falling into one of the groups.

Correlation between washup, wind direction and swell was performed using canonical correspondence analysis (Ter Braak, 1987). Wind direction and swell height were the environmental parameters investigated. These environmental parameters on the day of collection, one day previous to collection and two days previous to collection were entered into the analysis. For each analysis, two data files were made for entry into the Fortran program "CANOCO" (TerBraak, 1987). The first file contained the washup data at each site for each day of the year and the second file contained the environmental data for each day . The analysis produces an ordination of the washup data,on which the main environmental factors causing the data distribution are superimposed by the program.

2.4 Results

2.4.1 Bathymetry (fig. 2.2)

The Luderitz Lagoon, with a surface area of approximately 9.4 square kilometers, is for the most part less than 5 m deep. A deeper channel (5-6 m) runs up the middle of the Lagoon, originating from the deepest (9-10 m) area at the mouth of the Lagoon. The Lagoon floor slopes steeply, in the channel but for the rest, slopes are gradual. The southern end is flat and is less than 2 m deep.

Luderitz Bay is made up of three basins, North, Middle and South, divided from one another by two submarine ridges linking Penguin and Seal Islands with the mainland. The south basin is the deepest of the three with depths in the center of 8-9 m; north basin is next deepest at 8 m in the center and middle basin is the shallowest at 7 m in the center. Middle basin is the largest at 4.14 sq. km followed by south at 3.13 sq. km and lastly north basin at 2.8 sq. km.

Shearwater Bay lying to the west of Luderitz Lagoon, is a large bay with a surface area of approximately 5 square kilometers. The bay is, for the most part, over 5 meters deep except for a strip approximately 100 m wide around the shore line. The center of the bay is 10 m deep.

2.4.2 Sediments (fig. 2.3)

Sediment type B was dominant in the Bay and occurred to the west of the Lagoon mouth, and in small areas to the west and east of the central Lagoon. Type C was dominant in the Lagoon and occurred in the southern and eastern parts of the south basin and the eastern part of the north basin in the Bay system. Sediment type A was only found between Shark and Penguin and Penguin and Seal Islands and at the southern end of the lagoon.

2.4.3 Surveys

Survey I (August 1991; fig. 2.4)

The *Gracilaria* beds were estimated to cover an area of 8.3 square kilometers of which 2.5 sq. km were in the Lagoon and 5.8 sq. km in the Bay system. All attached material was found in water of less than 10 m and, apart from Radford Bay, no attached material was found shallower than 1 m. The highest biomass per m^2 was found on the inside of Seal Island (501-600 g wet wt.), off Agate Beach (301-400 g wet wt.), to the west of Shark Island (401-500 g wet wt.) and at Flamingo Bay (101-200 g wet wt.). At every other location where material was found attached the biomass was less than 100 g m^{-2} (wet wt.). The total biomass for the area was estimated at 850 tonnes of which 200 tonnes were in the Lagoon and 650 tonnes in the Bay.

In the Lagoon system, 33% of the bed surface area occurred between 3 to 4 meters and 24.5% occurred between 1 to 2 m. There was a rapid drop off in bed surface area deeper than 4 m and no part of the beds occurred below 10 m (fig. 2.5). In biomass terms there was a peak at 3-4 m (63 t wet wt. = 30%) and another between 5 to 6 m (47 t wet wt. = 23%) very little biomass occurred below 7m (fig. 2.6)

In the Bay system, a peak in the bed surface area occurred between 5 to 6 m (139 hect. = 23.9%). From this peak, percent surface area with depth decreased in deeper and shallower water and the beds did not grow deeper than 9 m. (fig. 2.7).

The peak in biomass occurred at 4 to 5 meters, this decreased rapidly in shallower water and gradually in deeper water (fig. 2.8).

Survey II (January 1992; fig. 2.9)
In this survey, the beds were estimated to cover an area of 8.4 square kilometers, 2.4 sq. km in the Lagoon and 6 sq. km in the Bay system, and all material was found growing between 1-11 m deep. The highest density per m^2 in the Bay system was found in Flamingo Bay (2000-2500 g wet wt.), in the middle of the north basin and inside of Seal Island (1000-1500 g wet wt.) and inside Penguin Island and off the northern end of Agate Beach (500-1000 g wet wt.) at every other station where material was found attached the density was less than 500 g m^{-2} (wet wt.). In the Luderitz Lagoon the highest density was found to the west of Shark Island at 100-200 g (wet wt.), whereas at every other station where attached material occurred, the density was less than 100 g m^{-2} (wet wt.). The total biomass of *Gracilaria* for the area was estimated at 3000 tonnes (wet wt.), of which 2850 tonnes were in the Bay and 150 tonnes in the Lagoon.

In the Lagoon system the distribution of bed surface area was relatively uniform from 1 to 7 m apart from a peak of 80 hect. (33%) at 3 to 4 m. Surface area decreased below 7 m and none occurred below 9 m (fig. 2.5). Biomass followed a similar pattern as surface area but the peak at 3-4 m was more pronounced (57 t wet wt. = 38%; fig. 2.6).

In the Bay system a peak in surface area occurred between 5-6 meters (159 hect. = 26%) with a gradual decrease in both shallower and deeper water. No part of the bed occurred above 1 m or below 11 depth (fig. 2.7). Biomass followed a similar pattern with a peak at 5-6 m (828 t wet wt. = 30%; fig 2.8).

All the beds consisted of a permanent underground thallus system from which aerial portions arose. Evidance from trial floating cultivation systems suggests that fragments which break free and sink to the bottom can form part of the underground system.

2.4.4 Associated fauna and flora.

At most sites where *Gracilaria* grew, in both the Lagoon and Bay, it was associated with the tube worm *Pectinaria capensis* (Pal.). This tube worm was also present in the very soft sediments in the channel and west side of the Lagoon at all depths tested. Inside Seal Island, the black mussel *Choromytilus meridionalis* (Kr.) grew with the *Gracilaria*, with the byssus threads intertwined with the *Gracilaria* thalli. These mussels probably came from a small floating mussel farm in the vicinity. Epiphytic *Ceramium diaphanum* (Lightfoot) Roth was found growing on the *Gracilaria* to the east of Penguin Island and north of Radford Bay on the east side of the Lagoon.

2.4.5 Washup

Figure 2.10 depicts the average monthly beach cast over the period 1987-1991. It can be seen that in the period August-November (generally September/October) washups are at the annual minimum. The amount of beach cast *Gracilaria* then increases to a maximum from April to July. The Lagoon contributed 22-31% each year to the total beach cast of the whole area, whereas the Bay system contributed 62.3-72.4%, and Shearwater Bay contributed 1.3-8.3% (Table 1).

YEAR	LAGOON	BAY	SHEARWATER
1987*	30%	67.6%	2.3%
1988	29.3%	62.3%	8.3%
1989	31%	62.7%	6.1%
1990	27.9%	70.6%	1.3%
1991	22%	72.4%	5.4%

Table 2.1 Contribution by Lagoon, Bay and Shearwater Bay to the total beach cast from 1987-1991. * Site collection data was not available for January and February 1987.

2.4.6 Comparison of swell, temperature and washup

In 1987 (fig. 2.10) sea temperature remained low throughout the year and swell, though initially small, gradually increased towards the middle of the year. Up until July the larger washups tended to occur during periods of large swell and conversely small washup tended to follow periods of small swell. Washup peaked in July and from then decreased to the year low in September/October. From July on, washup and swell seemed to have no correlation.

1988 was characterized by having a prolonged warm water anomaly from February to April with a peak in March. Temperature then dropped during winter and rose again to a relatively high level in December. Swells were larger than in 1987 with peaks in January, March, June, July, September and October. This was the record year for washups. As in 1987 the peak washups occurred in June and July with smallest washup in January, February and November.

In 1989 there was a prolonged warm water event, though less intense than in 1988, from January to May which peaked in February. Temperatures subsequently dropped during winter and gradually rose again towards the end of the year. Swell, though small at the beginning of the year, increased to a peak in June/July. Washup followed a relatively uniform curve starting small in January/February and steadily increasing to a peak in July then decreasing rapidly to a low in September.

In 1990 there was a period of warm water from January to April with a peak in February. As for previous years temperature dropped during winter to rise again towards the middle of the year. Swells were large, and in July the largest swell for many years was recorded. Washups were erratic and relatively small, but the largest biomass washed up after periods of large swell.

Temperatures remained low for the duration of 1991 though slightly higher in the first half. In the second half temperatures remained low but rose in December. Swell was small for the first 4 months but in May very large swells coincided with the largest washup of the year. From May, washup decreased to a minimum in August. Both swell and washup increased in December.

2.4.7 Wind and currents

The ocean at Luderitz is nutrient rich due to wind driven upwelling (see Chapter 1). Prevailing wind is south-south westerly and usually exceeds 40 kms h^{-1} (11 m $sec.^{-1}$, fig. 2.11). This wind causes wind chop, particularly in the Lagoon, of up to 1.5 meters. At the bottom of the Lagoon, water currents were found to run from north to south during nouth winds and surface water moved in the same direction as the wind. In the channel (fig. 2.2) during 40 kms h^{-1} South winds currents running from north to south of .44 ± .032 m sec^{-1} (± standard error) were recorded. During 32 kms h^{-1} winds, currents in the channel were .16 ± .015 m sec^{-1} from the north. In the southern end of the Lagoon currents were stronger on the western (.4 ± .038 m sec^{-1}) compared to the eastern side (.07 ± .02 m sec^{-1}) during 40 kms h^{-1} winds. Water motion was turbulent during south winds of less than 20 kms h^{-1} and during north wind. Currents during wind speeds greater than

40 kms h^{-1} could not be tested as under these conditions the Lagoon was too rough to work on.

In the Bay system a similar pattern of water movement was found, but currents were weaker than in the Lagoon under winds of the same strength and direction viz. .15 ± .02 m sec^{-1} from the north (at the bottom) during 40 kms h^{-1} south winds.

2.4.8 Correspondence analysis

The ordination diagrams (figs. 2.12-2.14) are the result of canonical correspondence analysis run for beach cast against environmental conditions two days prior to collection. From the relative position of the environmental vectors i.e. north and south and east and west wind vectors in opposite directions, it was evident that the environmental conditions two days prior to collection are the most applicable. Prevailing winds are south-south west and with north and east winds, swells are generally larger. For each year the data is influenced in one direction by the south and west wind combination and the other direction by the north and east wind, and swell vectors. A rough division into two groups can be made *viz.* Ang. Peq., Agate, Air. Bay, and SWB which are influenced by north and east winds and swell. All the other washup sites tend to be influenced more by South and West winds.

Figures 2.15 -2.22 give the monthly beach cast at individual sites in the Bay and Lagoon. Most of the Bay sites showed a seasonal pattern with peaks in autumn/winter (Agate), winter/spring (Aeroplane) and summer (Flamingo). Beach cast at LBC did not show a seasonal pattern and in the Lagoon no site showed a seasonal pattern of beach cast.

2.5 Discussion

The sediments in the Luderitz Bay and Lagoon are for the most part aeolian or marine in origin as no rivers or streams flow into the system, and with an average annual rainfall of 20 mm runoff is virtually zero. The distribution of these sediments appeared to be influenced by exposure to swell (fig. 2.10), and wind (fig. 2.11) driven currents. Generally, the more exposed Bay system had more coarse sediments than the Lagoon, presumably because swell disturbance is greater in the Bay and consequently finer sediments are removed. The sediment analysis gives particle sizes for each sample but this does not relate directly to the texture of the sediment presumably because organic matter and detritus is excluded from the analysis. An example of this is that the sediments on the east side of the Lagoon were observed to have a firmer texture than those on the west side even though their particle sizes were similar.

Beach cast *Gracilaria* has not been found outside the Luderitz Lagoon, Bay and Shearwater Bay systems. For many kilometers North and South of Luderitz rock lobster are harvested, and the fishermen involved have not reported finding any *Gracilaria*. The offshore sea bed around Luderitz has deposits of diamonds and many divers are involved in dredging the diamond bearing gravel and again *Gracilaria* has not been reported. Because of this evidence it is assumed that most if not all of the *Gracilaria* that breaks free from the beds at Luderitz is cast up on the beaches in the area. Furthermore it is probable that *Gracilaria* that breaks free is cast up on a beach soon after due to the strong currents that run on the bottom of the Lagoon and Bay. Free floating *Gracilaria* observed at various times was invariably cast up the following day.

Biomass of vegetatively reproducing populations have been found to be, spatially, very variable (Santelices *et al.*, 1984; Silva *et al.*, 1987 and Boraso de Zaixso, 1989). The growth pattern *viz.* that plants grow from an underground thallus system, become too large for the point of attachment and break off (Santelices and Doty, 1989), explains the spatial variability. Christie (1981) suggested that the spatial variation in biomass of *Gracilaria* growing in Langebaan Lagoon was caused by nutrient availability. This was, apparently, evidenced by the change in colour of the plants from deep red to yellow along a nutrient gradient from the nutrient rich mouth of the lagoon to the nutrient poor southern end of the Lagoon. This explanation seems doubtful as Jones (1959a) reported that *Gracilaria* plants growing in shallow water were bleached to a yellow colour and a depth gradient exists in Langebaan Lagoon from deep water at the mouth to the shallows at the southern end. Further to this, much of the southern end is intertidal. Colour variation due to genetic mutation has also been reported for this genus (van der Meer and Bird, 1977).

The extent of the underground system rather than the biomass per m^2 of the erect thalli is more important in understanding the recruitment of the system as when erect thalli break free they no longer play a role in increasing the total biomass unless reattachment occurs (Santelices *et al.*, 1984). Biomass estimates of free floating material are of little use.

As expected, the larger portion of the *Gracilaria* bed surface area occurred in the Bay system (figs. 2.4, 2.5, 2.7 and 2.9). In August 1991 the percentages in the Lagoon and Bay system were 30% and 70%, respectively and in January 1992, 28% and 72%, respectively. This corresponds well to the washup from these two areas in 1991 *viz.* 23.5% from the Lagoon and 76.5% from the Bay (percentage of annual total excluding Shearwater Bay).

The total surface area of the beds increased by an estimated 0.1 sq. km from August to January, manifested as a slight decrease in the Lagoon and an increase in the Bay (figs. 2.5 and 2.7). Terete *Gracilaria* populations have been reported to grow on coarse sand with organic detritus in Brazil (Silva *et al.*, 1987), fine soft substrata in Argentina (Boraso de Zaixso, 1989), soft sediments in Norway (Stokke, 1957; Rueness *et al.*, 1987) and soft mud in New Zealand (Nelson, 1989). At Luderitz the *Gracilaria* beds are associated with firm sediments (106-212 um) and it is the distribution of these "suitable" sediments that influences the distribution of the beds. On the east side of the Lagoon the *Gracilaria* grows on a plateau between 3-4 m, this is also where the firm sediment occurs (figs. 2.2 and 2.3). The sediments in the Bay are, for the most part firm except below 9-10 m and above 1m where they are hard and sandy and very little *Gracilaria* grows (figs. 2.4 and 2.9).

Biomass in the Bay increased by over 200% from August to January while the biomass in the Lagoon decreased by an estimated 38%. The increase can be attributed to faster growth rate with the onset of summer (see Chapter 3). Most of this increase in the Bay occurred from 4-7 meters partially because most of the bed surface area occurred at this depth but probably also because in shallower water despite faster growth rates (see Chapter 3), disturbance was greater and in deeper water growth rate was light limited (see Chapter 3). The decrease in Lagoon biomass was probably caused by disturbance as most of the bed occurred in shallower water than in the Bay. Although the Lagoon is more sheltered from swell than the Bay, the wind chop and wind driven currents are stronger in the Lagoon.

From figure 2.10, it is evident that large beach casts are preceded by periods of large swell. Swell follows a rough seasonal pattern with the largest occurring in winter. The effect of temperature on beach cast is not clear. *Gracilaria* is a warm water genus (McLachlan and Bird, 1984) and as such the sea temperature at Luderitz is usually suboptimal for growth. Engledow and Bolton (in press) working on *Gracilaria* from Saldanha Bay (South Africa) found the optimum temperature for growth to be 25° C and Baines (unpublished) found the optimum temperature to be 18° C for *Gracilaria* collected at Luderitz. It follows then that warm water anomalies such as in February to April 1988 caused an increase in growth of the *Gracilaria* and this was seen in the large amount of beach cast material that year. Another "warm water event" occurred in 1990 but the total beach cast for that year was much less than in 1988, probably due to large swells which occurred in April. The size of swell and when it occurs may thus be very important contributing factors to the total annual beach cast.

To understand the seasonal pattern of washup it is necessary to examine the system in detail. Figures 2.15-2.22 show the total washup per month for each area from 1987 to 1991, it can be seen that the main Lagoon washup sites lie to the south of the main *Gracilaria* beds. Currents in the Lagoon are driven predominantly by wind as the Lagoon is quite protected from swell. Most of the Lagoon washup occurs during the summer/autumn when southerly winds prevail (figs. 2.11 and 2.15-2.18) and swells are smaller. These winds set up counter currents along the bottom which ultimately result in the *Gracilaria* being cast up at sites south of the beds. Griffith (fig. 2.15) and Leibies (fig. 2.16) show marked seasonality though the annual total is variable. *Gracilaria* is cast up at Angola (fig. 2.17) during most of the year though greater amounts are cast during the summer and autumn and annual totals have declined. Radford (fig. 2.18) does not show a general pattern as it is a small shallow (1 m) bay and quite separate from the main Lagoon system.

Washups were markedly seasonal in the Luderitz Bay system at all sites except LBC (figs. 2.19-2.22). Most of the washup at Flamingo Bay occurred in summer/autumn, at Agate Beach, most washups occurred in autumn/winter and at Aeroplane Bay washups occurred in Winter. This pattern holds true for every year. The Aeroplane Bay "catchment area" (south basin, see figs. 2.1 and 2.2) is the deepest of the system which explains why washups occurred later than in the middle basin at Agate Beach. The washup at Flamingo increased over the study perion while washup at the other sites in the Bay system decreased. This, in the light of low temperature and high swell for the year, is puzzling. I think that the beds at Flamingo Bay have expanded dramatically since 1987. It is doubtful that the *Gracilaria* that washes out at Flamingo comes from beds that would normally supply other sites in the Bay, as the time of washup at Flamingo Bay did not change over the period. Swell did not seem to be important in controlling beach cast at Flamingo, as it was at Agate and Aeroplane (figs. 2.12-2.14), as washups occurred when swells were lowest, in summer. Flamingo Bay is open to wind chop formed by the south wind (which was strongest during summer) which travel the length of the Bay before running into the shallow Flamingo Bay, probably resulting in the *Gracilaria* being torn free.

The depth at which the beds occur effects the time of washup, as deep beds are less susceptible to detachment by swell. The situation is more complicated than this however, as plants grow more slowly at depth (see. chap. 3) and obviously they can attain a greater size before the point of attachment finally breaks.

The canonical correspondence diagrams confirm the assumptions made above; that south and west winds are particularly important for washups in the Luderitz Lagoon system and Flamingo Bay. These sites are shallow (<5 m) and consequently more susceptible to wind chop, and as mentioned above, the Luderitz

Lagoon system is more sheltered from swell than Luderitz Bay. In 1988 and 1989 the ordination diagrams clearly show that Luderitz Bay (with the exception of Flamingo Bay) washups are strongly influenced by swell and east and north winds while Luderitz Lagoon washups are strongly influenced by south and west winds (figs. 2.12-2.14) The swell component of 1987 appeared to have very little influence on washup in general and no influence at all on Agate Beach washup, probably because swell for 1987 was small (fig. 2.12).

2.6 CONCLUSIONS:

1) The three systems, *viz*. Lagoon, Bay and Shearwater, are independent of one another with very little or no exchange of *Gracilaria* between them. This is evidenced firstly by the similar percentage each contributes to the total washup every year and secondly, beach cast in the three systems is influenced by different parameters and the pattern of beach cast remained the same from year to year.

2) Beach cast in the Lagoon system is a more continuous process than in the Bay. This is because the *Gracilaria* beds in the Lagoon are shallower than in the Bay and so, though they grow faster (Chapter 3), they are more susceptible to disturbance and cannot attain a size as large as plants growing in the deeper beds in the Bay. The largest annual washups which occurred in winter came from the deep beds in the Bay. These plants grew undisturbed until dislodged by large winter swells.

3) The *Gracilaria* beds seem to cover most of the suitable substratum available. The absence of *Gracilaria* from the southern end of the Lagoon is because the water is shallow and wind driven currents severe. The beds at Flamingo have expanded in the last 5 years and the decrease in washup from the rest of the Bay system over

the same period was probably because of cooler water and unseasonally large swells which occurred early in the latter years.

Figure 2.1. Main *Gracilaria* washup sites in the Luderitz Lagoon and Bay system. Griffith, Angola, Radford, Aeroplane, LBC, Agate, Flamingo and Shearwater Bay.

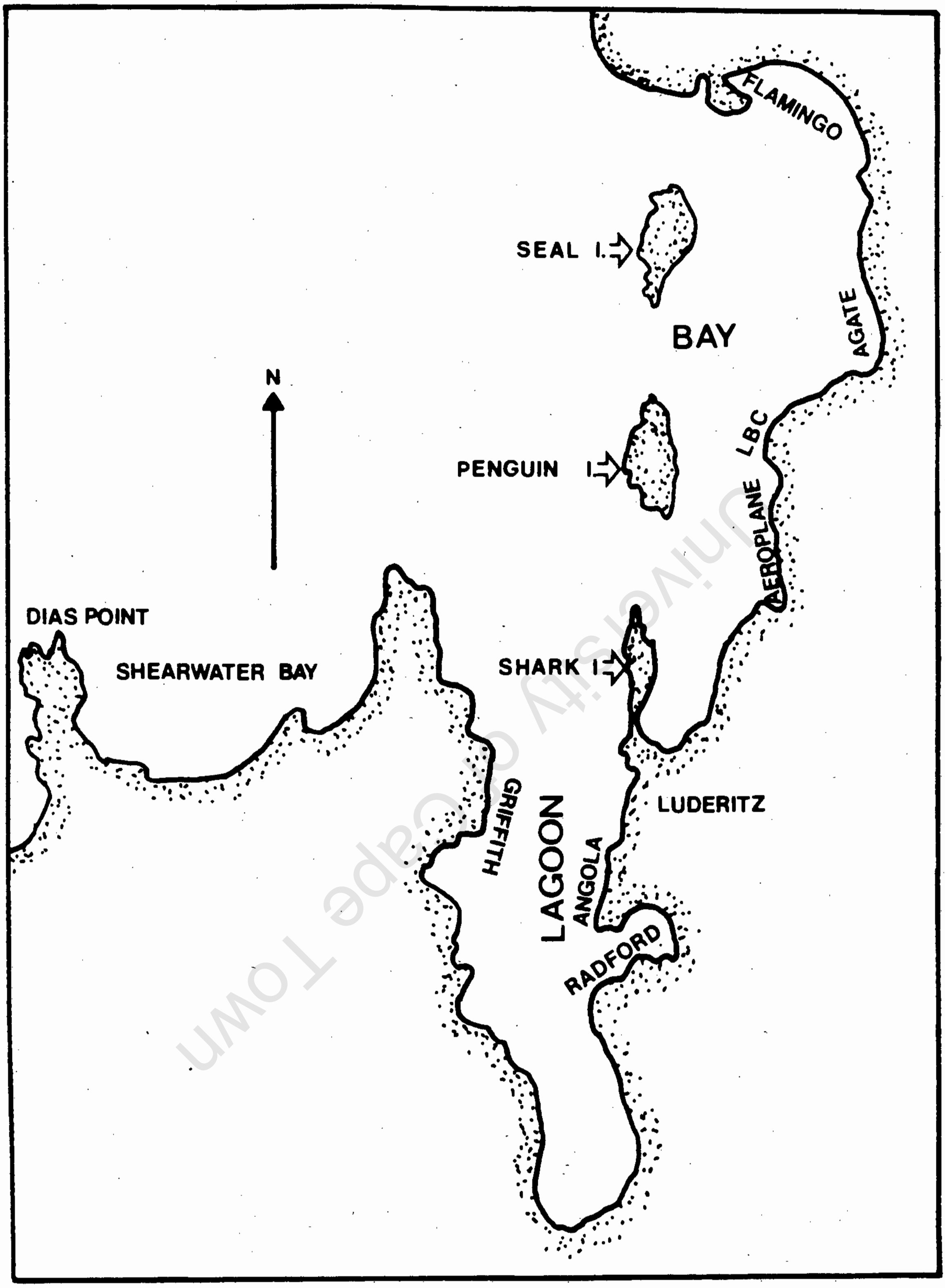

FLAMINGO
SEAL I.
BAY
AGATE
N
PENGUIN I.
LBC
AEROPLANE
DIAS POINT
SHEARWATER BAY
SHARK I.
LUDERITZ
GRIFFITH
LAGOON
ANGOLA
RADFORD

Figure 2.2. Bathymetric map of the Luderitz Lagoon and Bay system compiled from nautical charts and soundings taken during this study. Note the deep channel running up the center of the Lagoon and the three basins in the Bay system. Contours are at 1m intervals.

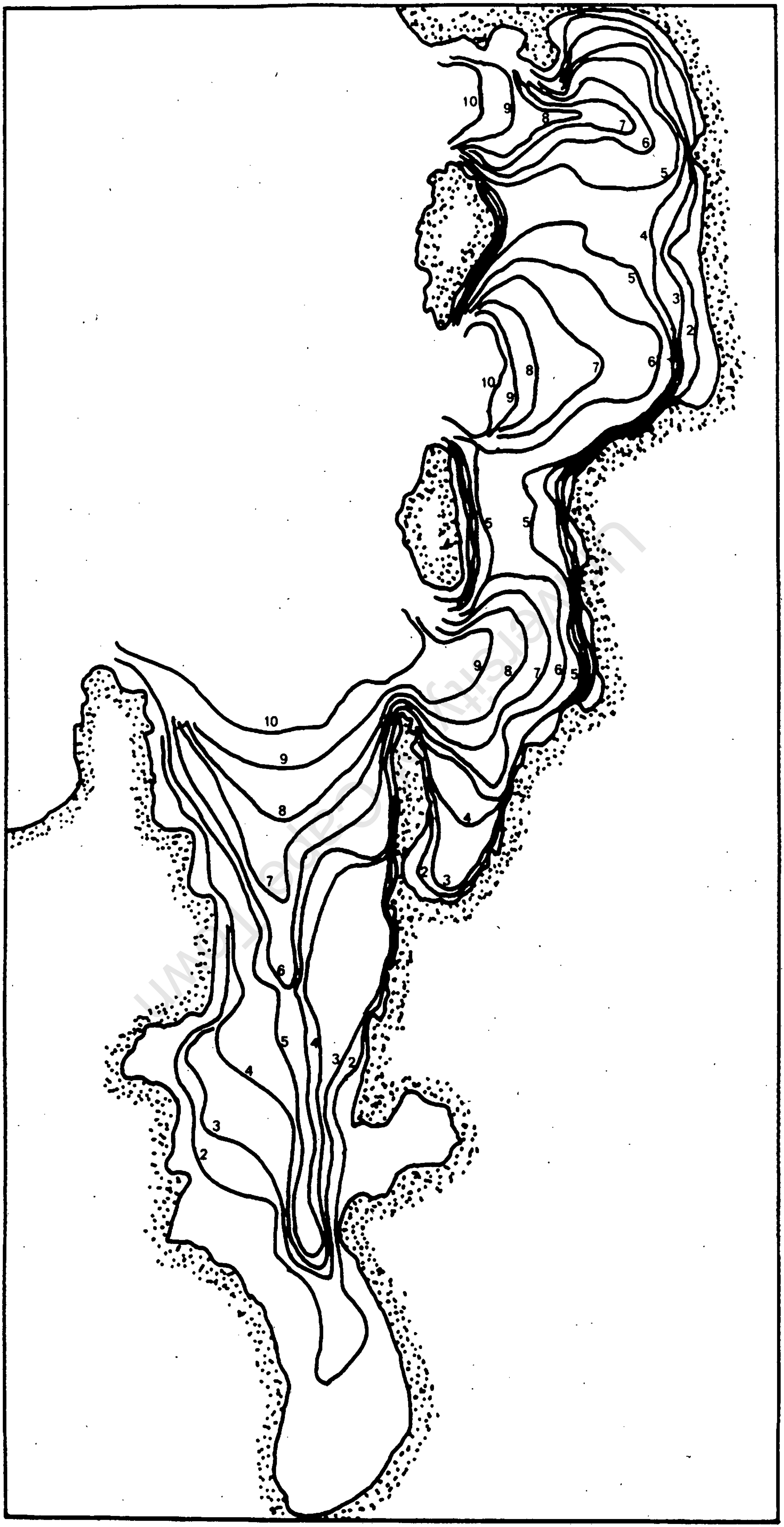

10
9
8
7
6
5
4
5
3
2
6
7
8
9
10
5
5
9
8
7
6
5
10
9
8
4
7
2
3
6
5
4
3
2
4
3
2

Figure 2.3. Distribution of sediments in the Luderitz Lagoon and Bay system. The sediments were catigorised based on 60% or more falling into one of three groups: A > 212 um; B = 106-212 um; C < 106 um; R = rock.

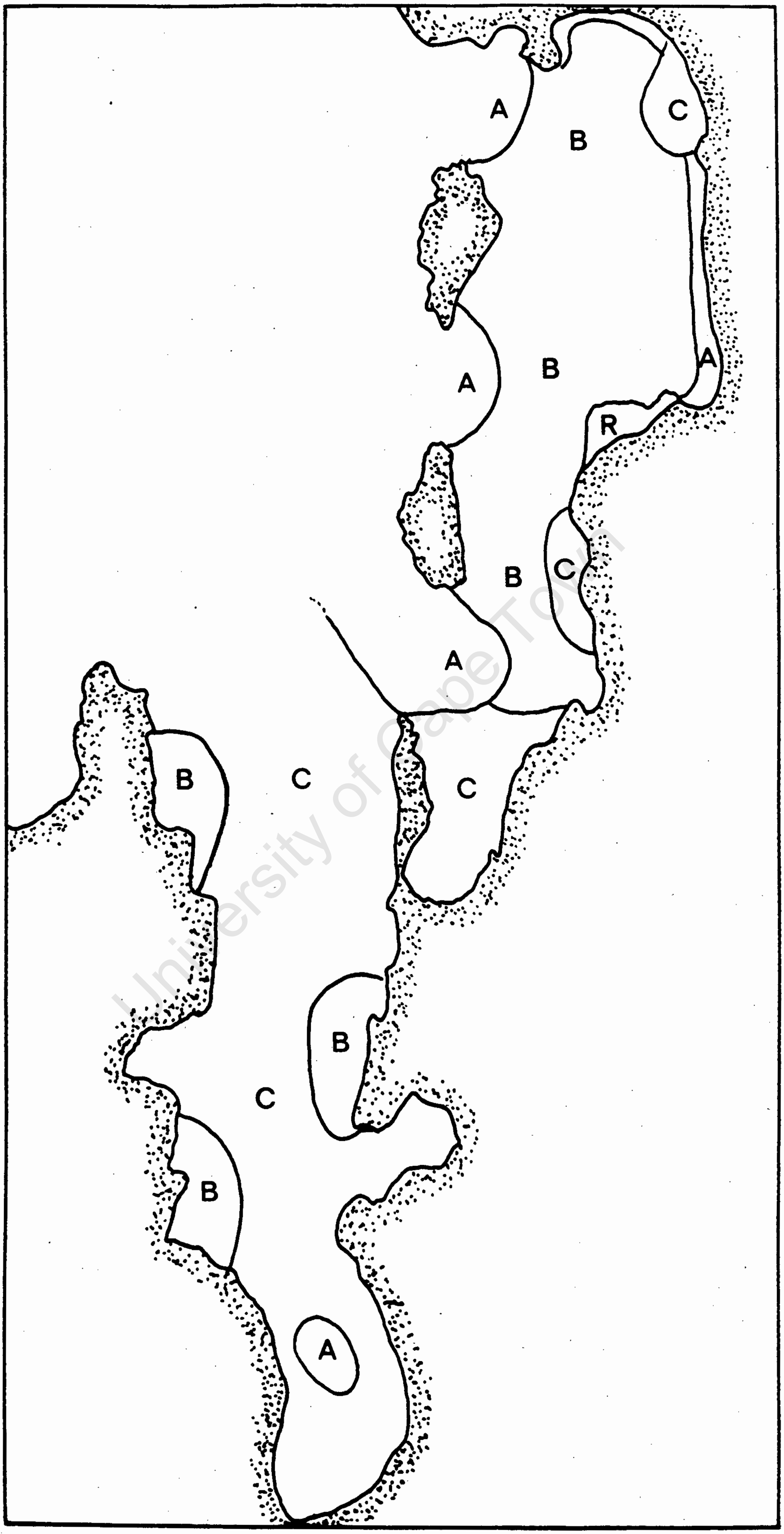

A
B
C
B
A
A
R
C
B
A
B
C
C
B
C
B
B
A

Figure 2.4. Distribution and density of *Gracilaria* in the Luderitz Lagoon and Bay in August 1991. The legend indicates the densities of the shaded areas. Black dots represent the dived stations. The speckled area in Radford Bay (fig. 2.1) represents a very shallow (< 1m) temporary bed which was quickly washed away. Black dots indicate the sites that were dived.

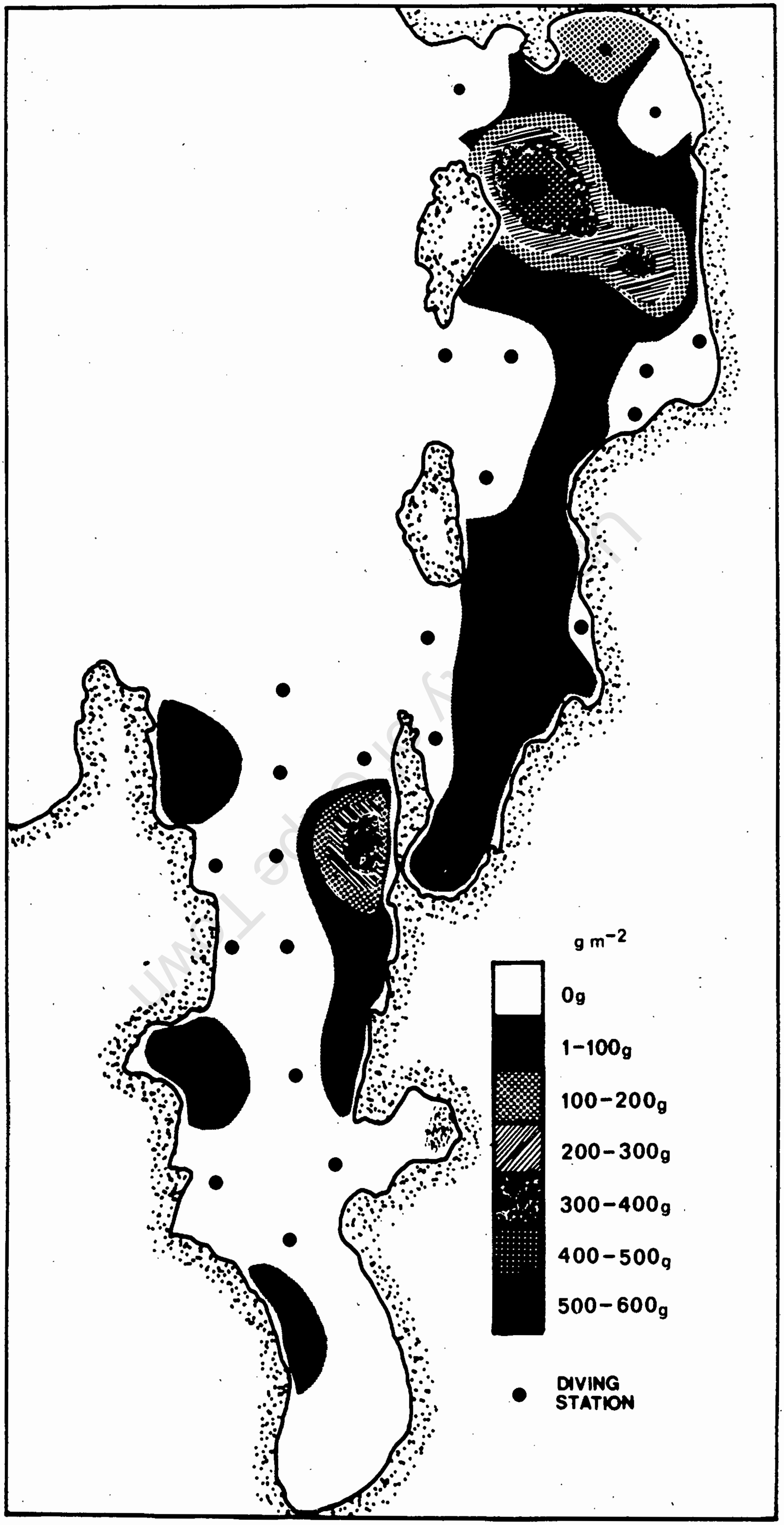
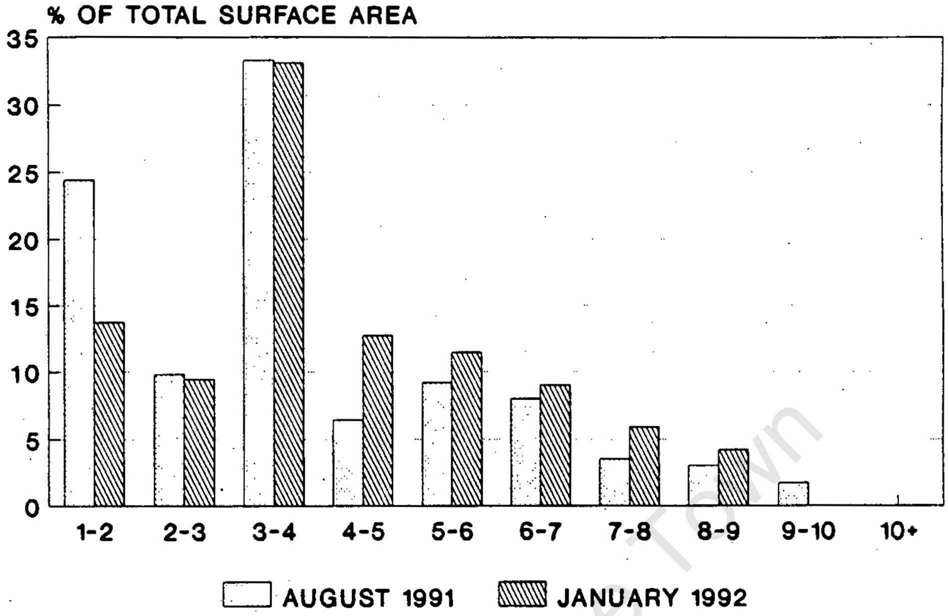

g m⁻²
0g
1-100g
100-200g
200-300g
300-400g
400-500g
500-600g
DIVING STATION

Figure 2.5. Area covered by *Gracilaria* beds at each depth in the Lagoon.

Figure 2.6. Biomass of *Gracilaria* at each depth in the Lagoon.

LAGOON



LAGOON

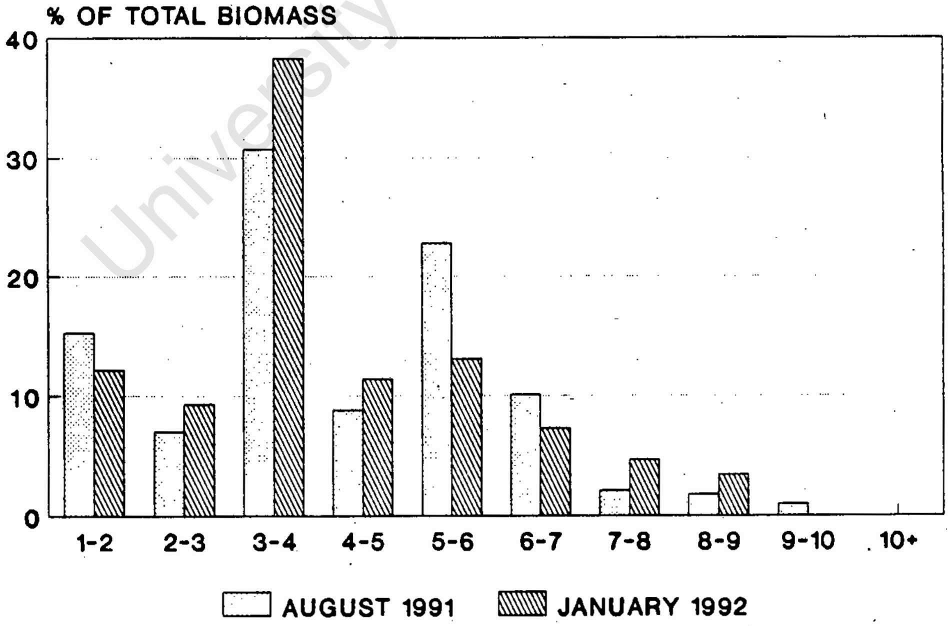
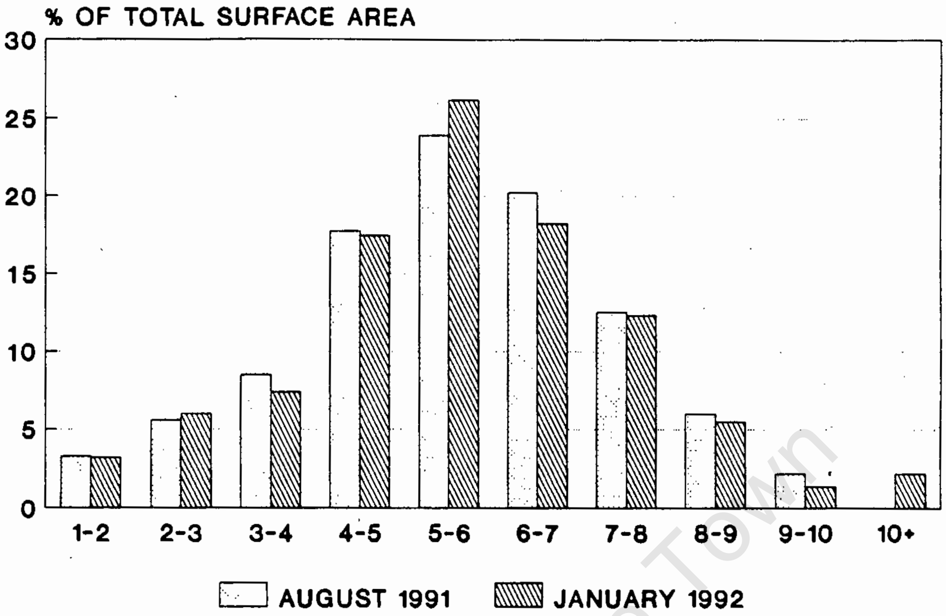


Figure 2.7. Area covered by *Gracilaria* beds at each depth in the Bay system.

Figure 2.8. Biomass of *Gracilaria* at each depth in the Bay system.

BAY


% OF TOTAL SURFACE AREA
30
25
20
15
10
5
0
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
9-10
10+
AUGUST 1991
JANUARY 1992

BAY

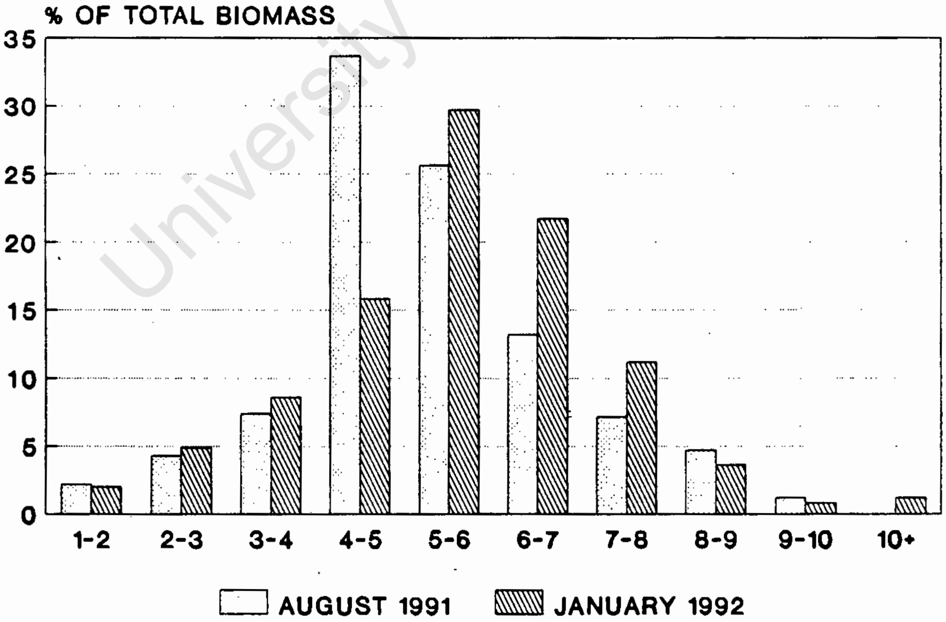

% OF TOTAL BIOMASS
35
30
25
20
15
10
5
0
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
9-10
10+
AUGUST 1991
JANUARY 1992

Figure 2.9. Distribution and density of *Gracilaria* in the Luderitz Lagoon and Bay in January 1992. Due to the magnitudinal difference in density between the Bay and Lagoon, a separate legend is given for each.

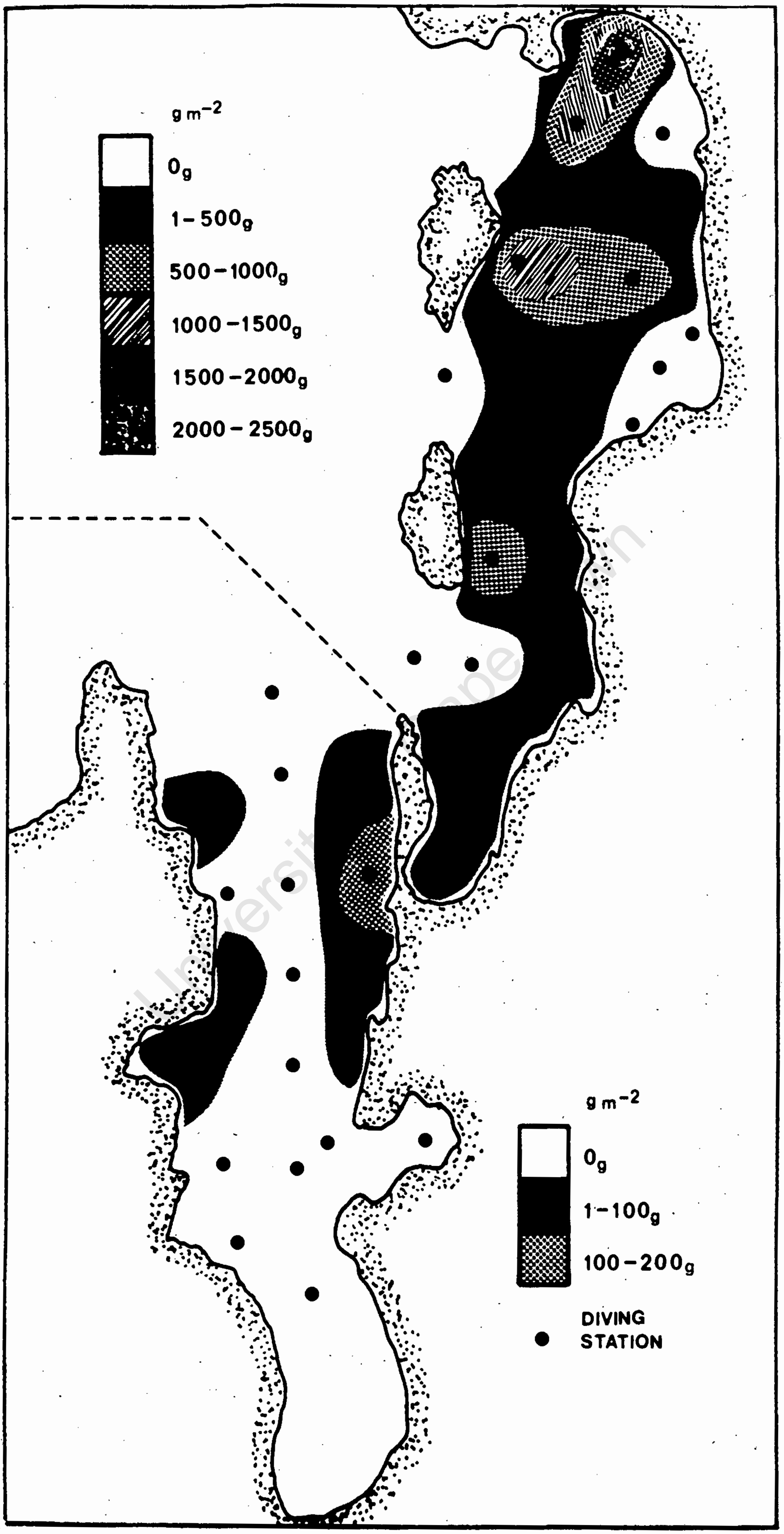

g m^{-2}
0g
1-500g
500-1000g
1000-1500g
1500-2000g
2000-2500g
g m^{-2}
0g
1-100g
100-200g
DIVING STATION

Figure 2.10. Total washup in the Luderitz area from 1987 to 1990 for each month. Average temperature and swell height for each month are superimposed.

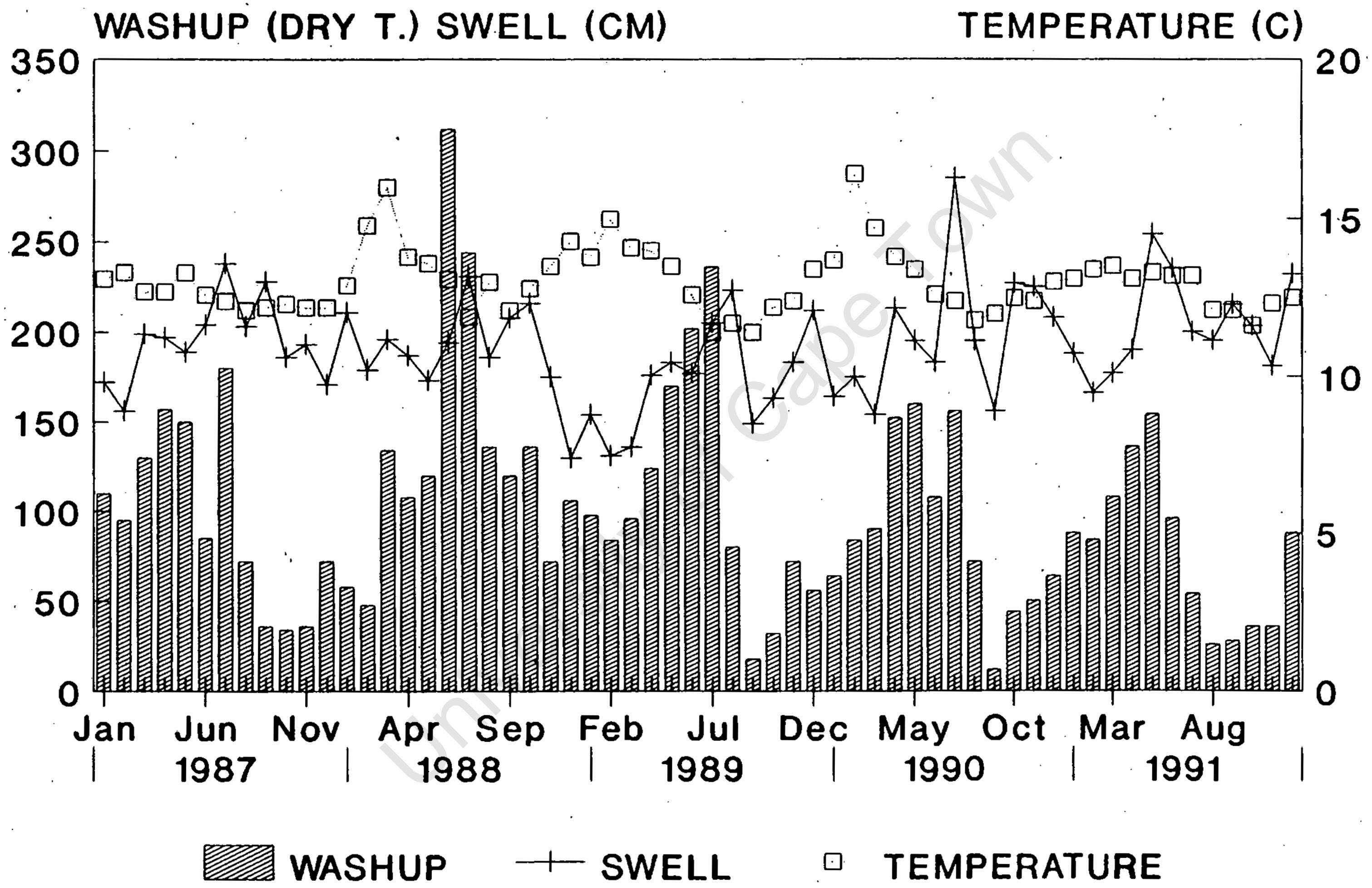

WASHUP (DRY T.) SWELL (CM)
TEMPERATURE (C)
350
300
250
200
150
100
50
0
20
15
10
5
0
Jan
Jun
Nov
Apr
Sep
Feb
Jul
Dec
May
Oct
Mar
Aug
1987
1988
1989
1990
1991
WASHUP
SWELL
TEMPERATURE

Figure 2.11. The occurrence and strength of South (+) and North (-) wind in the Luderitz area from 1987 to 1991. The data is given as a 21 day running average.

LUDERITZ WIND 1987-1991
SOUTH (+) NORTH (-)
21 DAY RUNNING AVERAGE

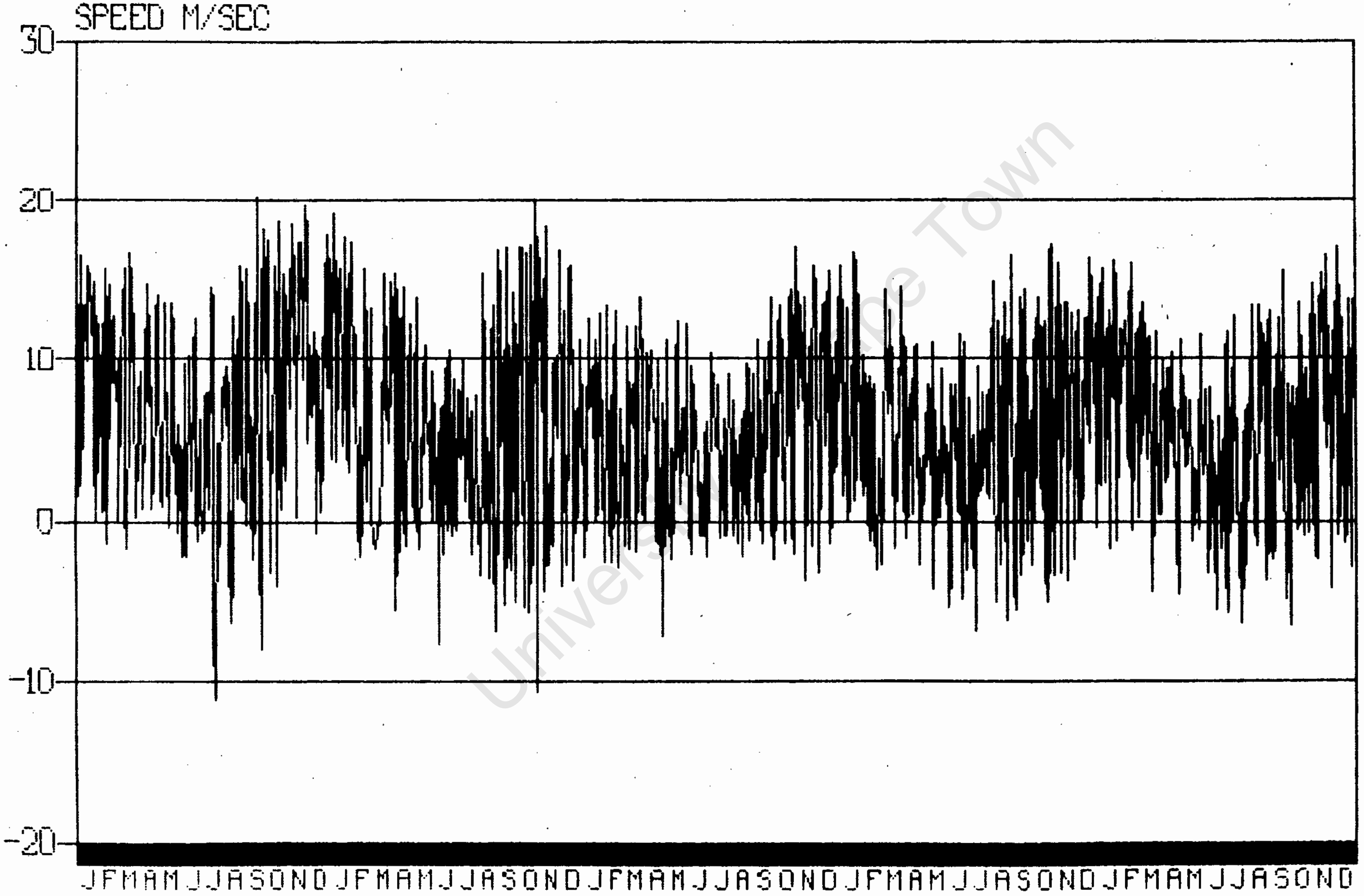


Figure 2.12. An ordination diagram resulting from canonical correspondence analysis of washup data and swell and wind data of two days previous to the collection of each washup for 1987. Vectors represent the influence of swell and wind from 4 quarters. The washup sites are Griffith Bay (grif1, grif2, grif3 and grif4), Radford (rad), Angola and Leibes (leib) in the Lagoon system and Aeroplane Bay (aer bay and ang peq), LBC (lbc1, lbc2 and lbc3), Agate Beach (Agate) and Flamingo Bay (fla bay) in the Bay system.

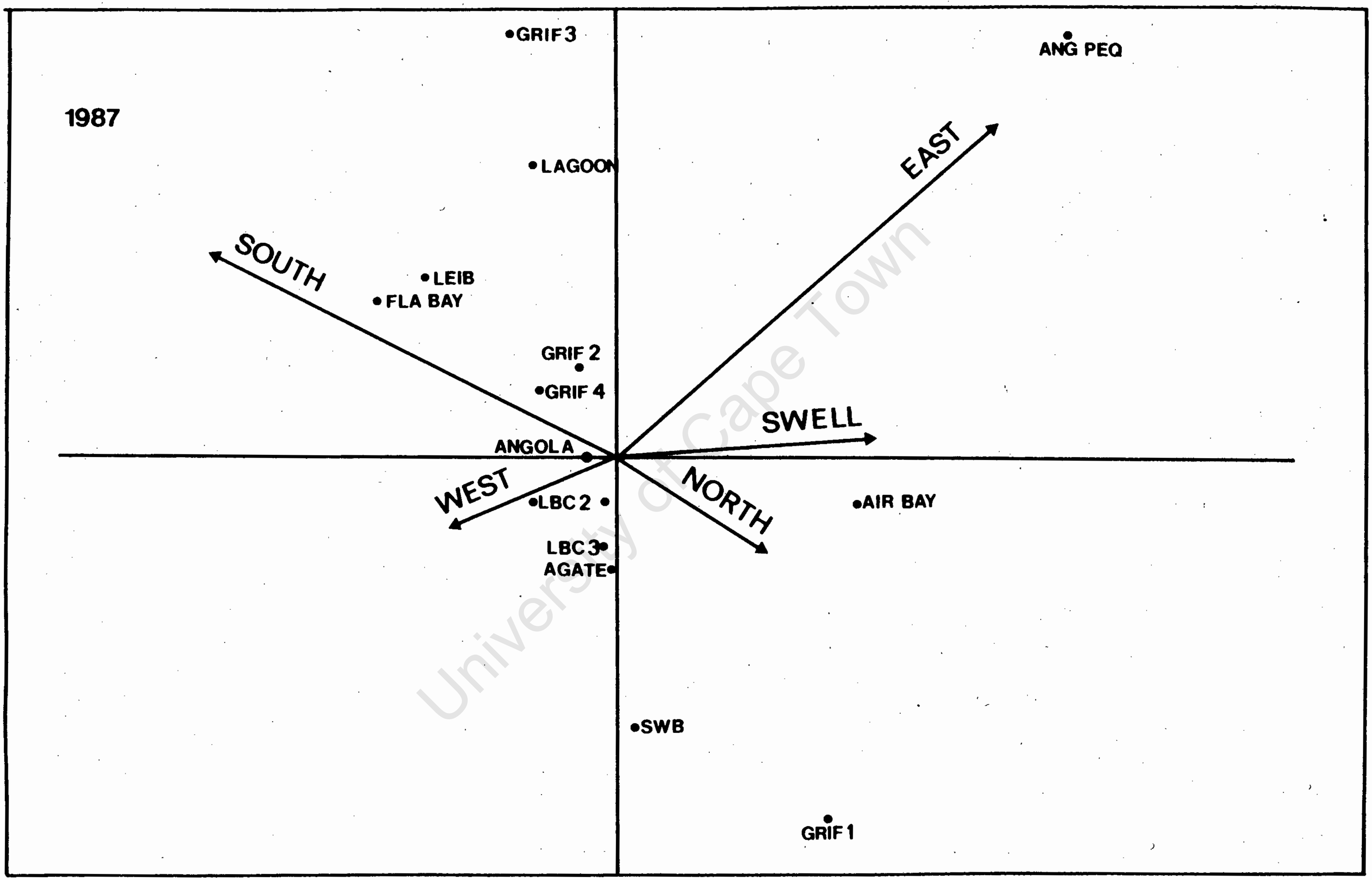

1987
GRIF 3
ANG PEQ
LAGOON
EAST
SOUTH
LEIB
FLA BAY
GRIF 2
GRIF 4
SWELL
ANGOLA
WEST
NORTH
LBC 2
AIR BAY
LBC 3
AGATE
SWB
GRIF 1

Figure 2.13. An ordination diagram resulting from canonical correspondence analysis of washup data and swell and wind data of two days previous to the collection of each washup for 1988. Vectors represent the influence of swell and wind from 4 quarters. The washup sites are Griffith Bay (grif1, grif2, grif3 and grif4), Radford (rad), Angola and Leibes (leib) in the Lagoon system and Aeroplane Bay (aer bay and ang peq), LBC (lbc1, lbc2 and lbc3), Agate Beach (Agate) and Flamingo Bay (fla bay) in the Bay system.

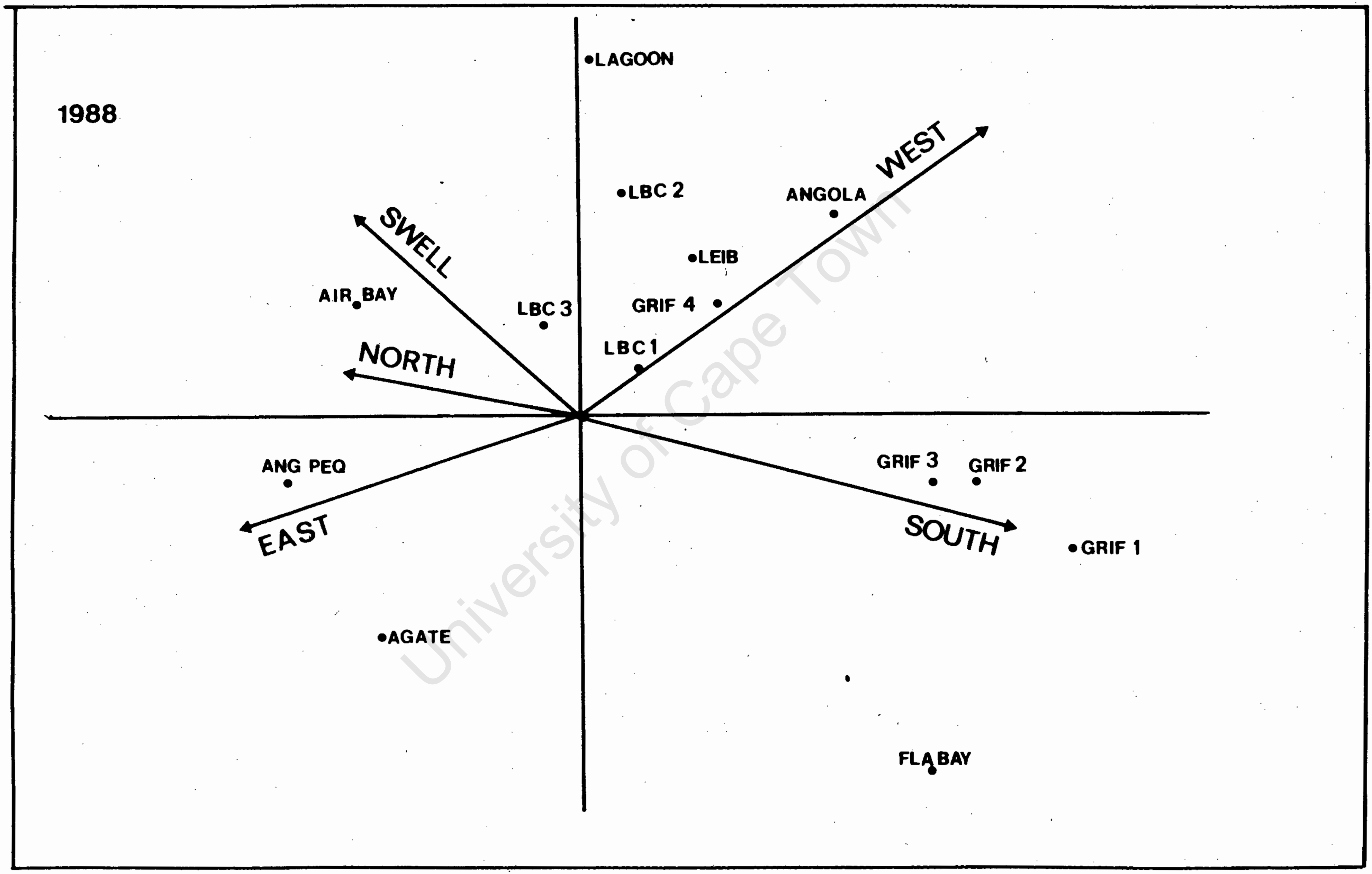

1988
LAGOON
LBC 2
ANGOLA
WEST
SWELL
LEIB
AIR BAY
LBC 3
GRIF 4
LBC 1
NORTH
ANG PEQ
GRIF 3
GRIF 2
EAST
SOUTH
GRIF 1
AGATE
FLA BAY

Figure 2.14. An ordination diagram resulting from canonical correspondence analysis of washup data and swell and wind data of two days previous to the collection of each washup for 1989. Vectors represent the influence of swell and wind from 4 quarters. The washup sites are Griffith Bay (grif1, grif2, grif3 and grif4), Radford (rad), Angola and Leibes (leib) in the Lagoon system and Aeroplane Bay (aer bay and ang peq), LBC (lbc1, lbc2 and lbc3), Agate Beach (Agate) and Flamingo Bay (fla bay) in the Bay system.

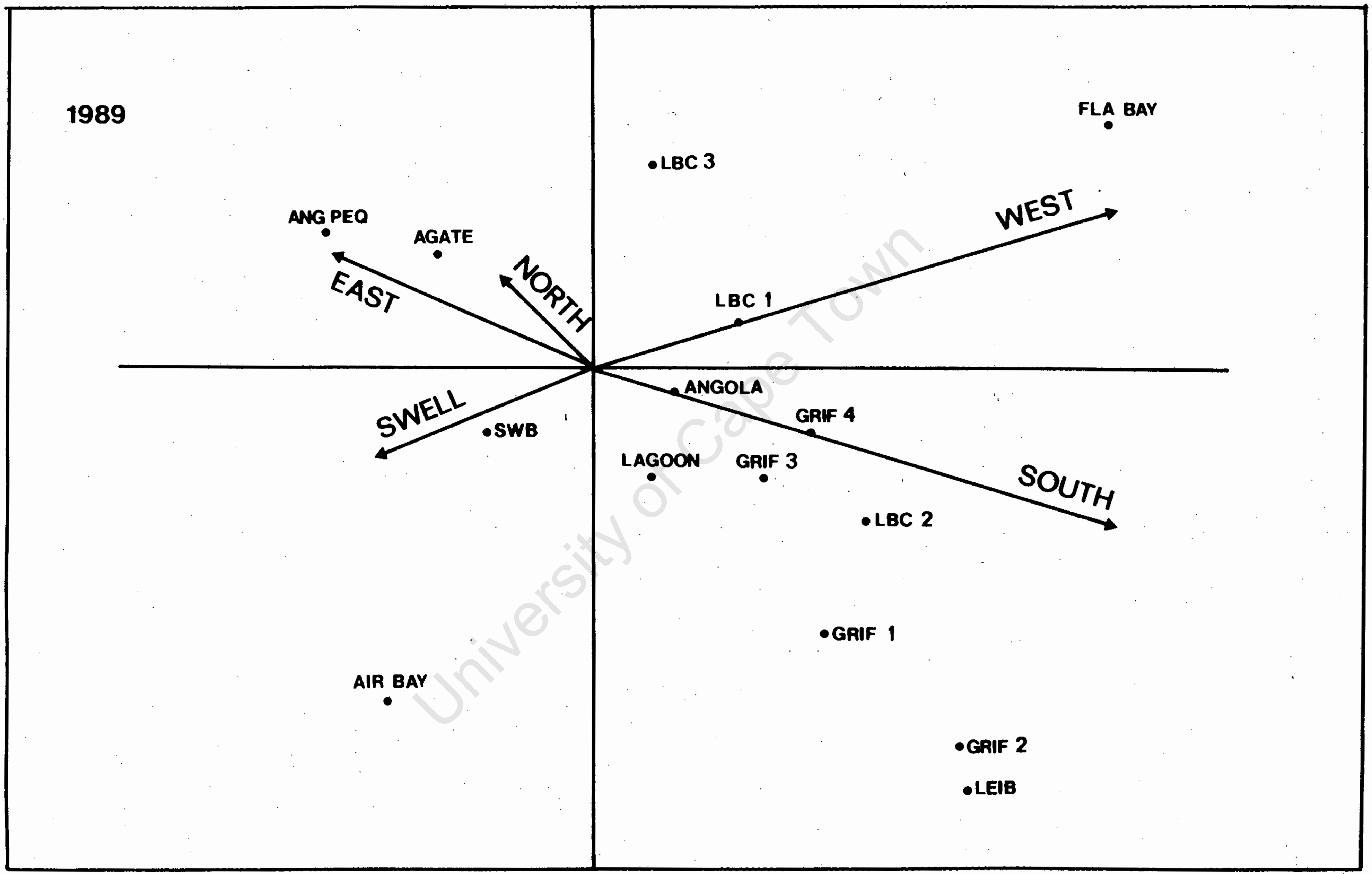
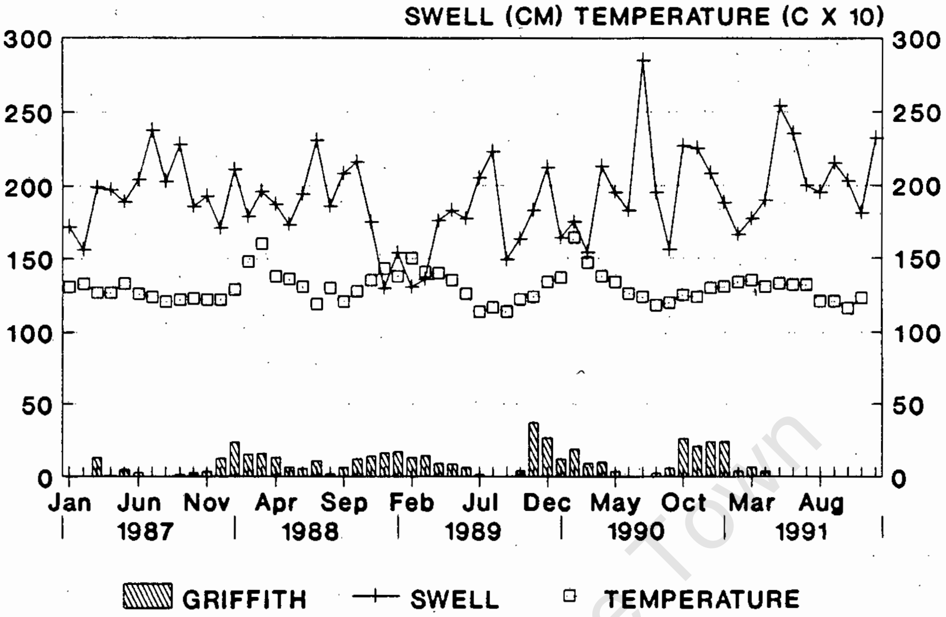

1989
FLA BAY
LBC 3
WEST
ANG PEQ
AGATE
NORTH
EAST
LBC 1
ANGOLA
SWELL
SWB
GRIF 4
LAGOON
GRIF 3
SOUTH
LBC 2
GRIF 1
AIR BAY
GRIF 2
LEIB

Figure 2.15. Monthly washup at Griffith Bay from March 1987 to December 1991. Average temperature and swell height for each month are also included.

Figure 2.16. Monthly washup at Leibes from March 1987 to December 1991. Average temperature and swell height for each month are also included.


SWELL (CM) TEMPERATURE (C X 10)
300
250
200
150
100
50
0
Jan
Jun
Nov
Apr
Sep
Feb
Jul
Dec
May
Oct
Mar
Aug
1987
1988
1989
1990
1991
GRIFFITH
SWELL
TEMPERATURE

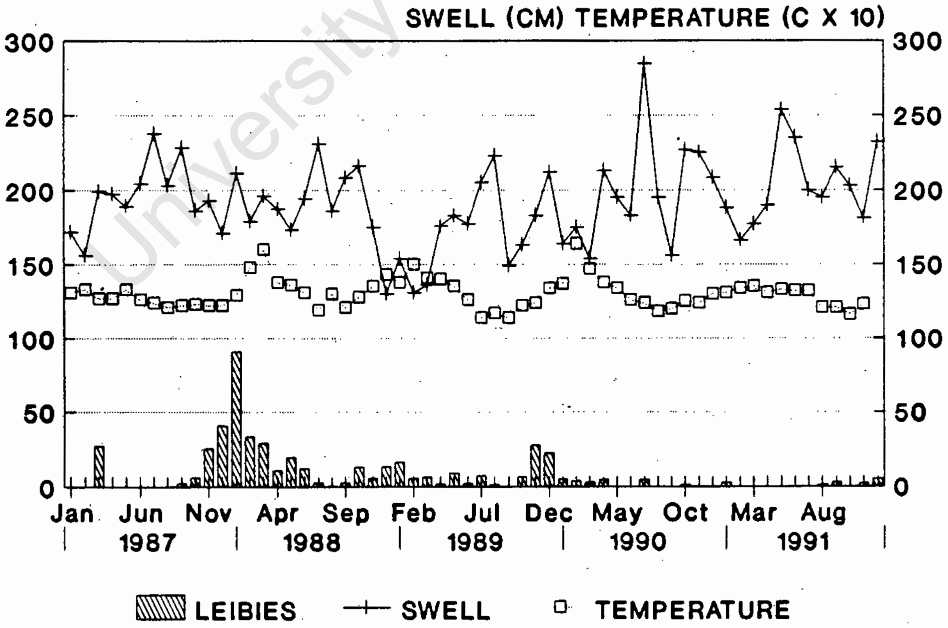
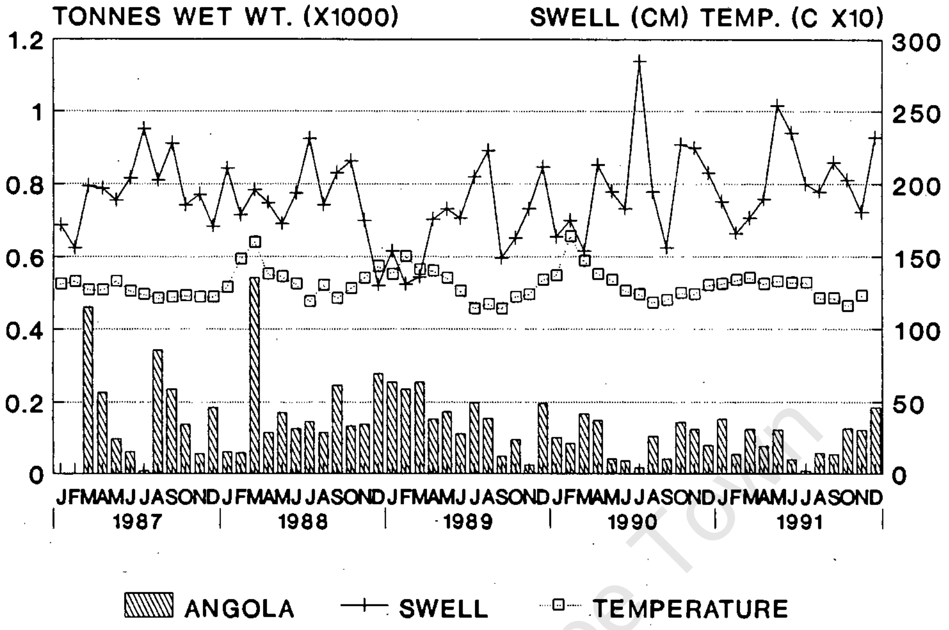

SWELL (CM) TEMPERATURE (C X 10)
300
250
200
150
100
50
0
Jan
Jun
Nov
Apr
Sep
Feb
Jul
Dec
May
Oct
Mar
Aug
1987
1988
1989
1990
1991
LEIBIES
SWELL
TEMPERATURE

Figure 2.17. Monthly washup at Angola from March 1987 to December 1991. Average temperature and swell height for each month are also included.

Figure 2.18. Monthly washup at Radford from March 1987 to December 1991. Average temperature and swell height for each month are also included.


TONNES WET WT. (X1000)
SWELL (CM) TEMP. (C X10)
1.2
1
0.8
0.6
0.4
0.2
0
300
250
200
150
100
50
0
JFMAMJJASONDJFMAMJJASONDJFMAMJJASONDJFMAMJJASONDJFMAMJJASOND
1987
1988
1989
1990
1991
ANGOLA
SWELL
TEMPERATURE

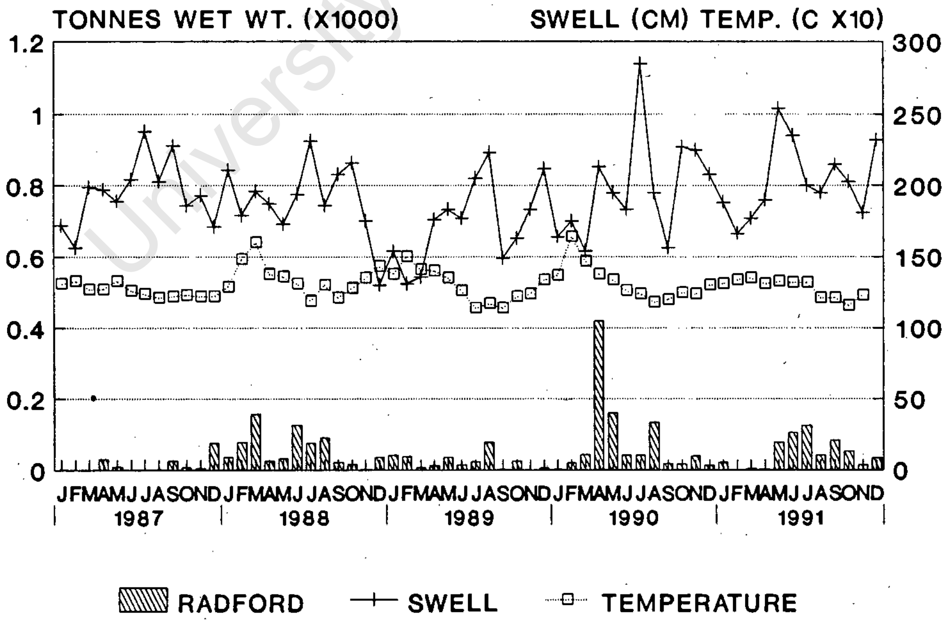
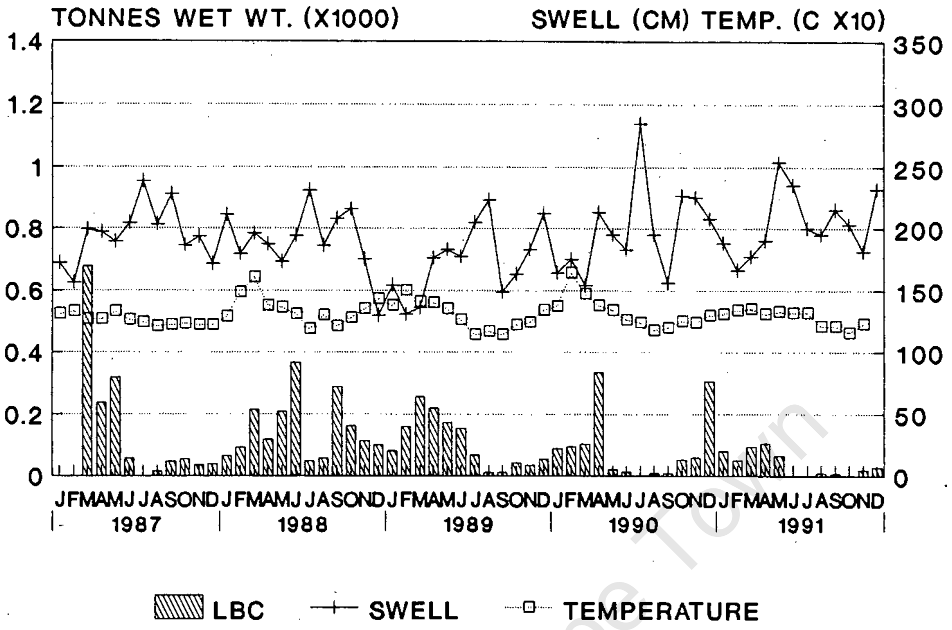

TONNES WET WT. (X1000)
SWELL (CM) TEMP. (C X10)
1.2
1
0.8
0.6
0.4
0.2
0
300
250
200
150
100
50
0
JFMAMJJASONDJFMAMJJASONDJFMAMJJASONDJFMAMJJASONDJFMAMJJASOND
1987
1988
1989
1990
1991
RADFORD
SWELL
TEMPERATURE

Figure 2.19. Monthly washup at LBC from March 1987 to December 1991. Average temperature and swell height for each month are also included.

Figure 2.20. Monthly washup at Flamingo Bay from March 1987 to December 1991. Average temperature and swell height for each month are also included.


TONNES WET WT. (X1000)
SWELL (CM) TEMP. (C X10)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
350
300
250
200
150
100
50
0
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1987
1988
1989
1990
1991
▨ LBC
SWELL
TEMPERATURE

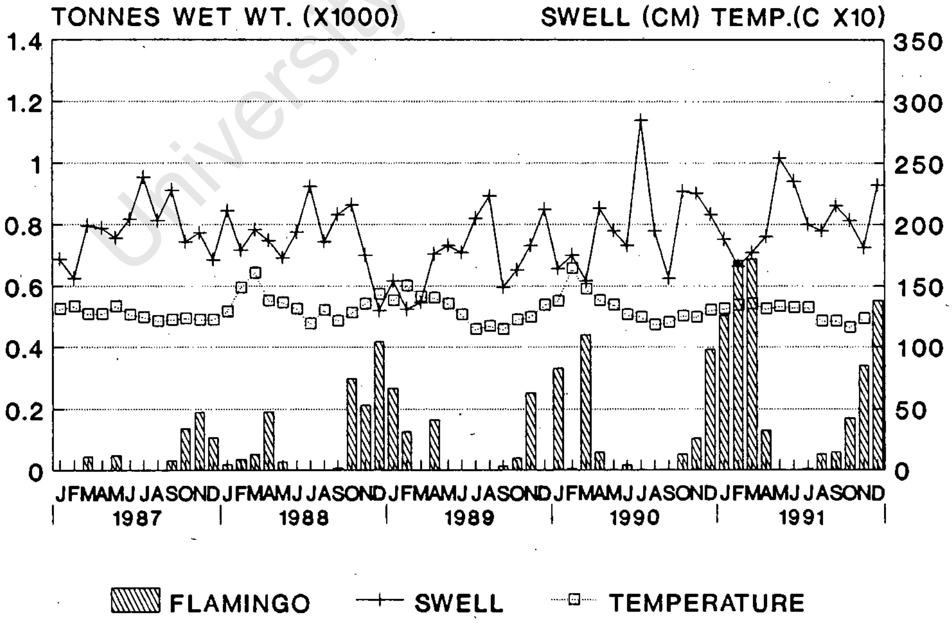

TONNES WET WT. (X1000)
SWELL (CM) TEMP.(C X10)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
350
300
250
200
150
100
50
0
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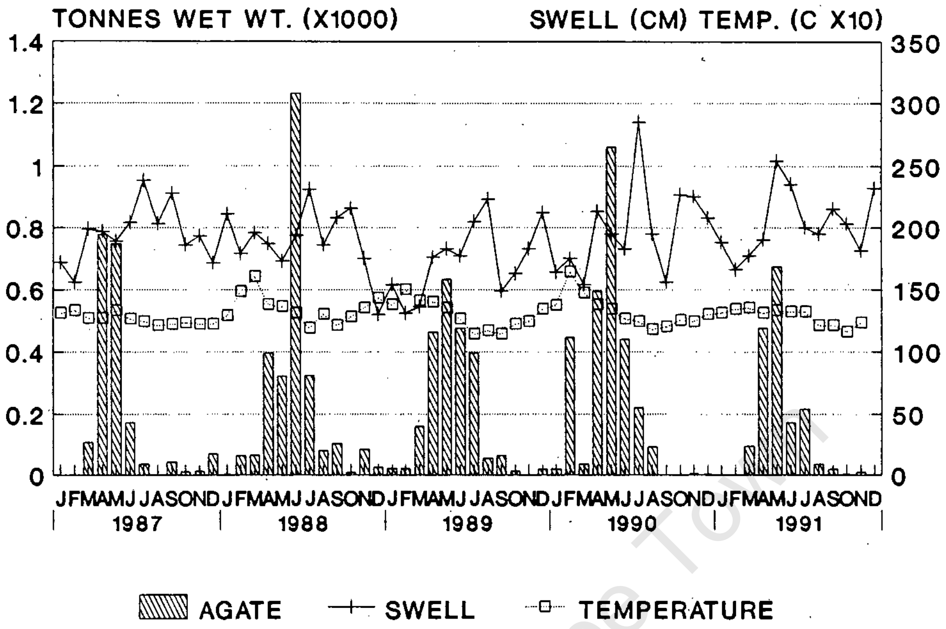
Figure 2.21. Monthly washup at Agate Beach from March 1987 to December 1991. Average temperature and swell height for each month are also included.

Figure 2.22. Monthly washup at Aeroplane from March 1987 to December 1991. Average temperature and swell height for each month are also included.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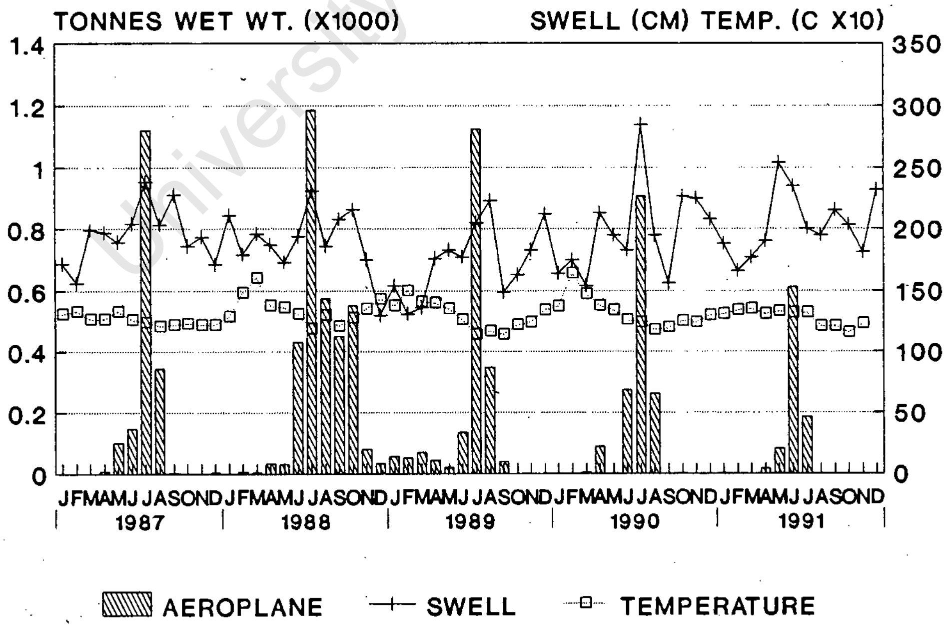
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SWELL (CM) TEMP. (C X10)
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CHAPTER 3

The effect of season and depth on the growth and agar content of *Gracilaria* at Luderitz.

3.1 Introduction

Growth studies are essential in gaining an understanding of the dynamics of natural seaweed populations and also in determining the potential of farming a seaweed species. Farming seaweeds is gaining popularity very rapidly, as natural stocks are unable to supply the demand (Santelices and Doty, 1989) and as end users require very specific end products that may be gained only from a particular strain of a seaweed species (Hansen, 1984).

Tank or pond cultivation has been attempted with a view to commercial cultivation of *Gracilaria* in Namibia (Rotmann, 1987) and Chile (Edding *et al.*, 1987) and in Taiwan pond cultivation is extensively practised on a commercial scale (Chiang, 1981). Hanisak (1987) reported on pilot scale cultivation of *G. tikvahiae* McLachlan from Florida involving a variety of temperatures *viz.* 12, 18, 30 and 24° C, intensive tank cultivation, non intensive pond cultivation and spray cultivation.

Vegetative *Gracilaria* populations are grown by attaching fragments to ropes on rafts or barges (Li, 1984; Ren *et al.*; 1984; Rueness *et al.* 1987) or by securing fragments to the bottom with stones or sand filled tubes (Pizarro and Barrales,

1986) or simply by inserting them into the substratum by hand or with forked sticks (Santelices and Doty, 1989).

Temperature, light, nutrient availability and perhaps photoperiod are the most important parameters in controlling seaweed growth. It is difficult to divorce temperature, light and photoperiod as in many localities, temperature, daylength and irradiance describe similar annual curves.

Gracilaria verrucosa (Huds.) Papenf. in Norway grows for much of the year in suboptimal conditions but reached a maximum growth rate of 5-8% d^{-1} in July and August when grown on ropes (Rueness *et al.*, 1987). In Great Britain *G. verrucosa* was found by Jones (1959b) to grow maximally (2.6% d^{-1}) during summer when temperature and light quantity were maximal. This, however, corresponded to the annual low for dissolved nitrogen and phosphorus. Defoliation was maximal in winter. Productivity of *G. verrucosa* strain G-16 from Florida was maximal in summer when temperature and irradiance were highest (Bird and Ryther, 1990).

Gracilaria sp. attached by sand filled tubes or stones to the substratum, in northern Chile, showed a maximum growth rate in summer, apparently opposite to the situation in the adjacent natural beds (Pizarro and Barrales, 1986). The conflicting results were explained by the natural beds being more susceptible to defoliation in summer due to poorer attachment. In China, *G. verrucosa* grew maximally in summer with an optimum temperature range of 12-20° C (Li *et al.*, 1984). Productivity of *Gracilaria* in tank culture in Chile was not correlated with light and temperature, though highest productivity was during spring and early summer; decreasing productivity in late summer was attributed to depletion of nutrients (Edding *et al.* 1987). In tank culture in Israel, *Gracilaria cf. conferta* (Schousboe) J. & G. Feldmann demonstrated two peaks in growth rate, one in early summer and one in late summer. In mid-summer, temperatures of 28.7° C were limiting (Friedlander *et al.* 1987).

DeBoer (1978) found the growth rate of *Gracilaria foliifera* (Forssk.) Borg., in outdoor culture, to increase with nitrogen concentration to a saturation point of about 1 m mole. Bird (1984), on the other hand, found the growth rate of *Gracilaria verrucosa* to increase with nitrate concentration to a value of 79 mg-at N l^{-1} (= 79 m mole nitrogen, Lobban *et al.*, 1985) with a light intensity of 50 uE m^{-2} s^{-1}. The critical internal nitrogen concentration for productivity of *Gracilaria tikvahiae* was 2% (Hanisak, 1987); at higher concentrations nitrogen was stored and at lower concentrations nitrogen was deficient. *Gracilaria tikvahiae* assimilated nitrogen at a constant rate in both light and dark periods (Hanisak, 1987) and when placed in nutrient enriched seawater for 6h, assimilated enough nitrogen for non-nutrient limited growth for 7-14 days (Ryther *et al.*, (1981). Though over fertilization does not increase or decrease growth rate after the threshold has been reached in *G. tikvahiae* (Hanisak, 1987), problems with epiphyte growth were encountered so a strategy of nutrient pulsing was developed (Ryther *et al.*, 1981; Lapointe, 1985). Nutrient pulses were given to keep the internal nitrogen level at or above 2%. Lapointe (1985) found that wild populations of *G. tikvahiae* in Florida were more limited by phosphorus than nitrogen.

Regardless of cultivation method, epiphytism has caused problems. In Norway epiphytic green algae were a problem between 0.5-1 m during the maximal period for *Gracilaria* growth (Rueness *et al.* 1987) while in Britain epiphytism was a major problem, not only because of the epiphyte biomass and consequent shading and drag but also because of the quantity of silt adhering to the seaweed (Jones, 1959a). In China epiphytism was found to be highest when growth rate of

Gracilaria was lowest (Li *et al.*, 1984) and in Chile shading was caused by floating *Ulva* settling on growth sites (Pizarro and Barrales, 1986).

Rueness *et al.* (1987) working on *Gracilaria verrucosa* in Norway obtained best growth from the surface down to 3 m and from 3-6 m growth was markedly reduced. They also found that the pigmentation of the plants varied with depth with bleaching occurring in the upper 3 m. Jones (1959a) found a similar bleaching in *G. verrucosa* grown in full daylight near the surface, which was explained as an effect of breakdown of the photolabile phycoerythrin.

Agar % yield was found to correlate negatively with growth, and gel strength correlated positively with growth rate in *Gracilaria verrucosa* strain G-16 (Bird and Ryther, 1990) in *G. foliifera* (DeBoer, 1978) in *Gracilaria* sp. (Yang, 1978) and in *G. sordida* W. Nelson in New Zealand (Christeller and Laing, 1989). Craigie and Wen (1984) found a positive correlation between temperature of growth and agar gel strength in *G. tikvahiae*; they also pointed out that agar from young tissue had a higher gel strength than that from mature tissue. In a *Gracilaria* species investigated by Macchiavello (1989), old tissue was found to have a higher agar content. Engledow and Bolton (in press) found no significant difference in agar % yield (32-34%) of *Gracilaria verrucosa* from Saldanha Bay (South Africa) following 4 weeks growth at different temperatures (10-20^{o} C) despite different growth rates at these temperatures.

Craigie and Wen (1984) suggest that reports of gel strength being positively correlated with nitrogen availability may be because growth rate increases with nitrogen availability and hence the ratio of young to old tissue increases. Nitrogen has been reported to play a role in agar yield by Hoyle (1978a). He found agar yield to be negatively correlated with nitrogen in the thalli (which was positively correlated with nitrogen in the sea) of *G. coronopifolia* J. Ag. and *G. bursa-pastoris* (Gmel.) Silva and Christeller and Laing (1989) found a similar result for *G. sordida*. Nitrogen secreted as ammonia from epifauna growing on *G. verrucosa* was found to have a negative effect on growth but a positive effect on gel strength (Cancino *et al.* 1987)

The seaweed industry at Luderitz depends on the beach cast of *Gracilaria* for it's survival. This beach cast is not constant through the year and fluctuates from year to year (Chapter 2). The research in this chapter aims to investigate the growth characteristics of the Luderitz *Gracilaria* with a view to supplying information on the dynamics of the natural population. The only means to expand the industry is through cultivation, and the results of this chapter are designed to provide a baseline for future cultivation activities.

3.2 Materials and methods

Gracilaria was collected at the same site, LBC 2 (fig. 3.1), for all investigations undertaken. LBC 2 was chosen as it is in a deep gully where unattached material could always be found. Temperatures were measured as in Chapter 2. and daylengths were calculated from the Basic computer program in Appendix I. Correlation analyses were performed with "Statgraphics" statistical package.

3.2.1 Growth with depth:

Material was brought back to the laboratory and manipulations were carried out in a 15.6 cubic meter cold room, at $12^{o} \pm 1^{o}$ C,. For experiment I, 10 cm (0.04 g) apical sections were excised and placed in fresh unfiltered seawater overnight. For experiment II, 20g portions were excised.

Experiment I:

Polyester (terylene) rope (6 mm, 3 chord) was chosen as a medium on which to grow the seaweed as it had a softer texture and higher specific weight than polyamide (nylon) rope (Anonymous, 1990a). Ropes to be outplanted were soaked in sea water for 24 h before seeding, to remove any toxins. A harbour lighter (barge), moored to the west of the harbour channel in 6.5m of water was chosen as the growth site (figs. 3.1 and 3.2)

Gracilaria was attached to eight replicate lengths of rope by opening the strands of the rope, inserting a 10 cm fragment and then closing the strand again. This was done from 0 m down to 5.5 m at 10 cm intervals on each rope. The ropes were suspended vertically from the lighter (4 on each side) with a 1 kg lead weight attached to the end of each rope to keep them vertical. The experiment was initiated on 17-11-1989 and terminated on 12-1-1990 (56 days duration).

Plant length was measured at 2 week intervals and on termination of the experiment, the wet weight of each plant was measured. To shake off excess water, plants were placed in a nylon netting bag attached to a 1 m string, which was then swung centrifugally, by hand, for approximately 5 seconds. (see fig 3.4) Contaminating epiphytes and epifauna were separated and weighed.

Experiment II:

In this experiment the primary aim was to grow enough biomass at each depth for agar analysis. The same site as for the previous experiment was chosen. Nylon netting tubes with 1.5 cm mesh size and 25 cm tube diameter (fully extended) were used to grow the seaweed. Twenty gram portions of seaweed, prepared as above, were placed into 4 replicate tubes above knots tied at 50 cm intervals. A 1 kg lead weight was again attached to the bottom end of each tube. Two tubes were suspended from each side of the lighter (figs. 3.1 and 3.2). The experiment was initiated on the 4-9-1991 and terminated on the 1-11-1991 (58 days duration). Plants were not disturbed for the duration of the experiment and on termination, biomass of each plant was measured as above. The plants were then sun dried for subsequent agar extraction.

3.2.2 Seasonal growth.

Based on the results of the growth with depth studies, a site was chosen in the Luderitz Lagoon (see fig. 3.3) to study the seasonal growth pattern of the *Gracilaria.* Untreated 1.5 m pine stakes were driven into the mud to a depth of 1 meter. Polyester ropes of 6 mm diameter and 5 m long were secured between stakes at the water/mud interface so that they lay on the bottom (fig .3.3). Twenty five replicate *Gracilaria* fragments were attached to each rope as above except the interval between fragments was 20 cm. The site was chosen so that at low spring tide the ropes were covered with 30 cm of water and at high springs 2 m of water covered the ropes. Five parallel ropes were placed in the site to initiate the experiment in February 1990 and at 14 day intervals one rope was removed and replaced by a new rope with *Gracilaria* attached in the same way.

By the time the 5th rope was removed it had been in place for 70 days and all subsequent ropes removed from the site had been growing for 70 days. The experiment was terminated in November 1991. When a rope was removed, all plants were treated and weighed as above and then sundried in preparation for later agar extraction.

3.2.3 Agar extraction.

Agar yield:

The agar extraction process used in this study is that of the industry at Luderitz. A 50g sample of the sundried seaweed was cleaned and dried for 40 minutes at 100° C. This dried seaweed was weighed and placed in a boiling flask with a 6% caustic soda solution in a ratio of 1 part seaweed to 25 parts caustic soda by volume. This mixture was heated to between 50-80° C until the seaweed turned light transparent green. The seaweed was then rinsed with fresh water until the seaweed water mixture reached a pH of 8-9, and the water was then poured off. Fresh water to the same ratio as seaweed to caustic soda was added, followed by sodium hypochloride to give a concentration of chloride in solution of 3000-5000 ppm. When the seaweed changed colour to pale yellow the action of the sodium hypochloride was neutralized by adding 10% sulphuric acid to a ph of 5. After rinsing with fresh water the ph was 6.

Fresh water was added to the bleached seaweed to just cover it and then brought to the boil. The pH was monitored and maintained at 6 by using acetic acid or 6% caustic soda. When all of the seaweed had disintegrated, filter aid (Diacalite Filteraid, Genulite Expanded Perlite, Chemserve Perlite, Cape Town) was added at a ratio of 1 part seaweed (dry) to 4 parts filter aid. The solution was then filtered through a hot Buchner funnel and flushed with small amounts of hot water. The filtrate was poured into gelling trays (30cm long, 5cm wide and 2cm deep)., allowed to gel in a fridge and then deep frozen (-30° C) over night. The gel trays were then thawed and excess water poured off, the gel was then fully dried in a drying oven at 50° C for 4-5 h. The dried gel was weighed and expressed as a % of the dry seaweed weight.

Gel strength:

A measured weight of agar powder (milled dry gel, as above) was placed in a boiling flask and cold water added to give a concentration of 1.5% by weight. This mixture was allowed to stand for ± 12 h after which it was boiled for 20 minutes until all of the agar had visibly gone into solution. The concentration was kept at 1.5% by adding hot water. After boiling, the solution was poured into gelling trays. After the trays stood for ± 20 h the gel strength was measured using a "gel meter" (Nikkansui-type, Japan Agar-Agar Marine Product Industry Association). A plunger of 1 cm^2 surface area was brought into contact with the surface of the gel and weights were added until the plunger penetrated the gel after 10 seconds.

3.2.4 Growth rate of plants with different starting weights.

To quantify the growth rate of plants with different starting weights at the seasonal growth site an experiment was set up adjacent to the "growth with season" site. Eight pine stakes were driven into the mud and four 5 m X 6mm polyester ropes were secured between the stakes. Fragments were attached, as in the seasonal growth experiment, at 20 cm intervals. The fragments on the first rope had a starting weight of 10 g, on the second 30 g, the third 50 g and on the fourth the fragments weighed 70 g. All ropes were placed in the growth site at the same time and allowed to grow for 11 days from 6-17 November 1990. After termination of the experiment the plants were shaken and weighed as before.

3.3 Results

3.3.1 Growth with depth I

Plant survival varied with depth. At the surface (0 cm) the plants were bleached and then died, at both 10 and 20 cm only one survived, at 30 cm 3, at 40 cm, 5 and from 50 cm down to 540 cm all eight plants survived at each depth. At 550 cm all plants were lost.

Apart from at 0 cm and 550 cm where no plants survived, the lowest specific growth rate was at 10 cm (2.6% d^{-1}; fig. 3.5). From 10 cm, biomass rapidly increased with depth to peak at 130 cm (9.9 ±1.4% d^{-1}; ± standard error). From this peak, specific growth rate decreased to a low of 3.9 ±0.32% d^{-1} at 530 cm. Based on figure 3.5, the optimum depth for growth was from 40 cm (8 ±1.7% d^{-1}) to 260 cm (8 ±1.3% d^{-1}) depth.

Epiphyte contamination was a problem from the surface to approximately 2 m. *Ceramium diaphanum* (Lightfoot) Roth. and a *Polysiphonia* species were the most common, but juvenile *Porphyra* and *Ulva* and an unidentified, juvenile, foliaceous Rhodophyte were also present. From 2 m to 5 m, contamination was predominantly by the hydroid *Tubularia warreni,* Ewer. whereas below 5 m no contaminating organisms were visible. Contamination became a problem after 30 days of growth but was mostly attached to the ropes and did not occur beyond a ± 5 cm radius of the rope, and as such the growth of *Gracilaria* was not significantly affected.

Plants growing from 0-50 cm had a yellow/green colour whilst at the bottom of the ropes the plants were deep red. Between these extremes there was a gradual colour transition.

3.3.2 Growth with depth II

This experiment, though less detailed than the first growth with depth experiment, gave a similar growth with depth profile (fig. 3.6), though overall the growth rates were very much lower. The highest growth rate was attained from 0.5 m (3.23

±.21% d^{-1}) to 1.5 m (2.94 ±.39% d^{-1}). From these optima the growth rates decreased with depth to a low of 1.32 ± 2% d^{-1} at 4 m. At the surface, growth rate was 2.4 ± .13% d^{-1}.

3.3.3 Exponential growth.

Given the initial weight, and the weight of fragments after 14, 28, 42, 56, and 70 days, a "best fit" straight line was fitted to the data as a regression on a log scale. This converted to the exponential curve in figure 3.7. This curve represents a growth rate of 12.1% d^{-1} which was slightly higher then the actual growth rate based on the initial and final weight ie. 11.6% d^{-1}. This "best fit" curve did not fit very well, however, as the data point at 56 days was above and at 70 days was below the curve. Another "best fit" curve was calculated as above based on the initial weight and the weight after 14, 28, 42, and 56 days. This curve fitted all the data points very well and represented a growth rate of 12.5% d^{-1}. It thus appears that the fragments grew exponentially at least until day 56.

3.3.4 Growth rate with season (fig. 3.8)

Growth rate roughly followed a seasonal pattern with highest growth from late spring through summer to autumn and lowest growth in winter. The rapid growth rate period was extensive covering the 6 months from October to April. The lowest growth rates (over 70 day periods) occurred in July/August 1990 (7.9 ±1.1% d^{-1}) and in June 1991 (8.8 ±1.1% d^{-1}). Over the duration of the experiment the growth rates appeared to be higher in the high growth rate period at the beginning of 1990 then the 1990/1991 high growth period but the difference was not significant ($p > .1$). Rate of growth correlated positively with daylength and temperature ($p < .01$) though the correlation with daylength was stronger ($r = .635$, $p = .0015$) than temperature ($r = .5464$, $p = .0085$). Temperature points (fig. 3.8) were taken from a 70 day running average run for the period. Over the experimental period, temperature was highest during March 1990 (15.3° C) and gradually decreased to the year minimum during September (11.8° C). From then, temperature increased to 13.1° C at the end of December 1990 and remained between 13-13.5° C from December to June 1991 followed by a drop to 12.5° C in August 1991.

The isopod *Paridotia reticulata* was found in most samples, but at times of high *Gracilaria* growth rate, the ratio of isopod to *Gracilaria* reached problematic proportions (fig. 3.9). In April 1990 isopods comprised over 20% (900 g pooled) of the total sample weight (4500 g pooled). This dropped to almost negligible amounts in winter and climbed again to 10% (240 g) of the total sample weight (2400 g) in April 1991.

3.3.5 Growth rate vs. plant size.

It was established that *Gracilaria* grew exponentially in autumn 1990 (at 30-200 cm deep; fig. 3.7). It appeared that as plants increased in size their growth rate decreased (fig. 3.7 and S.E. bars on fig. 3.8). Figure 3.10 depicts 4 exponential growth curves based on the starting and finishing weights of the 4 size classes. The 10g class had a specific growth rate of 12.1% d^{-1}, the 30g class grew at 11.3% d^{-1}, the 50g class at 8.7% d^{-1} and the 70g class at 5.7% d^{-1}.

3.3.6 Agar.

Sufficient biomass (50 g dry) was gained for one agar extraction at each depth from the surface down to 2.5 m. The plants from 3, 3.5 and 4 m were combined to give a biomass sufficient for agar extraction (fig. 3.11). The % agar yield showed an inverse relationship with % growth rate (this data set may not be large enough for a proper correlation) except for the combined 3 m sample. Highest % yield was 2.5 m (17.8%) and lowest at 0.5 (14.2%).

Results of agar extractions on samples taken from the growth with season site from March 1990 to March 1991, show that % yield correlated negatively with temperature, daylength and growth rate (r = -.2176, -.8109 and -.33 respectively, fig. 3.12). However, only daylength had a significant correlation $p < .001$. The % yield was highest in winter at 20 ±1.3% and lowest in autumn at 11.72 ±.26%.

3.3.7 Environmental parameters.

The annual variation in daylength was small, with a 10 h shortest day and 13 h longest day. Temperature, though relatively constant, did show a slight seasonal pattern, high in late summer and autumn and low in winter and spring. In February/March 1990 sea temperatures were unusually high (fig. 3.8)

3.4 Discussion

The results of both growth with depth experiments were superficially similar. The most immediate difference is that the growth rates for experiment II were very much lower (maximum = 3.23% d^{-1}) than experiment I (maximum = 9.86% d^{-1}). This difference, however, was due to the different seeding methods employed, and nevertheless the growth trend with depth can be compared.

The most obvious explanation for the pattern of growth with depth is light availability, as in Luderitz Bay and Lagoon a defined thermocline can only exist in the absence of mixing by the wind and this is a rare occurrence. Namibia falls into a global region where the annual average sum of photosynthetically active radiation reaching the water surface is 3000-3800 MJ m^{-2} yr^{-1} (Luning, 1990). As solar energy passes through the sea the quantity is reduced and the quality altered

(Lobban *et al.*, 1985; and Luning, 1981). Engleman's (1883; in Saffo, 1987) theory of chromatic adaptation has lost support through lack of confirmatory evidence (Ramus *et al.*, 1976; Saffo, 1987) so it cannot be said that red algae are better adapted for photosynthesis in deeper water.

Quantities of light, below the saturation level for photosynthesis of a particular plant will reduce photosynthesis and hence growth. Decrease in light intensity through absorption depends on the turbidity of the water (Luning, 1990). The coastal waters of Namibia, through upwelling (Chapter 1) and resultant productivity, are normally turbid but the added effect of wind driven water motion (Chapter 2) in the Luderitz Bay and Lagoon result in very turbid water with a Secchi disk depth of 1-2 m usual in the Lagoon (Noli pers. comm..). Under these conditions 10% of the surface light reaches from 1.35-2.7 m. This turbidity is highest when southerly winds are strongest (late spring through summer to early autumn; Chapter 2). Both experiments were conducted during this turbid season.

The lower limit of the peak growth rate for experiment I (±260 cm), which was conducted during the highest annual irradiance (17 November 1989 to 12 January 1990) was deeper than for experiment II (± 150 cm). This may be because of the lower seasonal irradiance during the duration of experiment II (4 September 1990 to 1 November 1990). The upper limit of optimal growth, in experiment II was probably also shallower than experiment I, but as only 0.5 m depth intervals were tested in experiment II, this cannot be stated with certainty.

McLachlan and Bird (1986) found little evidence that species of *Gracilaria* are sensitive to high levels of radiation, yet Beer and Levy (1983) and Friedlander *et al.* (1987) found the optimal photon fluence rate for growth of *Gracilaria* tips to be 100 uE m^{-2} s^{-1} (uE = uMol photons), photon fluence rates above and below this value were limiting. Engledow and Bolton (in press) found 80 umol m^{-2} s^{-1} to be saturating for growth of *Gracilaria* from Saldanha Bay (South Africa), growth decreased rapidly at intensities below the saturation level and at intensities in the range 160-850 umol m^{-2} s^{-1} growth leveled off though at a lower rate than at 80 umol m^{-2} s^{-1}. Baines (unpublished), working on *Gracilaria* collected at Luderitz, found the saturating level to be 70 umol m^{-2} s^{-1} and at 80 and 100 umol m^{-2} s^{-1} growth was reduced by 50%. It is likely that at the optimum depth for growth, light was at the saturating level. Below this optimum, light was limiting and above photoinhibition may have been the limiting factor. Even though the light saturation range for *Gracilaria* may be broad there is a point where light intensity becomes inhibitory (Luning, 1990) and *Gracilaria* at Luderitz, being a sublittoral species, was certainly inhibited by the high light intensity at the surface.

Rueness *et al.* (1987) found Norwegian *Gracilaria verrucosa* to grow best at 3 m in summer but they suggest that heavy fouling above 3 m may have been the factor reducing growth in shallow water. In experiment I fouling was mostly confined to the rope and as such did not effect the growth of the *Gracilaria*. The bleaching of plants close to the surface, in experiment I and II, has also been reported by Jones (1959a) and Rueness *et al.* (1987). Jones further stated that bleached plants demonstrated lower growth rates than "fully pigmented" plants. In this investigation the bleached plants at the surface did show a lower growth rate than the less bleached plants at 0.5 to 2 m depth but the deeply pigmented plants in deeper water had the lowest growth rate.

The use of the following units to express growth rate; % per day, doublings per day and doubling time, all describe an exponential type of growth. This growth rate is usually assumed to be constant over the experimental period (Jones, 1959a +b; DeBoer, 1978; Lapointe, 1985; Friedlander *et al.*, 1987; Li *et al.*, 1984;

Eckman and Pedersen, 1990; Engledow and Bolton, in press). For this assumption to be true in pond/tank or culture dish conditions, temperature and light need to be constant, nutrients non-limiting and densities maintained so as to prevent shading - a situation approaching steady state (Mclachlan and Bird, 1986). In the field, all of the above elements fluctuate, and the loss of material through fragmentation or grazing can also effect results.

Constant growth rates can only be maintained over short periods of time, whereas during longer periods, growth rates are less (Mclachlan and Bird, 1986). This is evident from figure 3.7 where growth rate based on 56 days from the start, was 12.5% d^{-1} and on 70 days from the start was 11.6% d^{-1}. The important consideration is not the duration of the experiment but the size of the plants as larger plants are more susceptible to self-shading as well as shading each other, and fragmentation. Figure 3.10 shows growth curves for 4 starting weights of *Gracilaria* all grown concurrently over 11 days. Growth rate was inversely related to starting weight. Grazing of the plants was discounted as evidence of grazing was not found and plants shading each other, though it must have played a role, was not thought to be the most important factor as the plants were well spaced on the lines (20 cm apart) and due to the water currents, were in constant motion. Self-shading and loss of plant material through water motion are thought to have been the main reasons for the apparent reduction in growth rate.

Growth rate should follow the annual cycle of daylength but is usually also effected by levels of nutrients and temperature (McLachlan and Bird, 1986). The seasonal growth curve correlated well ($p < .01$) with the annual daylength cycle and temperature curve (fig. 3.8). The highest growth rate was recorded during March/April 1990 when the highest temperatures for the experimental period were measured. The same year, the lowest growth rate was in late winter to early spring presumably because temperatures were still low even though daylength was increasing. The prolonged high growth rate period in summer 1990/1991 may be explained by the sea temperature increasing through the summer to peak in autumn. Lowest growth rates in 1991 were found in June when daylength was shortest. It is possible that *Gracilaria* exhibits an annual photoperiodic rhythm in growth rate, which was further influenced by temperature.

Though light intensity was not measured in this study, it is assumed that the annual cycle of photoperiod and light intensity are very similar as atmospheric obstruction of the solar radiation by clouds etc. is rare. Santelices and Fonck (1979) found the growth of Chilean *Gracilaria* to correlate with seasonal changes in light intensity and water temperature. Namibia has a similar marine climate to that of Chile and the latitude of Luderitz (26^{o} 40' S) is close to that of Coquimbo (30^{o} S), the site studied by Santelices and Fonck (1979). Friedlander and Zelikovitch (1984) found the growth of a *Gracilaria* species in Israel to correlate with temperature and not light intensity. They suggested that light was always saturating. Friedlander and Zelikovitch (1984) carried out their experiments in shallow (1 m) ponds where the light intensity never fell below 700 umol m^{-2} s^{-1} and as *Gracilaria* was found to be light saturated at or below 100 umol m^{-2} s^{-1} (Beer and Levy, 1983; Friedlander *et al.*, 1987; Engledow and Bolton, in press and Baines, unpublished), it was not surprising that light intensity did not correlate with growth. As a consequence of the turbid water in the Luderitz area (particularly the Lagoon), light penetration is poor and probably often below saturation levels for the seaweed, particularly during high tide when the experimental site was in 2 m of water.

The growth rates obtained in this study, 8-11.9% d^{-1}, are among the highest for any field cultivation reported. *Gracilaria* sp. grown on rafts in China (Ren *et al.*, 1984) had comparable rates (12% d^{-1} in summer); in New Zealand immersed

Gracilaria sordida had peak growth rates of 4-5% d^{-1} (Pickering *et al.*, 1990) while *Gracilaria cornea* J. Ag. grown on ropes in Venezuela had growth rates of 1.4-2.4% d^{-1} (Rincones Leon, 1989). Rueness *et al.* (1987) reported a peak of 8% d^{-1} for *G. verrucosa* grown on ropes in Norway in summer and Jones (1958b) found the peak growth rate for *G. verrucosa* in Britain to occur in May (2.6% d^{-1}). The growth rates for Luderitz are in excess of the typical range (5-10% d^{-1}) for *Gracilaria* species as reviewed by McLachlan and Bird (1986). Indeed these results are higher than many reported for pond, tank and aquaria culture reviewed by the latter authors.

The isopod *Paridotea reticulata* was found in large numbers, during summer and autumn, sheltering amongst the *Gracilaria* thalli. Other epifauna included juvenile rock lobster, octopus and unidentified fish species. However, no evidence of grazing by the isopods or the other epifauna was found.

Agar % yield had a strong negative correlation with daylength ($p < .001$) and a negative, though not significant, correlation with growth rate and temperature. Similarly, Bird and Ryther (1990) found agar % yield of *Gracilaria verrucosa* G-16, in Florida, to be lowest in summer when growth rate, irradiance and temperature were highest. Also working on *G. verrucosa*, Daugherty and Bird (1988) found % yield to decrease with increasing salinity and temperature and the % yield of *G. sordida* was found to decrease with increasing temperature and nitrogen levels suboptimal for growth (Christeller and Laing, 1989). In each of these investigations the ranges of temperature and salinity were large; 5-30° C and 16-40‰ (Bird and Ryther, 1990), 11-45° C and 17-33‰ (Daugherty and Bird, 1988) and 10-30° C, salinity constant (Christeller and Laing, 1989). In the Luderitz Lagoon the maximum temperature variation is from 10-20° C and salinity does not vary significantly due to water mixing and the lack of fresh water input (Chapter 2.).

Upwelling is most active on the coast from September to March when the southerly wind strength is highest. With increased upwelling comes an increase in the nutrient content of the water (Bailey, unpubl.) and this period corresponds to the decrease in % agar yield in figure 3.12. De Boer (1978) found agar % yield to decrease with increase in nitrogen up to a saturation level of 2-3 um. Hoyle (1978a) found the agar % yield of *G. bursapastoris* and *G. coronopifolia* to be inversely related to the nitrogen content of the thalli which was positively related to the ambient sea water nitrogen levels. He went as far as to state that the important factor effecting agar seasonality is the nitrogen concentration of the ambient sea water. Eckman *et al.* (1991) found increased agar yield from *Gracilaria sordida* grown in enriched culture, and conversley, found highest yields from uninriched cultures. In Hoyle's (1978a) investigation the nitrogen levels never exceeded 2 um. The Luderitz nitrate levels rarely if ever drop below 10 um (Noli pers. comm.. figs. 3.13 and 3.14), well above the saturation point of 2-3 um found by DeBoer (1978), and as such are unlikely to effect agar yield.

3.5 Conclusions

1) The optimum depth for growth was between .5m and 2-2.5m. The controlling factor was light availability as a defined thermocline rarely exists in the Luderitz Lagoon or Bay. Light inhibited growth in water shallower than .5m.

2) Seasonal growth followed the daylength cycle, the growth rate being maximal and minimal when daylengths were correspondingly maximal and minimal. Temperature also acted to alter the seasonal pattern dictated by the daylength cycle, growth rate increasing with higher temperature.

3) The apparent decrease in growth rate as plants grew larger was attributed to self-shading and the loss of material through water motion.

4) Agar % yield correlated negatively with daylength, and in the growth with depth experiment agar yield correlated negatively with growth rate.

Figure 3.1. Map of the Luderitz area showing the seasonal and growth with depth study sites.

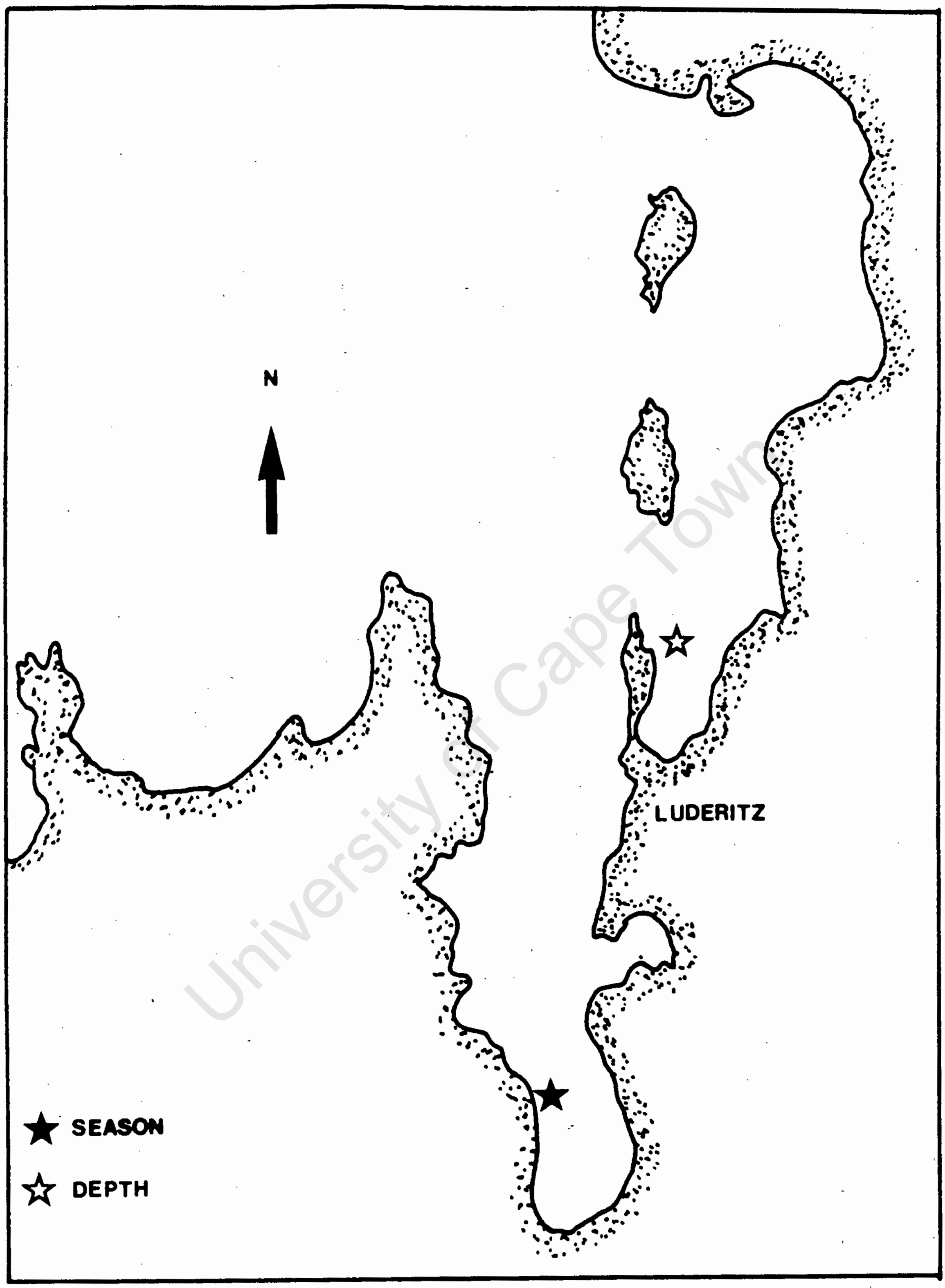
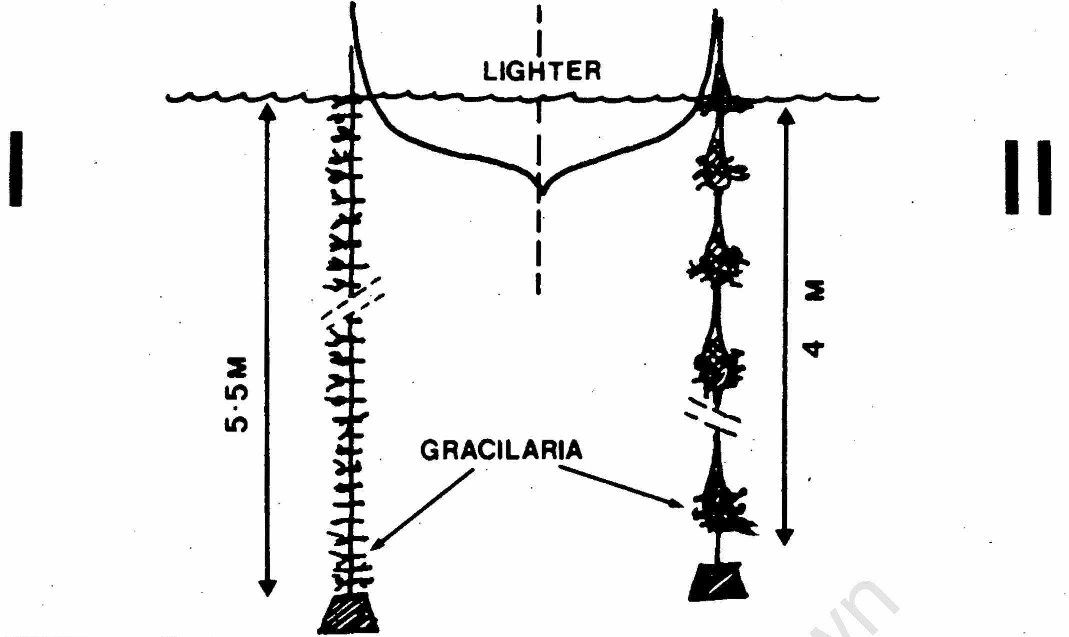
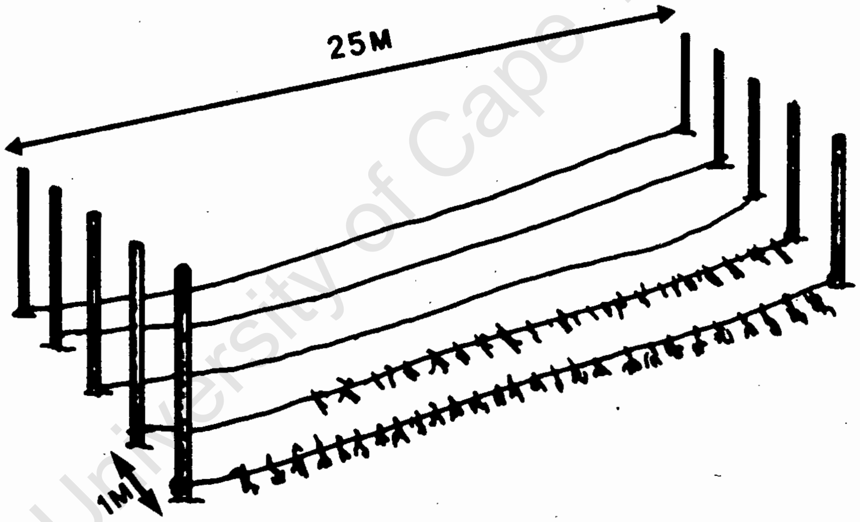

N
LUDERITZ
★ SEASON
☆ DEPTH

Figure 3.2. Growth with depth experiments I and II. In experiment I Gracilaria fragments were secured in the strands of 6 mm rope. In experiment II tubular netting was used, a knot was tied at the required depths to form a string of bags.

Figure 3.3. Seasonal growth study site. Stakes were hammered into the mud and seeded ropes secured between the stakes.

Figure 3.4. Method of extracting excess water for weighing purposes. The netting bag was swung for 5 seconds.


I
LIGHTER
II
5·5M
4 M
GRACILARIA


25M
1M

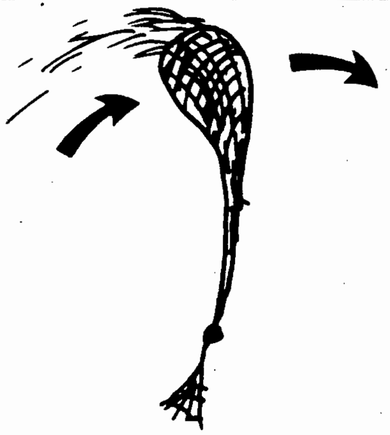


Figure 3.5. Growth rate from the surface down to 5.5 m at 10 cm intervals during summer. Each point represents an average of 8 plants ± 1 standard error.

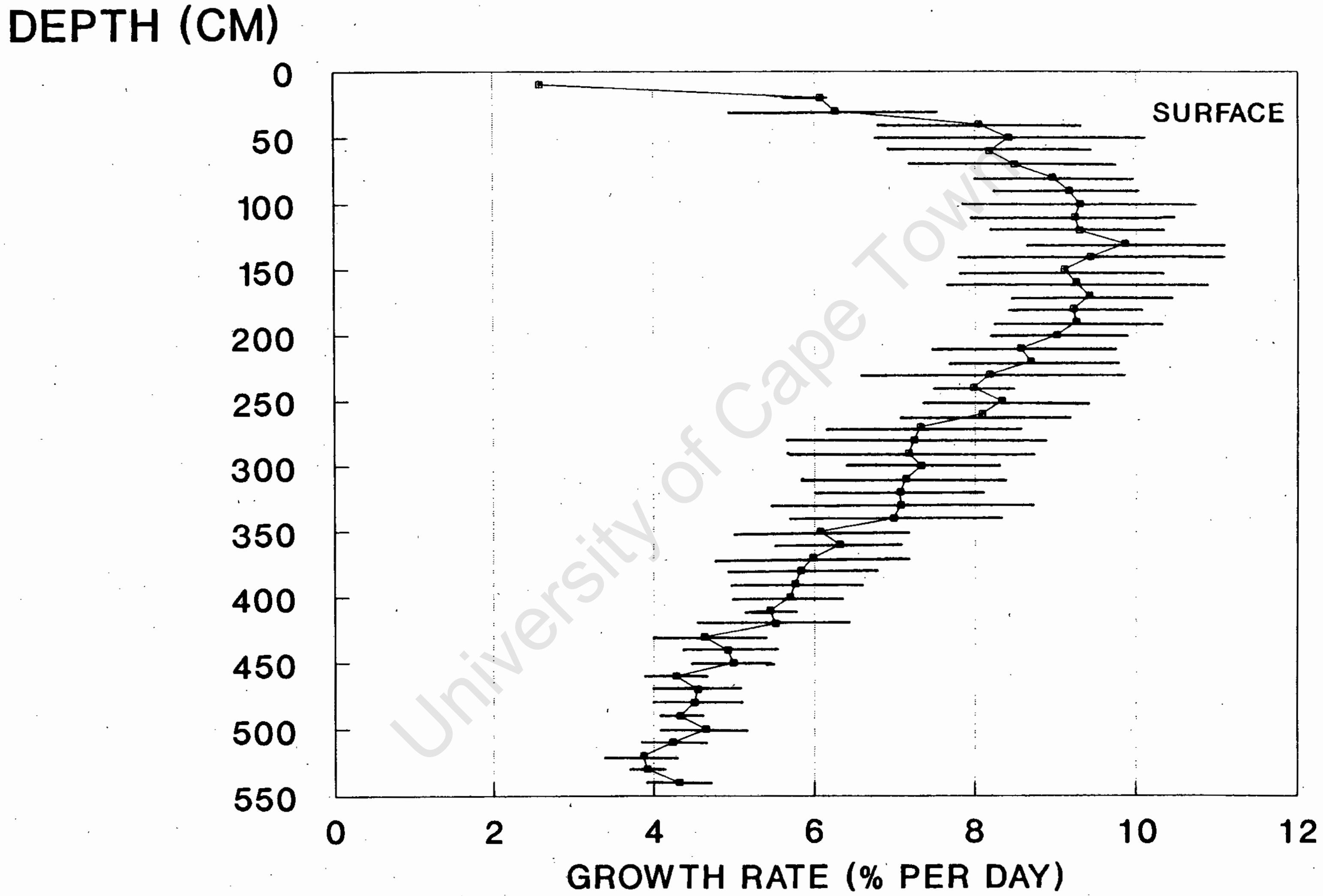

DEPTH (CM)
0
50
100
150
200
250
300
350
400
450
500
550
SURFACE
0
2
4
6
8
10
12
GROWTH RATE (% PER DAY)

Figure 3.6. Growth rate from the surface down to 4 m at 0.5 m intervals during spring. Each point represents an average of 4 plants ± 1 standard error.

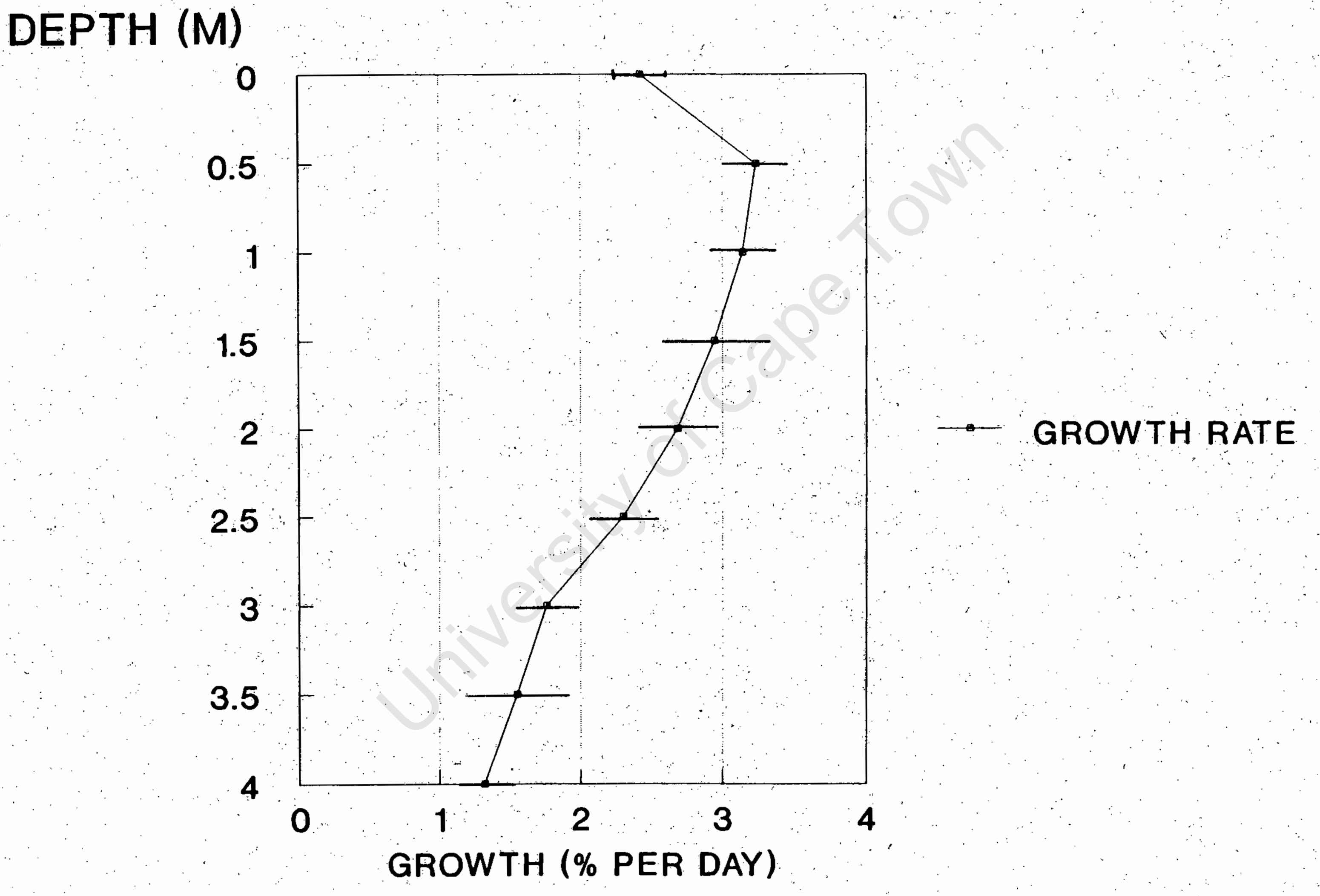
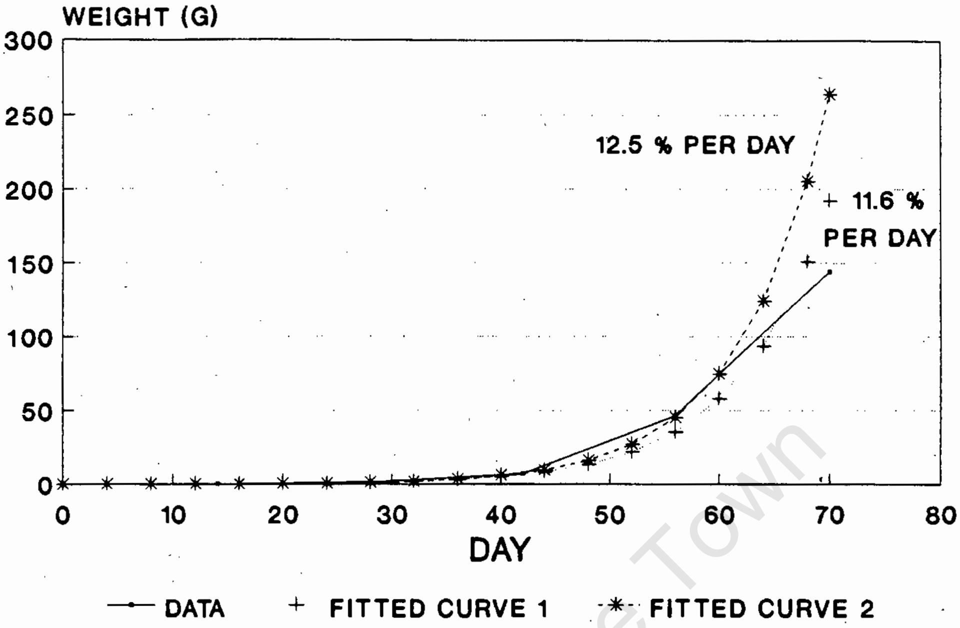

DEPTH (M)
0
0.5
1
1.5
2
2.5
3
3.5
4
0
1
2
3
4
GROWTH (% PER DAY)
GROWTH RATE

Figure 3.7. Exponential growth: The solid line represents the average weight of 25 plants weighed at 2 week intervals over 70 days. The exponential curve, represented by the dashed line, is based on the starting weight and the weight at day 70. The dash, dot exponential curve is based on the starting weight and the weight at day 56.

Figure 3.8. Growth expressed as % per day from March 1990 to August 1991. Twenty five 10 cm fragments were allowed to grow for 70 days. Each point represents the average rate of growth of the 25 plants ± 1 standard error. Sea temperature and daylength data points represent the mean for the 70 day growth period of each set of plants. Daylengths were obtained from a "Basic" computer program run for the Luderitz latitude at 0^o solar declination.


WEIGHT (G)
300
250
200
150
100
50
0
0
10
20
30
40
50
60
70
80
DAY
12.5 % PER DAY
11.6 % PER DAY
DATA
FITTED CURVE 1
FITTED CURVE 2

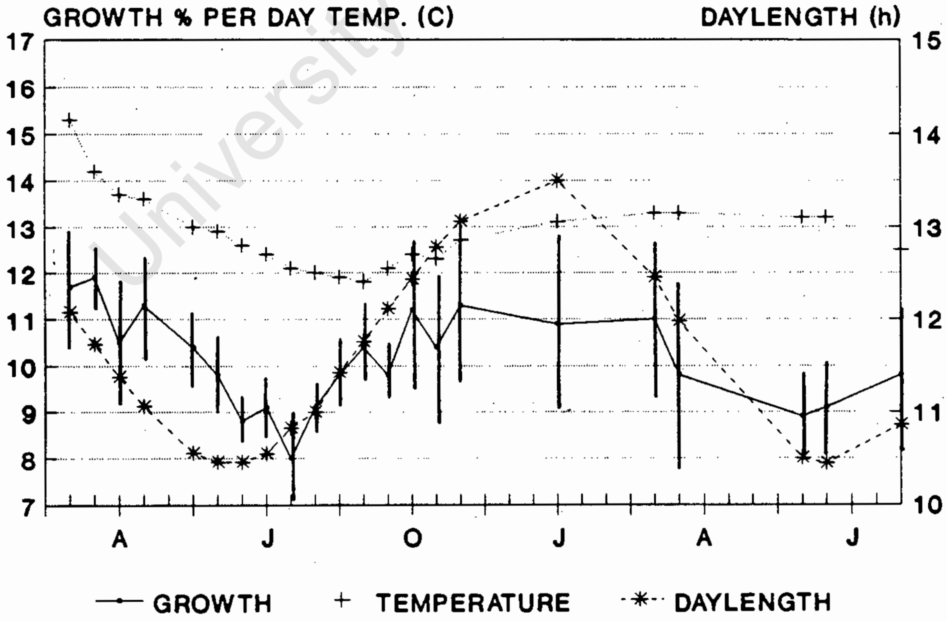
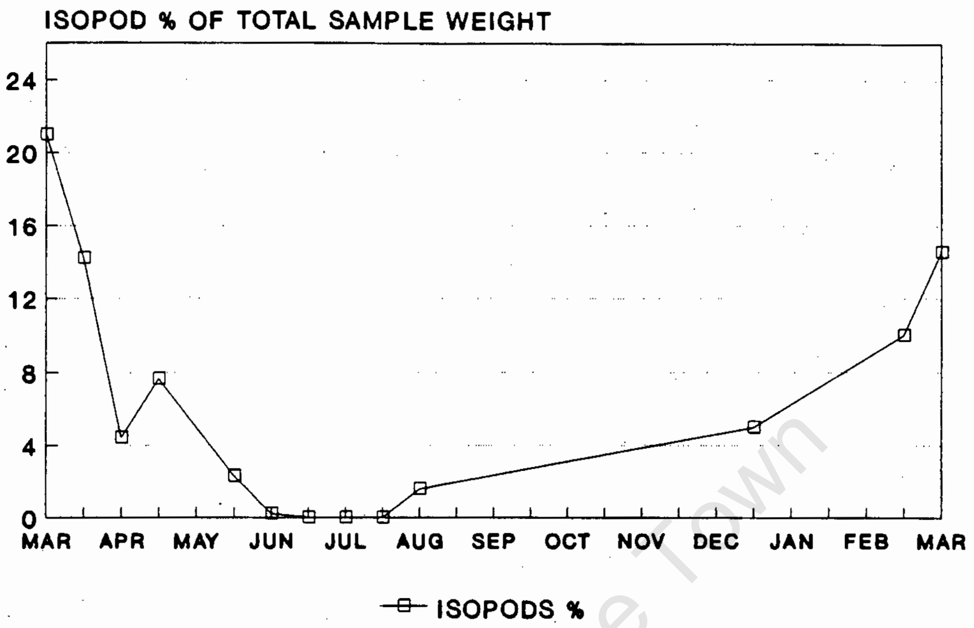

GROWTH % PER DAY TEMP. (C)
DAYLENGTH (h)
17
16
15
14
13
12
11
10
9
8
7
15
14
13
12
11
10
A
J
O
J
A
J
GROWTH
TEMPERATURE
DAYLENGTH

Figure 3.9. Isopods (*Paridotea reticulata*) per 25 plant sample from March 1990 to August 1991. Each point represents the % weight of each 25 plant sample.

Figure 3.10. Plants were grown for 11 days with different starting weights, 10g, 30g , 50g and 70g. The 4 exponential growth curves are extrapolated from the weight gain of the 4 size classes over the 11 days. The figures next to the exponential curves are the growth rate in % per day.


ISOPOD % OF TOTAL SAMPLE WEIGHT
24
20
16
12
8
4
0
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
ISOPODS %

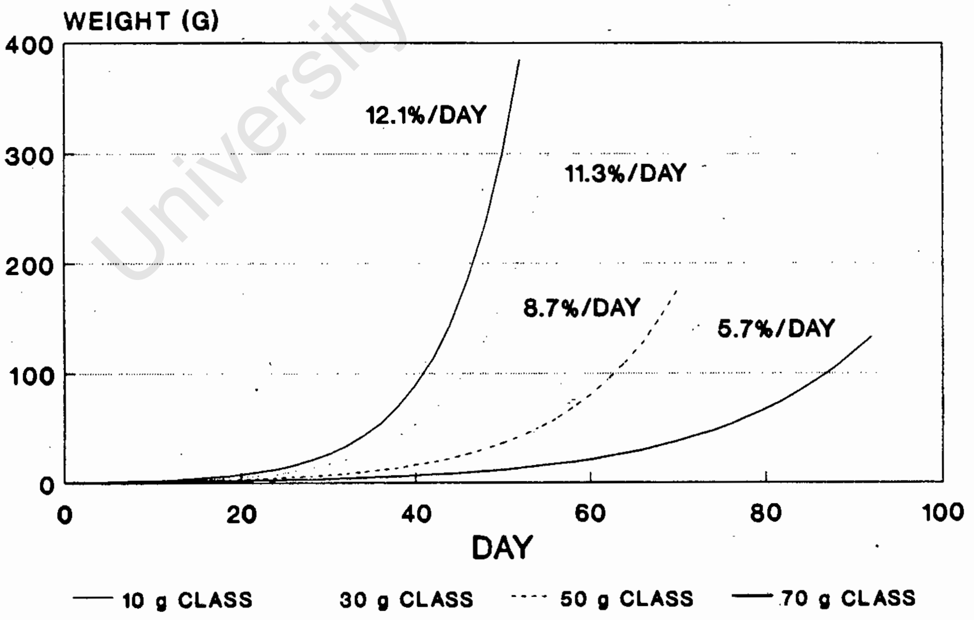
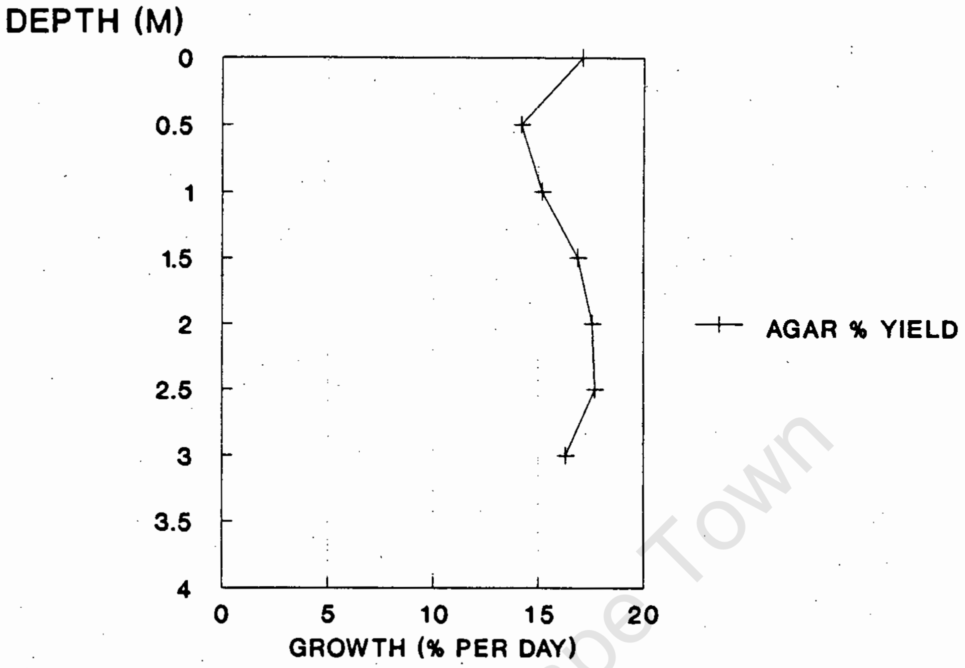

WEIGHT (G)
400
300
200
100
0
0
20
40
60
80
100
DAY
12.1%/DAY
11.3%/DAY
8.7%/DAY
5.7%/DAY
10 g CLASS
30 g CLASS
50 g CLASS
70 g CLASS

Figure 3.11. Agar yield for plants grown from the surface down to 4 m at 0.5 m intervals. Yield is expressed as a % of the seaweed dry mass.

Figure 3.12. Agar yield from seaweed collected at the seasonal growth study site. Yield expressed as a % of dry seaweed mass. Standard errors are given where enough material was available for replication (n = 4).


DEPTH (M)
0
0.5
1
1.5
2
2.5
3
3.5
4
0
5
10
15
20
GROWTH (% PER DAY)
AGAR % YIELD

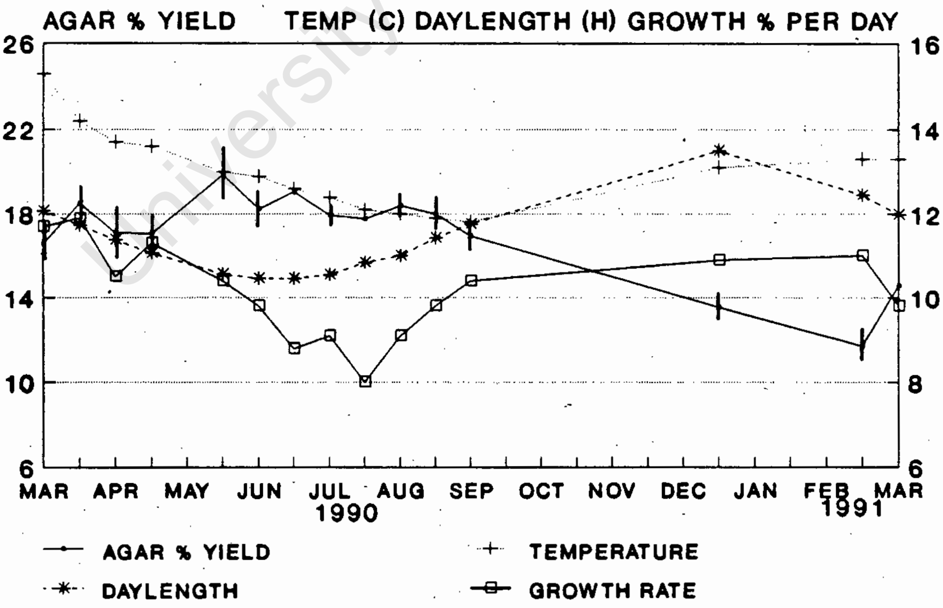
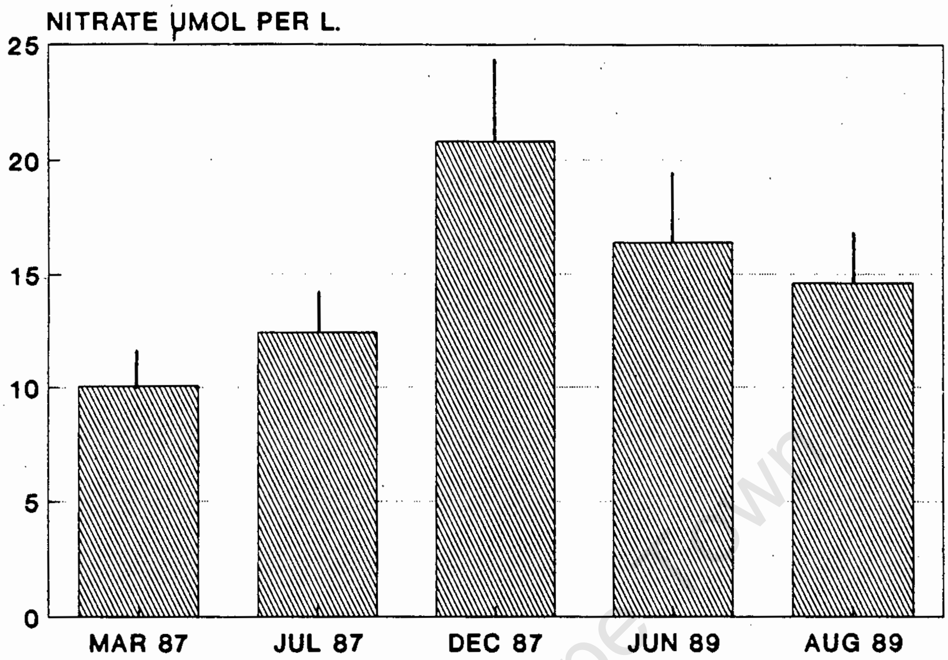
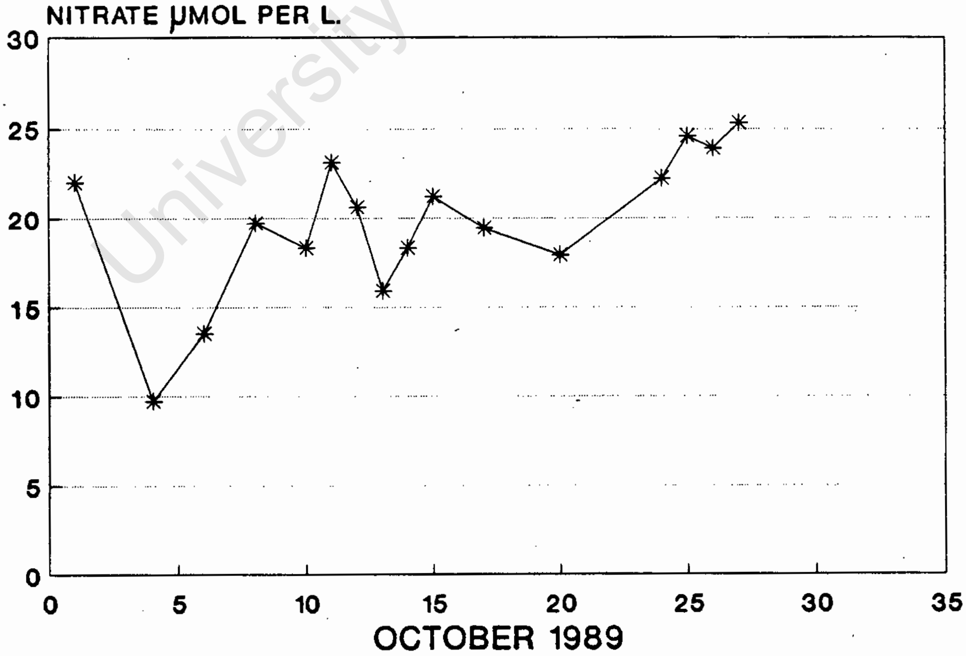

AGAR % YIELD
TEMP (C) DAYLENGTH (H) GROWTH % PER DAY
26
22
18
14
10
6
16
14
12
10
8
6
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
1990
1991
AGAR % YIELD
TEMPERATURE
DAYLENGTH
GROWTH RATE

Figure 3.13. Nitrate and phosphate concentrations for arbitrary months from 1987 to 1989 (± S. E. n = 6 - 14).

Figure 3.14. Nitrate and phosphate concentration in the Luderitz Lagoon during October 1989.


NITRATE µMOL PER L.
25
20
15
10
5
0
MAR 87
JUL 87
DEC 87
JUN 89
AUG 89


NITRATE µMOL PER L.
30
25
20
15
10
5
0
0
5
10
15
20
25
30
35
OCTOBER 1989

CHAPTER 4

A deterministic simulation model predicting washups from the *Gracilaria* population at Luderitz

4.1 Introduction.

As a subject for modeling, the *Gracilaria* population at Luderitz is relatively straightforward because the environmental parameters in the area do not have a large seasonal variation (Chapter 3) and the life history of the Luderitz *Gracilaria* is relatively uncomplicated (Chapter 2).

There is virtually no fresh water input into the system, and hence salinity remains constant. Due to continuous upwelling, nutrients appear never to be limiting and sea water temperature varies relatively little except for occasional, short, warm water events. As Luderitz has a desert climate and sea fog rarely extends into the Lagoon and Bay, sunlight is constant and unobstructed and due to a latitude of 26^{o} 39' S, variation in daylength is small (Chapter 3).

Fertile *Gracilaria* has never been found in this area and it is thus assumed that the population reproduces solely through vegetative fragmentation. The plants grow continuously throughout the year and there is no dormant stage. The *Gracilaria* stands are virtually monospecific with little epiphytism and no interspecific competition on the muddy substratum.

Friedlander *et al.* (1990) constructed a model to describe the growth of *Gracilaria conferta* (Schousboei) J et G Feldmann in tank culture. Their model successfully simulated the control of seasonal growth rate by irradiance and temperature. Their approach was to model growth rate as a function of the above variables. These variables did not have a linear relationship with growth rate throughout a year as high temperature and high irradiance were found to be inhibitory in summer so the model consisted of two parts - summer and non-summer. The model was constructed as an analysis of covariance-type, where variance in the response (growth rate) variable due to the environmental variables was isolated. Water temperature accounted for twice as much variation as irradiance and together they accounted for 57% of the variation in growth rate.

An additional parameter to be considered is the presence of different life-history phases in most seaweed populations. Ang and DeWreede (1990) developed matrix models for different life history types and applied them to populations of *Sargassum siliquosum* J. Ag. and *Laminaria longicruris* Pyle. In their matrices the number of columns and rows depended on the number of life history phases and stages. The columns gave information on the reproduction (sexual and vegetative) of each phase and the rows gave information of recruitment into each phase by the other phases. By entering information on the contribution each phase (through various reproductive means) gave to other phases, the life-history of a population could be modeled. Ang *et al.* (1990) developed this approach further and made a matrix simulation model of an *Iridaea splendens* (Setchell *et* Gardner) Papenfuss population in Canada, with a view to determining the effect of future harvesting.

A matrix model is made up of one or more sets of information arranged in columns and rows. Each column and row accounts for an element to be modeled and each column/row position is related to another position in the matrix or another matrix by an expression or equation. A simulation model aims to produce a solution that resembles the response being modeled, simulating the effect of factors or variables on that response.

The primary objective of this chapter is to simulate the pattern of washup from the *Gracilaria* beds at Luderitz as a function of growth rate (and the factors affecting it) and water motion. This model should explain the seasonal and annual washup over the years and with given environmental information, short term predictions should be possible.

4.2 Materials and Methods.

Chapter 2 dealt with the distribution, production and dynamics of the natural *Gracilaria* beds at Luderitz while chapter 3 concentrated on the growth characteristics of the plant. From a combination of these chapters, the basic data to be fed into the model was extracted.

The seasonal growth data (chapter 3.) was smoothed using 6th order polynomial smoothing (Statgraphics, 1986) to give a uniform curve of seasonal growth. This method was designed for smoothing time series data, the number of orders indicates the "tension" of the smoothing. For instance, 1st order polynomial smoothing (the most "taught") gives a straight line regardless of the variation in the data being smoothed, 2nd order would give a crude representation of a data set with one peak. The longer a seasonal data set ie. the more peaks and troughs in the data, -the more orders are required. There comes a point where increasing the number of orders does not improve the smoothing and for the present data, this was found to be 6.

At a similar depth to the seasonal growth site, the daily growth rates at the growth with depth experiment I (Chapter 3) were 48% lower over the same months. Overall daily growth rates for the year were lowered using this percent difference. This overall lowering of growth rates was necessary as the seasonal growth study was conducted in an area of the Lagoon where temperatures were normally ±4° C higher than that for most of the Lagoon and Bay. On the other hand, the growth with depth experiments were conducted in the harbour area where temperatures are similar to most of the Lagoon and Bay. The change in growth rate with depth was obtained from the growth with depth experiments (Chapter 3).

Before a model based on monthly growth rate of individual plants was chosen, another type of matrix model was considered. Through the diving surveys (chapter 2) an estimation of the standing biomass was made so an attempt was made to construct a model based on biomass. The increase in biomass through monthly growth could not be balanced by the washup (production) per month. This was because it was impossible to determine the contribution portions of the *Gracilaria* beds, at each depth, made to each washup. This resulted in biomass orders of magnitude greater than even the total washup for a year accumulating in the model.

The present model was based on growth of individual plants as these represent the basic unit of the population. Three main principles were followed; firstly that plants grow until a size where, through water motion, the point of attachment can no longer hold is reached. Secondly, plants are cast on the shore soon after they break free, thirdly the underground thallus system remains intact after plants break free to regenerate new plants, and finally that all life-history phases behave the same.

An estimation of the size range plants at each depth can achieve before removal by "normal" water motion was made.
These estimations were based on observations during the diving surveys, growth studies and collection of drift (Table 4.1).

DEPTH	**WEIGHT**
1-2 m	30 ± 20 g
2-3 m	70 ± 20g
3-4 m	100 ± 30g
4-5 m	150 ± 30g
5-6 m	180 ± 40g
6-7 m	200 ± 40g
7-8 m	220 ± 50g
8-9 m	250 ± 50g
9-10 m	270 ± 50g

Table 4.1. Estimations of maximum biomass of plants at each depth.

The model was constructed on a computer spread sheet as a series of 3 12 X 9 (12 months X 9 depths) matrices for each year. Matrix 1 represented the average daily growth rate per month for each depth (Table 4.2 and 4.3.) and matrix 2 the total growth rate per month for each depth. Matrix 3 was the natural log (ln) of plant biomass for each month at each depth.

The matrices were related to each other as follows:

Matrix I to Matrix II

$A_{ij} * 30 = B_{ij}$

where: A = ave. daily growth rate at month i_{1-12} and depth j_{1-9}

B = tot. monthly growth rate at month i_{1-12} and depth j_{1-9}

Each month was assumed to have 30 days.

Matrix II to Matrix III

$\ln C_{ij} + B_{i+1j} = \ln C_{i+1j}$

where: C = biomass at month i_{1-12} and depth j_{1-9}

B = growth rate at month i_{1-12} and depth j_{1-9}

When biomass is given as ln, then total growth rate for a month is added to the ln of biomass to give the ln of biomass of the next month (+1).

DEPTH	1-2M	2-3M	3-4M	4-5M	5-6M	6-7M	7-8M	8-9M	9-10M
MONTH									
1988									
JAN	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
FEB	.0674	.0595	.0481	.0632	.0309	.0277	.0254	.0236	.0229
MAR	.0758	.0669	.0542	.0407	.0348	.0312	.0285	.0265	.0258
APR	.0652	.0576	.0466	.0350	.0299	.0268	.0245	.0228	.0222
MAY	.0547	.0483	.0391	.0294	.0251	.0225	.0206	.0192	.0186
JUN	.0526	.0464	.0376	.0283	.0241	.0216	.0198	.0184	.0179
JUL	.0495	.0437	.0354	.0266	.0227	.0203	.0186	.0173	.0168
AUG	.0515	.0455	.0368	.0277	.0236	.0212	.0194	.018	.0175
SEP	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
OCT	.0589	.052	.0421	.0317	.0270	.0242	.0222	.0206	.02
NOV	.06	.053	.0429	.0323	.0275	.0247	.0226	.021	.0204
DEC	.059	.0521	.0421	.0317	.0271	.0242	.0222	.0207	.0201
1989									
JAN	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
FEB	.0574	.0507	.041	.0309	.0263	.0236	.0216	.0201	.0195
MAR	.0658	.0581	.0470	.0354	.0302	.0270	.0248	.023	.0224
APR	.0552	.0487	.0394	.0297	.0253	.0227	.0208	.0193	.0188
MAY	.0547	.0483	.0391	.0294	.0251	.0225	.0206	.0192	.0186
JUN	.0526	.0464	.0376	.0283	.0241	.0216	.0198	.0184	.0179
JUL	.0495	.0437	.0354	.0266	.0227	.0203	.0186	.0173	.0168
AUG	.0515	.0455	.0368	.0277	.0236	.0212	.0194	.018	.0175
SEP	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
OCT	.0589	.052	.0421	.0317	.0270	.0242	.0222	.0206	.02
NOV	.06	.053	.0429	.0323	.0275	.0247	.0226	.021	.0204
DEC	.059	.0521	.0421	.0317	.0271	.0242	.0222	.0207	.0201
1990									
JAN	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
FEB	.0774	.0683	.0553	.0416	.0355	.0318	.0291	.0271	.0263
MAR	.0558	.0493	.0399	.03	.0256	.0229	.021	.0195	.019
APR	.0552	.0487	.0394	.0297	.0253	.0227	.0208	.0193	.0188
MAY	.0547	.0483	.0391	.0294	.0251	.0225	.0206	.0192	.0186
JUN	.0526	.0464	.0376	.0283	.0241	.0216	.0198	.0184	.0179
JUL	.0495	.0437	.0354	.0266	.0227	.0203	.0186	.0173	.0168
AUG	.0515	.0455	.0368	.0277	.0236	.0212	.0194	.018	.0175
SEP	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
OCT	.0589	.052	.0421	.0317	.0270	.0242	.0222	.0206	.02
NOV	.06	.053	.0429	.0323	.0275	.0247	.0226	.021	.0204
DEC	.059	.0521	.0421	.0317	.0271	.0242	.0222	.0207	.0201
1991									
JAN	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
FEB	.0574	.0507	.041	.0309	.0263	.0236	.0216	.0201	.0195
MAR	.0558	.0493	.0399	.03	.0256	.0229	.021	.0195	.019
APR	.0552	.0487	.0394	.0297	.0253	.0227	.0208	.0193	.0188
MAY	.0547	.0483	.0391	.0294	.0251	.0225	.0206	.0192	.0186
JUN	.0526	.0464	.0376	.0283	.0241	.0216	.0198	.0184	.0179
JUL	.0495	.0437	.0354	.0266	.0227	.0203	.0186	.0173	.0168
AUG	.0515	.0455	.0368	.0277	.0236	.0212	.0194	.018	.0175
SEP	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
OCT	.0589	.052	.0421	.0317	.0270	.0242	.0222	.0206	.02
NOV	.06	.053	.0429	.0323	.0275	.0247	.0226	.021	.0204
DEC	.059	.0521	.0421	.0317	.0271	.0242	.0222	.0207	.0201

Table 4.2. Growth coefficients for each month and each depth from 1988 to 1991. This is the first matrix of the model.

A.

LOW TEMPERATURE

DEPTH	1-2M	2-3M	3-4M	4-5M	5-6M	6-7M	7-8M	8-9M	9-10M
MONTH									
JAN	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
FEB	.0574	.0507	.041	.0309	.0263	.0236	.0216	.0201	.0195
MAR	.0558	.0493	.0399	.03	.0256	.0229	.021	.0195	.019
APR	.0552	.0487	.0394	.0297	.0253	.0227	.0208	.0193	.0188
MAY	.0547	.0483	.0391	.0294	.0251	.0225	.0206	.0192	.0186
JUN	.0526	.0464	.0376	.0283	.0241	.0216	.0198	.0184	.0179
JUL	.0495	.0437	.0354	.0266	.0227	.0203	.0186	.0173	.0168
AUG	.0515	.0455	.0368	.0277	.0236	.0212	.0194	.018	.0175
SEP	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
OCT	.0589	.052	.0421	.0317	.0270	.0242	.0222	.0206	.02
NOV	.06	.053	.0429	.0323	.0275	.0247	.0226	.021	.0204
DEC	.059	.0521	.0421	.0317	.0271	.0242	.0222	.0207	.0201

B.

MEDIUM TEMPERATURE

DEPTH	1-2M	2-3M	3-4M	4-5M	5-6M	6-7M	7-8M	8-9M	9-10M
MONTH									
JAN	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
FEB	.0674	.0595	.0481	.0362	.0309	.0277	.0254	.0236	.0229
MAR	.0658	.0581	.047	.0354	.0302	.027	.0248	.023	.0224
APR	.0652	.0576	.0466	.035	.0299	.0268	.0245	.0228	.0222
MAY	.0547	.0483	.0391	.0294	.0251	.0225	.0206	.0192	.0186
JUN	.0526	.0464	.0376	.0283	.0241	.0216	.0198	.0184	.0179
JUL	.0495	.0437	.0354	.0266	.0227	.0203	.0186	.0173	.0168
AUG	.0515	.0455	.0368	.0277	.0236	.0212	.0194	.018	.0175
SEP	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
OCT	.0589	.052	.0421	.0317	.027	.0242	.0222	.0206	.02
NOV	.06	.053	.0429	.0323	.0275	.0247	.0226	.021	.0204
DEC	.059	.0521	.0421	.0317	.0271	.0242	.0222	.0207	.0201

C.

HIGH TEMPERATURE

DEPTH	1-2M	2-3M	3-4M	4-5M	5-6M	6-7M	7-8M	8-9M	9-10M
MONTH									
JAN	.0597	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
FEB	.0647	.0595	.0481	.0362	.0309	.0277	.0254	.0236	.0229
MAR	.0758	.0669	.0542	.0407	.0348	.0312	.0285	.0265	.0258
APR	.0652	.0576	.0466	.0350	.0299	.0268	.0245	.0228	.0222
MAY	.0574	.0507	.0410	.0309	.0263	.0236	.0216	.0201	.0195
JUN	.0526	.0464	.0376	.0283	.0241	.0216	.0198	.0184	.0179
JUL	.0495	.0437	.0354	.0266	.0227	.0203	.0186	.0173	.0168
AUG	.0515	.0455	.0368	.0277	.0236	.0212	.0194	.018	.0175
SEP	.0579	.0511	.0414	.0311	.0265	.0238	.0218	.0203	.0197
OCT	.0589	.0520	.0421	.0317	.0270	.0242	.0222	.0206	.02
NOV	.06	.0530	.0429	.0323	.0275	.0247	.0226	.021	.0204
DEC	.059	.0521	.0421	.0317	.0271	.0242	.0222	.0207	.0201

Table 4.3. Growth coefficients for hypothetical years incorporating low, medium and high temperatures between February and April.

if $\ln C_{ij} \geq \ln M_j$ or if the biomass is washed out by swell (see text) then $\ln C_{i+1j}$ = -3.218

where: M = maximum attainable biomass for each depth j_{1-9} (Table 4.4)

-3.218 = ln of starting biomass after a plant has broken free (ln .04g). The model cannot run without a seed, this starting biomass represents a fragment of approximately 10cm long.

Monthly washup.

$W_i = \text{sum}(C_{ij1-9}*p)$ if $C_{ij} \geq M_j$ or if the biomass is washed out by swell (see text).

where: W = washup at month i_{1-12}

p = a multiplication factor based on the % surface area of the *Gracilaria* beds at each depth j1-9 (fig 4.4). This information was extracted from Chapter 2.

At a given depth, *Gracilaria* did not wash out until a biomass, at least equal to the maximum (fig. 4.1) for that depth was achieved.

Washup was then represented as a 3 month running average to smooth the data and simulate the continuous process of actual washup.

DEPTH	STARTING WEIGHTS (ln)	MULTIPLICATION FACTORS BASED ON % SURFACE AREA
1-2M	-1.64	.027
2-3M	3.69	.06
3-4M	2.37	.154
4-5M	.99	.224
5-6M	.38	.229
6-7M	.01	.143
7-8M	-.26	.094
8-9M	-.46	.04
9-10M	-.54	.009

Table 4.4. Model seeding weights and division factors based on % surface area of *Gracilaria* beds at each depth.

The seed of the model i.e. the starting weights of the plants at each depth (Table 4.4) were obtained by running a portion of the model from August to December (after the major winter swells and washup) with an initial weight at each depth of .04g (= a ±10 cm apical fragment as used to seed seasonal growth experiments in chapter 3.). The environmental conditions for this run were those for August to December 1987 as the first year to be modeled was 1988. In the model, after plants were washed up the subsequent starting weight was again .04g. The model was run continuously for the 4 years so that the finishing biomass at each respective depth for one year became the initial biomass at each respective depth for the following year.

Temperature was incorporated into the model in matrix I as a rise in growth rate during the warm water events of 1988, 1990 and to a lesser extent 1991 (fig. 4.2) These elevations were based on the seasonal growth study (chapter 3), the beginning of which was conducted over the 1990 warm water event. Elevations in growth rate of .01, for every 1.5^{o} C rise in temperature above normal, were ascribed to the relevant months (February - April; Table 3).

Swell was incorporated in matrix III as three categories *viz.* small (< 2m; where plants broke free when they reached their estimated maximum size; medium (2-2.5m; where all plants to a depth of 4-5m were broken free); large (> 2.5m; where all plants to a depth 6-7m were broken free.

In addition to the continuous 1988-1991 model, investigatory models using combinations of swell and temperature were built to determine the effect each had on washup. High, low and medium (Table 4.2) temperatures were tested for small swell, medium and large swell occurring in autumn and medium and large swell occurring in winter.

The output of the model did not directly give information on the quantity of *Gracilaria* that washed up during a year, it did, however give information on the pattern and relative size of washups. By comparison with actual washup data, the model output was calibrated to give an approximate figure in tonnes.

4.3 Results.

Growth rate at 1-2m below chart datum was estimated to vary between 4.9-6% d^{-1} in a year where no warm water anomaly occurred, at 9-10m growth rate varied from 1.6 - 2 % d^{-1} over the year (Table 4.2 A and Table 4.3 1991). Using the two parameters of sea temperature, swell size and swell frequency (fig.2) and their effect on growth rate and washup the model simulated the actual washup pattern well (fig. 4.3) with a correlation coefficient of .564 $p<.001$ (in other words it described 56.4% of the variation) over the 4 years. The actual and simulated total washup for each year correlate very well with a coefficient of .96 ($p<.05$; fig 4.4). Simulated washup related to actual washup approximately as 1 model unit = 8.5 tonnes (dry) of *Gracilaria.*

From 1988 to 1991 the simulated washup from the portion of the *Gracilaria* population at 5-6m was by far the greatest at over 3612t (dry). Washup from portions of the population at 3-4m, 4-5m, 6-7m and 7-8m were between 1000 to 1600t (dry) and the smallest contributions came from m 1-2m and 9-10m (Table 4.5 and fig. 4.5).

DEPTH	CONTRIBUTION TO WASHUP 1988-1991. Tonnes (dry).
1-2M	82
2-3M	355
3-4M	1011
4-5M	1292
5-6M	3612
6-7M	1445
7-8M	1581
8-9M	782
9-10M	187

Table 4.5. Contribution of each depth to the total washup from 1988 to 1991.

Variations in temperature and swell were incorporated into the model to gain some basic rules of the system. In a simulated year where no large swell occurred (which had not been the case over the study period) washup under low and medium temperatures peaked in the second half of the year while under high temperature washup peaked in the middle of the year. The total annual washup under these conditions were the largest of any combination tested, low temperature = 1428t, medium temperature = 1963t and high temperature = 2065t (figs. 4.6, 4.7, 4.8 and 4.9)

In years with medium autumn or winter swell (figs. 4.7, 4.8, 4.9, 4.10 and 4.11), total washups were similar, 1181t, 1717t and 1819t (low medium and high temperature respectively) for autumn swell and 1164t, 1734t and 1802t (low, medium and high temperature respectively) for winter swell. The peak washups for low and medium temperatures occurred in winter/spring and for high temperature, peak washup was in winter.

When large autumn and winter swells were simulated (figs. 4.7, 4.8, 4.9, 4.12 and 4.13), lower washup occurred in the year of large autumn (756t, 1088t and 1300t, low, medium and high temperature respectively) swell than in the year of large winter swell (977t, 1453t and 1700, low, medium, and high temperature respectively), There was a peak in washup in autumn and another, lower peak in washup in spring/summer for all temperatures. In the event of large winter swell the peak in washup occurred in winter for all temperatures.

Figure 4.14. shows the total annual washups from the simulation models of varying swell and temperatures. Small swell yielded the largest washup, medium autumn and winter swell yielded similar quantities, large winter swell yielded less and large autumn swell yielded the smallest quantity.

4.4 Discussion

Seasonal growth rate was controlled primarily by light availability but also by temperature (chapter 3). In Luderitz, light availability follows a seasonal pattern that varies little from year to year but the seasonal pattern of temperature does vary from year to year and this variation is usually manifest as an elevation between February and April, called a warm water event. The most intense warm water event of the study occurred in 1988 (fig. 2.10). The resulting rise in growth rates and the occurrence of medium sized swells in winter (fig. 2.10) resulted in the largest washup of the study period (fig. 4.3). The main temperature features of the other three years were, the moderately warm water at the beginning of 1989 and the warm water at the beginning of 1990. The main swell features were the medium winter and summer (December) swell in 1989, the medium autumn swell in 1990 followed by large winter swell and medium spring/summer swell, and finally the large autumn swell of 1991 (fig. 4.2). These "events", when incorporated into the model, explain the decrease in total annual washup from 1988-1991. Unexplained or poorly explained "crashes" in seaweed stocks such as in Saldanha Bay in South Africa (Rotmann, 1990) are the bane of the industry. In the absence of other disturbance factors such as harvesting (Santelices and Doty, 1989), dredging (Rotmann, 1990) or obvious herbivore grazing (Chapter 3; Anderson, pers. comm.) in the Lagoon and Bay, variations in yield must be environmentally controlled.

From this simulation model the most important elements of the population are readily evident. The portion of the population growing between 5-6m (fig. 4.5) has the most influence on washup. The large surface area of the *Gracilaria* bed at this depth (Chapter 2) is responsible, even though plants which grow in shallower water have a faster growth rate (Table 4.2 and 4.3) and those growing in deeper water can attain a greater biomass (Table 4.1). In the model, large swell affected the population to a depth of 7m, which includes the portion of the population that contributes the most to the total annual washup (fig 4.5). Because large winter swell is an annual event in Luderitz (Fig 4.2) it follows that washup is also maximal in winter, however, in the event of a large autumn swell (fig 4.12) the effect in the model was a drastic reduction in total annual washup (fig 4.14). The medium autumn swell in 1990 played a major role in the lower washup despite a warm water event at the beginning of that year.

Short term predictions can be made in the form of alternatives. Once the temperatures for the beginning of the year are known, a set of different swell scenarios can be run through the model and the predictions made as, if...... then......, statements.

The fact that the population can be modeled using relatively simple methods involving a few parameters indicates stability in the underground thallus system.

4.5 Conclusions

1) The absence of sexual reproduction makes the Luderitz *Gracilaria* population a straightforward subject for modeling. A small number of variables can be incorporated into the model to gain a satisfactory simulation.

2) The portions of the population that contribute most to the total production of the system occur between 4-7m, especially at 5-6m.

3) The time of occurrence of large swell is very important in determining the total annual production.

4) Temperature plays an important role in increasing growth rate and hence production but this effect can be nullified by the occurrence of large swells.

5) The model is robust enough to produce simulations based on wide variations of the environmental variables and is a useful predictive tool.

Figure 4.1. Flow diagram of the relationship of *Gracilaria* growth and environmental factors. Factors on the left directly influence (black arrows) growth whereas those on the right influence (shade arrows) the factors on the left and washup.

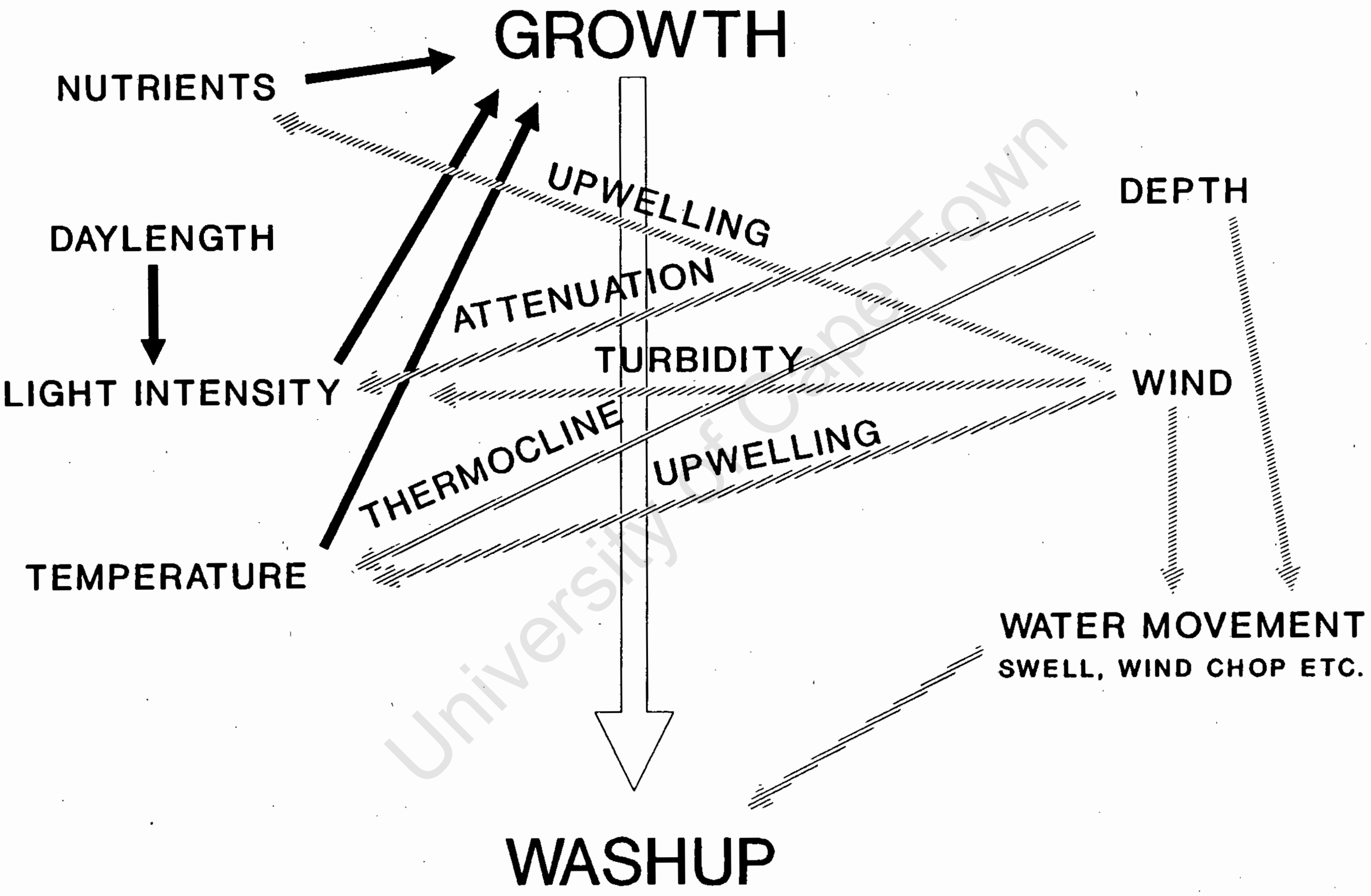
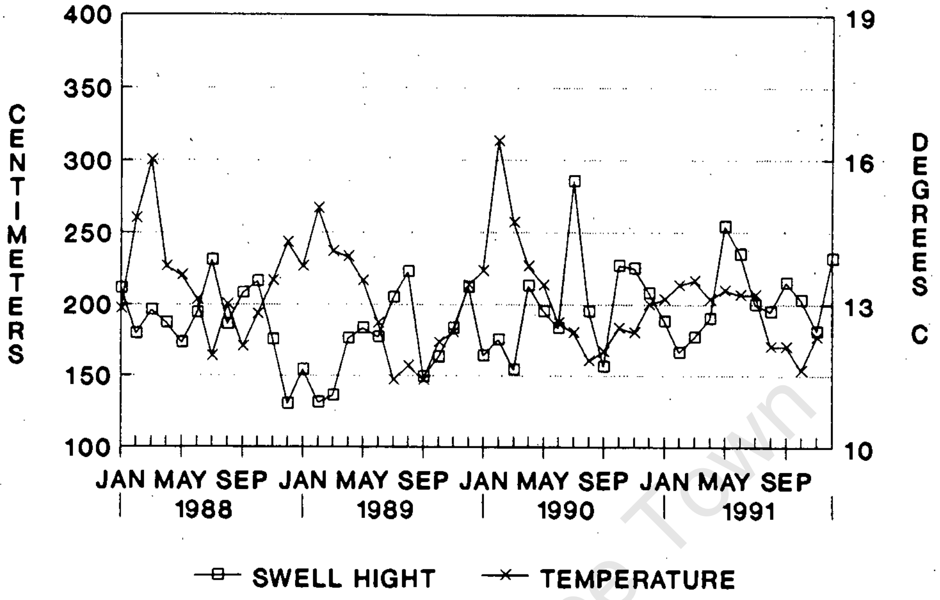

GROWTH
NUTRIENTS
DAYLENGTH
LIGHT INTENSITY
TEMPERATURE
UPWELLING
ATTENUATION
TURBIDITY
THERMOCLINE
UPWELLING
DEPTH
WIND
WATER MOVEMENT
SWELL, WIND CHOP ETC.
WASHUP

Figure 4.2. Mean monthly temperature and swell for 1988, 1989, 1990 and 1991.

Figure 4.3. Actual washup and simulated washup from 1988-1991. The simulated values are given as "model units". 8.5 tonnes (dry) = 1 model unit.


SWELL AND TEMPERATURE
1988 TO 1991

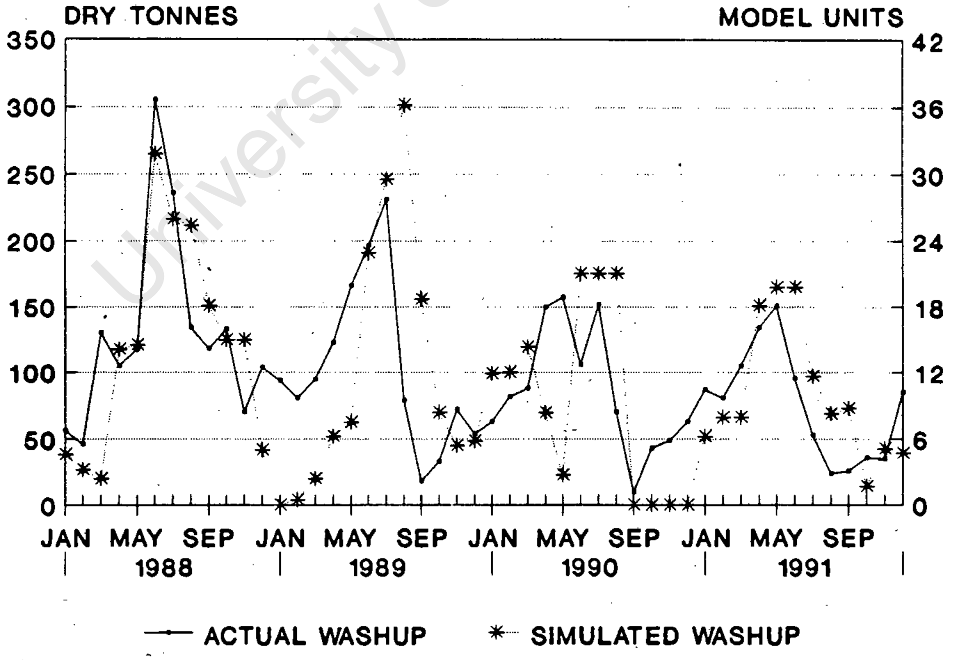
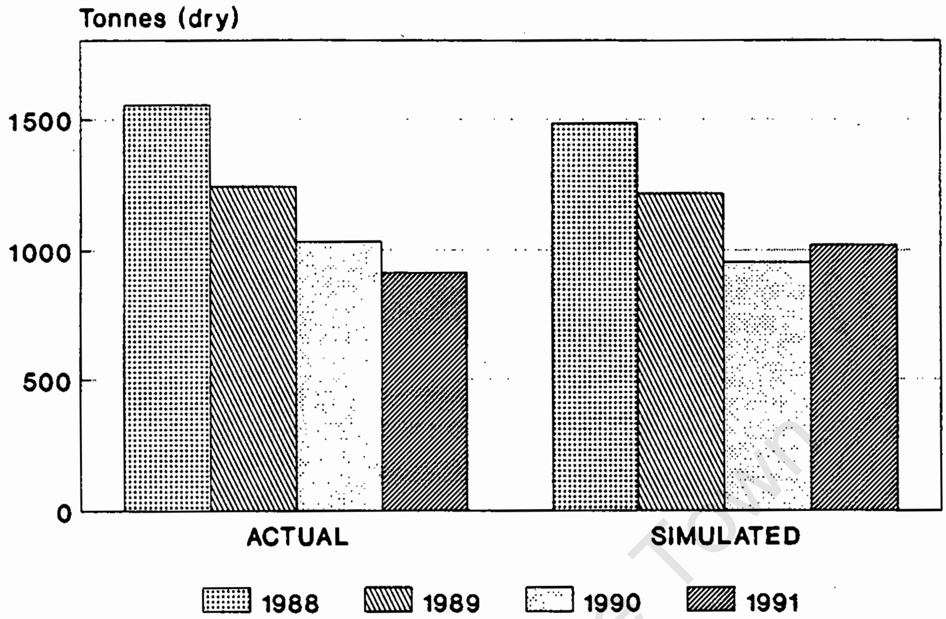

ACTUAL VS. SIMULATED WASHUP

Figure 4.4. The actual and simulated washups for 1988, 1989, 1990 and 1991.

Figure 4.5. The contribution of each depth to the total washup from 1988-1991.

ACTUAL VS. SIMULATED WASHUP
% CONTRIBUTION FOR EACH YEAR



BIOMASS CONTRIBUTIONS FROM EACH DEPTH
FROM 1988-1991

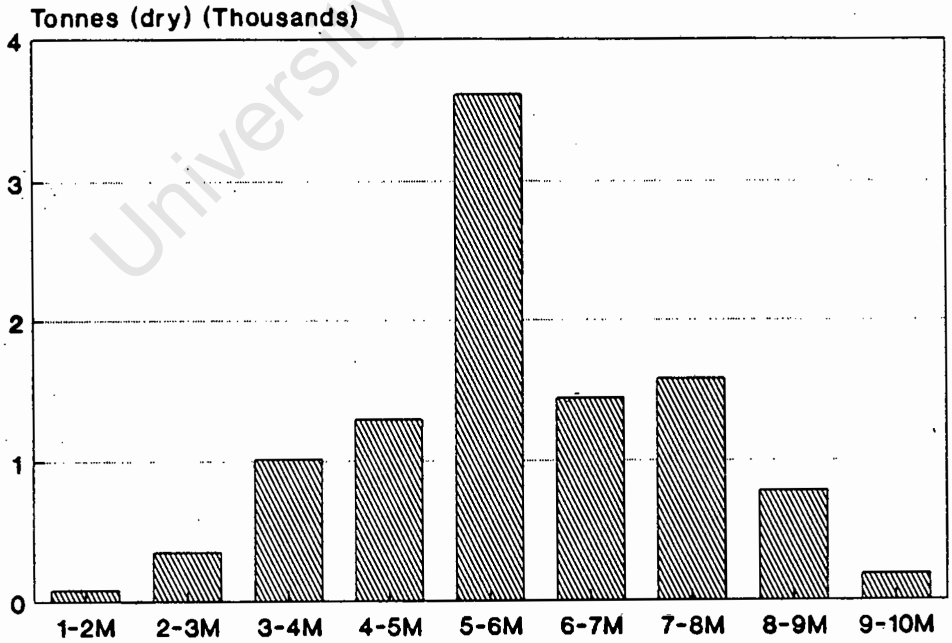
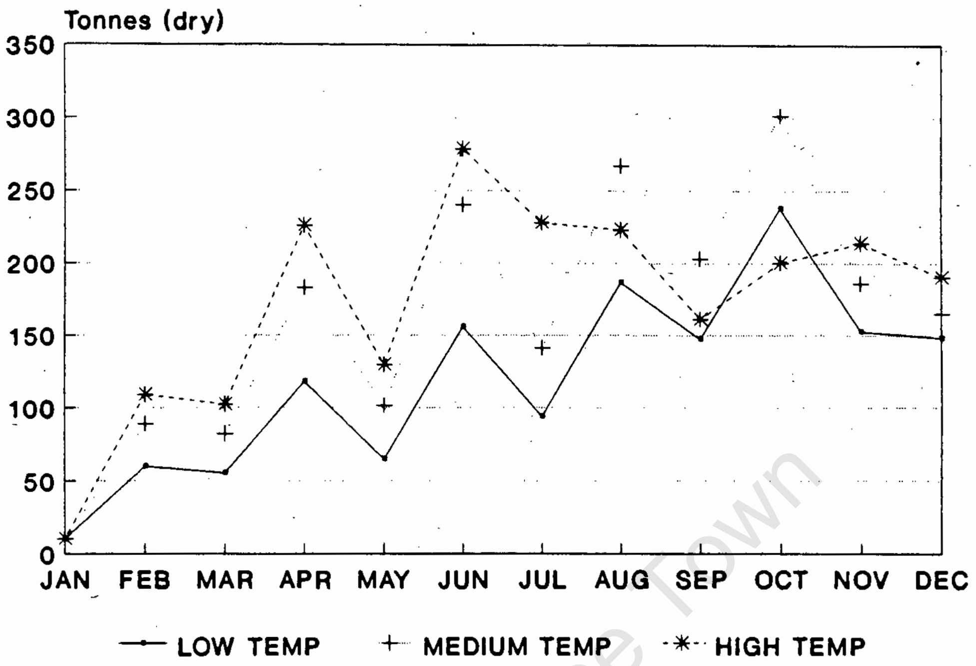


Figure 4.6. The simulated effect of small swell and low, medium and high temperature on annual washup.

Figure 4.7. The simulated effect of low temperature and various swell on annual production.

SMALL SWELL AND VARYING TEMPERATURE



LOW TEMP. VARIOUS SWELL

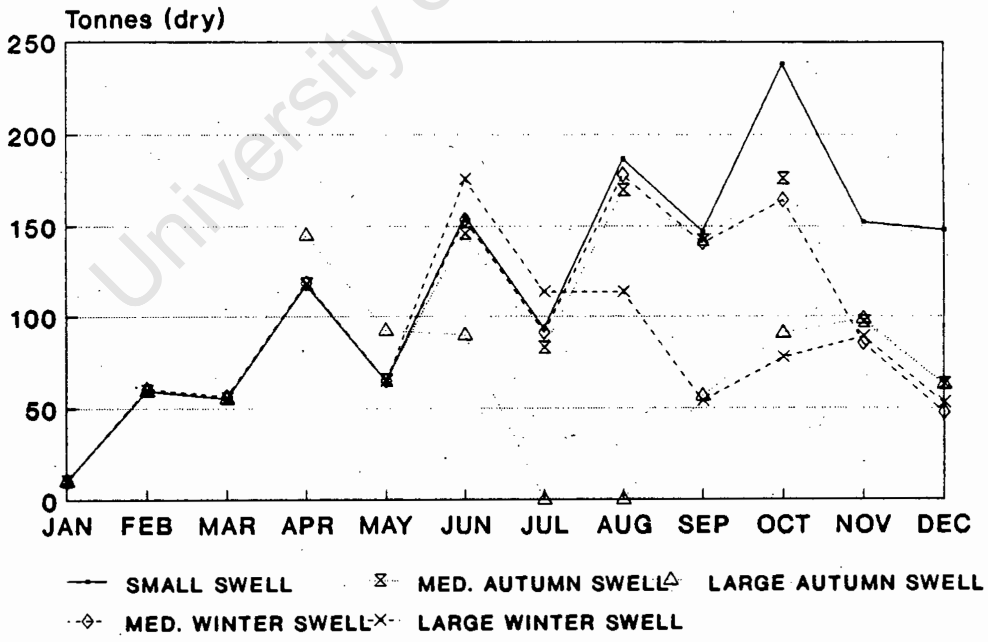
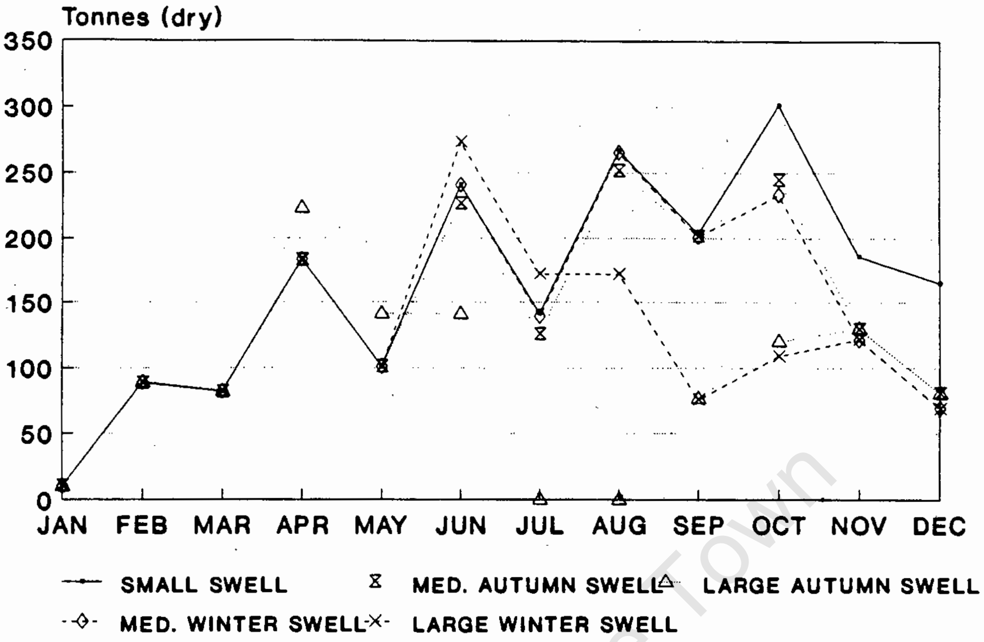
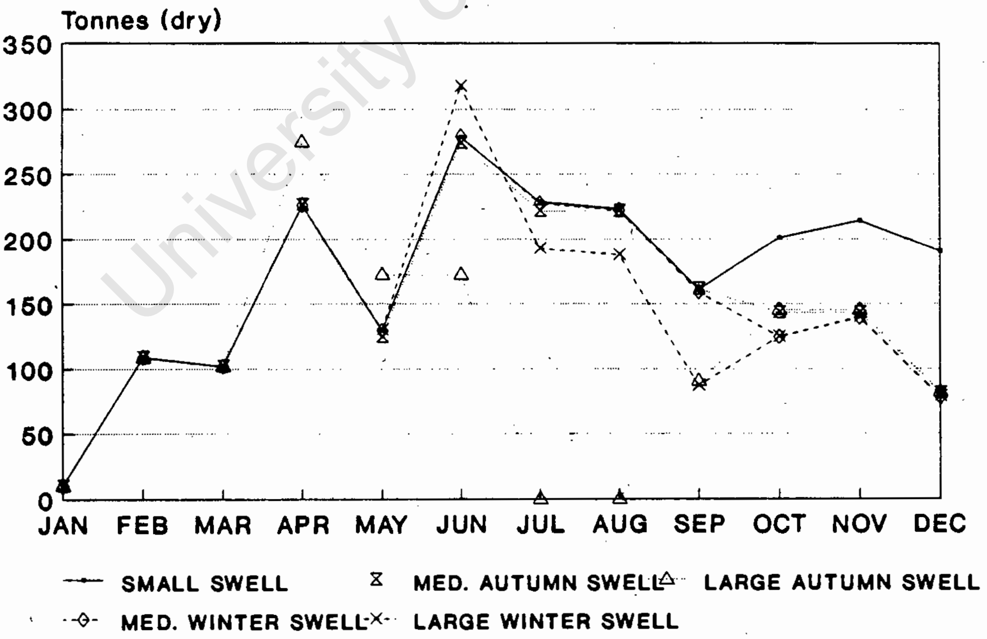


Figure 4.8. The simulated effect of medium temperature and various swell on annual production.

Figure 4.9. The simulated effect of high temperature and various swell on annual production.



MEDIUM TEMP. VARIOUS SWELL

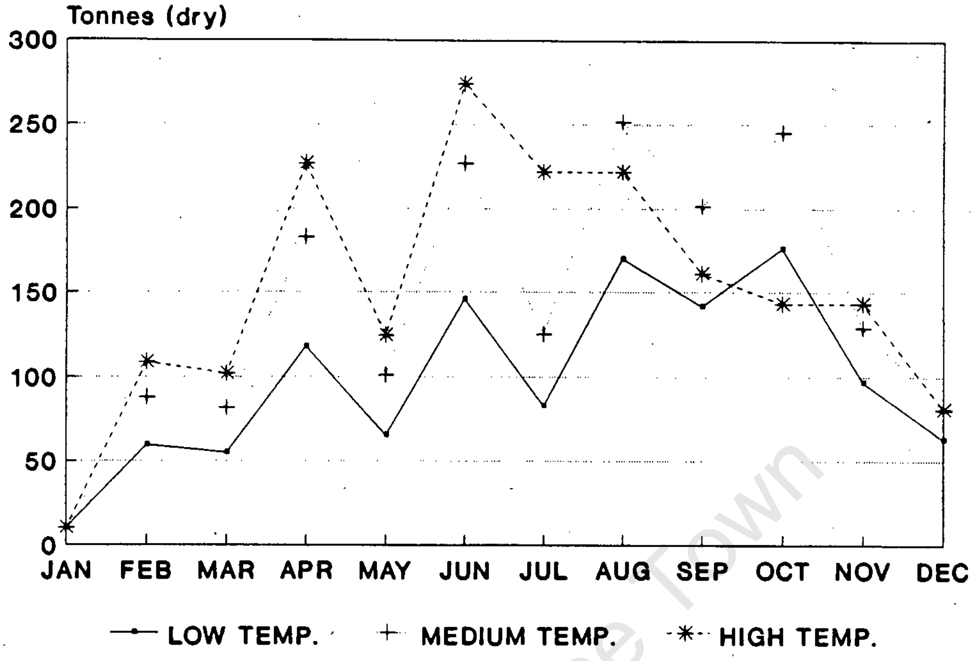


HIGH TEMP. VARIOUS SWELL

Figure 4.10. The simulated effect of medium Autumn swell and low, medium and high temperature on annual production.

Figure 4.11. The simulated effect of medium Winter swell and low, medium and high temperature on annual production.

MEDIUM AUTUMN SWELL VARYING TEMP.



MEDIUM WINTER SWELL VARYING TEMP

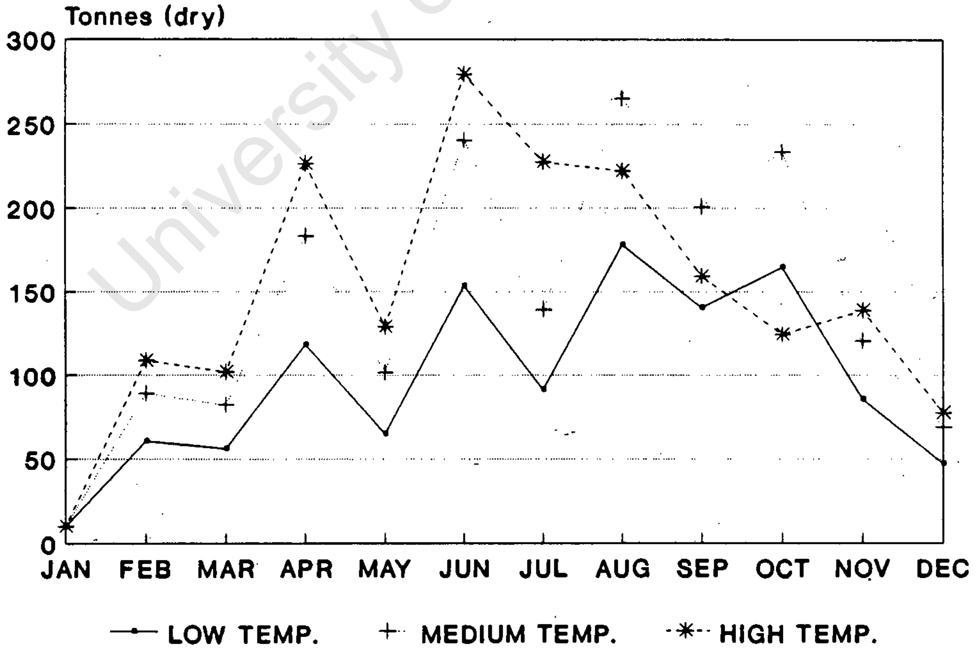
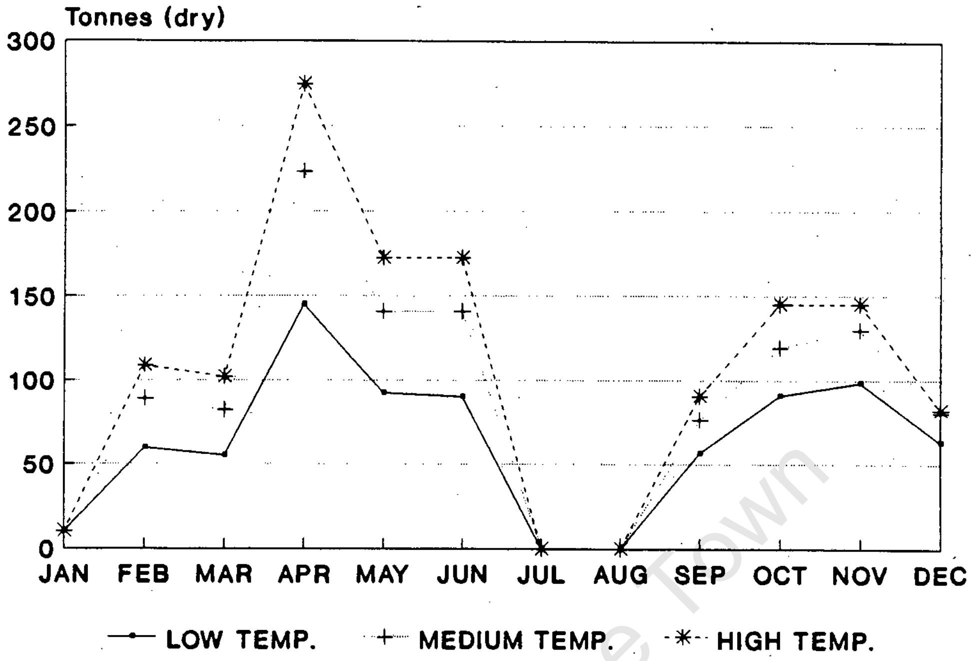


Figure 4.12. The simulated effect of large Autumn swell and low, medium and high temperature on annual production.

Figure 4.13. The simulated effect of large Winter swell and low, medium and high temperature on annual production.

LARGE AUTUMN SWELL AND VARYING TEMP.



LARGE WINTER SWELL VARYING TEMP.

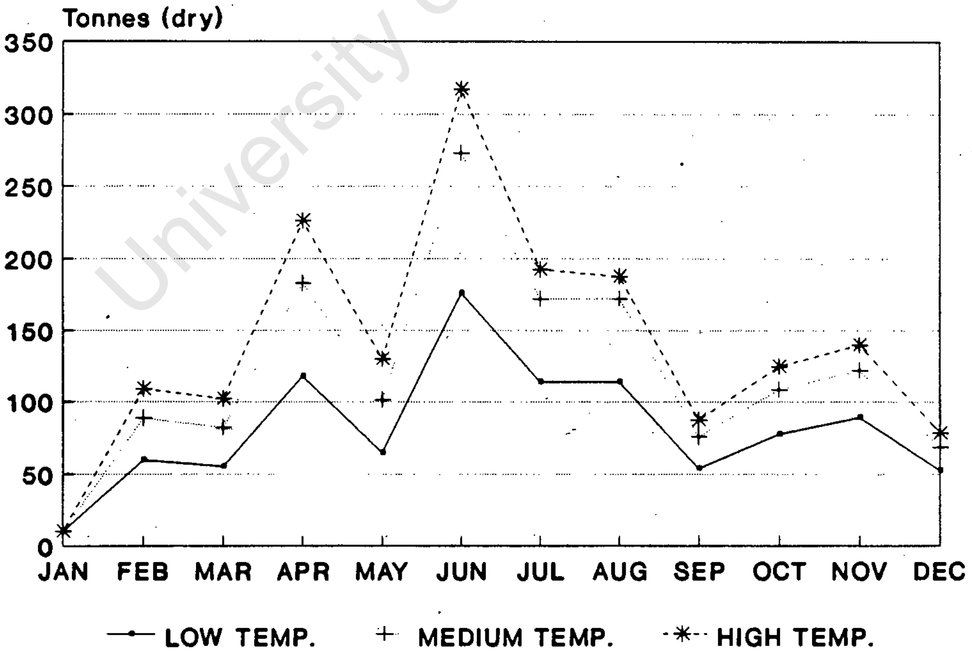
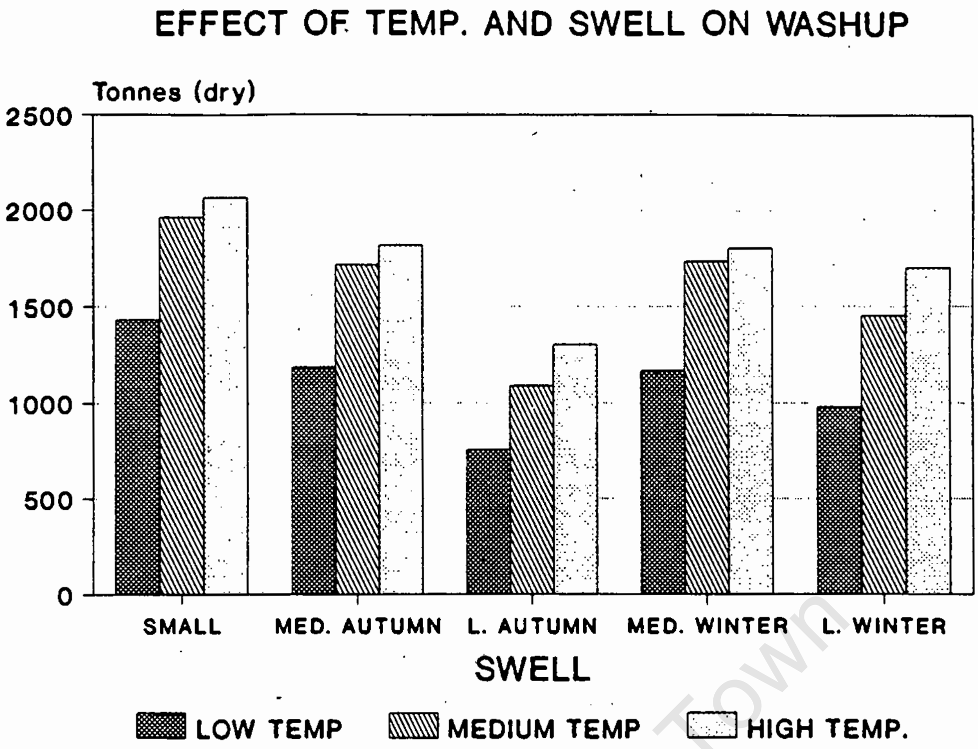


Figure 4.14. Simulated total annual production for various temperature and swell conditions


EFFECT OF TEMP. AND SWELL ON WASHUP
Tonnes (dry)
2500
2000
1500
1000
500
0
SMALL
MED. AUTUMN
L. AUTUMN
MED. WINTER
L. WINTER
SWELL
LOW TEMP
MEDIUM TEMP
HIGH TEMP.

CHAPTER 5

THE EFFECTS OF WAVE EXPOSURE ON MORPHOLOGY, AND SEASONAL GROWTH OF SHALLOW WATER POPULATIONS OF *LAMINARIA SCHINZII*.

5.1 Introduction

Early taxonomists did not take the effect of environment on morphology into account when separating species of *Laminaria*. As a result over 100 species have been described, many of which have since been discounted (Kain, 1979). *Laminaria* species have been divided into two sub-genera *viz.* the *Simplices* and the *Digitatae*; the fronds of the Simplices are undivided whereas the fronds of the Digitatae are split into leaves or digits. This splitting is caused by changes in the frond structure and are not merely tears (Killian, 1911 in Kain, 1976b). Kain (1976b) found that holes punched into the fronds of *Laminaria hyperborea* initiated the splitting of a digit.

Experimental investigation into the authenticity of the species was probably spurred on by experiments such as those by Sundene (1964) where, through transplanting from exposed to sheltered sites and *vice versa*, one morphological form was grown into another. These investigations cast doubt over many species particularly in the Simplices where taxa were not as well defined as in the Digitatae.

Detailed morphological studies (Chapman, 1973), and later, crossing studies (Chapman, 1974) led to the conclusion that *Laminaria saccharina* (L.) Lamour and *Laminaria longicruris* Pyle. from Nova Scotia were conspecific though Yarish *et* *al*. (1990) expressed some concern regarding Chapman's (1974) interpretations. Species variation of the diagnostic criteria of stipe length and hollow or solid stipe were found to overlap (Chapman, 1974). The interpretation of Yarish *et al.* (1990) indicated that stipe length and hollow diameter exhibited considerable variation regardless of exposure and that stipe length and hollowness were controlled by a strong genetic component. Luning (1975) produced viable hybrids from crosses between smooth and bullate *Laminaria saccharina* and Bolton *et al.* (1983) successfully crossed a variety of *L. saccharina* populations from the Pacific and Atlantic and *L. longicruris* from Nova Scotia with *L. ochotensis* Miyabe from Japan and found no evidence that *L. saccharina* can be environmentally induced to produce the long hollow stipes of *L. longicruris*. These experiments indicate that many of the morphological differences in the genus may be ecotypic. Similarly, many species from the Digitatae complex have been successfully crossed by tom Dieck (unpubl.). Battacharya and Druehl (1990) have investigated the use of restriction analysis of ribosomal DNA for three *Laminaria* species. They suggested that this should be a useful method for differentiating between *Laminaria* taxa. DNA restriction analysis is powerful and reliable as the coding of DNA is not environmentally variable or plastic.

Distribution:

Laminaria species occur throughout the temperate and cold oceans of the northern hemisphere with species richness peaking in the north western and north eastern coasts of the Pacific. Most of the *Digitatae* occur in the Atlantic. Only 4 species of the genus have been reported from the southern hemisphere (Kain, 1979) and all of these are confined to the Atlantic. *Laminaria pallida* (Grev.) J. Ag. and *Laminaria schinzii* Fosl., both digitate, have been described from the west coast of South Africa and the Namibian coast (Bolton, 1986; Molloy, 1990; Luning, 1990). *Laminaria schinzii* appears to be closely related to *L. pallida* (tom Dieck, unpubl.;

Luning, 1990). Young sporophytes are not distinguishable from one another and on the Cape peninsula (out of the range of *L. schinzii*) occasional hollow stiped *Laminaria* plants occur (pers. obs.) tom Dieck (unpubl) has shown that *L. schinzii*, *L. pallida* and *L. brasiliensis* appear to be fully interfertile, and a cross between these and European *L. ochroleuca* was partially successful. The southern hemisphere species do not, however, cross with other digitate northern hemisphere species. Stegenga *et al.* (in prep.) refer to the two taxa as *Laminaria pallida var. schinzii* and *Laminaria pallida var pallida.* The two other southern hemisphere species occur at 40-100 m depth off the coast of Brazil, *Laminaria brasiliensis*, a digitate form and *Laminaria abyssalis* the only southern hemisphere Simplices member, both described by Joly and Oliviera Filho (1967). Some doubt has been cast as to the distinction between these two species, and it is possible that *L. abyssalis* is an environmentally induced undivided form of *L. brasiliensis* (Oliveira, *pers. comm.*).

Growth morphology and environment:

Parke (1948) found that growth of the frond of *Laminaria saccharina* was continuous, with tissue being formed in a meristematic region at the proximal end of the lamina and old tissue eroded from the distal end. Mann (1972) reported a similar growth pattern in *L. longicruris* and *L. digitata.* Chapman (1973) found that stipes of *L. agardhii* Kjell (=*L. saccharina*) and *L. longicruris* were longer and more often hollow in sheltered and deeper sites. Kain (1976a) found a similar relationship between stipe length and hollow stipe occurrence for *L. faeroensis* Borgesen (= *L. saccharina*, Kain, 1976a) from the Shetland Isles. In Norway, Sundene (1962, 1964) found that *L. digitata* had narrow fronds in wave exposed habitats, which, when transplanted to sheltered habitats increased in width. Blade thickness in *L. hyperborea* (Gunn.) Foslie was greater at exposed sites and in shallower water (Kain, 1977) and Gerard and Mann (1979) found the blades of *L. longicruris* to be narrower and thicker in exposed locations. From these studies it would seem that in sheltered and deeper sites stipes are longer and more often hollow and in more exposed sites fronds are narrower and thicker, the latter in both simple and digitate North Atlantic species.

Growth with depth:

The standing crop of *L. hyperborea* from the Isle of Man was highest in shallow water (0-5m) and decreased with depth to a maximum of 27.4m. Fronds, though larger in deeper water, were thinner due to less water movement (Kain, 1977). Boden (1979) grew *L. saccharina* plants on vertically suspended lines from 1 down to 12m at 3 meter intervals. Growth peaked at 9m, below which light was limiting, and above which high temperature was limiting. Though biomass of *L. longicruris* and *L. digitata* showed a significant peak at 0-5m there was otherwise no significant relationship between biomass and depth. *Laminaria brasiliensis* Joly and *L. abyssalis* Joly were only found in waters deeper than 40m off the coast of Brazil (Joly and Oliveira Filho, 1967). At this depth water temperature seems to be low enough for survival of the two species, while shallower, temperature is too high. In Norwegian populations of *Laminaria hyperborea* the upper and lower limits at which plants were found were 5 to 32m in exposed sites and 0 to 26m in sheltered sites (Kain, 1977). Biomass of *L. hyperborea* decreased with depth in the Isle of Man, and the main contributing factors were identified as light and water motion which decreased with depth (Kain, 1977).

Seasonal growth:

A strong correlation has been demonstrated between *L. longicruris* seasonal growth and nitrogen availability (Chapman and Craigie, 1977). In winter when light conditions were not optimal, growth rate increased corresponding to a peak in dissolved nitrogen utilizing stored carbon. Where sufficient nitrogen was available all year round, seasonal growth followed the seasonal light cycle (Gagne *et al.*, 1982). In Norway seasonal growth of *L. digitata* was found to be controlled by sea temperature and daylength (Sundene, 1964). High sea temperatures caused a minimum growth rate in summer in southern Norway and low light caused a minimum growth rate in winter in northern Norway. Both northern and southern Norway had peak growth rates in late winter/early spring. (Sundene, 1964). Dieckmann (1980) measured the growth rate of *L. pallida* at 8m and 14m. Seasonal blade elongation rate was found to be between 1-13 mm. day^{-1} with the peak in spring and early summer, both the maximum and minimum seasonal growth rates were lower in the 14m site. Rate of growth was thought to be controlled by an annual rhythm triggered by photoperiod with the onset of rapid growth coincining with the shortest days and decreasing before the longest days were reached. Luning (1986) found the annual formation of a new frond in *L. hyperborea* to be a short day photoperiodic response. The response was triggered when day lengths fell below 12h and temperatures were below 15° C, and could be inhibited by a 1h light break in the middle of the dark period (night break) of an other wise inducing light/dark regime. Photoperiodic responses that are triggered when light falls below a critical daylength are termed "short day" and those that are triggered by daylengths longer than a critical daylength are termed "long day" (Dring, 1984). The fact that most reported short day responses can be inhibited by a night break indicates that it is the timing of the dark period that is important (Luning, 1990).

Southern African kelp beds:

Laminaria pallida grows as an understory kelp to *Ecklonia maxima* (Osbeck) Papenfuss down to 8m depth in wave exposed conditions in the south-western Cape region of South Africa. In waters from 8-20 meters *L. pallida* is the dominant kelp (Jarman and Carter, 1981). On the northern Cape coast *Laminaria schinzii* Foslie grows with *E. maxima* from Cape Columbine into Namibia (Anderson *et al.*, 1989). Field *et al.* (1980) found that total kelp biomass decreases northwards along the west Cape coast from a maximum on the Cape peninsula and suggested that decreasing water clarity may be the reason. Jarman and Carter (1981) estimated the standing crop of *L. pallida* and *E. maxima* to be 217,960 and 336,370 tons wet weight respectively between Cape Point and Cape Columbine.

Namibian kelp beds:

Upwelling along the Namibian coast insures that the annual average sea temperature ranges are relatively low for temperate seas (12-14.8 °C for Luderitz and 12-18.4 °C for Swakopmund). This upwelled cool water is rich in nutrients and, because of high rates of primary and secondary production, light penetration tends to be low except for short periods between upwelling cycles.

From Cape Columbine, on the western Cape coast of South Africa, to northern Namibia a long hollow-stiped variety, *L. schinzii* grows and ultimately becomes the dominant kelp (Anderson and Bolton, 1985; Anderson *et al.*, 1989; Molloy, 1990), and seems to compete with *E. maxima*. In the southern part of the Namibian coast, where substratum is suitable, it occurs in dense beds interspersed with a few *E. maxima* plants. The beds are restricted to rocky areas which, on the Namibian coast, occur very intermittently (Molloy, 1990). The ±80 km stretch of rocky coast around Luderitz is the largest expanse of rock on the 1500 km coast which, for the most part, is sandy with rocky outcrops (Molloy, 1990).

Commercial harvesting of *L. schinzii* has been carried out on a trial basis in the Luderitz area. Blades were cut 2 cm above the meristem, dried and exported for human consumption. Harvesting commenced in April 1987 and ended in March 1989 with a total of 137 tonnes (wet) harvested. The harvest was discontinued because the consumers found the texture of the blades unsuitable (Molloy, 1990; Critchley *et al.*, 1991).

Estimates of standing stock for *L. schinzii* or *E. maxima* from the north west Cape and Namibian coasts are not available and there are no published estimates of the standing stock of *L. schinzii* for any part of its distribution. Molloy (1990) estimated a standing stock available to a given harvesting technique for a 20km stretch of the coast at Luderitz at 300 tonnes (wet) per year. The harvesting technique involved manually cutting individual blades 2 cm above the meristem and the removal of all blades from a harvested plant. Only the shallow portions of the beds (1-1.5m deep) were harvested.

The environment in which Namibian *Laminaria* grows differs from that in which most other Laminariales grow in that the seasonality of environmental variables is relatively little. Light availability varies less than at higher latitudes due to daylength and light intensity variation decreasing with increasing latitude and continuous upwelling ensures a relatively small water temperature range (12-14.8^{o} C, running average of 23 days over 10 years for Luderitz, Molloy, 1990) and relatively constant nutrient availability.

This investigation aims to study the morphology of *Laminaria schinzii* in the Luderitz area and to investigate the effects of variations in water motion on morphology and seasonal growth.

5.2 Materials and Methods

The adult *L. schinzii* (fig. 5.1) has a hollow stipe (the only hollow stiped member of the Digitatae complex reported) up to a maximum of 5m long (personal observation). The stipe is widest in the mid region, becoming narrower at the distal and proximal ends and is very often verrucate. *Laminaria pallida* (fig. 5.1) stipes grow to a maximum of 3m, are slightly conical and are also often verrucate, and they may occasionally be partially hollow (personal observation). The fronds of both species are similar.

The three sites, Shear Water Bay, Dias Point and Grossebucht were chosen to represent sheltered, semi-exposed and exposed habitats respectively (fig. 5.2). Shear Water Bay is sheltered from the open ocean swells (fig. 5.2) by Dias Point. The prevailing south-south westerly winds (fig. 5.3) for the area are off shore at this site, as a result very little wind induced wave action is experienced.

Dias Point site is partially sheltered from swell by the position of Seal Rock, lying to the south-south west. This rock and the Dias Cross Rock both contributed to lessening the effects of wind induced wave action.

The Grossebucht site is open to the full force of the Atlantic swell. The shore is steep attaining 10m depth just 150 m off-shore so the outer regions of the kelp bed are of little protection to the inner portion. The prevailing south-south westerly winds are offered no obstruction at the site. Because of wave exposure the site proved very difficult to work at except on very calm days.

For each depth (0-0.5m, 1m and 2m below mean low water) at each site four 1 X 1 meter quadrats were randomly placed, by throwing a rock with a float attached into the bed to choose the spot. All plants inside the quadrats were removed by cutting - just above the holdfast so the holdfast was not included in weight measurements. The plants were brought back to the shore and stipe length and weight, frond length and weight, total weight, and frond thickness of each individual were measured, and fertility state was noted. All plants from the 4 quadrats at each site were pooled for intersite analysis of morphological characters.

Samples of the fronds (20 per depth per site) were taken back to the laboratory so that specific density could be calculated. Each sample was a large piece cut mid-way along the blade. From each blade sample one 2X2 cm square was cut, blotted and the thickness measured with a vernier callipers. The piece was then weighed on a scale accurate to 10^{-3}g and the density calculated as:

$$\text{density} = \text{weight} / (\text{area} \times \text{thickness})$$

This measurement of density was used to calculate surface area as :

$$\text{surface area} = \text{blade weight} / \text{thickness} / \text{density}$$

The thickness of a frond was found to be uniform except in the area of the transition between stipe and frond, where thickness was greater. The meristematic region was up to 1mm thicker than the blades, which had a uniform thickness. On many specimens the stipe was already flattened up to 20 cm proximal to the region where the stipe widened to become the frond.

Stipe lumen diameter was measured independently of the other characters. All mature plants (those with stipes reaching the surface at low tide) were removed from three $1m^2$ quadrats at 1m depth at each site. The plants were cut midway along the stipe and the lumen diameter and stipe diameter measured.

To measure the attachment strength of the *Laminaria* plants, a chain (2 cm link width) was secured to the base of the stipe with 8-10 coils of 6 mm nylon rope. The chain was run out of the kelp bed to the shore and attached to a 300 kg suspension scale. The scale was in turn coupled to a hand cranked winch which was secured to a crack in the rock with a steel rod. The chain was cranked in until the holdfast lost its attachment and the reading taken. Approximately 28% of the stipes broke due to the cutting action of the rope, and these were not included in the analysis. Because of the method used no plants were more than 20 m away from the shore and only plants in 1 m of water were chosen. Measurements of all plants extracted in this manner were made, as above.

Seasonal growth of the fronds was monitored following the method of Parke (1948), also used widely by other authors including Sundene (1964), Mann (1972) Mann *et al.* (1979) and Egan and Yarish (1990). Holes were punched with an empty .22 hornet rifle shell (5mm diameter) 40 cm from the stipe frond transition zone at two weekly or at monthly intervals. Thirty plants were punched at each site (Shearwater Bay, Dias Point and Grossebucht) but subsequently not all of the plants could be found for measurement. Only plants at 1 m depth were punched. Position for punching the holes and later measurement of hole migration along the frond was carried out using the apparatus in figure 5.4. This apparatus was used successfully by Sundene (1964) and serves to remove ambiguity when deciding where the stipe ends and frond begins.

To determine the position of the meristematic tissue of the fronds, holes were punched at 10 cm intervals from 30cm distal to the stipe/frond transition zone to the end of the blade. The fronds were remeasured after 2 weeks and the progression of each hole noted. One blade on each of 10 plants at each site was punched in this manner.

Sea surface temperature data was obtained from Dias Point Lighthouse on a daily basis (where it was measured with a mercury thermometer accurate to 0.1°C) and at Luderitz harbour temperature was taken every working day. Raw wind data, in the form of speed and direction taken 7 times per day, was also obtained from Dias Point Lighthouse. The 7 readings for each day were combined to produce an average speed from 4 quarters as a 20 day running average.

Linear regressions (by minimizing the sum of squares of the residuals for the fitted line), discriminant analysis and Mann - Whitney tests, for comparison of two samples, of the data on morphology at different sites were performed with the "Statgraphics" computer program (STSC, Inc).

5.3 Results

5.3.1 Stipe length (Table 5.1, fig. 5.5)

At each site stipes were longest at 2m depth and shortest at 0-0.5m. Stipes at 0-0.5m were longest at Grossebucht and shortest at Shearwater Bay, at 1m they were longest at Shearwater Bay and shortest at Dias Point and at 2m they were longest at Grossebucht and shortest at Dias Point. The differences in stipe length was not significant between: Shearwater Bay and Dias Point or between Grossebucht and Dias Point, at 0-0.5 m depth, 1m at Grossebucht and Dias Point, 2m at Shearwater Bay and Dias Point and 1m at Shearwater Bay and 2m at the Dias Point. At all other sites and depths stipes had significantly different weights at $p < 0.001$ except at 1m at Shearwater Bay and Grossebucht where the significance was $p < 0.05$.

5.3.2 Frond length (Table 5.1, fig. 5.6)

Fronds were longest at 2m and shortest at 0-0.5m at each site. At 0-0.5m frond length was greatest at Dias Point and least at Shearwater Bay, at 1m fronds were

STIPE LENGTH	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	$Z = .025$ N.S.
SWB0 X GROSS0	$Z = 3.6$ $p < 0.001$
DP0 X GROSS0	$Z = 1.5$ N.S.
SWB1 X DP1	$Z = -3.4$ $p < 0.001$
SWB1 X GROSS1	$Z = -2.3$ $p < 0.05$
GROSS1 X DP1	$Z = -.03$ N.S.
SWB1 X SWB2	$Z = .55$ N.S.
SWB2 X DP2	$Z = .07$ N.S.
SWB2 GROSS2	$Z = 2.8$ $p < 0.01$
DP2 X GROSS2	$Z = 4.2$ $p < 0.001$
BLADE LENGTH	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	$Z = 6$ $p < 0.001$
SWB0 X GROSS0	$Z = 4.6$ $p < 0.001$
DP0 X GROSS0	$Z = 1.1$ N.S.
DP0 X DP1	$Z = 1.6$ N.S.
GROSS0 X GROSS1	$Z = 1.2$ N.S.
SWB1 X DP1	$Z = .8$ N.S.
SWB1 X GROSS1	$Z = -.69$ N.S.
DP1 X GROSS1	$Z = -.6$ N.S.
DP2 X GROSS2	$Z = -.5$ N.S.
SWB2 X GROSS2	$Z = -2.5$ $p < 0.01$
DP1 X GROSS0	$Z = -2.2$ $p < 0.05$
SWB1 X DP0	$Z = 1.5$ N.S.
DP0 X GROSS1	$Z = .38$ N.S.
SWB2 X DP2	$Z = -2.9$ $p < 0.001$
TOTAL WEIGHT	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	$Z = 4.5$ $p < 0.001$
SWB0 X GROSS0	$Z = 5.1$ $p < 0.001$
DP0 X GROSS0	$Z = .5$ N.S.
DP0 X DP1	$Z = 2.4$ $p < 0.01$
SWB1 X DP1	$Z = -2.3$ $p < 0.05$
SWB1 X GROSS1	$Z = -1.3$ N.S.
DP1 X GROSS1	$Z = .5$ N.S.
SWB2 X DP2	$Z = -1.2$ N.S.
SWB2 X GROSS2	$Z = 0$ N.S.
DP2 X GROSS2	$Z = 1$ N.S.
DP0 X GROSS1	$Z = 3.2$ $p < 0.001$
DP1 X GROSS0	$Z = -2.1$ $p < 0.05$
STIPE WEIGHT	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	$Z = 1.5$ N.S.
SWB0 X GROSS0	$Z = 4.4$ $p < 0.001$
DP0 X GROSS0	$Z = 2.9$ $p < 0.001$
DP0 X DP1	$Z = 5$ $p < 0.001$
SWB X DP1	$Z = -3.1$ $p < 0.001$
SWB1 X GROSS1	$Z = -1.5$ N.S.
DP1 X GROSS1	$Z = 1.2$ N.S.
SWB1 X SWB2	$Z = 2.3$ $p < 0.05$
SWB2 X DP2	$Z = .5$ N.S.
DP1 X DP2	$Z = 4.6$ $p < 0.001$

FROND WEIGHT	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	$Z = 5$ $p < 0.001$
SWB0 X GROSS0	$Z = 5$ $p < 0.001$
DP0 X GROSS0	$Z = -.09$ N.S.
DP0 X DP1	$Z = 1.3$ N.S.
GROSS0 X GROSS1	$Z = 1.9$ $p < 0.05$
SWB1 X DP1	$Z = -1.9$ N.S.
SWB1 X GROSS1	$Z = -1.2$ N.S.
DP1 X GROSS1	$Z = .2$ N.S.
DP2 X GROSS2	$Z = -.05$ N.S.
SWB2 X GROSS2	$Z = -1.6$ N.S.
SWB2 X DP2	$Z = -1.8$ N.S.
FROND SURFACE AREA	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	$Z = 4.5$ $p < 0.001$
SWB0 X GROSS0	$Z = 3.8$ $p < 0.001$
DP0 X GROSS0	$Z = -1.09$ N.S.
DP0 X DP1	$Z = 1.5$ N.S.
GROSS0 X GROSS1	$Z = 1.6$ N.S.
SWB1 X DP1	$Z = -2.3$ $p < 0.05$
SWB1 X GROSS1	$Z = -3.1$ $p < 0.001$
DP1 X GROSS1	$Z = -.5$ N.S.
SWB2 X GROSS2	$Z = -2.5$ $p < 0.01$
SWB2 X DP2	$Z = -2.3$ $p < 0.01$
DP2 X GROSS2	$Z = 1.6$ N.S.
STIPE WEIGHT PER CENTIMETER LENGTH	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	$Z = 1.1$ N.S.
SWB0 X GROSS0	$Z = 4.5$ $p < 0.001$
DP0 X GROSS0	$Z = 3.7$ $p < 0.001$
SWB1 X DP1	$Z = -2.5$ $p < 0.01$
SWB1 X GROSS1	$Z = .17$ N.S.
DP1 X GROSS1	$Z = 2$ $p < 0.05$
SWB2 X DP2	$Z = .9$ N.S.
SWB2 X GROSS2	$Z = 2.1$ $p < 0.05$
DP2 X GROSS2	$Z = 1.6$ N.S.
FROND WIDTH	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	$Z = 3.5$ $p < 0.001$
SWB0 X GROSS0	$Z = 3.1$ $p < 0.001$
DP0 X GROSS0	$Z = -.6$ N.S.
DP0 X DP1	$Z = 1.3$ N.S.
SWB1 X DP1	$Z = -3.1$ $p < 0.001$
SWB1 X GROSS1	$Z = -3.5$ $p < 0.001$
DP1 X GROSS1	$Z = -.2$ N.S.
GROSS0 X GROSS1	$Z = 1.1$ N.S.
GROSS2 X GROSS1	$Z = -2.6$ $p < 0.001$
SWB2 X DP2	$Z = -1.5$ N.S.
SWB2 X GROSS2	$Z = -2.2$ $p < 0.05$
DP2 X GROSS2	$Z = -1.3$ N.S.
DP1 X GROSS0	$Z = -1.7$ N.S.

BLADE THICKNESS	
COMPARISON	SIGNIFICANCE
SWB0 X DP0	Z = 10.4 p < 0.001
SWB0 X GROSS0	Z = 11.9 p < 0.001
DP0 X GROSS0	Z = 8.4 p < 0.001
SWB1 X DP1	Z = 1.6 N.S.
SWB0 X SWB1	Z = 1.5 N.S.
DP0 X DP1	Z = -3.4 p < 0.001
SWB1 X SWB2	Z = -2.7 p < 0.001
SWB0 X SWB2	Z = -2.5 p < 0.01
DP1 X DP2	Z = -1.9 p < 0.05
GROSS1 X GROSS2	Z = -.7 N.S.
GROSS0 X GROSS2	Z = -.9 N.S.
GROSS0 X GROSS1	Z = -.4 N.S.

Table 5.1. Comparison of the morphological characters (Mann -Whitney test) of plants from 0-0.5m, 1m and 2m at Shearwater Bay, Dias Point and Grossebucht. Test statistic (Z) and degree of significance indicated. N.S. = not significant. Tests were performed where a significant difference was uncertain, all other comparisons were significant at $P < 0.001$.

again longest at Dias Point but were shortest at Grossebucht and at 2m they were longest at Shearwater Bay and shortest at Grossebucht. The difference in frond length, however, was not significant between: 0-0.5m at Dias Point and Grossebucht, 0-0.5m and 1m at Dias Point, 0-0.5m and 1m at Grossebucht, 1m at all 3 sites, 2m at Dias Point and Grossebucht, 1m at Shearwater Bay and 0-0.5m at Dias Point, and 0-0.5m and 1m at Grossebucht. All other differences were significant at $p < 0.001$ except between: 2m at Shearwater Bay and Grossebucht ($p < 0.01$) and 1m at Dias Point and 0-0.5m at Grossebucht ($p < 0.05$).

5.3.3 Total weight (Table 5.1, fig. 5.7)

At all sites weight of plants was greatest at 2m and least at 0-0.5m. At 0-0.5m plants were heaviest at Grossebucht and lightest at Shearwater Bay, at 1m they were heaviest at Shearwater Bay and lightest at Dias Point and at 2m they were heaviest at Grossebucht and again, lightest at Dias Point. The differences in total weight were not significant between: 0-0.5m at Dias Point and Grossebucht, 1m at the Shearwater Bay and Grossebucht, 1m at Dias Point and Grossebucht and 2m at all 3 sites. All other differences were significant at $p < 0.001$ except between 0-0.5m and 1m at Dias Point ($p < 0.01$), 1m at Shearwater Bay and Dias Point and 0-0.5m at Dias Point and Grossebucht ($p > 0.05$).

5.3.4 Stipe weight (Table 5.1, fig. 5.8)

Stipes were heaviest at 2m and lightest at 0-0.5m at each site. At 0-0.5m there were heaviest at Grossebucht and lightest at Shearwater Bay, at 1m they were heaviest at Shearwater Bay and lightest at Dias Point and at 2m they were heaviest at Grossebucht and lightest at Shearwater Bay. The difference in stipe weight was not significant between: 0-0.5m at Shearwater Bay and Dias Point, 1m at Shearwater Bay and Grossebucht, 1m at the Dias Point and Grossebucht, and 2m at the Shearwater Bay and Dias Point. All other differences were significant at $p < 0.001$ except between 1m and 2m at Shearwater Bay ($p < 0.05$).

5.3.5 Frond weight (Table 5.1, fig. 5.9)

At all sites frond weight was greatest at 2m and least at 0-0.5m. At 0-0.5m frond weight was greatest at the Dias Point and least at Shearwater Bay, at 1m it was greatest at Shearwater Bay and least at Dias Point and at 2m frond weight was greatest at Shearwater Bay and least at Grossebucht. The differences in frond weight were not significant between: 0-0.5m at Dias Point and Grossebucht, 1m at all 3 sites and 2m at all 3 sites. All other differences were significant at $p < 0.001$ except between 0-0.5m and 1m at Grossebucht ($p < 0.05$).

5.3.6 Frond Surface area (Table 5.1, fig. 5.10)

Frond surface area was largest at 2m and smallest at 0-0.5m at all sites. At 0-0.5m it was largest at Dias Point and smallest at Shearwater Bay, at 1m it was largest at Shearwater Bay and smallest at Grossebucht and at 2m it was also largest at Shearwater Bay and smallest at Grossebucht. The differences in surface area were not significant between: 0-0.5m at Dias Point and Grossebucht, 0-0.5m and 1m at Dias Point, 0-0.5m and 1m at Grossebucht, 1m at Dias Point and Grossebucht, and 2m at Dias Point and Grossebucht. All other differences were significant at $p < 0.001$ except between Dias Point and Grossebucht at 2m, Shearwater Bay and Dias Point at 2m ($p < 0.01$) and Shearwater Bay and Dias Point at 1m ($p < 0.05$).

5.3.7 Stipe weight per unit length (Table 5.1, fig. 5.11)

Stipes were heavier per unit length at 2m and lighter at 0-0.5m at all sites. At 0-0.5m they were heaviest at Grossebucht and lightest at Dias Point, at 1m they were also heaviest at Grossebucht and lightest at Dias Point and at 2m they were heaviest at the Grossebucht and lightest at Shearwater Bay. The differences were not significant between: 0-0.5m at Shearwater Bay and Dias Point, 1m at Shearwater Bay and Grossebucht, 2m at Shearwater Bay and Dias Point, and 2m at Dias Point and Grossebucht. All other differences were significant at $p < 0.001$ except between Dias Point and Grossebucht at 1m and Shearwater Bay and Grossebucht at 2m ($p < 0.05$).

5.3.8 Frond width (Table 5.1, fig. 5.12)

Fronds were widest at 2m and narrowest at 0-0.5m at all sites. At 0-0.5m they were widest at Dias Point and thinnest at Shearwater Bay, at 1m they were widest at Shearwater Bay and narrowest at Dias Point and at 2m they were widest at Shearwater Bay and narrowest at Grossebucht. The differences were not significant between: 0-0.5m at Dias Point and Grossebucht, 0-0.5m and 1m at Grossebucht, 2m and 1m at Grossebucht, 2m at Shearwater Bay and Dias Point, 2m at Dias Point and Grossebucht, and 1m at Dias Point and 0-0.5m at Grossebucht. All other differences were significant at $P < 0.001$ except between Shearwater Bay and Grossebucht at 2m ($p < 0.05$) and 0-0.5m and 1m at Dias Point ($p < 0.01$).

5.3.9 Frond thickness (Table 5.1, fig. 5.13)

Frond thickness was greatest at 0-0.5m and least at 2m at all sites. At all depths thickness was greatest at Grossebucht and least at Shearwater Bay. The differences were not significant between: 1m at Shearwater Bay and Dias Point, 0-0.5m and 1m at Shearwater Bay and all three depths at Grossebucht. All other differences were significant at $p < 0.001$ except between 0-0.5m and 2m at Shearwater Bay ($p < 0.01$) and 1m and 2m at Dias Point ($p < 0.05$).

5.3.10 Stipe lumen diameter (Table 5.1, fig. 5.14)

When stipe lumen diameter was regressed against stipe diameter, slopes of 1.12, 1.37 and 1.07 were obtained for the sheltered, semi-exposed and exposed site respectively.

5.3.11 Discriminant analysis

Figure 5.15 shows the result of discriminant analysis of the variables at the 3 depths for each of the 3 sites. The separation is based on the 9 parameters shown in figures 5.5 to 5.13. The two discriminant functions used to separate the data account for 75.9% of the total variation. The data in the ordination is separated along a diagonal. At one extreme is the 2m site at Grossebucht followed by the 1m site and then the 0-0.5m site at Grossebucht. At the other extreme is the 2m site at Shearwater Bay followed by the 2m site at Dias Point and much less the 1m site at Shearwater Bay. The 0-0.5m sites at Shearwater Bay and Dias Point and the 1m site at Dias Point are centrally positioned

5.3.12 Species composition

Ecklonia maxima (fig. 5.1) did not grow at the sheltered site nor at 2-2.5m at the exposed site. Plant density results were too variable to be of use.

5.3.13 Seasonal growth (fig. 5.16 a to c).

The fronds at all 3 sites grew all year round and displayed a seasonal pattern with the growth rate varying from 5 mm d^{-1} to 10.5 mm d^{-1}. Maximal growth occurred between September and November and the lowest growth rates were recorded from March to July. Over the whole experimental period, at each site, growth rate followed the same general pattern but the growth rate at the exposed site was generally 1-2mm d^{-1} less than at the other two sites apart from a brief period during March 1991 and another during December 1991.

5.3.14 Attachment strength.

At 1m depth at the 3 sites there was no significant difference in attachment. It took 52 ±13.3 kg to remove plants from the substratum at the sheltered site, 50 ±6.9 kg at the semi-exposed site and 59 ±3.3 kg at the exposed site. Attachment for mature plants did not correlate with plant size.

5.4 DISCUSSION

From the work of previous authors it seems that exposure has a great influence on the morphology of members of the Laminariales. This was demonstrated by *Laminaria schinzii* growing at three sites on the Namibian coast viz. Grossebucht, Dias Point and Shearwater Bay.

For convenience the three sites were classified as sheltered (Shearwater Bay), semi-exposed (Dias Point) and exposed (Grossebucht). The discriminant analysis, however, indicates that the division is not so clear-cut as the depth at each site must be considered as well. If the 3 deepest (2m) sites are linked with a diagonal axis, the axis represents an exposure gradient. So, based on the plant morphology, from the discriminant analysis, the position of each site and depth along an exposure gradient are given in table 5.2.

Grossebucht 2m	Exposed
Grossebucht 1m	
Grossebucht 0-0.5m	
*Dias Point 0-0.5m	
*Dias Point 1m	
*Shearwater Bay 0-0.5m	
Shearwater Bay 1m	
Dias Point 2m	
Shearwater Bay 2m	
	Sheltered

Table 5.2 The position of the various sites along an exposure gradient. * indicates sites that are similar.

All three sites at Grossebucht are more exposed than any site at Dias Point or Shearwater Bay. The most sheltered site was at 2m at Shearwater Bay followed by 2m at Dias Point and 1m at Shearwater Bay. The shallow 0-0.5m site at Dias Point and Shearwater Bay and the 1m site at Dias Point are similar and intermediate. It follows then, that the morphological characteristics of plants growing at exposed and sheltered site are as in table 5.3.

EXPOSED (2m at Grossebucht)	**SHELTERED** (2m at Shearwater Bay)
Long stipe,	Short stipe,
Heavy stipe,	Light stipe,
Low frond surface area,	High frond surface area,
Heavy stipe/unit length,	Light stipe/unit length,
Narrow frond,	Wide frond,
Thick frond,	Thin frond,
Short frond,	long frond,
Light frond.	heavy frond,
Both exposed and sheltered plants are heavy.	

Table 5.3 The morphological characteristics of exposed and sheltered plants.

5.4.1 Stipe morphology:

Though Chapman (1973) reported that *Laminaria longicruris* stipes tended to be hollow and longer in calmer waters and Druehl (1967a) reported that, the closely related, *L. groenlandica* stipes were longer in exposed water, reports from the Digitatae complex (including this report) all indicate that stipes were longer in exposed habitats. Stipes of the sheltered form of *L. hyperborea* (f. *cucullata*) had shorter stipes (Kain, 1971). *Laminaria digitata* stipes were shorter in sheltered conditions in Nova Scotia (Sharp and Carter, 1986) and in the Pacific digitate species, *L. setchellii,* plants were taller in exposed habitats (Klinger and DeWreede, 1988). In more exposed conditions *Laminaria schinzii* had a thicker stipe, this was also the case in *L. digitata* (Sundene, 1962) and *L. setchellii.* At each site for the 3 depths investigated, stipe weight, length and thickness increased with depth the only exception being between plants which grew at 1m and 2m at the sheltered site.

A complicating factor, which must be considered is the occurrence of *Ecklonia maxima* at some of the sites. *Laminaria pallida* is an understory species to *E. maxima* on the west Cape coast of South Africa (Velimirov *et al.*, 1977; Dieckmann, 1980 and Field *et al.* 1980) and it is possible that *L. schinzii* tends towards an understory species in the presence of *E. maxima.* This may be an explanation as to why at 1m stipes were shorter at the more exposed Grossebucht and intermediate Dias Point site than at the more sheltered Shearwater Bay site. Further evidence of this is that at 1m at Dias Point the stipe lumen diameter was smaller, relative to the stipe diameter, than at the other sites at the same depth, tending towards the solid stipe of *L. pallida.*

A long stipe in deeper water obviously serves to keep the frond closer to the light and in more turbulent water due to greater surface reflection (Cousens, 1982) a very long stipe would be advantageous. Koehl (1986) suggested that a long flexible alga in a wave exposed environment may "move back in the opposite direction before the slack in the plant has been taken up". In the case of *L. schinzii* the narrower portion of the stipe just above the holdfast, and the long stipe, aid in flexibility. In the Simplices group of *Laminaria, L. saccharina* and *L. longicruris* tend towards long hollow stipes in sheltered conditions (Kain, 1976; Gerard and Mann, 1979), however at the southern limit of *L. longicruris,* in moderate exposure, long hollow stiped populations occur (Egan and Yarish, 1990). In contrast, hollow stiped *L. schinzii* dominates on the high wave energy coast of Namibia, and likewise the hollow stiped *Ecklonia maxima* dominates on the high energy south western Cape coast of South Africa (Jarman and Carter, 1981) and *Nereocystis luetkeana* (also hollow stiped) thrives in exposed waters on the west coast of North America (Koehl, 1986).

5.4.2 Frond morphology

The smaller frond surface area of plants in more exposed sites was accounted for by a decrease in frond width rather than frond length. There was a close positive correlation between exposure and blade thickness; a similar trend has been reported for *Laminaria digitata* (Sundene, 1962) and *L. longicruris* at 10m (Gerard and Mann, 1979).

No significant difference was found in the thickness of fronds between depths contrary to Kain's (1977) findings that at a given site fronds of *Laminaria hyperborea* were thinner in deeper water. Kain (1977) suggested that the logarithmic decrease in water motion with depth was responsible. Most of her study sites were deeper than 2m, however. It is possible that the thinning of fronds with decreasing exposure only occurs in conditions of extreme shelter, such as in deeper water in fjords.

The advantage of a small surface area in high wave action is a result of reduced water resistance and also that thicker blades are more robust. The flow of nutrients across the surface of the fronds increases with high water motion (Lobban *et al.*, 1985 and De Boer, 1981) and thus the lower surface area to volume ratio is not such a disadvantage. However, once maximum uptake rate is reached it is a disadvantage to have a low surface area to volume ratio.

Total plant weight was lower at the sites of intermediate exposure than the other sites (though not very significantly). These plants did not possess the heavy stipes of the exposed site nor the heavy fronds of the sheltered site. This resulted in a lighter plant than at either wave exposure extremes.

It may not have been necessary for plants growing at the exposed site, despite the higher wave action, to have a higher attachment strength as due to smaller blade surface area, water resistance was reduced. Conversely an attachment strength equivalent to that of the exposed site may have been necessary for plants at the sheltered site because of their increased water resistance due to larger blade surface area. The sheltered site, though sheltered in comparison to the exposed site was not as sheltered as a Norwegian fjord and so did have some degree of water motion. Where conditions approaching those in the fjords of Norway exist, such as in parts of the Luderitz Lagoon, water temperatures are too high for *Laminaria* growth and very little rocky substratum occurs (Chapter 3).

5.4.3 Seasonal growth

Seasonal growth for subtidal Laminariales in general, show a seasonal pattern of growth with a maximum in spring or early summer and a minimum in late summer to early winter (Kain, 1989). This seasonal growth pattern is demonstrated by *Laminaria schinzii* as well though the seasonal difference in growth rate was small at 6 mm d^{-1}. This may be because of the relatively low latitude of the area viz. 26° S as Kain (1989) found a strong correlation between seasonality and latitude in the Laminariales, seasonality being greater with higher latitude. Working on *L. pallida* Dieckmann (1980) found a very similar seasonal pattern to that reported here but the seasonal difference in growth rate, between maximum and minimum, was more marked (12mm d^{-1} at his 8m study site) then that of *L. schinzii* (5.5mm d^{-1}). This more pronounced seasonality was probably because of the higher latitude (33° 59' S) of Oudekraal, his study site on the Cape peninsula of South Africa. At a deeper (14m) site Dieckmann (1980) found the overall growth rates to be lower and exhibit less pronounced seasonality than at the 8m site so it is unlikely that depth was responsible for the lower seasonality reported in this study as the sites were at a depth of 1m. The seasonal variation in growth rate reported here for *L. schinzii* is one of the lowest reported for any Laminarian (Kain, 1989) and the winter growth is one of the highest reported.

To explain this growth pattern, the seasonality of sea temperature, light and nutrients must be investigated. The regulating force of the marine climate in this area is the wind. Southerly wind which drives the upwelling of cold nutrient rich water is present all year round but is less frequent in winter (fig. 5.3). This cooling effect was more notable in spring than summer when the heating effect of the sun was reduced due to lower seasonal irradiation. It can be said that when north or reduced south winds blew upwelling did not occur or was reduced and consequently nutrient levels were lower (5-10 umol l^{-1} nitrate off shore at

Luderitz, Bailey, unpubl.; 4.2 umol l^{-1} on shore at the Cape Peninsula South Africa, Dieckmann, 1980) and temperatures higher ie. from March to July which corresponds to the seasonal low growth in *L. schinzii.* The increase in growth rate in spring is correlated with an increase in south wind and hence upwelling of cool nutrient rich water.

The fact that growth was depressed in summer despite upwelling and high light conditions indicated that some other factor was responsible. Dieckmann (1980) found a similar occurrence in *L. pallida.* Bailey (unpubl.) found upwelling on the Namibian coast to be most intense in the Luderitz region and that the highest nutrient concentrations were in the near shore region. Annual off shore nitrate concentration varied between 5 and 20 umols l^{-1} (Bailey, unpubl.). Growth rate of *Laminaria saccharina* was found to be saturated at 10-20 umol nitrate (Chapman *et al.*, 1978) and so it is doubtful that nutrient availability was the most important controlling factor. In this investigation reproductive material was found year round with no obvious seasonal pattern so it is not likely that sporogenesis was more active in the summer and consequently depressed growth rate. The most likely controlling factor of the observed seasonal growth pattern is daylength. The onset of rapid growth in winter is triggered by a critical daylength in anticipation of increased light and nutrient availability. A short day photoperiodic response for seasonal growth has been demonstrated in *L. hyperborea* (Luning, 1986) where the critical daylength triggered the formation of a new frond.

Warm temperature anomalies due to north wind, as happened in March 1991 and February 1992 (fig. 5.16 d), depressed growth rate. The effect was immediate indicating that *Laminaria schinzii* was reacting to high temperatures. The optimum temperature for growth of small sporophytes of *L. schinzii* in the laboratory was 15° C (tom Dieck, unpubl.) which occurred very rarely during this study so the effect of temperature on the seasonal growth pattern is probably small as the highest growth rates were recorded during the lowest temperatures (10-11^{o} C). It is, however, difficult to separate the importance of nutrients from temperature as the two are closely correlated on this coast (Bailey, unpubl.).

The competition between *Laminaria schinzii* and *Ecklonia maxima* was probably one for light. Both kelps have floatation organs. *Ecklonia maxima* in <8m of water has a sufficiently long stipe to keep its frond at the surface and at these depths dominates the kelp beds of the west Cape coast of South Africa (Field *et al.* 1980); below this depth *Ecklonia* is absent, *L. pallida* being the sole component of the kelp bed. Because of its long hollow stipe. *L. schinzii* can compete with *E. maxima,* particularly, as on this coast the maximum stipe length for *E. maxima* is 5m - the same as *L. schinzii*. The competitive edge of *E. maxima* was probably reduced due to some factor such as steepness of the shore, which allowed *L. schinzii* to outcompete it. It must be remembered that *E. maxima* finds its northern most limit in the vicinity of Luderitz (Molloy, 1990). It is difficult to explain this limit by considering environmental factors, especially as at the southern end of the distribution, *E. maxima* extends further into warmer water than *L. pallida*. If *L. schinzii* is outcompeting *E. maxima* in Namibia why does this not occur further south? This would be a fascinating study of the ecology and ecogenetics of two competing species, but outside the scope of the present study.

5.5 Conclusions

1. *Laminaria schinzii* adapted well to growth in sheltered and exposed sites. This adaptation was manifest as a decrease in frond surface area, increase in frond thickness and increase in stipe length and weight with increased exposure. Larger

surface area in more sheltered habitats was caused largely by an increase in frond width.

2. Attachment strength did not vary with degree of exposure, indicating that a decrease in water resistance rather than an increase in attachment strength was the adaptive avenue evolved to cope with wave exposure.

3. The plant morphological difference between sites was obvious only in deeper water. In shallow water differences, though evident, were not marked.

4. In shallow kelp beds (0-2m), plants which grow in deeper sites (2m) are heavier than those from shallower sites(0-1m), regardless of exposure.

5. In the presence of *Ecklonia maxima* it appeared that *Laminaria schinzii* tends towards an understory species with shorter stipe. These shorter stiped plants had a smaller lumen diameter to stipe diameter ratio which indicated a close relationship to the short, solid stiped *L. pallida.*

6. Seasonal growth followed a pattern reported for many other Laminariales. An annual growth rhythm triggered by photoperiod is hypothesized to be responsible but nutrients may also have played a minor role. Temperature was sub-optimal for growth for most of the study and highest growth occurred during lowest temperatures, and thus temperature had no significant effect.

Figure 5.1. Habit drawing of *Laminaria schinzii* (1), *Laminaria pallida* (2) and *Ecklonia maxima* (3). Stipe cross sections also shown. Maximum stipe lengths for the Luderitz area are indicated.

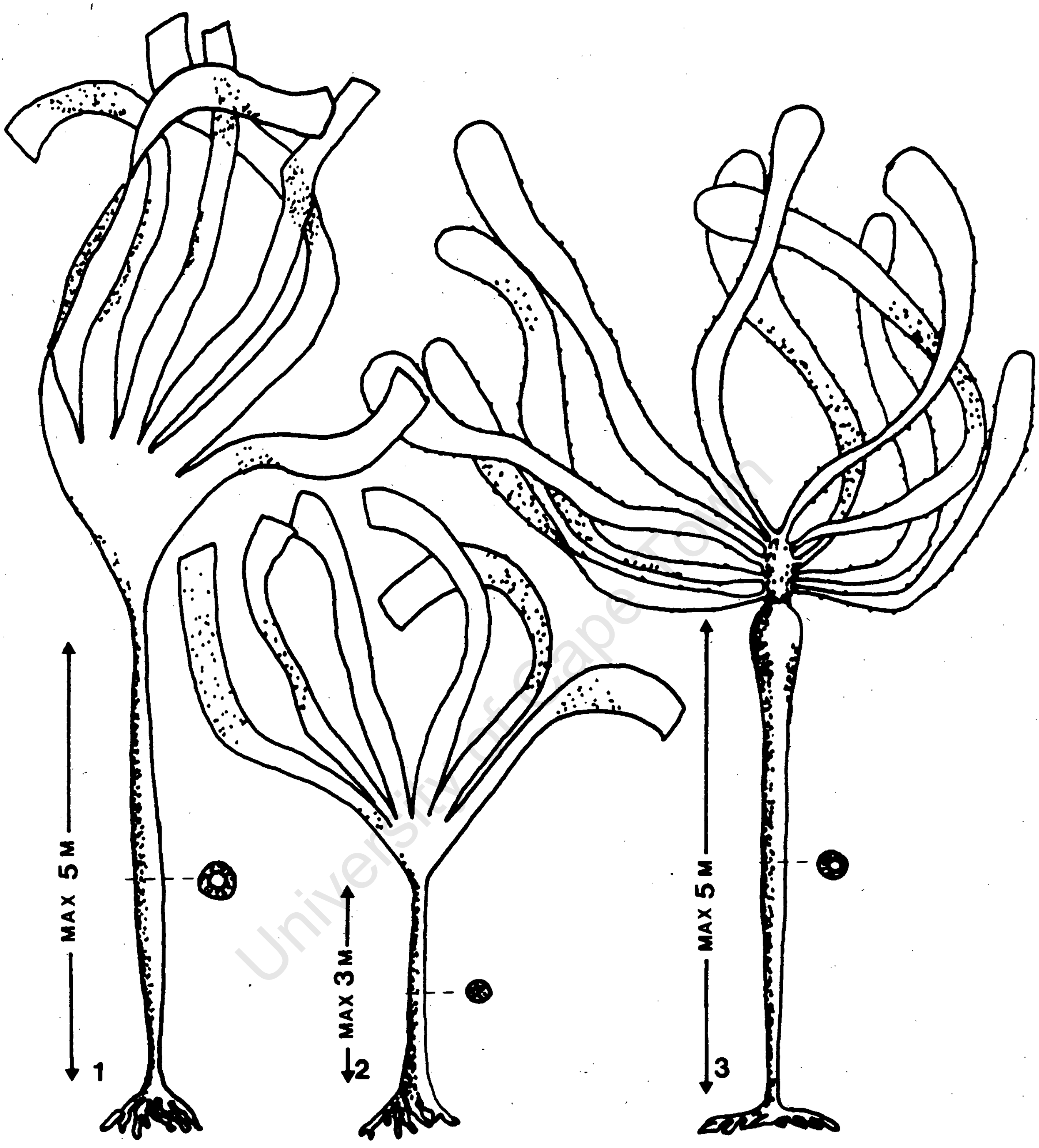

MAX 5 M
1
MAX 3 M
2
MAX 5 M
3

Figure 5.2. Map of Luderitz area with blowups of the Dias Point, Shearwater Bay area and the Grossebucht area. Swell direction is indicated on the blowups. Also shown is a wind frequency rose for the Luderitz area based on a 20 year database.

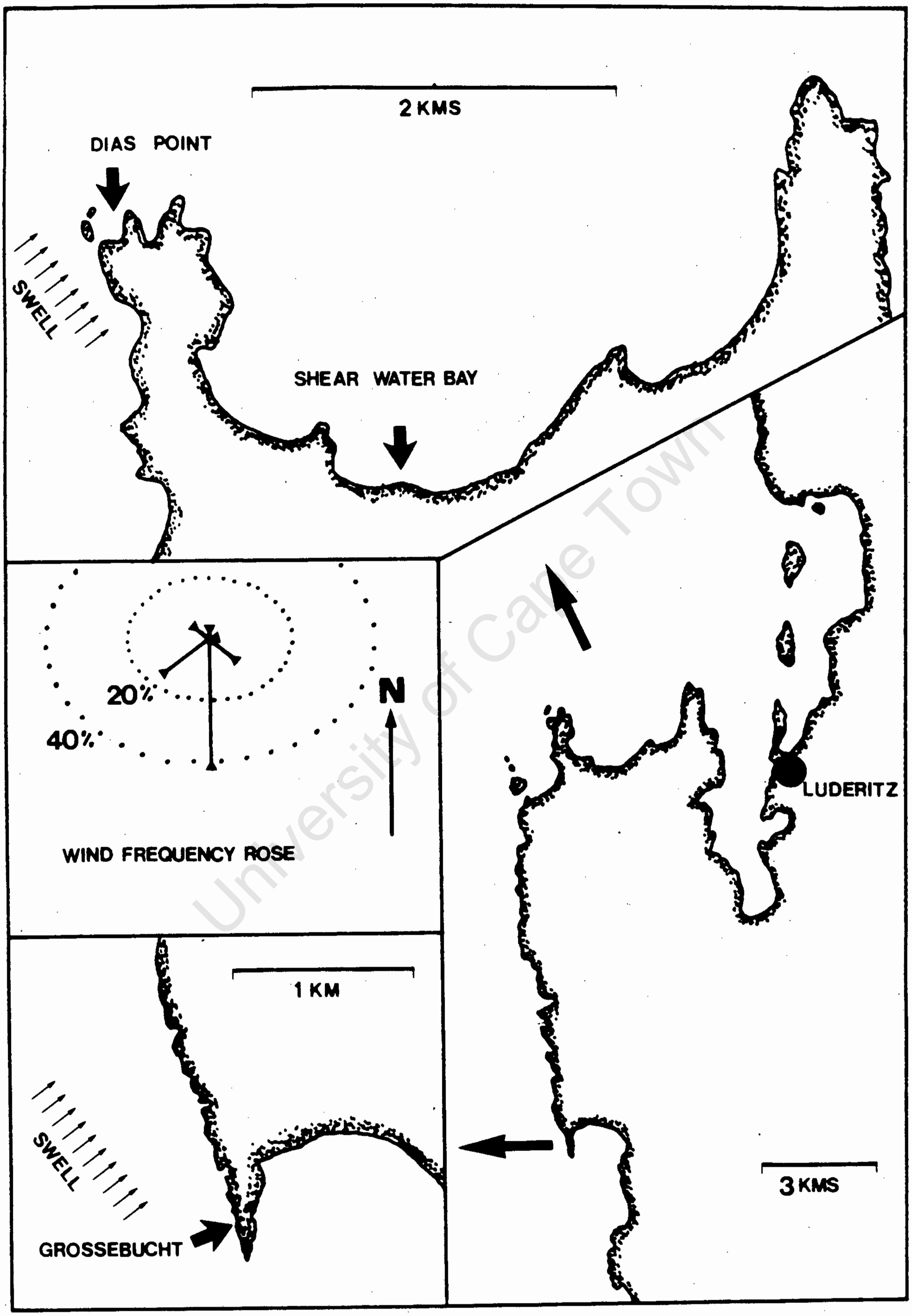
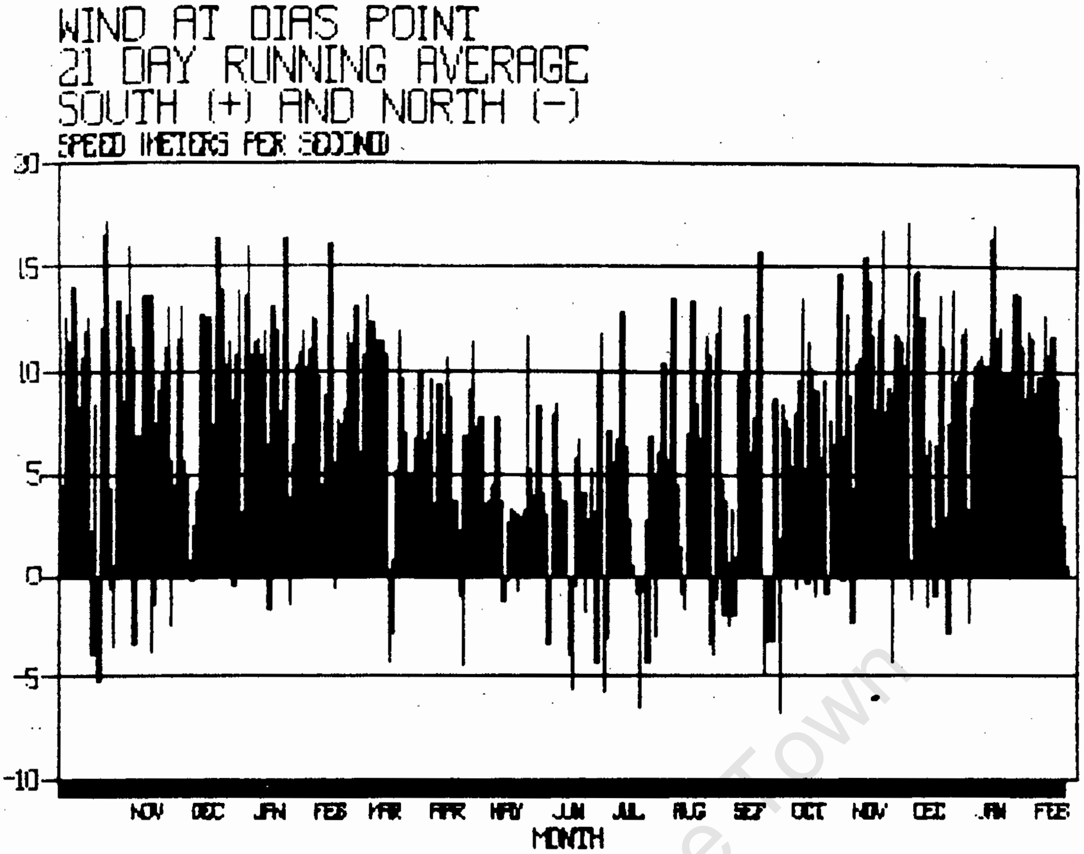

2 KMS
DIAS POINT
SWELL
SHEAR WATER BAY
20%
40%
N
WIND FREQUENCY ROSE
LUDERITZ
1 KM
SWELL
GROSSEBUCHT
3 KMS

Figure 5.3. South (+) and North (-) wind occurrence and speed over the seasonal growth experimental period. Data presented as a 21 day running average.

Figure 5.4. Apparatus for measuring progression of punched holes along the blades of *Laminaria pallida.* Transparent perspex was used to construct it with a hole at the 40 cm mark to facilitate re-punching.


WIND AT DIAS POINT
21 DAY RUNNING AVERAGE
SOUTH (+) AND NORTH (-)
SPEED (METERS PER SECOND)
30
15
10
5
0
-5
-10
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MONTH

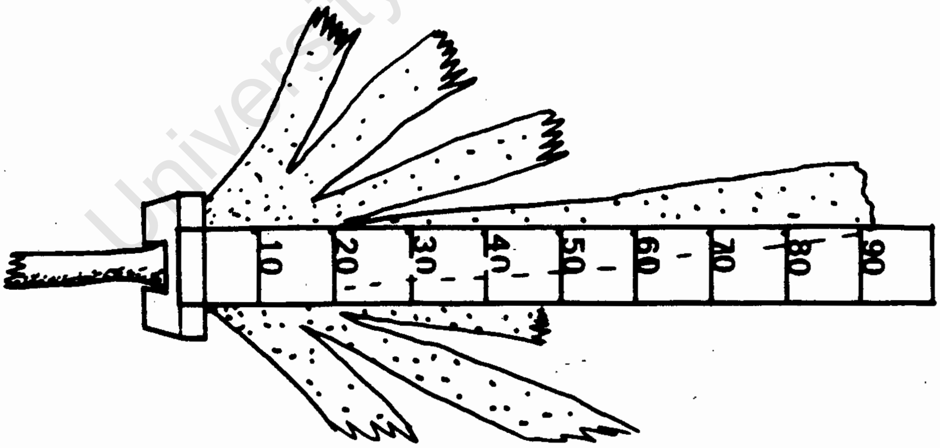
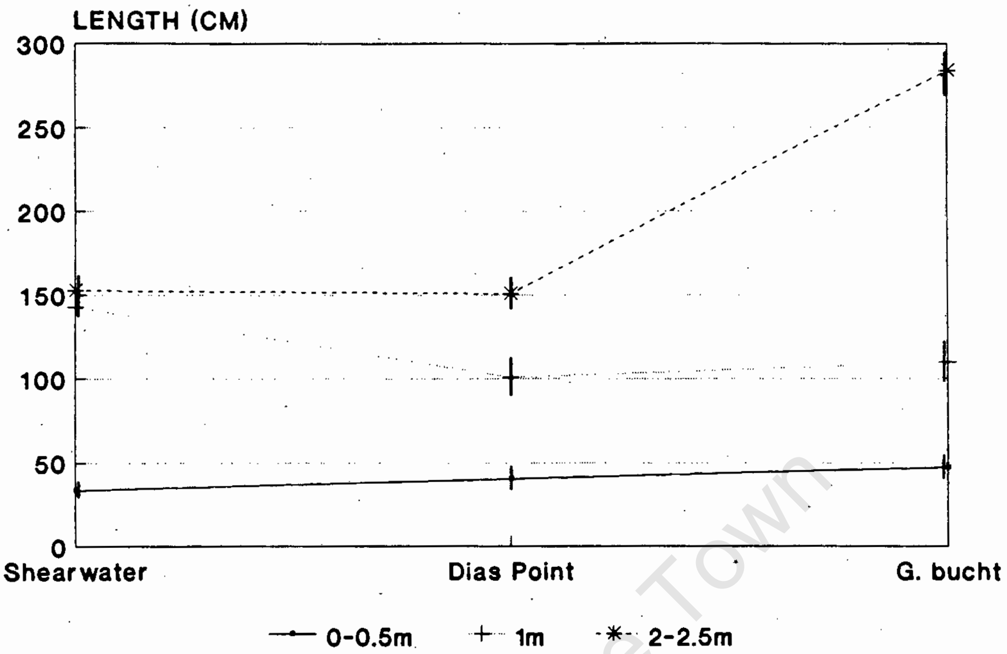

10
20
30
40
50
60
70
80
90

Figure 5.5. Mean length of stipes ± standard error (SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht.

Figure 5.6. Mean length of fronds (± SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht.

STIPE LENGTH



FROND LENGTH

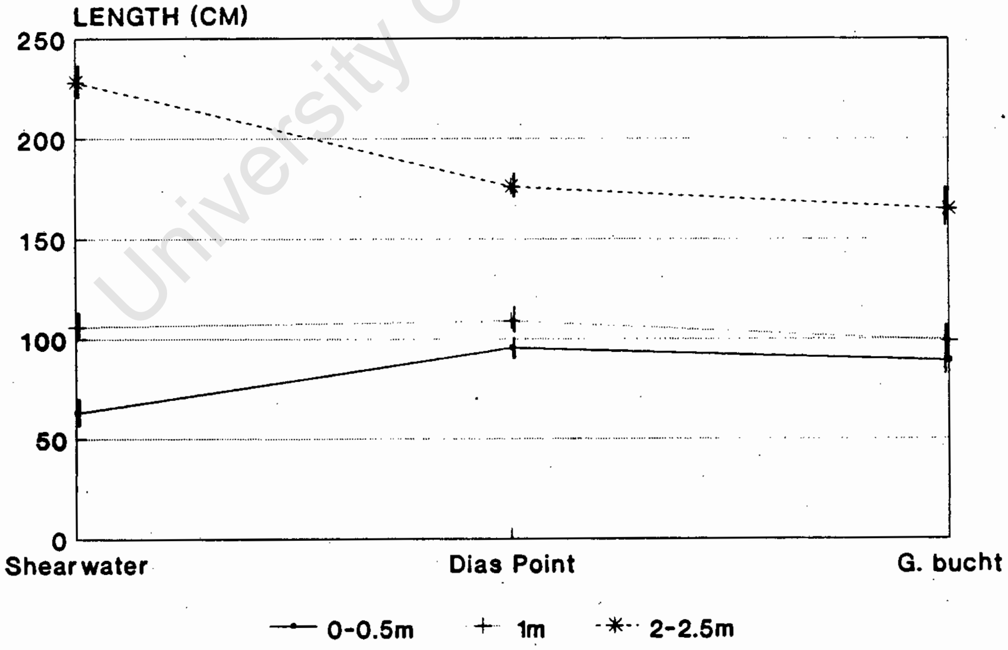
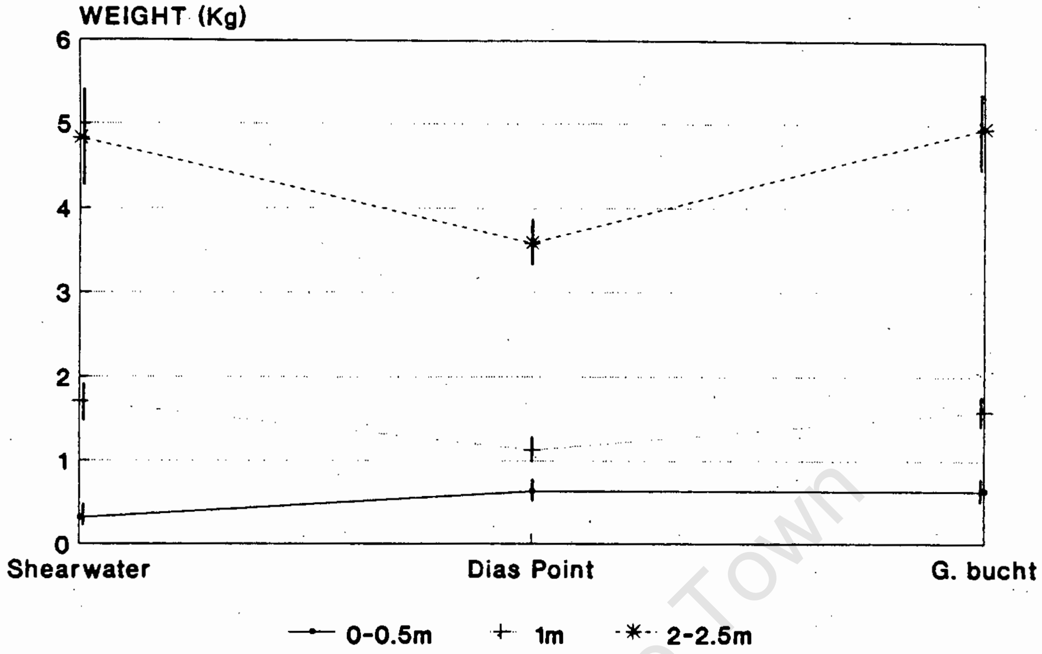
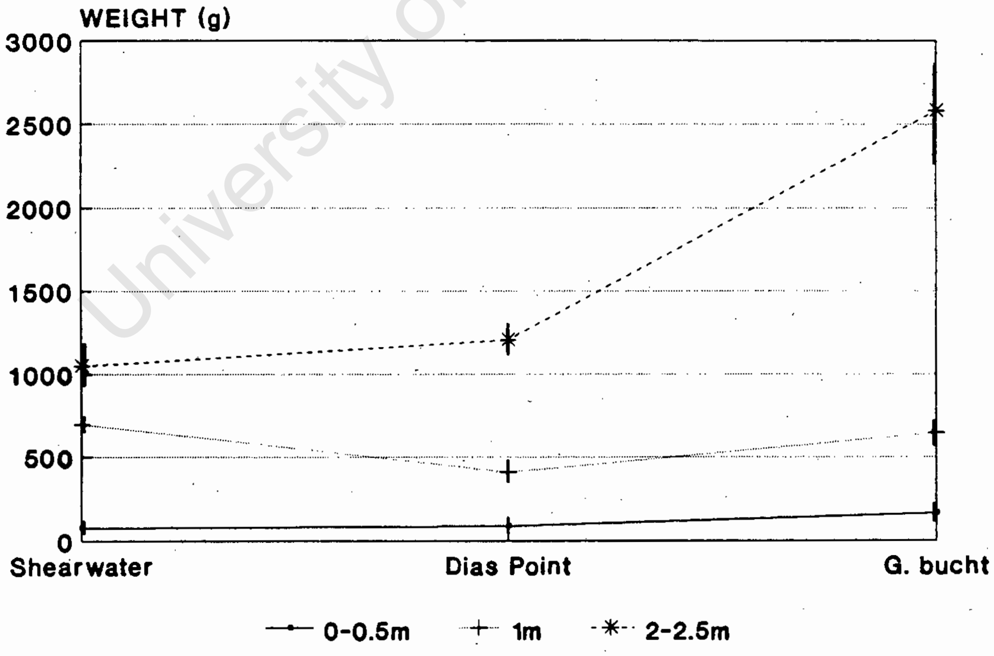


Figure 5.7. Mean total weight of plants (± SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht.

Figure 5.8. Mean total weight of stipes (± SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht.



TOTAL WEIGHT

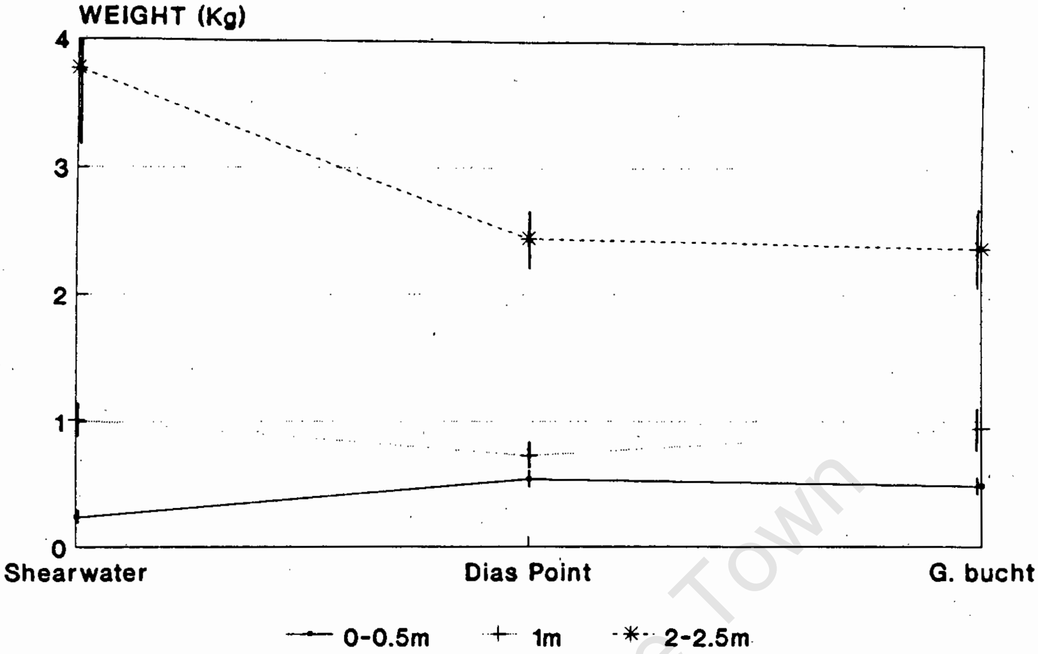


STIPE WEIGHT

Figure 5.9. Mean total weight of fronds (± SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht.

Figure 5.10. Mean frond surface area (± SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht

FROND WEIGHT



FROND SURFACE AREA

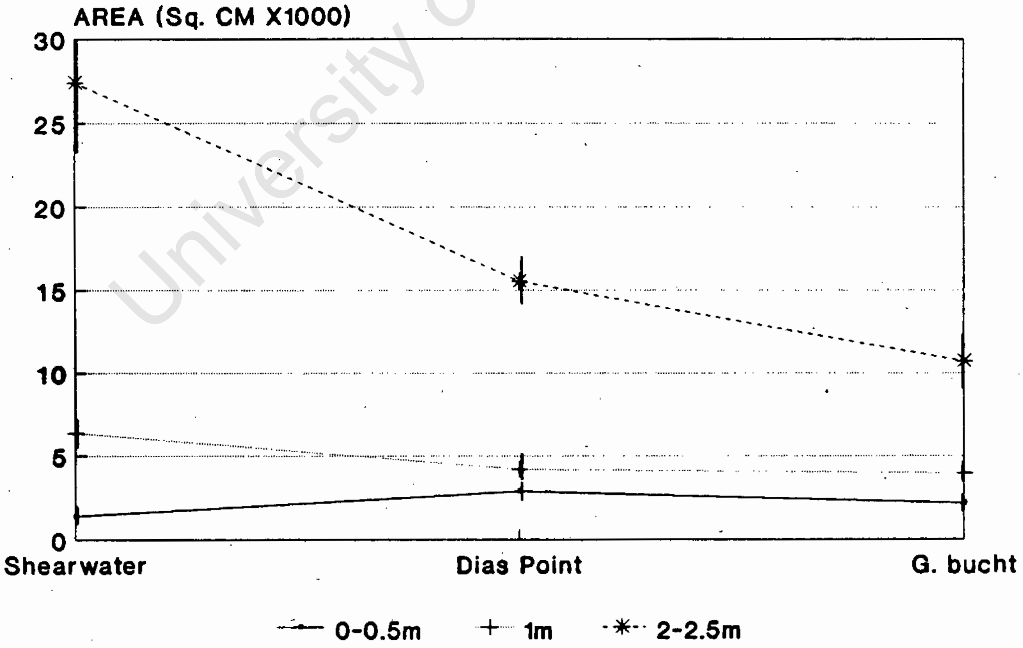
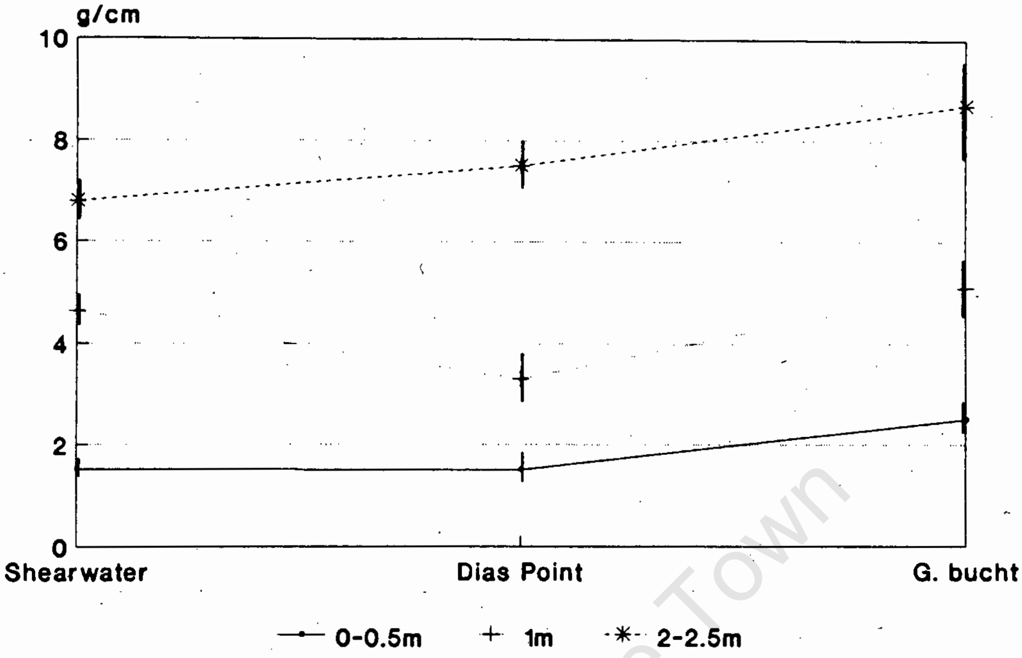


Figure 5.11. Mean stipe weight per unit length (± SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht.

Figure 5.12. Mean frond width (± SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht.

STIPE WEIGHT PER UNIT LENGTH



FROND WIDTH

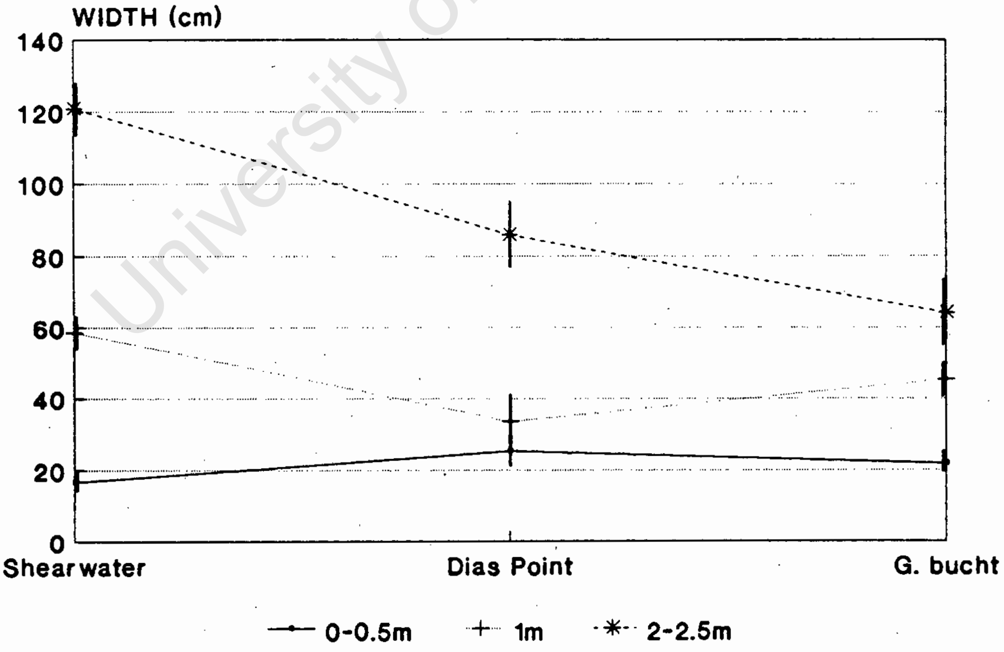
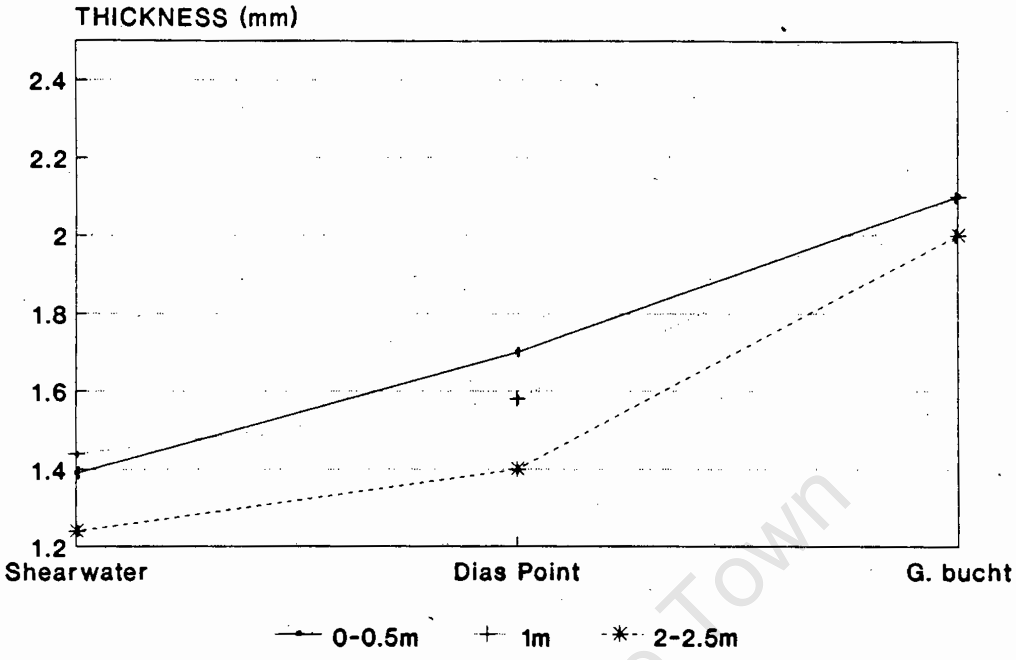
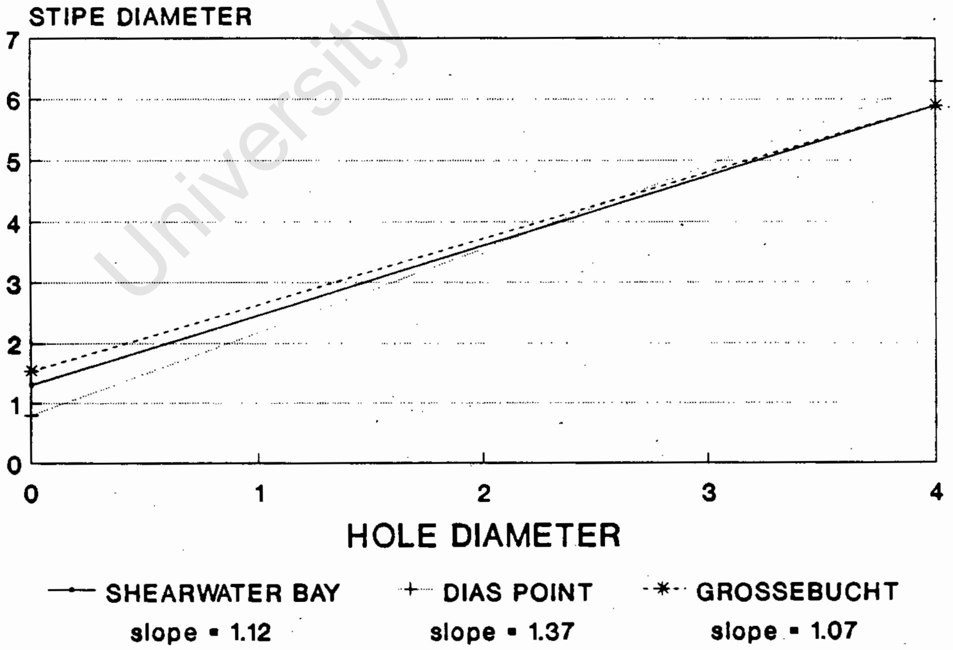


Figure 5.13. Mean frond thickness (± SE) at 0-0.5m, 1m and 2-2.5m depth at Shearwater Bay, Dias Point and Grossebucht.

Figure 5.14. Regression of stipe diameter against stipe lumen diameter at 1m at Shearwater Bay, Dias Point and Grossebucht. Slopes are given in the legend.



FROND THICKNESS



REGRESSION OF STIPE DIAMETER AGAINST LUMEN DIAMETER

Figure 5.15. Discriminant analysis of all measured characters of plants at 0-0.5m, 1m and 2m depth at Shearwater Bay, Dias Point and Grossebucht. Diagonal dashed line A-B links the deepest sites and represents an exposure gradient (A: exposed and B: sheltered) The dashed line C-D represents a depth gradient (C: shallow and D: deep).

1 = Shearwater Bay 0-0.5m
2 = Shearwater Bay 1m
3 = Shearwater Bay 2m
4 = Dias Point 0-0.5m
5 = Dias Point 1m
6 = Dias Point 2m
7 = Grossebucht 0-0.5m
8 = Grossebucht 1m
9 = Grossebucht 2m

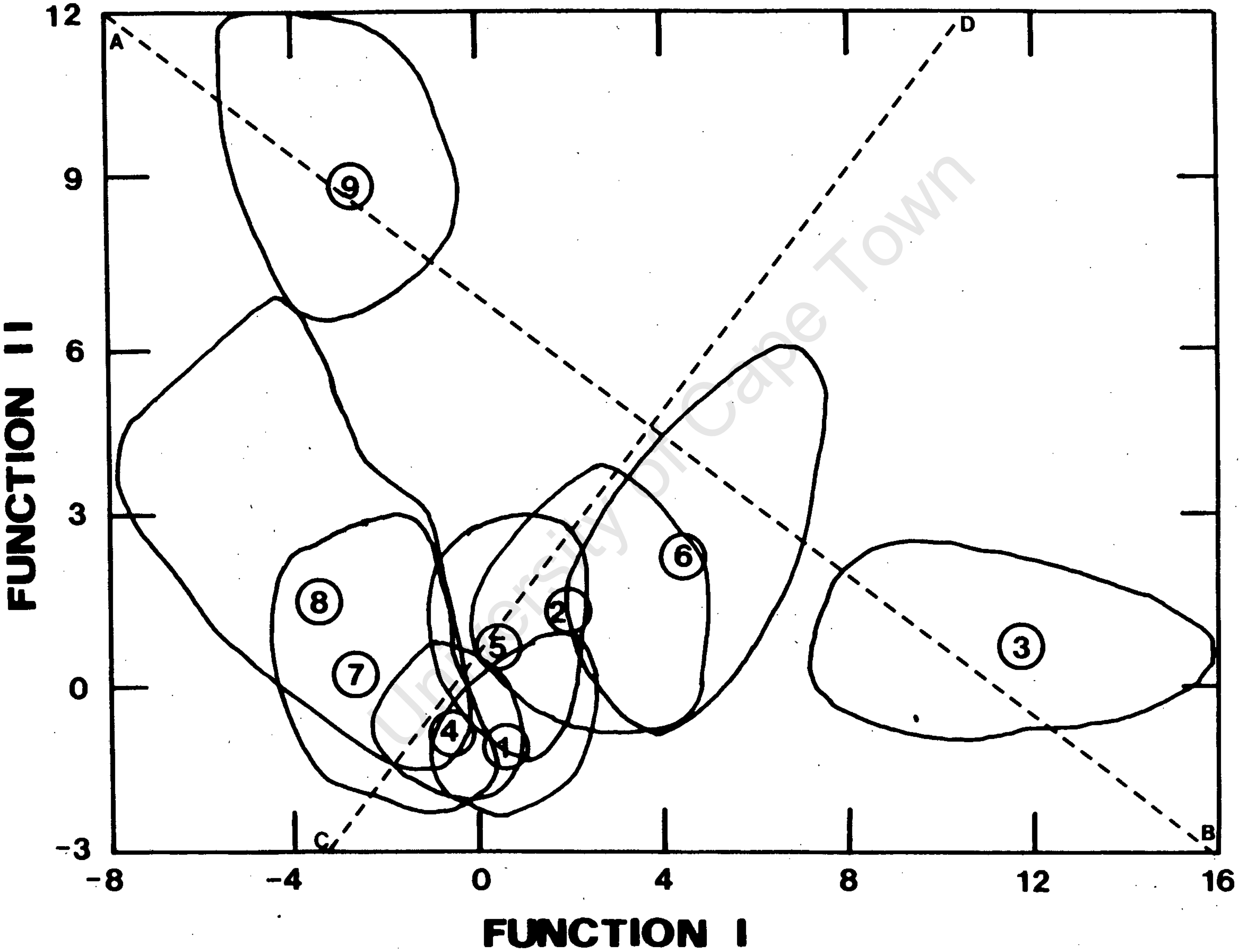

12
9
6
3
0
-3
-8
-4
0
4
8
12
16
FUNCTION II
FUNCTION I
A
B
C
D
1
2
3
4
5
6
7
8
9

Figure 5.16. Seasonal growth curves from November 1990 to April 1992 for: A. Shearwater Bay; B. Dias Point; C. Grossebucht at 1m depth. Each point represents a mean of between 15 to 30 plants (see text). D. mean temperature over each growth rate period.

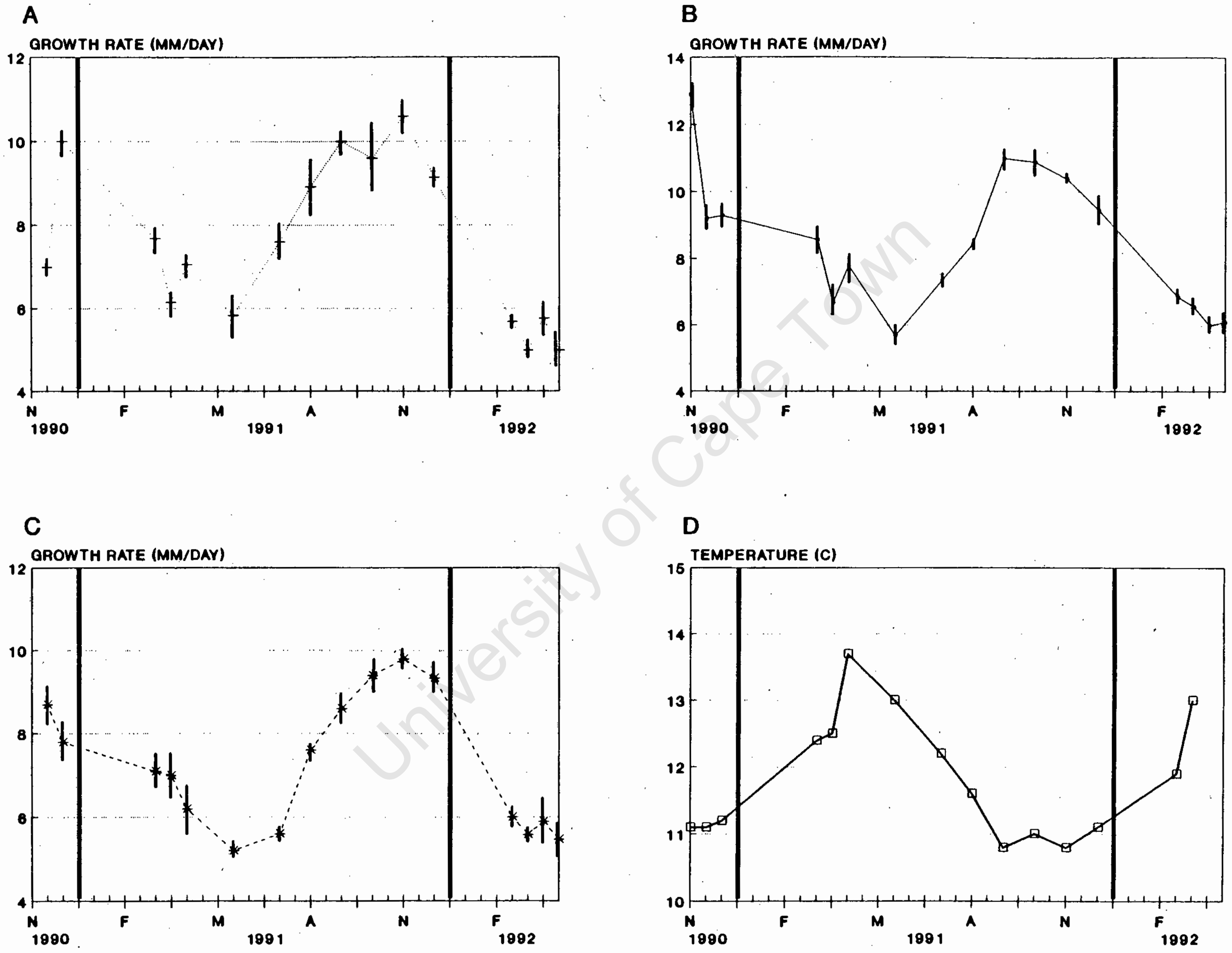
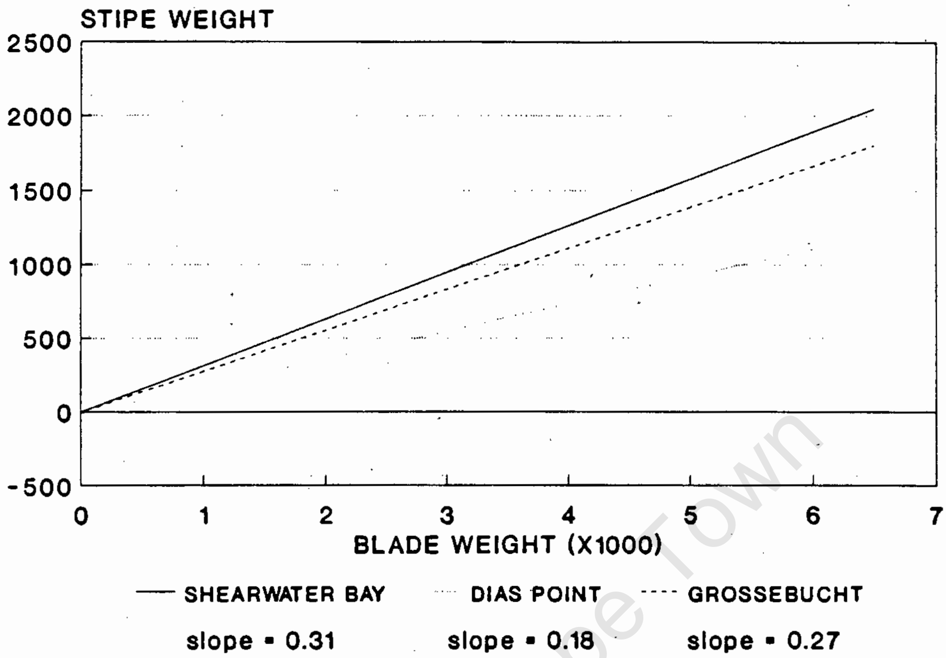

A
GROWTH RATE (MM/DAY)
12
10
8
6
4
N
F
M
A
N
F
1990
1991
1992
B
GROWTH RATE (MM/DAY)
14
12
10
8
6
4
N
F
M
A
N
F
1990
1991
1992
C
GROWTH RATE (MM/DAY)
12
10
8
6
4
N
F
M
A
N
F
1990
1991
1992
D
TEMPERATURE (C)
15
14
13
12
11
10
N
F
M
A
N
F
1990
1991
1992

Figure 5.17. Regression of stipe weight against frond weight at Shearwater Bay, Dias Point and Grossebucht at 0-0.5m depth. Regression slopes are indicated in the legend.

Figure 5.18. Regression of stipe weight against frond weight at Shearwater Bay, Dias Point and Grossebucht at 1m depth. Regression slopes are indicated in the legend.

REGRESSION OF STIPE WEIGHT AGAINST FROND WEIGHT AT 0-0.5M DEPTH



REGRESSION OF STIPE WEIGHT AGAINST FROND WEIGHT AT 1M DEPTH

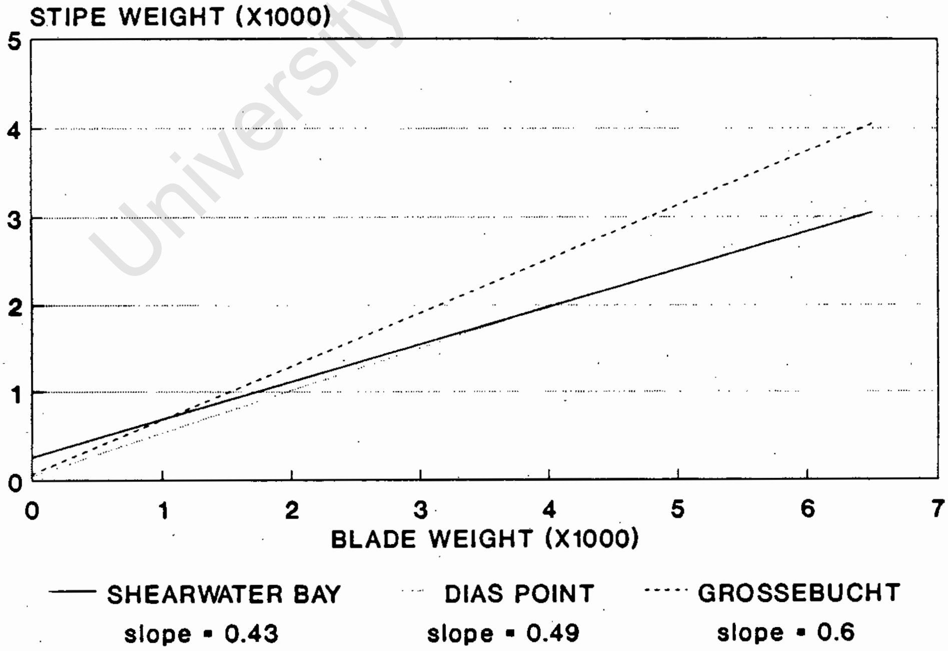
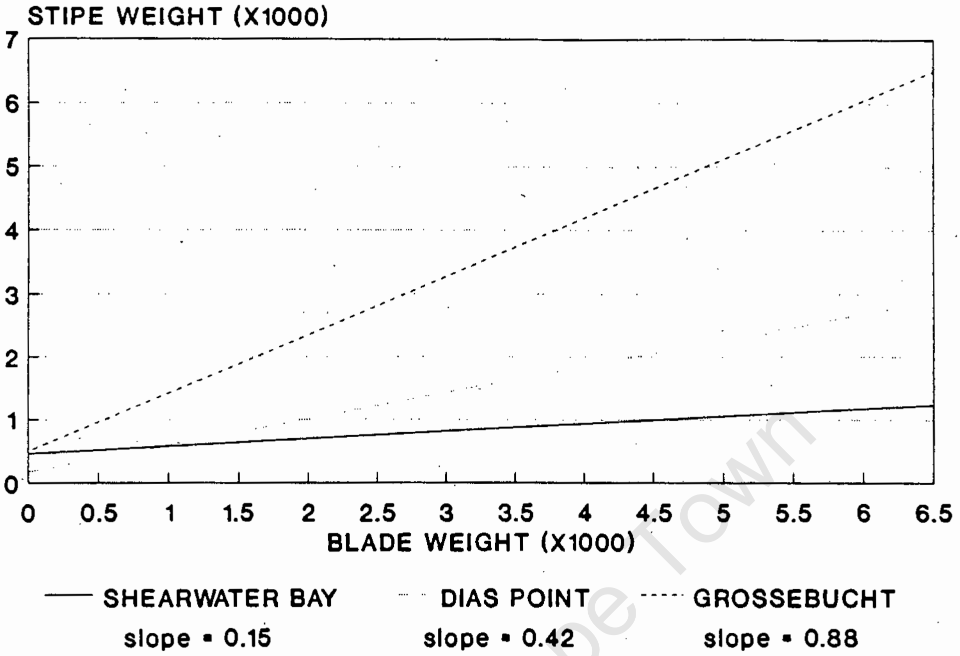
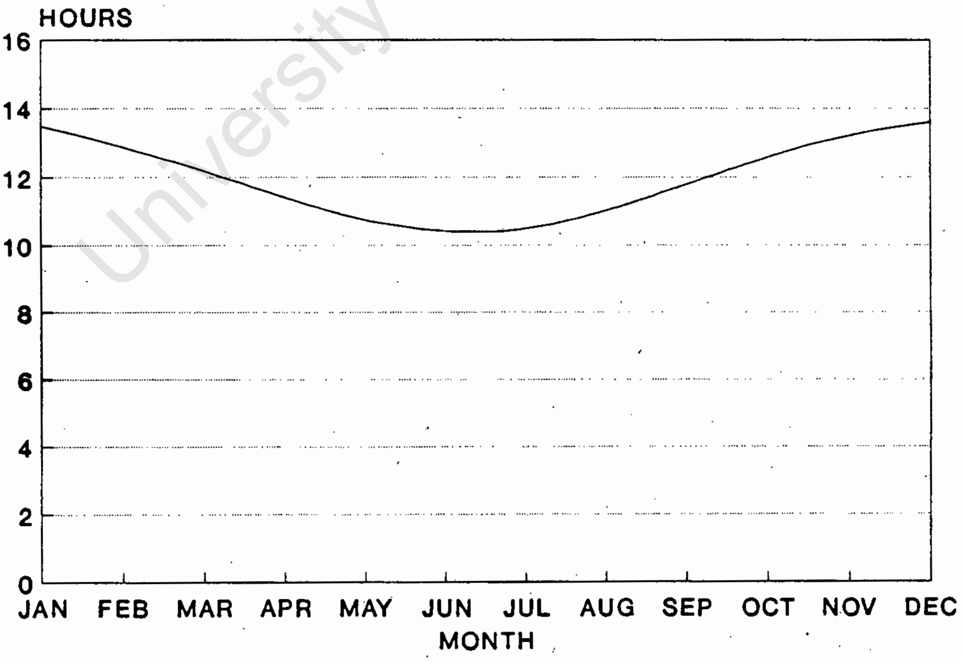


Figure 5.19. Regression of stipe weight against frond weight at Shearwater Bay, Dias Point and Grossebucht at 2-2.5m depth. Regression slopes are indicated in the legend.

Figure 5.20. Daylength curve for a year at the Luderitz latitude (26^{o} 39' S).

REGRESSION OF STIPE WEIGHT AGAINST FROND WEIGHT AT 2-2.5M DEPTH





CHAPTER 6

Seasonal growth of eulittoral seaweeds, with special reference to species of economic potential

6.1 Introduction

The intertidal habitat is the most environmentally variable of all marine ecosystems. Due to tidal cycles, the environment exhibits both marine and terrestrial characteristics and as such the plants that grow here must be able to survive extremes of both habitats. Intertidal seaweed stocks, from an exploitation point of view, are an attractive proposition as they can easily be collected.

Molloy (1990) gave a brief introduction to the seaweeds of possible economic importance on the Namibian coast and indicated that of the intertidal species, *Porphyra capensis*, *Aeodes orbitosa*, *Gigartina radula*, *Gigartina stiriata* and *Iridaea capensis* had potential for economic exploitation. In South Africa these species have been harvested at some time (*Gigartina radula* and *G. stiriata*) or have shown potential for harvesting (*Porphyra capensis*, *Iridaea capensis* and *Aeodes orbitosa*; Anderson *et al.*, 1989). As mentioned in Chapter 1., some work has been done on the distribution of Namibian seaweeds. Information on seasonality and response to environmental variables of these Namibian seaweeds is, however, unavailable.

The extent of the intertidal region, as the name suggests, depends primarily on tidal amplitude but the upper limits can be pushed further up the shore by exposure to wave action (Stephenson, 1944). Stephenson and Stephenson (1972) show that slope and aspect can also effect the upper and lower limits of organisms living on sea shores. Since the beginning of the last century, researchers have reported on the occurrence of zones of organisms growing on intertidal rocky surfaces (Doty, 1957) but as the limits of these zones are not merely dictated by tidal levels, researchers prefer to refer to biological zones rather than physical zones (Dring, 1982). The three main biological boundaries are 1) the upper limit of *Verrucaria*, blue-green algae and *Littorina*, 2) the upper limit of barnacles and 3) the upper limit of Laminarians, where these organisms are present (Dring, 1982).

Doty (1957) stated that the most important factors to organisms living along shores are light, temperature, wind, wave action, fog, tides, rain, human activity and ice. The latter three factors can be discounted in the case of Namibian shores as due to the (sub) tropical latitude (17° 30' S to 28° 20' S) and the coastal desert conditions, temperatures are never freezing and rain is a very rare occurrence. Human activity is minimal as the coast has a tiny population, major industrial pollution is absent and presently, no intertidal seaweeds are harvested.

Luning (1981) reviewed the effects of light on the biology of seaweeds. Eulittoral species are photosynthetically saturated at higher irradiance levels (500 umol m^{-2} s^{-1}) than sublittoral species (200 umol m^{-2} s^{-1}) and deep water red algae (100 umol m^{-2} s^{-1}). Growth saturation levels of light have been reported to be less than half the saturation point for photosynthesis the probable explanation being that the photosynthesis saturation experiments were of short duration but these levels of light, on the long term, may be inhibitory (Luning, 1981). All intertidal seaweeds are exposed to full sunlight at some period; the duration of this emersion increases higher up the shore to a point where populations highest on exposed shores may only be wetted by sea spray and large swells. Distruction of algal cells by UV light was mentioned by Luning (1990), this effect is probably more evident closer to the tropics.

As light passes through water, intensity is decreased and quality altered (Luning, 1990) and thus intertidal seaweeds are subjected to a range of different intensities and altered spectra throughout the course of the tidal cycle.

Intertidal seaweeds must be able to survive the range of ambient sea temperature as well as ambient air temperature, (which is usually much greater). Luning (1990) summarized the optimal water temperatures for growth of seaweeds from different regions as; 10-15° C for cold temperate species, 10-20° C for warm temperate species and 15-30° C for warm temperate to tropical species. Air temperatures, particularly in upwelling areas such as the Namibian coast, are usually far in excess of water temperatures. Further to this, exposed intertidal rock may become much hotter than the air, in the absence of wind, due to direct solar energy (Biebl, 1970).

Seaweeds absorb nutrients through their thalli from the surrounding seawater and thus intertidal seaweeds can only absorb nutrients when they are submerged. Nutrient uptake is influenced by light through photosynthesis stimulating growth and supplying energy for active transport and temperature which increases nutrient diffusion and cell metabolism (DeBoer, 1981). When submerged, intertidal seaweeds are exposed to the full nutrient concentration of ambient water through the relatively high water motion that exists in the intertidal environment (DeBoer, 1981).

Water motion, apart from affecting nutrient uptake, has very direct physical influence on the intertidal environment. Individuals may be damaged or torn free and increased exposure serves to increase the upper limits of the biological zones (Dring, 1982). "For intertidal species it is frequently observed that plants growing on exposed shores are usually tougher, shorter, narrower and often have stronger attachment structures than those growing in calmer situations" (Norton *et al.*, 1981). Koehl (1986) examined seaweed morphological change with exposure from an engineering perspective and discussed trade-offs that seaweeds in high energy habitats have to make, such as thicker plants having smaller surface area for photosynthesis.

The width of the intertidal is dictated by the tidal amplitude of the area. Tidal amplitude varies depending on the position of the moon and sun relative to the earth; at Luderitz the maximum amplitude is 1.8 m (Molloy, 1990). Tidal cycles may be diurnal (one high tide every day), semi-diurnal (two high tides, almost of equal height, per day), which is the case at Luderitz and mixed (two tides per day of quite different height; Doty, 1957). Water levels can be increased or decreased by the action of wind and swell.

The factors controlling zonation have not been satisfactorily explained although desiccation tolerance, the effect desiccation has on photosynthetic rate, and recovery of photosynthesis after desiccation play an important role (Dring 1982: Luning, 1990). Seaweeds do not have specialized morphological structures such as stomata to regulate the loss of water (Luning, 1990) so they have no protection against the factors controlling desiccation such as temperature, wind, humidity and the duration of emersion.

Competition, whether between individuals of the same species or different species or with animals, is an important part of a seaweeds' existence in the intertidal. Reviewing previous research, Luning (1990) suggested that the upper limits of the eulittoral zones are controlled by desiccation and the lower limits by competition. Carpenter (1990) reviewed competition from a physiological perspective and suggested that competition for space, light and nutrients would be the areas of most fruitful future research. Maggs and Cheney (1990) reviewed laboratory studies of competition.

Seasonality of intertidal seaweeds depends on the seasonality of the environmental variables they are subjected to ie. sea temperature, air temperature, light intensity, daylength, nutrient availability, humidity and cloud cover. Murray and Horn (1989) working on intertidal shores in the northeast Pacific, found that the "fleshy" seaweed biomass was maximal in late spring to late summer and the coralline seaweed biomass was maximal in winter or spring. The "fleshy" seaweed maximum correlated positively with daylength, upwelling and air temperature and the coralline maximum correlated positively with swell height, precipitation and seawater temperature. On an intertidal shore of the Cape Peninsula of South Africa, McQuaid (1985) found the seasonality of the dominant seaweed species to correlate most strongly with the height of lowest tides after a lag was incorporated. When optimal tidal conditions, high sea temperature and radiation coincided then biomass was particularly high. Seasonal biomass of *Gigartina radula* on the Cape peninsula was found to peak in the late summer (Bolton and Levitt, in press) and the seasonality of *Aeodes orbitosa* and *Iridaea capensis* on the same shores was found to be more marked than that of *Gigartina radula* with a summer maximum and winter minimum.

6.2 Materials and methods.

On the coast of Namibia, there are very few sheltered shores and thus two shores were chosen for this study to represent exposed and semi-exposed sites. The shore at Grossebucht (fig. 6.1), orientated in a north-south direction, is open to the full force of the Atlantic swell and the prevailing south westerly winds. At Halifax, the shore is in a recess on the north-south orientated shore and is offered some protection to the south. The shore at Grossebucht was very much more steep (dropping 235 cm in 35 m fig. 6.1) than the shore at Halifax (dropping 85 cm in 38 m; fig. 6.2). The rock on both shores was a dark metamorphic type crisscrossed with cracks and crevices. No boulders, rocks or sand were present on either shore.

In February 1990, five quadrat positions were randomly chosen on each shore from the high water mark to the bottom of the eulittoral zone (kelp bed edge) in the case of Halifax and as far down as possible due to swell at Grossebucht (40 cm higher than the bottom of the eulittoral zone; figs. 6.1 and 6.2). In February 1991 the number of quadrats was increased to 15 on each shore, ie. three replicates at each level, the results of which were averaged. An electric drill fitted with a 7 mm bit and connected to a portable generator was used to drill holes into the rock at each corner of each quadrat. Into these holes brass bolts of 8 mm diameter were hammered and a tag attached. This method was successful as very few of the bolts were lost over the duration of the experiment. On each visit to the shores, the percentage cover of all species in each quadrat was estimated and the quadrat photographed from the vertical using colour slide film. These slides were later projected onto a 20X20 cm grid divided into 2X2 cm squares so that the corner bolts of the quadrats were projected onto the corners of the square. The percentage cover of the dominant species was accurately calculated by first mapping, with a pen, the cover of each species. Then the number of squares, or portions thereof, covered by the seaweeds were added together and expressed as a percentage.

Sea surface temperatures (0.5m depth) were recorded once every day at Dias Point; air temperature, cloud cover, humidity and swell height were recorded three times each day at Dias Point by the Dias Point lighthouse staff, and an average of the three readings was calculated. Daylengths for each day were calculated using a "Basic" program (Appendix I). The program calculates daylengths for every day of the year when the latitude of the site in question is entered. Predicted lowest tides for each day at Luderitz were taken from the tide tables (Anonymous, 1990 and 1991). The environmental data for each sampling date was calculated as a mean of the interval since the previous sampling date. For February 1990 (the first sample) the mean of the previous 6.8 weeks (the length of a lag period, see data analysis) was calculated.

Shore profiles were made using a transect line marked off in meters and two poles (one 15 cm shorter than the other). Starting at the upper shore the top of the shorter pole, the top of the longer pole, further down the shore and the horizon were lined up, the distance between the poles which represented a drop of 15 cm was noted. The shorter pole was then moved to the position of the longer and the longer pole moved down the shore again until the tops of the two poles and the horizon were again in line and so on to the bottom of the eulittoral zone.

Data analysis were performed using the cross-correlation analysis with 6.8 week lag periods and the principal components analysis of "Statgraphics" (STSC, Inc., 1987). The cross-correlation analysis estimates the correlation between one time series at time t and a second at time $t+k$ as a function of the lag or time interval k. The program chooses the lag period as the average interval between sampling. For example the use of one lag period meant that the environmental conditions 6.8 weeks prior to the sampling dates were correlated to the sampling data. Principal components analysis (PCA) reduces the number of variables by finding linear combinations of the variables that explain most of the variation. PCA was performed on the abiotic variables to determine the seasonality of these variables, and on the maximum correlations between the abiotic and biotic variables (after cross-correlation).

6.3 Results.

6.3.1 Seasonality of abiotic variables.

Both sea and air temperature (fig. 6.3) peaked in late summer to early winter (13.2° C and 19.4° C, respectively, for 1990 and 12.7° C and 20° C for 1991) with seasonal lows in spring (10.8° C and 14.9° C, respectively, in 1990 and 10.8° C and 15.6° C, respectively, in 1991). Cloud cover (fig. 6.4) did not show an obvious seasonal pattern but did peak in spring (2.9 octers in 1990 and 2.78 in 1991) and humidity (fig. 6.4) peaked in autumn to early summer 1990 (78%) and then dropped to 60%, the lowest during the experimental period, in June 1990. Humidity, however, did not demonstrate a seasonal pattern. Low tides (fig. 6.5) were lowest in late winter early spring (15.2 cm and 14.2 cm above chart datum, respectively, in 1990 and 1991) and highest in autumn (22.9 cm and 24 cm for 1990 and 1991, respectively). Swell (fig. 6.5) was generally low from February to May and there was a trend towards larger swells from the start to the end of the experimental period. The lowest swells recorded were in May 1990 and the largest in July 1991. Daylengths (fig. 6.6), show a difference of 3 hours between maximum and minimum.

6.3.2 Abiotic variable correlations (table 6.1).

Sea temperature and air temperature correlated positively ($r = .8$, $p < .001$) without a lag and with two lag periods they both correlated positively ($r = .74$, $p < .01$ and $r = .81$ $p < .001$, respectively) with daylength. Low tide, with one lag period, correlated positively with daylength ($r = .89$, $p < .001$) and sea temperature and air temperature, with one lag period correlated positively with low tide ($r = .87$, $p < .001$ and $r = .75$, $p < .01$ respectively). Without a lag, humidity correlated positively with cloud cover ($r = .56$, $p < .05$). Cloud cover correlated negatively with air temperature ($r = -.65$, $p < .05$), swell correlated negatively with lowtide ($r = -.62$, $p < .05$), and daylength correlated negatively with cloud cover.

6.3.3 Seasonality of seaweed cover.

At Halifax and Grossebucht the highest cover of fleshy seaweeds was found on the upper shore (H1 and G1), midshore (H2, G2 and G3) had the lowest cover and the lower shore (H3, H4, H5, G4 and G5) had intermediate cover (figs. 6.7 and 6.8). The midshore had the highest concentrations of limpets (*Patella granularis* L. and *P. granatina* L.) there were no limpets on the upper shore and the lower shore was occupied by *P. argenvillei* Krauss..

Porphyra capensis was the only seaweed growing at level G1 and G2 (figs 6.7 and 6.9). Percentage cover at G1 was maximum from September 1990 to May 1991 and minimum during winter 1990 and autumn 1991 (maximum = 96.5 ± 2% (± standard error), minimum = 19.7%). At G2 the cover of *Porphyra* was maximum at the beginning of the study (February 1990, 68.5%) then decreased to zero in July 1990 and remained zero for the rest of the study except for July and August 1991 where cover was .5 to .6%.

Total "fleshy" seaweed cover at G3 (fig. 6.7) was maximal during spring through summer to early autumn. Maximum cover was at the beginning of the study, February 1990 (48.5%) with a very similar cover the following spring (47.2%). The winter minimum cover for 1990 was 30% and 1991 was 26.4 ± 6.1%. The dominant seaweed of G3 was *Chordariopsis capensis* with minor amounts of *Cladophora capensis, Leathesia difformis* and *Splachnidium rugosum* also present. The cover of *Chordariopsis* (fig. 6.10) followed a seasonal pattern very similar to the total fleshy seaweed seasonal pattern.

At level G4 (fig. 6.7) total cover of fleshy seaweeds was maximum in late spring through summer to early autumn with the seasonal low in winter to early spring. Peak cover was in February 1991 at 54.4 ± 6% and minimum in July 1990 (7.3%). The combined cover of *Gigartina radula* and *Gigartina stiriata* at G4 (fig. 6.11) was below 10% throughout the study except in October 1991 (13.3 ± 1.7%) and showed little seasonality. Cover of *Aeodes orbitosa* at G4 (fig. 6.12) was also low but exhibited a seasonal pattern with a peak in autumn 1991 (34.7 ± 7%) and seasonal minimum in winter to spring. *Iridaea capensis*, though absent for most of the study, did appear in summer 1990/91 and reached a maximum cover in December of 4.9%.

Fleshy seaweed cover at G5 (fig. 6.7) was maximal in late spring 1990 through summer and autumn to early winter 1991 (peak in December of 68.4%) and minimal in winter 1990 (28.2% in July) and late winter to early spring 1991 (25.8 ± 5% in August). The cover of *Gigartina* (fig. 6.11) being a major component of G5 was similar to the total cover pattern. The peak was in May 1991 at 54.4 ± 8%. Cover of *Plocamium rigidum* (fig. 6.10) did not show seasonality with peaks of 17.2% in September 1990 and 17 ± 4% in July 1991.

Porphyra capensis (fig. 6.9) was the only seaweed present at H1 (fig. 6.8), from 81% in February 1990 cover dropped to 0% in spring and peaked at 95.6 ± 5% in February 1991, the lowest cover for 1991 was 60.2 ± 4% in August.

Porphyra capensis (fig. 6.9), *Ulva* and *Nothogenia ovalis* were the only seaweeds at level H2 (fig. 6.8). From a peak of 93% in February 1990 cover dropped to below 10% for the rest of the study period. *Porphyra* disappeared after a peak of 39.4% in February 1990 and reappeared briefly in May 1991 (4.5 ± 1.5%).

Level H3 (fig. 6.8) was dominated by *Aeodes orbitosa* (fig. 6.12). Maximum cover of fleshy seaweeds occurred from late summer through autumn to winter (with a peak of 94.8 ± 2.8% in February 1991) and minimum cover occurred in late winter and spring (22.6% in October 1990 and 14.5 ± 4% in July 1991). *Aeodes orbitosa* cover followed a similar pattern.

Total cover of fleshy seaweeds did not show seasonality at level H4 (fig. 6.8), from a maximum of 93.9% at the beginning of the study (February 1990) cover dropped to 30.6% in June 1990 and from there fluctuated but the trend was a gradual increase towards the end of the study. *Aeodes orbitosa* (fig. 6.12) cover decreased from 21.8% in February 1990 to 0% in July 1990, remained at 0% until February 1991 (9.1 ± 2%) and then peaked in March 1991 at 30.5 ± 7%. From this peak cover decreased gradually towards the end of the study period. Cover of *Gigartina* (fig. 6.11) remained below 20% for the duration of the study but peaked in early winter 1990 (12% in May) and autumn to early winter 1991 (15.9 ± 2% in February). From a peak of 61.8% in February 1990, cover of *Codium* (fig. 6.10) dropped to 10% in July 1990, rose to 30.8% in December 1990 then dropped to 14.5 ± 2% in March 1991 and rose again to 55.8 ± 7% in August 1991.

The total fleshy seaweed cover of level H5 (fig. 6.8) from a peak of 60.1% at the beginning of the study, dropped to 11.9% in October 1990 and rose towards the end of the study to 50.6 ± 2.6% in October 1991. *Gigartina* (fig. 6.11) followed a similar pattern from a high of 27.5 ± 2.7% at the beginning of the study to 2.4% in October 1990 to 28.4 ± 1.9% at the end of the study. The highest *Aeodes orbitosa* (fig. 6.12) cover at H5 (fig. 6.8) occurred at the beginning of the study at 17.6%; for the rest of the study cover remained below 5%.

6.3.4 Relationships between abiotic variables and total fleshy seaweed cover (table 6.2).

Sea temperature correlated negatively with total fleshy seaweed cover at G1 (r = -.67, p < .01) after 2 lag periods, G3 (r = -.69, p < .01) after 1 lag period, G4 (r = -.79, p < .01) after 2 lag periods and G5 (r = -.66, p < .05) after 2 lag periods.

Air temperature correlated positively with total fleshy seaweed cover at H1 (r = .55, p < .05) without a lag and correlated negatively with G4 (r = -.61, p < .05) after 2 lag periods and H3 (r = -.58. p < .05) with 2 lag periods.

Cloud cover did not correlate with seaweed cover at any site.

Humidity correlated positively with total fleshy seaweed cover at G3 (r = .69, p < .01) without a lag and H4 (r = .61, p < .05) without a lag.

Low tide correlated positively with G3 (r = .63, p < .05) after 2 lag periods, G4 (r = .61, p < .01) without a lag, G5 (r = .55, p < .05) without a lag, H1 (r = .59, p < .05) without a lag and H3 (r = .84, p < .001) without a lag.

Swell did not correlate positively with any site but correlated negatively with H3 (r = -.59, p < .01) without a lag.

Daylength correlated positively with G1 (r = .55, p < .01) without a lag, G3 (r = .78, p < .01) without a lag, G4 (r = .76, p < .01) without a lag, G5 (r = .72, p < .01) without a lag and H3 (r = .69, p < .01) with 1 lag period.

6.3.5 Relationships between abiotic variables and seaweed species cover (table 6.3).

Sea temperature correlated negatively with cover of *Porphyra* at G1 (r = -.67, p < .01) after 2 lag periods, *Aeodes* at G3 (r = -.74, p < .01) after 2 lag periods, *Chordariopsis* at G3 (r = -.75, p < .01) after 1 lag period, *Aeodes* at G4 (r = -.69, p < .01) after 2 lag periods, *Iridaea* at G4 (r = -.7, p < .01) after 1 lag period and *Gigartina* at G5 (r = -.68, p < .01) after 2 lag periods.

Air temperature correlated negatively with *Aeodes* at G3 (r = -.67, p < .01) with 2 lag periods, *Chordariopsis* at G3 (r = -.62, p < .05) with 1 lag period, *Iridaea* at G4 (r = -.71, p < .01) after 1 lag period, *Plocamium* at G5 (r = -.56, p < .05) without a lag, *Aeodes* at H3 (r =-.62, p < .05) with 2 lag periods Aeodes at G4 (r = -.63, p < .05) with 2 lag periods and *Gigartina* at H4 (r = -.55, p < .05) after 2 lag periods. Air temperature correlated positively with *Porphyra* at H1 (r = .55, p <.05) without a lag period.

Cloud cover did not correlate with any seaweed cover and humidity correlated positively with cover of *Codium* at H4 (r = .6, p < .05) without a lag period.

Low tide correlated positively with cover of *Aeodes* at G4 (r = .82, p < .001), *Gigartina* at G5 (r = .67, p < .01), *Porphyra* at H1 (r = .59, p < .05), *Aeodes* at H3 (r = .82, p < .001) and *Gigartina* at H4 (r = .82, p < .001) all without a lag. There was a negative correlation between low tide and cover of *Chordariopsis* at G3 (r = -.6, p < .05) with 2 lag periods.

Swell correlated positively with cover of *Plocamium* at G5 (r = .63, p < .05) without a lag and daylength correlated positively with *Chordariopsis* (r = .59, p < .05) and *Gigartina* at H4 (r = .71, p < .01) both with 1 lag period and *Porphyra* at G1 ($r = .55$, $p < .05$), *Aeodes* at G3 ($r = .71$, $p < .01$), *Aeodes* at G4 ($r = .78$, $p < .01$), *Gigartina* at G5 ($r = .71$, $p < .01$) and *Aeodes* at H3 ($r = .67$, $p < .01$) all without a lag.

6.3.6 Ordination.

Principal components analysis (PCA) of the abiotic variables (fig. 6.13) and the sampling dates (fig. 6.14) show that seasonality was skewed i.e. summer and winter were not the extremes and chronologically close months such as February and December had very different climates. The first two axes accounted for 76.3% of the variation with the first axis accounting for 43.9%. There was a good separation of the variables along axis I from those that increase in autumn-early winter (sea temperature, air temperature and low tide) and those that increase in late winter and spring (swell and cloud).

A PCA ordination of the maximum correlations between the abiotic and biotic variables (after cross-correlation, figs. 6.15 and 6.16) described 67.9% of the variation with the first two axes, the first axis accounted for 41.9%. With this analysis the abiotic variables exhibit a clear separation along both axes. Axis I was thought to represent spring (-ve) to autumn (+ve) and Axis II, winter (-ve) to summer (+ve). Most of the component scores for Halifax fall in the autumn/winter sector of the ordination when sea temperature , air temperature, humidity and low tide were increasing and component scores for Grossebucht fall in the winter/spring sector when swell was increasing and the summer/autumn sector when daylength was increasing. The exceptions are *Porphyra* at G2 which fell amongst the Halifax scores and *Aeodes* at H3 and *Gigartina* at H4 which fell amongst the Grossebucht scores. *Iridaea* at G4 and *Plocamium* at G5 fell in the autumn/winter sector when swell was increasing.

6.4 Discussion

The shore at Grossebucht is more exposed to wave action than that at Halifax and the difference is exaggerated by the steepness of the shore at Grossebucht (fig. 6.1). Gentle slopes tend to reduce the effect of wave exposure (Dring, 1982). The large difference between the upper macrophyte limit and the edge of the kelp beds, between the sites (85 cm and 230 cm, respectively) indicates the large difference in wave exposure.

6.4.1 Seasonality of total fleshy seaweed cover (figs. 6.7 and 6.8)

Seasonal patterns in total cover were more evident at Grossebucht than Halifax, particularly in the lower shore. At Grossebucht cover was at a minimum during winter 1990 and increased for a prolonged period from spring through summer to autumn and decreased again in winter. The longest periods of maximum growth were at G1 and G5. On the other hand, at Halifax only H1 and H3 exhibited a seasonal pattern which was at a minimum in spring and maximum in autumn/winter. Though the lack of seasonality in total cover at H4 masks the seasonality of the component species, this is not the case in H5. Site H5 abutted on the kelp fringe and so it may have been the thrashing of kelp fronds rather than variations in growth which resulted in a pattern that did not correlate with any abiotic variable tested. McQuaid (1985) found heavy grazing by *Patella cochlear*, to have an impact on macrophyte growth in this zone on the Cape Peninsula of South Africa. *Patella cochlear*, however, does not occur on the Namibian coast nor does the "cochlear" zone, which is characterized by low macrophyte biomass and high densities of *P. cochlear*. The high cover at G2 and H2 at the beginning of the study and the subsequent reduction to very low cover in the case of H2 and disappearance in the case of G2, cannot be explained by the abiotic variables tested. The fact that this phenomenon occurred on both shores suggests that the causal factor was environmental or at least triggered by an environmental factor or factors.

The direct effect of the single variables tested in this study can be discounted but they may have acted in concert or one or more of them may have influenced the population of the limpet *Patella granitina* and *P. granularis* which inhabits this zone and grazes on seaweed sporelings. This level on each shore was dominated by *Porphyra capensis.* McQuaid (1985), working on a shore on the Cape Peninsula of South Africa also found *P. capensis* to appear and disappear without apparent explanation. The irregular appearance may relate to the effects of environmental and/or biotic factors on the conchocelis phase, the whereabouts of which has never been documented in this species, and subsequent recruitment by the macroscopic gametophytes.

6.4.2 Species seasonality (figs. 6.9 to 6.12).

The main species under scrutiny in this study, *Porphyra capensis*, *Aeodes orbitosa* and the two *Gigartina* species all demonstrated a seasonal pattern of percentage cover at most levels on the two shores. Seasonality was most marked in *P. capensis* and least in *Gigartina* with *Aeodes orbitosa* intermediate. This was found to be true of *A. orbitosa* and *G. radula* growing on the Cape west coast of South Africa (Bolton and Levitt in press). The exceptions were G2 and H2 as mentioned before and H5 where no seasonality could be found for any species. Percentage cover for each of the main species on both shores at all levels peaked in autumn with the exception of the aforementioned G2, H2 and H5. *Iridaea capensis*, though a minor component of these shores, is a potentially exploitable carrageenophyte. This seaweed was absent for most of the study then appeared at G4 in spring 1990, peaked in December 1990 and disappeared again the following autumn correlating negatively with sea and air temperature. Abundant stands of *I. capensis* were found to occur predominantly on sand affected shores on the west coast of South Africa (Bolton and Levitt, in press); neither of the shores in this study were affected by sand. Other species were included in this study not because of economic potential but because of their dominance (*Codium* and *Chordariopsis*) or because of apparent competition (*Plocamium*).

6.4.3 Relationships between abiotic and biotic variables (tables 6.1, 6.2 and 6.3). The most influential factor on sea temperature in the Luderitz area is upwelling. The prevailing south westerly winds which drive the upwelling of the Benguela system were said to show little seasonality north of about 31° S (Branch and Griffiths, 1988). Stander (1964) however, stated that the most active upwelling season for the northern Benguela was late winter and spring. Bailey (unpubl.), after analyzing Dias Point wind data suggested that August/September to January/February was the period of maximum south westerly winds. After analyzing a 10 year sea surface temperature data set from Luderitz harbour, Roux (pers. comm..) found that spring was the season of lowest temperature and autumn to early winter the period of highest. This is also evident from figure 6.2. It is not surprising that air temperature correlated well with sea temperature as the recording station was right on the coast and the prevailing winds came off the sea.

The seasonality of daylength and light intensity show the same pattern world wide, highest in summer and lowest in winter. So, there is a situation where the two most important abiotic factors viz. light and temperature (Doty, 1957) have different annual maxima and minima; the two do correlate well but only with a lag of 3 months.

Sea temperature, air temperature, cloud cover and humidity are all affected by upwelling and the factors that cause it, though no correlation could be found between humidity and temperature but cloud cover correlated negatively with air temperature. On the other hand, low tide, swell and daylength are independent of the above variables though strong correlations do exist between some variables in the two groups (table 6.1).

Though sea temperature did have a significant negative correlation with most of the biotic variables at Grossebucht it is unlikely that higher sea temperatures were inhibiting growth and vice versa. Firstly, sea temperature variation for the area is small (fig. 6.3) and secondly, intertidal seaweeds usually have a wide tolerance of temperatures (Luning, 1990). Air temperature, on the other hand, has a wider variation than sea temperature and as such may indeed have had an influence as indicated by the significant negative correlations at Grossebucht. The effect of air temperature, however, would have been somewhat decreased by the timing of low tides as at Luderitz, low spring tides fall in the morning and evening (Anon., 1990b and 1991). Due to less wave exposure and consequent splash it is surprising that air temperature did not have a more significant effect on the seaweeds at Halifax.

Cloud cover did not correlate with any biotic variable because cover of cloud is so small on this coast and that which does exist, does not follow a seasonal pattern (fig. 6.4). Humidity exhibited little seasonality but did correlate with total seaweed cover at G3 and H4 and with *Codium* at H4.

Intertidal seaweeds have been reported to be well adapted to their environment (Quadir *et al.*, 1979), seaweeds from higher up the shore had a higher photosynthetic rate when emerged and those from lower had a higher photosynthetic rate when submerged. On the Cape Peninsula of South Africa, Levitt and Bolton (1991) found that upper shore *Porphyra capensis* had a high photosynthetic rate when emersed, mid-shore *Gigartina radula* did not have as high a photosynthetic rate and lower shore *Bifurcaria brassicaeformis* Kuetz. had the lowest rate when emersed. They suggested that the plants were physiologically adapted to their position on the shore but that the morphology of the thalli also played a role in this difference. Duration of emersion and submersion depends on the position on the shore and the tidal cycles. Tides not only follow daily cycles but also follow longer term biweekly and annual cycles (fig. 6.5; Doty, 1957; McQuaid, 1985) and these cycles could affect cover of macrophytes. The pattern of low tides correlated well with many of the biotic variables and the best correlations of any biotic and abiotic variables were found between low tide and *Aeodes* at G4 and H3, *Gigartina* at H4 and total cover at H3 (table 3). After one lag period, low tide correlated very well ($p < .001$) with daylength (table 6.1) and daylength correlated with more biotic variables that any other abiotic variable (table 6.3). It is difficult to say that one was more important than the other because of this intercorrelation, but the two probably enhance each other.

Swell had a significantly positive correlation with lower shore *Gigartina* and *Plocamium* at Grossebucht. It is possible that through the removal of other seaweeds by large swell, a competitive edge was given to these seaweeds. Also, the high exposure of Grossebucht may have raised the level of *Plocamium,* which is predominantly subtidal (Simons, 1976). *Gigartina radula* is common down to 5m on the Cape Peninsula but from its light saturation levels it is especially adapted to an intertidal existence (Levitt and Bolton, 1990)

The PCA ordination of the abiotic variables (figs. 6.13 to 6.16) shows that seasonality is not as obvious as has been shown in other areas (Murray and Horn, 1989; McQuaid, 1985) so it is not surprising that on a PCA ordination of abiotic and biotic correlations, the biotic component scores are widely and irregularly distributed in the ordination. The fact that the 2 axes represent opposite seasons, axis I spring and autumn and axis II summer and winter indicates that on the Namibian coast autumn and spring are not merely intermediary between summer and winter with similar environmental factors, but are very different. The change in environmental factors from summer to autumn was sudden and the return through winter to summer was more gradual. Despite the very different environments of each season, most of the seaweeds showed remarkable seasonality with daylength and temperature being the important factors. This seasonality was found at every level on the two shores and in contrast to Murray and Horn's (1989) findings, the macrophyte cover on the upper shore exhibits the strongest seasonality. The two shores were different in the degree of wave action they were exposed to as well as having different slopes. Cover of *Aeodes* was greater at the semi-exposed and cover of *Gigartina* was greater at the exposed site, and total cover of fleshy seaweeds tended to peak later at Halifax than Grossebucht. Degree of exposure was probably responsible for the smaller cover of *Aeodes* at Grossebucht as this species has been documented as preferring shelter and indeed the largest *Aeodes* thalli are found in sheltered lagoons (pers. obs.; Bolton and Levitt, in press).

6.5 Conclusions.

1) Intertidal seaweeds on the Namibian coast show marked seasonality despite small variations in two important environmental factors *viz.* temperature and light.

2) Autumn was the season of maximum cover for most species tested but these maxima also often spanned summer and early winter.

3) Differences in exposure result in changes in abundance e.g. *Aeodes* was more prolific at Halifax and *Gigartina* more prolific at Grossebucht, and peak coverage tended to occur later in the less exposed shore.

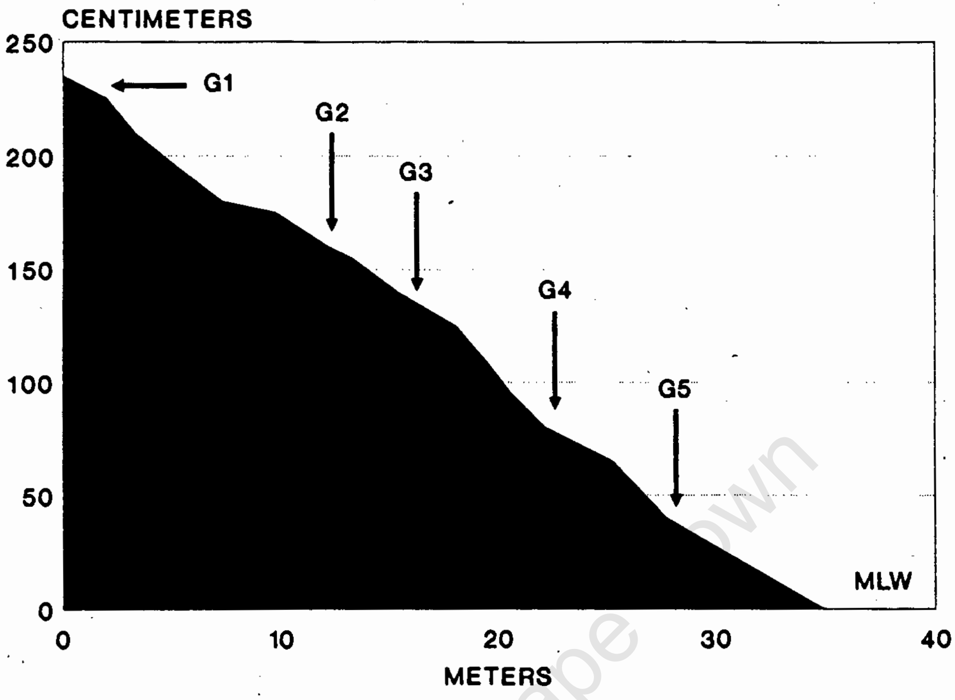
4) The 4 marine seasons at Luderitz are quite different from one another. On the basis of only 2 environmental variables (temperature and daylength) this can be seen: summer = low temperature, long daylength; autumn = high temperature, medium daylength; winter = high temperature, short daylength and spring = low temperature, medium daylength.

5) The optimum time for harvesting *Porphyra capensis*, *Aeodes orbitosa* and the two *Gigartina* species would be late summer through autumn to early winter. but impact on recruitment would first have to be determined.

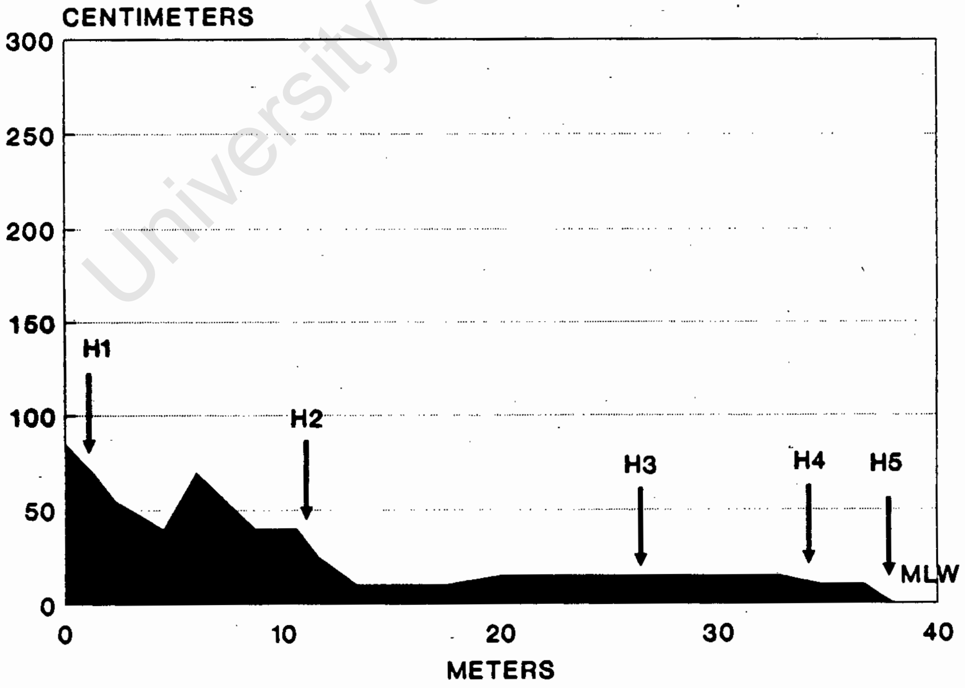
6) Due to intercorrelation between many of the abiotic variables such as sea temperature, air temperature, low tide and daylength (after lag periods), it is difficult to separate their respective importance. Laboratory studies would be needed for this purpose.

Figure 6.1. Profile of the shore at Grossebucht with the position of the permanent quadrats indicated.

Figure 6.2. Profile of the shore at Halifax with the position of the permanent quadrats indicated.



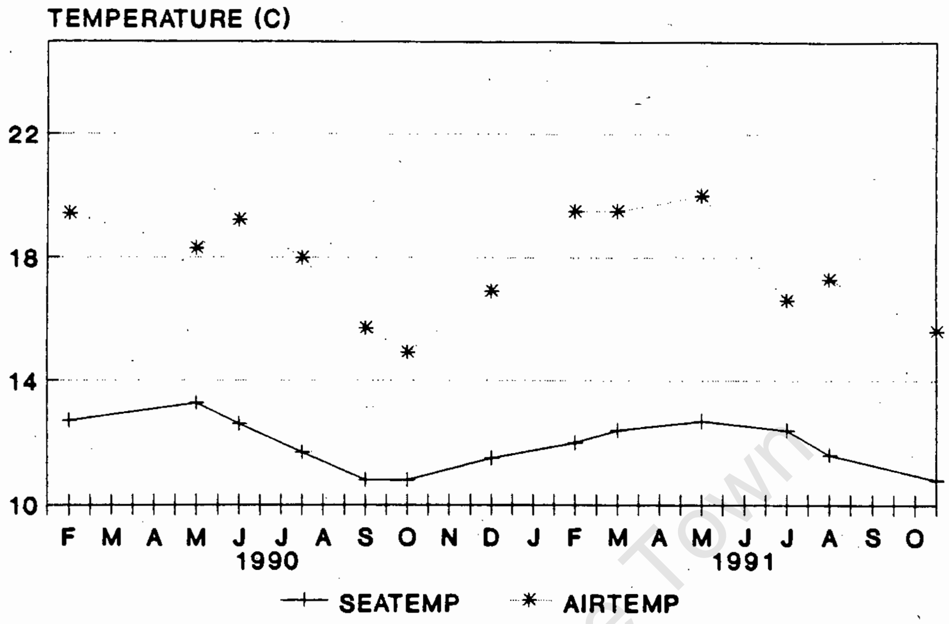
GROSSEBUCHT



HALIFAX

Figure 6.3. Sea temperature and air temperature over the experimental period. Each point is the mean of the interval between sampling dates, the first point is the mean of the previous 6 weeks.

Figure 6.4. Cloud cover and humidity over the experimental period. Each point is the mean of the interval between sampling dates and the first point is the mean of the previous 6 weeks. Cloud cover is given in octers (1 octer = one eighth of the sky).


TEMPERATURE (C)
22
18
14
10
F M A M J J A S O N D J F M A M J J A S O
1990
1991
SEATEMP
AIRTEMP

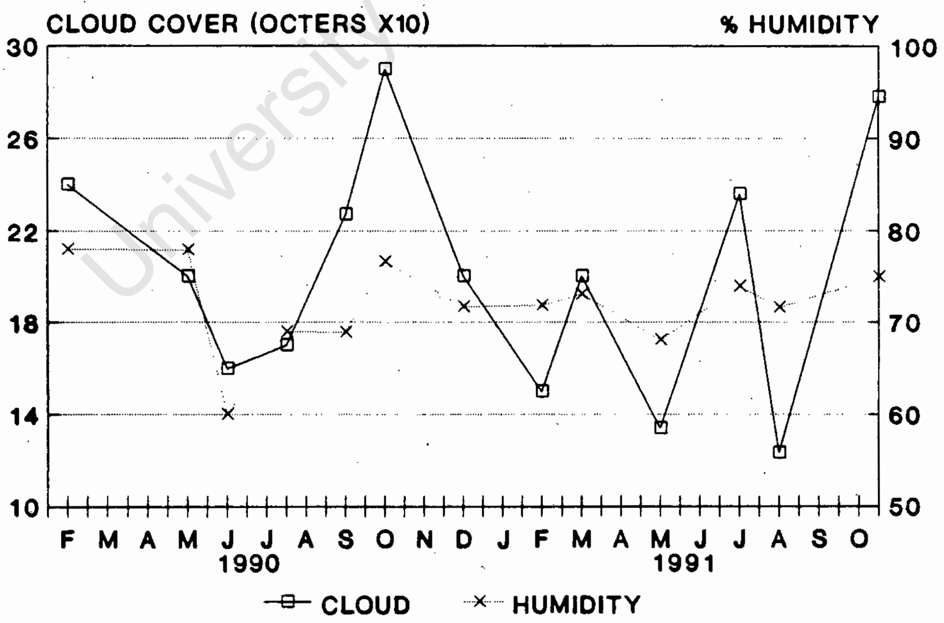
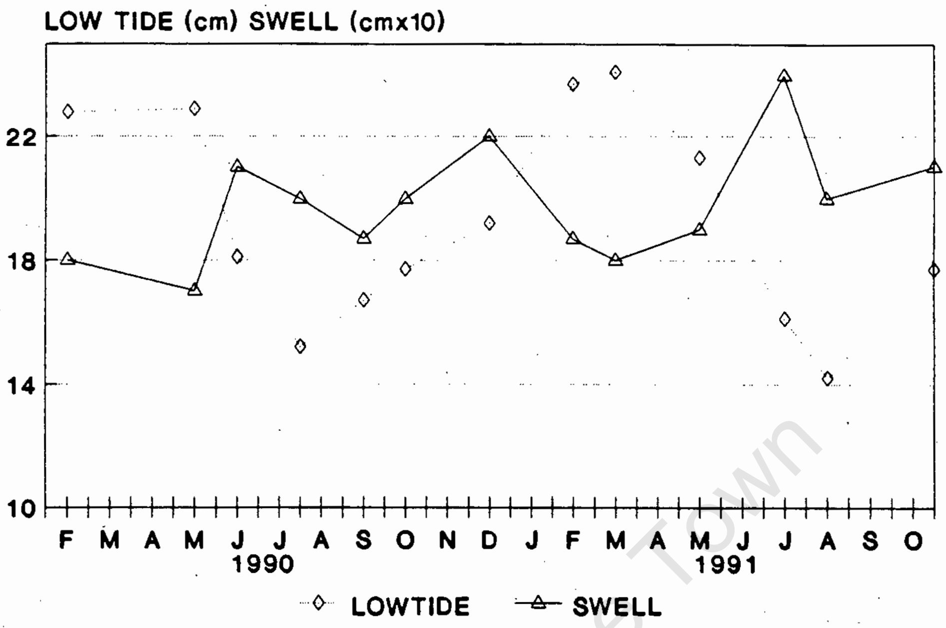

CLOUD COVER (OCTERS X10)
% HUMIDITY
30
26
22
18
14
10
100
90
80
70
60
50
F M A M J J A S O N D J F M A M J J A S O
1990
1991
CLOUD
HUMIDITY

Figure 6.5. Lowtide (average of the lowest per day)and swell height over the experimental period. Each point is the mean of the interval between sampling dates, the first point is the mean of the previous 6 weeks.

Figure 6.6. Daylengths obtained from a "Basic" computer program (appendix I) for the Luderitz latitude. Each point is the mean of the interval between sampling dates and the first point is the mean of the previous 6 weeks.


LOW TIDE (cm) SWELL (cmx10)
22
18
14
10
F M A M J J A S O N D J F M A M J J A S O
1990
1991
LOWTIDE
SWELL

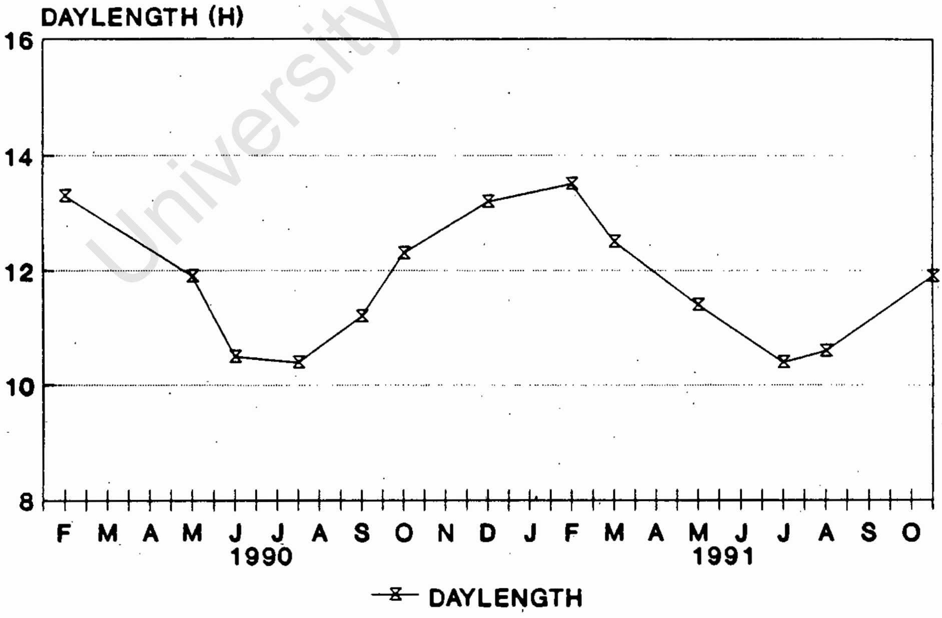
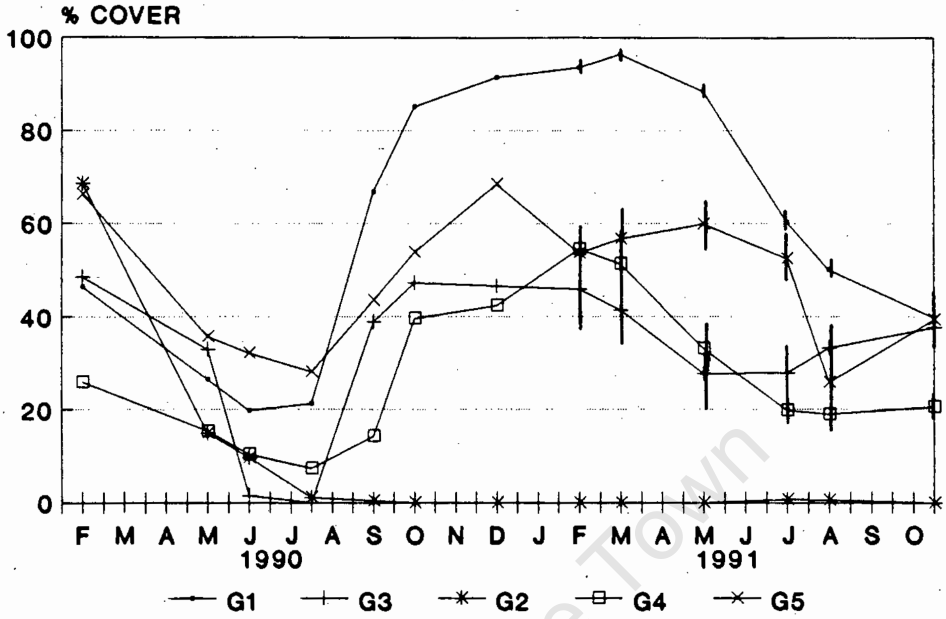
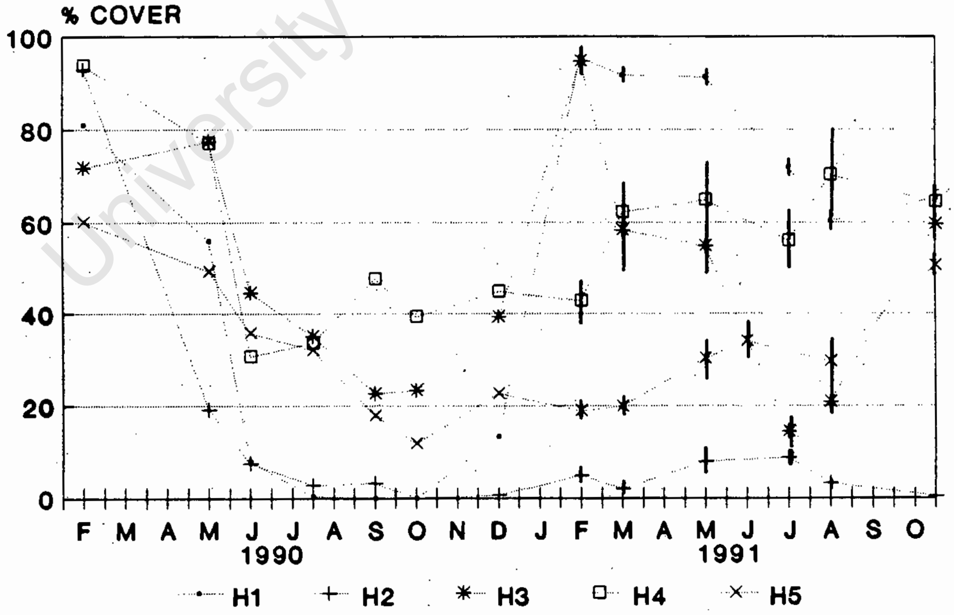

DAYLENGTH (H)
16
14
12
10
8
F M A M J J A S O N D J F M A M J J A S O
1990
1991
DAYLENGTH

Figure 6.7. Total fleshy seaweed cover all 5 levels at Grossebucht, Standard errors (± 1) are given as from Feb. 1991

Figure 6.8. Total fleshy seaweed cover for all 5 levels at Halifax. Standard errors (± 1) are given as from Feb. 1991.



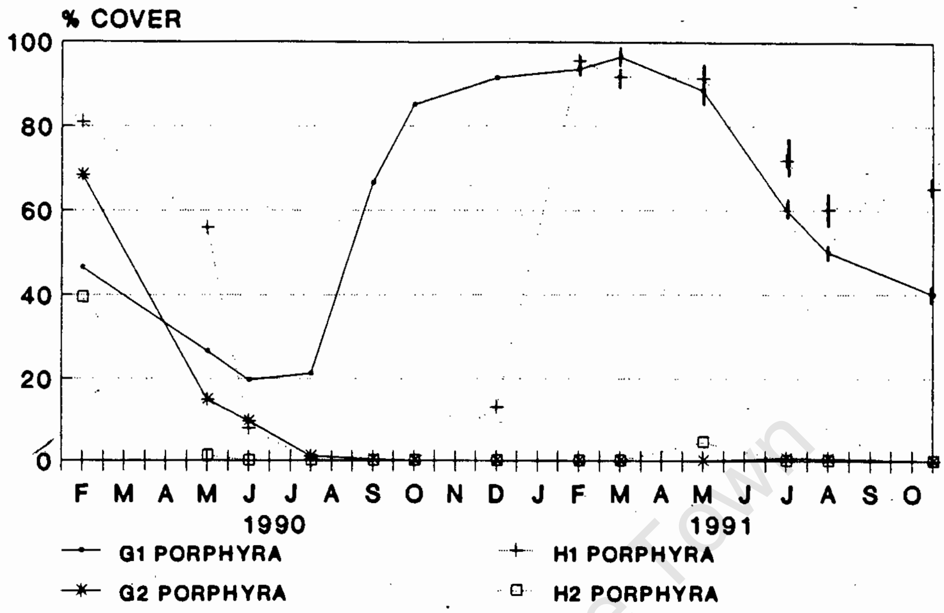
% COVER
100
80
60
40
20
0
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1990
1991
G1
G3
G2
G4
G5



% COVER
100
80
60
40
20
0
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1990
1991
H1
H2
H3
H4
H5

Figure 6.9. Cover and occurrence of *Porphyra capensis* on both shores. Standard errors (± 1) are given as from Feb. 1991.

Figure 6.10. Cover and occurrence of other major dominants (*Codium isaacii*, *Chordariopsis capensis*, *Iridaea capensis* and *Plocamium rigidum*) on both shores. Standard errors (± 1) are given as from Feb. 1991.


% COVER
100
80
60
40
20
0
F M A M J J A S O N D J F M A M J J A S O
1990
1991
G1 PORPHYRA
G2 PORPHYRA
H1 PORPHYRA
H2 PORPHYRA

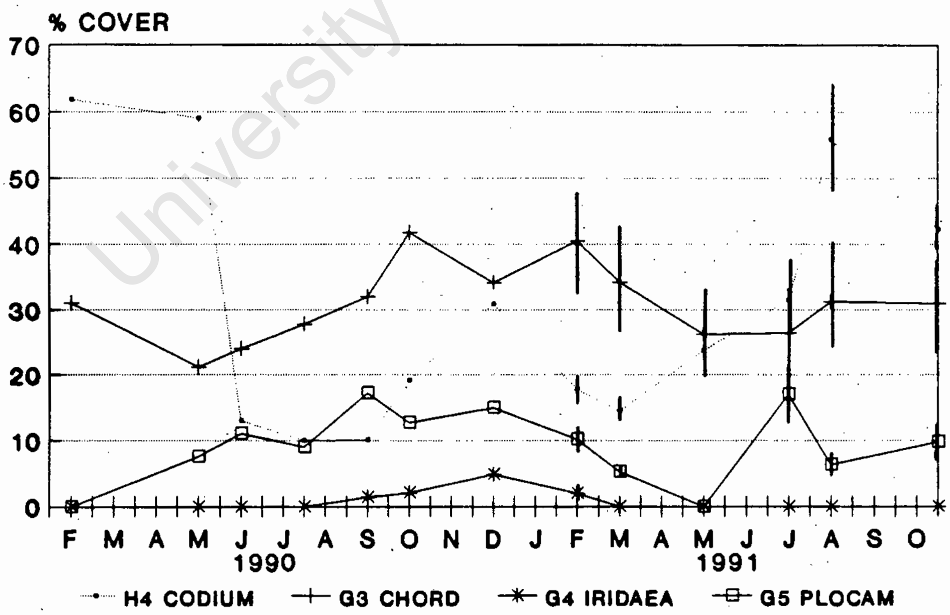
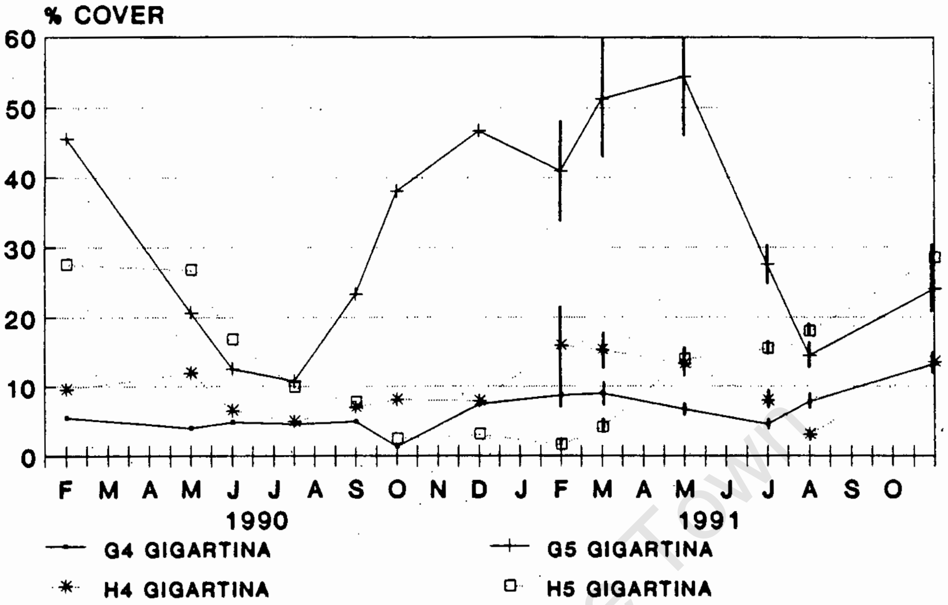

% COVER
70
60
50
40
30
20
10
0
F M A M J J A S O N D J F M A M J J A S O
1990
1991
H4 CODIUM
G3 CHORD
G4 IRIDAEA
G5 PLOCAM

Figure 6.11. Cover and occurrence of *Gigartina* (*G. radula* and *G. stiriata* combined), on both shores. Standard errors (± 1) are given as from Feb. 1991.

Figure 6.12. Cover and occurrence of *Aeodes orbitosa* on both shores. Standard errors (± 1) are given as from Feb. 1991.


% COVER
60
50
40
30
20
10
0
F M A M J J A S O N D J F M A M J J A S O
1990
1991
G4 GIGARTINA
G5 GIGARTINA
H4 GIGARTINA
H5 GIGARTINA

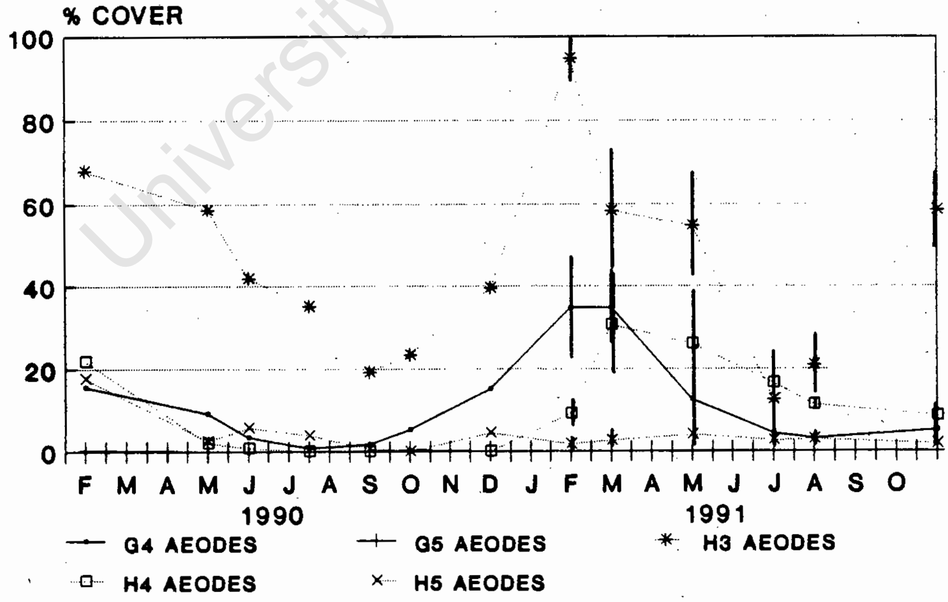
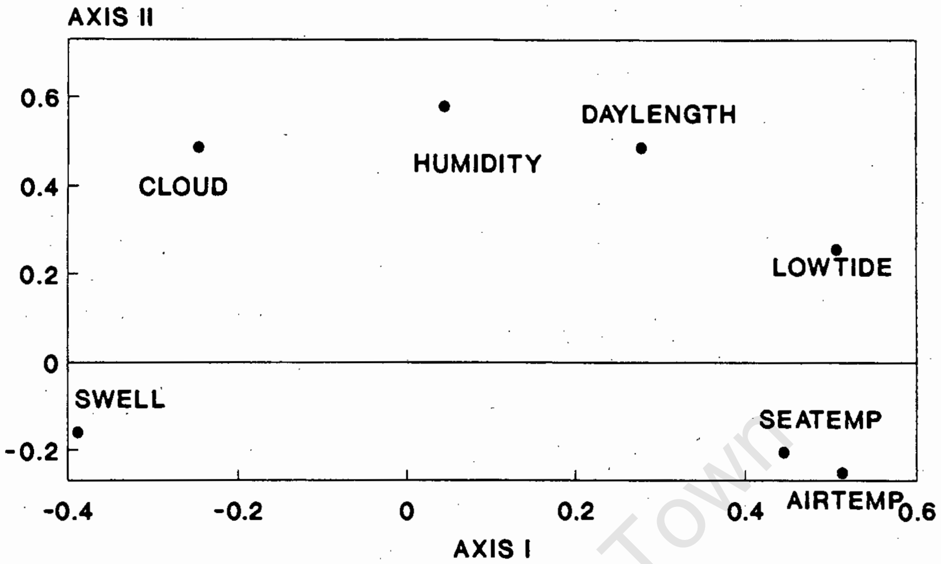

% COVER
100
80
60
40
20
0
F M A M J J A S O N D J F M A M J J A S O
1990
1991
G4 AEODES
G5 AEODES
H3 AEODES
H4 AEODES
H5 AEODES

Figure 6.13. Principal components analysis (PCA) of abiotic variables. Axis I accounted for 43.9% of the variation and axis II, 32.4%.

Figure 6.14. Sampling date scores for the PCA of figure 15.


AXIS II
0.6
0.4
0.2
0
-0.2
CLOUD
HUMIDITY
DAYLENGTH
LOWTIDE
SWELL
SEATEMP
AIRTEMP
-0.4
-0.2
0
0.2
0.4
0.6
AXIS I

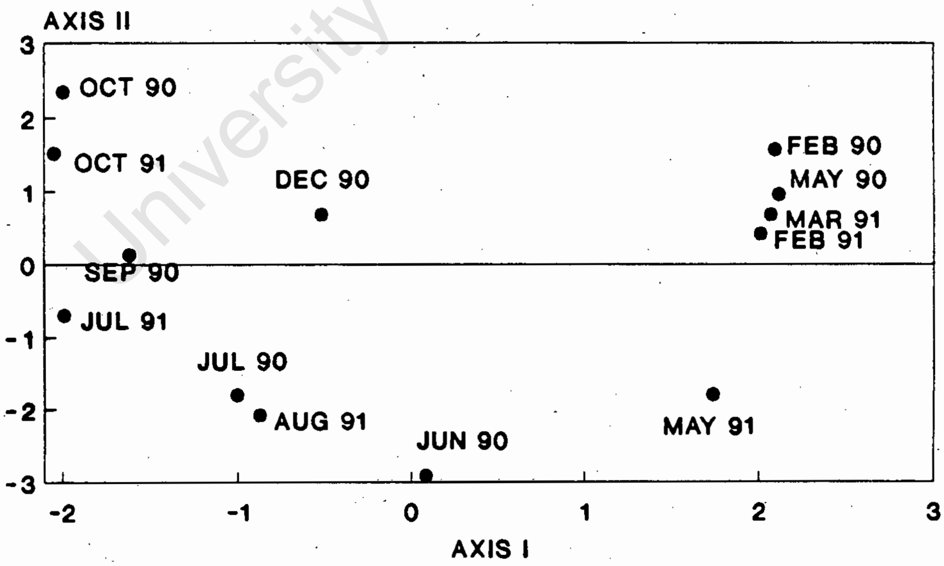
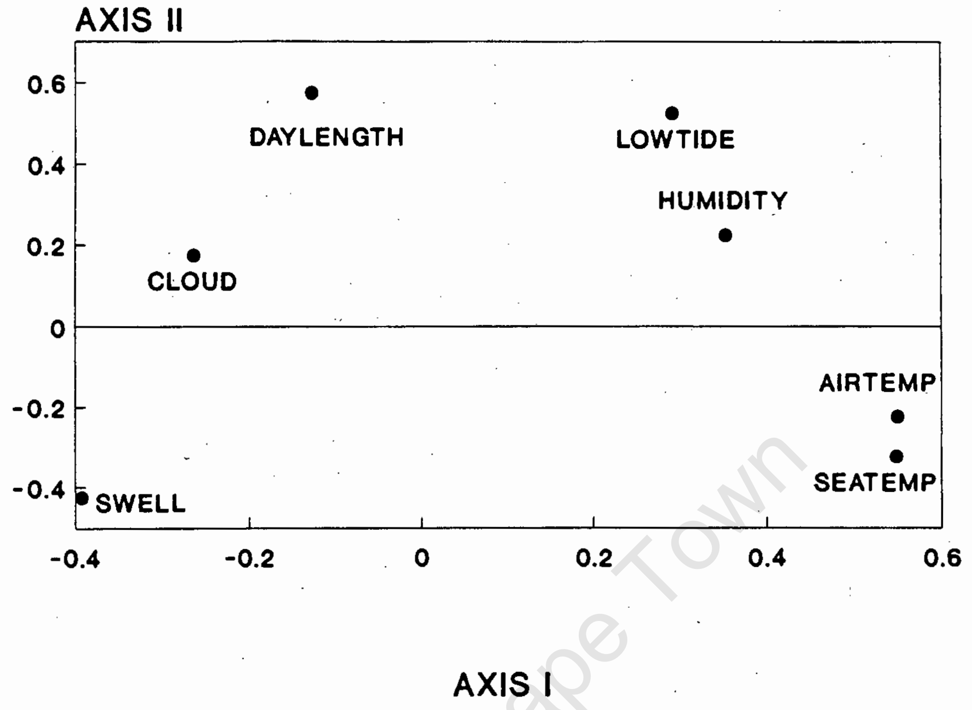

AXIS II
3
2
1
0
-1
-2
-3
OCT 90
OCT 91
DEC 90
SEP 90
JUL 91
JUL 90
AUG 91
JUN 90
MAY 91
FEB 90
MAY 90
MAR 91
FEB 91
-2
-1
0
1
2
3
AXIS I

Figure 6.15. Principal components analysis of the correlations (including the respective lag periods) between the abiotic and biotic variables. Axis I accounted for 42% of the variation and axis II 29.9%.

Figure 6.16. Species cover and total fleshy seaweed cover scores for the PCA of figure 17. Por = *Porphyra*, Gig = *Gigartina*, Aeo = *Aeodes*, Irid = *Iridaea*, Cod = *Codium*, Plo = *Plocamium* and Chord = *Chordariopsis*.


AXIS II
0.6
0.4
0.2
0
-0.2
-0.4
DAYLENGTH
LOWTIDE
HUMIDITY
CLOUD
AIRTEMP
SEATEMP
SWELL
-0.4
-0.2
0
0.2
0.4
0.6
AXIS I

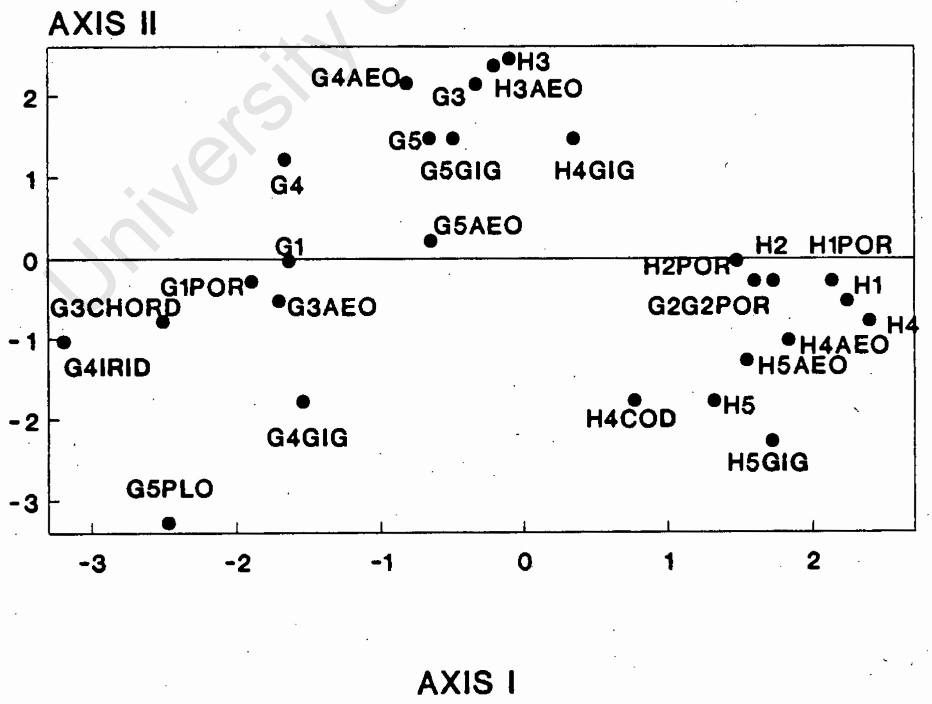

AXIS II
2
1
0
-1
-2
-3
G4AEO
H3
G3
H3AEO
G5
G5GIG
H4GIG
G4
G5AEO
G1
H2
H1POR
H2POR
G1POR
H1
G3CHORD
G3AEO
G2G2POR
H4
G4IRID
H4AEO
H5AEO
H5
H4COD
G4GIG
H5GIG
G5PLO
-3
-2
-1
0
1
2
AXIS I

Table 6.1. Correlation matrix of abiotic variables. Significance level (based on Student's t distribution) and number of lag periods required for maximum correlation (1 lag period = 6 weeks) are given.

	SEATEMP	AIRTEMP	CLOUD	HUMIDITY	LOWTIDE	SWELL	DAYLEN.
SEATEMP	1.00						
AIRTEMP	.8*** (0 lag)	1.00					
CLOUD	-.41 n.s. (0 lag)	-.65* (0 lag)	1.00				
HUMIDITY	.43 n.s. (2 lags)	.49 n.s. (2 lags)	.56* (0 lag)	1.00			
LOWTIDE	.87*** (1 lag)	.75** (1 lag)	-.5 n.s. (2 lags)	.29 n.s. (0 lag)	1.00		
SWELL	-.4 n.s. (1 lag)	-.44 n.s. (0 lag)	.47 n.s. (2 lags)	.39 n.s. (2 lags)	-.62* (0 lag)	1.00	
DAYLEN	.74** (2 lags)	.81*** (2 lags)	-.56* (2 lags)	.5 n.s. (0 lag)	.89*** (1 lag)	-.41 n.s. (1 lag)	1.00

Significance: * = $p < .05$, ** = $p < .01$, *** = $p < .001$, n.s. = not significant

Table 6.2. Correlation matrix of total fleshy seaweed cover at each level and abiotic variables. Significance level (based on Student's t distribution) and number of lag periods (1 lag period = 6 weeks) required for optimum correlation are given

	SEATEMP	AIRTEMP	CLOUD	HUMIDITY	LOWTIDE	SWELL	DAYLEN.
G1 Total	-.67** (2 lags)	-.36 n.s. (2 lags)	.14 n.s. (1 lags)	-.34 n.s. (1 lag)	.37 n.s. (0 lag)	-.01 n.s. (0 lag)	.55* (0 lag)
G2 Total	.41 n.s. (0 lag)	.33 n.s. (0 lag)	.19 n.s. (0 lags)	.32 n.s. (0 lag)	.36 n.s. (0 lag)	-.36 n.s. (0 lag)	.35 n.s. (0 lag)
G3 Total	-.69** (1 lags)	-.46 (2 lags)	.4 n.s. (0 lags)	.69** (0 lag)	.63* (2 lag)	-.22 n.s. (0 lag)	.78** (0 lag)
G4 Total	-.79** (2 lags)	-.61* (2 lag)	.22 n.s. (2 lags)	.27 n.s. (0 lag)	.61* (0 lag)	.3 n.s. (2 lag)	.76** (0 lag)
G5 Total	-.66* (2 lag)	-.4 n.s. (2 lags)	.27 n.s. (0 lags)	.32 n.s. (0 lag)	.55* (0 lag)	-.22 n.s. (1 lag)	.72** (0 lag)
H1 Total	.49 n.s. (0 lag)	.55* (0 lag)	-.2 n.s. (0 lags)	.34 n.s. (0 lag)	.59* (0 lag)	-.24 n.s. (0 lag)	.51 n.s. (1 lag)
H2 Total	.43 n.s. (0 lag)	.35 n.s. (0 lag)	.17 n.s. (0 lags)	.36 n.s. (0 lag)	.37 n.s. (0 lag)	-.35 n.s. (0 lag)	.36 n.s. (0 lag)
H3 Total	-.44 n.s. (0 lag)	-.58* (0 lag)	.49 n.s. (2 lags)	.42 n.s. (2 lag)	.84*** (0 lag)	-.59* (0 lag)	.69** (1 lag)
H4 Total	.4 n.s. (0 lag)	.25 n.s. (0 lag)	-.24 n.s. (2 lags)	.61* (0 lag)	.34 n.s. (0 lag)	-.44 n.s. (0 lag)	.22 n.s. (0 lag)
H5 Total	.44 n.s. (0 lag)	.22 n.s. (0 lag)	.15 n.s. (0 lag)	.32 n.s. (2 lag)	.14 n.s. (0 lag)	-.16 n.s. (1 lag)	-.03 n.s. (1 lag)

Significance: * = $p < .05$, ** = $p < .01$, *** = $p < .001$, n.s. = not significant

Table 6.3. Correlation matrix of species cover and abiotic variables. Significance level (based on Student's t distribution) and number of lag periods (1 lag = 6 weeks) for maximum correlation are given.

	SEATEMP	AIRTEMP	CLOUD	HUMIDITY	LOWTIDE	SWELL	DAYLEN.
G1 Porphyra	-.67** (2 lags)	-.36 n.s. (2 lags)	.14 n.s. (1 lags)	-.34 n.s. (2 lag)	.37 n.s. (0 lag)	.24 n.s. (2 lag)	.55* (0 lag)
G2 Porphyra	.41 n.s. (0 lag)	.33 n.s. (0 lag)	.19 n.s. (0 lag)	.32 n.s. (0 lag)	.36 n.s. (0 lag)	-.36 n.s. (0 lag)	.35 n.s. (0 lag)
G3 Aeodes	-.74** (2 lags)	-.67** (2 lags)	.34 n.s. (1 lag)	.18 n.s. (0 lag)	-.53 (2 lag)	.13 n.s. (1 lags)	.69** (0 lag)
G3 Chordariop	-.75** (1 lag)	-.62* (1 lags)	.27 n.s. (0 lags)	.26 n.s. (0 lag)	-.6* (2 lags)	.42 n.s. (1 lag)	.59** (1 lag)
G4 Aeodes	-.69** (2 lag)	-.63* (2 lag)	.36 (2 lag)	.21 n.s. (1 lag)	.82*** (0 lag)	-.38 n.s. (0 lag)	.78** (0 lag)
G4 Gigartina	-.17 n.s. (0 lags)	-.39 (2 lag)	.28 n.s. (2 lag)	.15 n.s. (2 lag)	-.2 n.s. (1 lag)	.61* (2 lag)	.23 n.s. (0 lag)
G4 Iridaea	-.7** (1 lags)	-.71** (1 lags)	.51 (1 lags)	-.31 n.s. (1 lag)	-.54 (2 lags)	.24 n.s. (0 lag)	.53 (0 lag)
G5 Gigartina	-.68** (2 lag)	-.39 n.s. (2 lag)	.13 n.s. (1 lags)	.3 n.s. (0 lag)	.67** (0 lag)	-.2 n.s. (0 lag)	.71** (0 lag)
G5 Aeodes	-.35 n.s. (1 lag)	-.31 n.s. (2 lags)	.53 n.s. (1 lag)	.47 n.s. (0 lag)	-.32 n.s. (2 lags)	-.2 n.s. (0 lag)	.41 n.s. (0 lag)
G5 Plocamium	-.44 n.s. (1 lag)	-.56* (0 lag)	.16 n.s. (0 lag)	-.3 n.s. (2 lags)	-.45 n.s. (0 lag)	.63* (0 lag)	-.31 (0 lags)
H1 Porphyra	.49 * (0 lag)	.55* (0 lag)	-.2 n.s. (1 lags)	.34 n.s. (0 lags)	.59* (0 lag)	-.25 n.s. (0 lag)	.51 n.s. (1 lag)
H2 Porphyra	.32 n.s. (0 lag)	.33 n.s. (0 lag)	.18 n.s. (0 lags)	.33 n.s. (0 lag)	.35 n.s. (0 lag)	-.33 n.s. (0 lag)	.4 n.s. (0 lag)
H3 Aeodes	-.47 n.s. (2 lag)	-.62* (2 lag)	.51 n.s. (0 lag)	.45 n.s. (0 lag)	.82*** (0 lag)	-.53 n.s. (0 lag)	.67** (0 lag)
H4 Aeodes	.43 n.s. (0 lag)	.54 (0 lag)	-.3 n.s. (1 lags)	.17 n.s. (0 lags)	.47 (1 lag)	-.19 n.s. (0 lag)	.53 (0 lag)
H4 Gigartina	-.53 (2 lag)	-.55* (2 lag)	-.43 (2 lag)	.22 n.s. (2 lag)	.82*** (0 lag)	-.38 n.s. (0 lag)	.71** (1 lag)
H4 Codium	.3 n.s. (0 lag)	-.08 n.s. (1 lag)	.26 n.s. (1 lags)	.6* (0 lag)	.11 n.s. (0 lag)	.19 n.s. (0 lag)	-.21 n.s. (2 lag)
H5 Gigartina	.43 n.s. (1 lag)	.28 n.s. (2 lags)	-.15 n.s. (1 lag)	.25 n.s. (1 lag)	.17 n.s. (2 lags)	-.12 n.s. (0 lag)	-.21 n.s. (1 lags)
H5 Aeodes	.45 n.s. (0 lag)	.47 n.s. (0 lag)	.1 n.s. (1 lag)	.18 n.s. (2 lags)	.29 n.s. (0 lag)	-.2 n.s. (1 lag)	.29 n.s. (0 lag)

Significance: * = p < .05, ** = p < .01, *** = p < .001, n.s. = not significant

CHAPTER 7

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APPENDIX I

"Basic" computer program to calculate daylength at a given latitude and solar declination by M. D. Guiry (Molloy, unpublished).

```
10 REM daylength calculates daylength for any day at a given latitude
20 PRINT CHR$(26)
30 PRINT "D A Y L E N G T H  P R O G R A M"
40 INPUT "Solar elevation (in degrees) ";L
50 PRINT:INPUT "Latitude (in degrees) ";L
60 RD= 3.14159/180
70 FOR I= 1 TO 365
80 D= D +1
90 D1=D*.9856
100 LM=279.1 + D1 + 1.915 * SIN ((356.5 + D1)*RD)
110 SD=.3978 * SIN(LM * RD): SD = ATN(SD/SQR(-SD*SD+1))
120 DL=SD/RD
130 PRINT "Solar declination = ";DL
140 DL = (SIN(B*RD)-SIN(L*RD)*SIN(SD))/COS(L*RD)/COS(SD)
150 DL = -ATN(DL/SQR(-DL*DL + 1))+1.5708
160 DL = DL/RD/7.5
170 LPRINT "Daylength = "; INT(DL); "h";(DL - INT(DL))*60; "min"
180 NEXT I
0
```