BIOLOGICAL STRUCTURE OF AN AGULHAS BANK SUBTIDAL REEF COMMUNITY AND CONSUMPTION ESTIMATION FOR A DOMINANT SPECIES

by

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DECLARATION

The study described here formed part of an investigation into the organic matter flow between three environments. I was responsible for the planning and design of all phases of the study, leading the field surveys and the experimental work carried out in the laboratories of the National Research Institute for Oceanology. This study represents original work by the author and has not been submitted in any form to another University. Where assistance was afforded by others it has been duly acknowledged in the text.

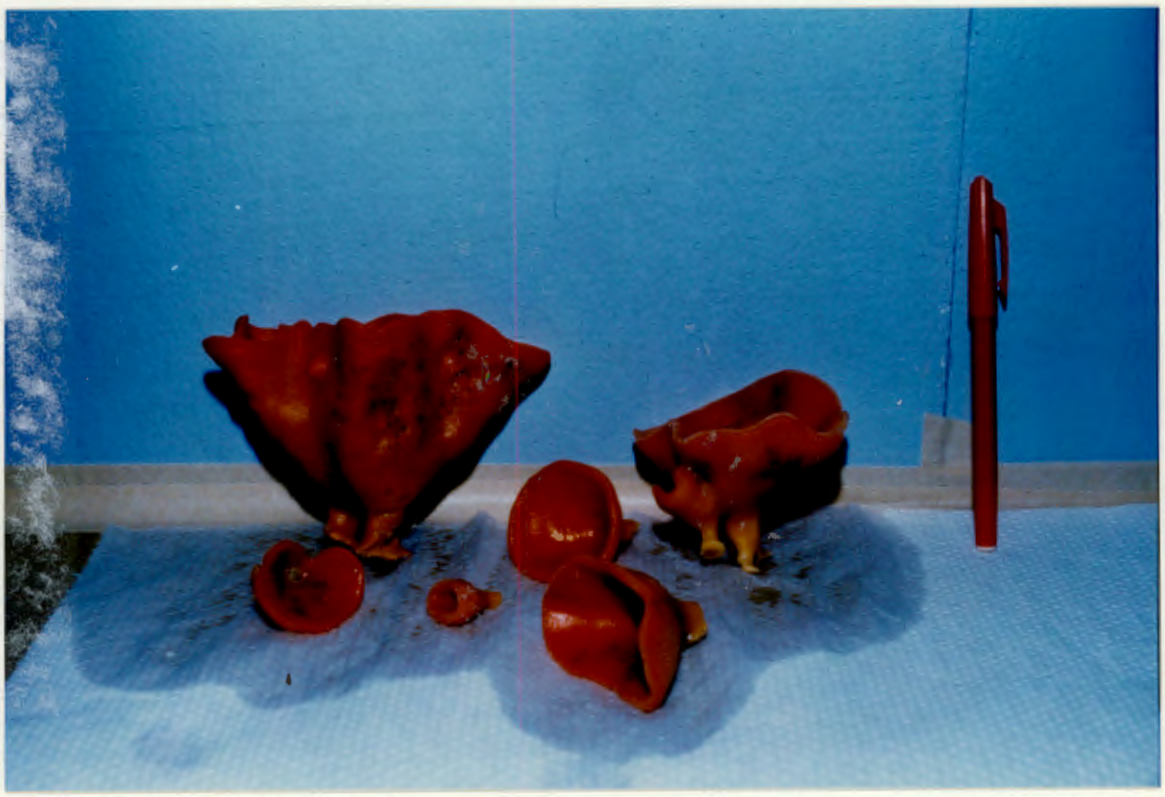

PLATE 1: Spirastrella sp.

CONTENTS

ABSTRACT

This thesis reports on an investigation into some aspects affecting and contributing to the flow of organic matter through a subtidal reef environment. In particular, the contribution of Porifera to the organic matter pool in terms of biomass and the consumption of organic matter by a dominant Porifera species are assessed. Further, reef fauna biomass and community structure, as well as Porifera respiration, the subsurface temperature regime above the subtidal reef and the amount of organic matter available for utilization are examined.

The range, distribution and time scales of the temporal and vertical temperature fluctuations above the reef were measured. The temperatures were recorded with the use of a temperature profile recorder (Aanderaa Type TR-2). The average temperature varied between 17°C and 18°C and a well-mixed water column was present over the seven-month period (13/03/1986 to 02/10/1986) with the exception of cold bottom water intrusions during the summer months. It was established that the reef fauna are subjected to fluctuations within a temperature range of at least 9°C, sudden cold bottom water intrusions and two entirely different temperature regimes.

The concentration of total suspended particulate matter present in the immediate vicinity of the reef ranged from 8,28 $mg\ell^{-1}$ to 34,8 $mg\ell^{-1}$ at the 14 sampling stations, with a mean value of 20,6 $mg\ell^{-1}$. A mean value 1,18 $mg\ell^{-1}$ (5,7%) was obtained for the organic content of the particles while the mean inorganic content was 19,42 $mg\ell^{-1}$. It is suggested that the high inorganic fraction could be ascribed to the presence of the high turbidity layer observed at various sampling stations. The dissolved organic carbon values ranged from 0,23 $mg\ell^{-1}$ to 3,58 $mg\ell^{-1}$ with a mean value of 1,29 $mg\ell^{-1}$. The variability in the amount and composition of seston available for utilization is a dominant feature of the reef environment.

A biomass survey was carried out during March and June 1986 on board the RV Meiring Naudé. Porifera accounted for 33% of the total ash-free dry weight obtained by means of the random quadrat method. The dominance of the filter feeders (73%) was evident. Micropredators accounted for 20% while grazers and deposit feeders made up a small percentage of the total. The results obtained from the belt counts also reflect the dominance of Porifera, Bryozoa and Cnidaria. From the combined data it was concluded that a mean ash-free dry mass of 170 gm^{-2} is present on the aeoleonite reef and that attached algae appears to be a minor nutritional source.

The oxygen consumption rate of Spirastrella was measured by means of a closed respirometer system. Routine oxygen consumption increased linearly with weight with values of the exponent b ranging between 0,66 and 0,68 at the three experimental temperatures. No significant differences could be detected between respiration rates measured at 12°C, 16°C or 20°C. A minimum consumption rate of 5,7 $mgCm^{-2}d^{-1}$ was estimated for the Spirastrella community while the corresponding value for the whole filter feeding community (biomass=123 gm^{-2}) was 466,9 mg $Cm^{-2}d^{-1}$.

The filtration rate of Spirastrella was measured indirectly by recording the rate of decrease in algal concentration in a static volume of ambient water. The filtration rates increased linearly with weight with values of the exponent b ranging between 0,57 and 0,61 while no differences could be detected between filtration rates at 12°C, 16°C or 20°C.

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GENERAL INTRODUCTION

The Marine Biology Division of the National Research Institute for Oceanology is at present investigating the movement of organic matter between the water column, unconsolidated sediments and reef environments on the Agulhas Bank, with the object of quantifying these fluxes. For these purposes it is essential to estimate the organic matter flow through each of these environments. An investigation of the flow necessitates quantitative determinations of the components affecting and contributing to the organic matter flux. Major components are the production and consumption of organic matter as well as the biomass and particulate and dissolved organic matter present in the environment.

The present study contributes to the theme by providing particulate and dissolved organic matter measurements, a biomass distribution and a consumption estimate for the reef environment. The study also provides some basic information with regard to the ecology of a subtidal reef.

The survey was carried out on a subtidal aeoleonite reef system on the Agulhas Bank. This extensive offshore reef area lies seaward of the breakers parallel to the coast between Mossel Bay and Walker Point (Figure 1.1). The research site is located at the westernmost point of the reef and south of the Great Brak River mouth (Figure 1.2).

The community structure of the reef environment was established through biomass measurements. This was achieved by quadrat clearance and belt count methods. The results confirmed that sponges are the dominant component of the reef fauna. Therefore specimens of a dominant Porifera genus, Spirastrella, were used for estimating the consumption of organic matter by the reef fauna.

Two methods were used to estimate the consumption:

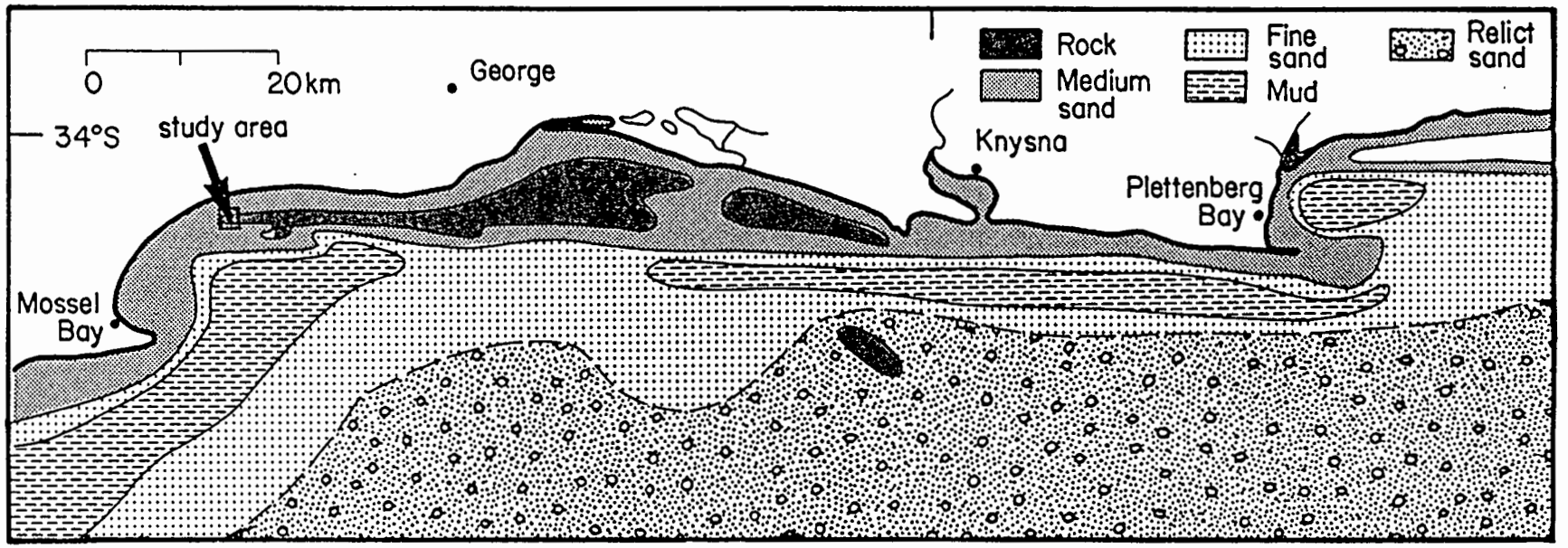

FIGURE 1.1: Schematic illustration of the sedimentary character of the inner Agulhas Bank.

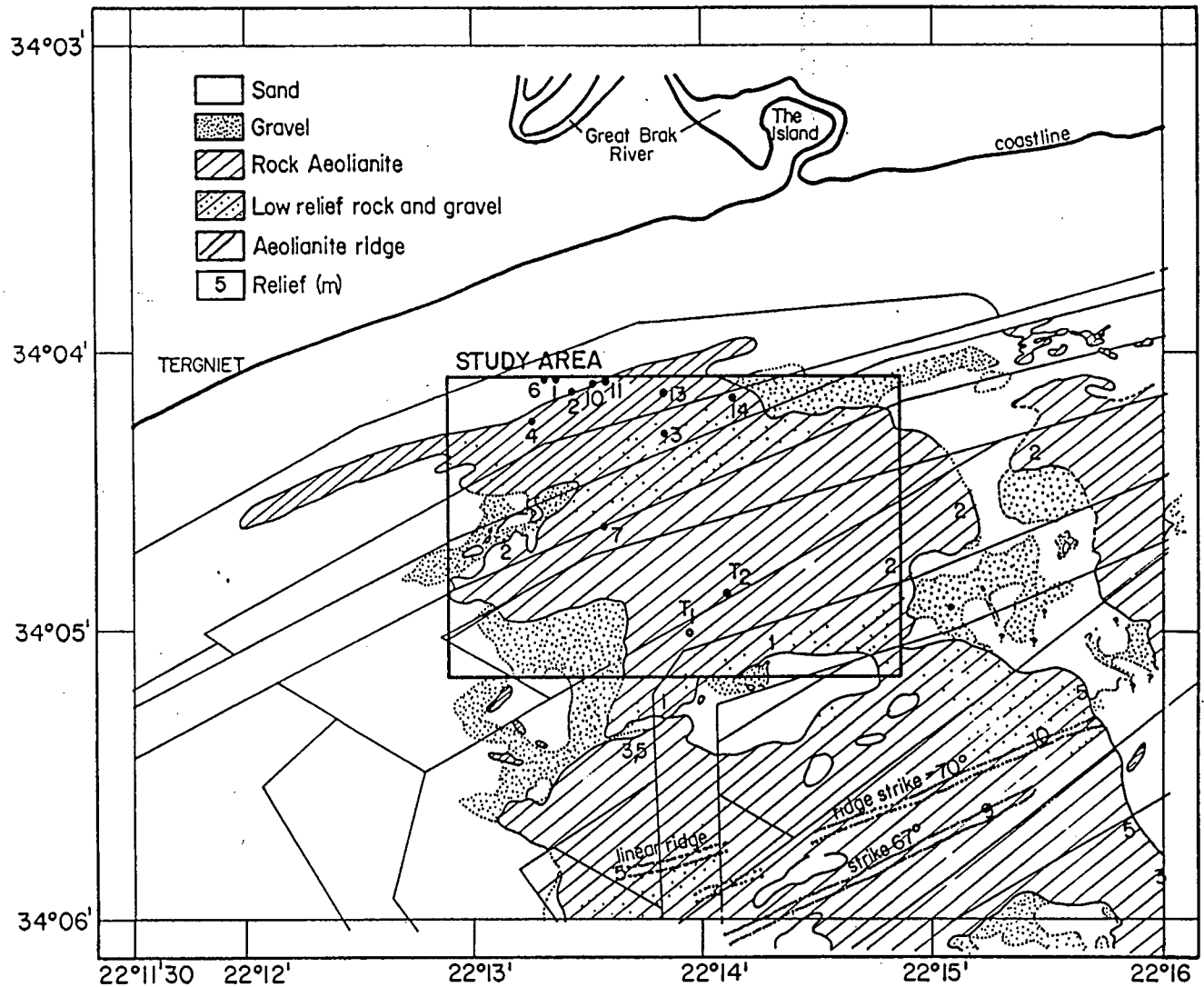

FIGURE 1.2: The study area on the Cape south coast. Water sample stations (1-14) and thermistor deployment positions (T_1, T_2) are indicated.

(1) The indirect consumption estimate was done by measuring oxygen consumption and thus estimating basal metabolism. By determining and including the effect of temperature a minimum consumption estimate can be obtained. These values can be related to field data using biomass measurements to arrive at energy expenditure per square metre.

(2) Organic matter consumption was also estimated by measuring the actual consumption rate. This was done by measuring the relative changes in proportions of different sized particles after a fixed period of time in a closed system containing a Spirastrella sp.

The first two chapters are supportive to the rest of the study. In Chapter 1 the spatial and temporal temperature fluctuations in the vicinity of the reef are investigated and discussed because the temperature regime forms an integral part of the indirect minimum consumption estimate. Quantitative measurement of the organic matter available as a food source to the reef fauna is an important step towards understanding the flow of organic matter through the reef environment. Sea-water obtained from the reef was filtered through a series of filter papers and the organic matter content of each fraction measured (Chapter 2). Chapter 3 deals with the biomass distribution of the reef community, while the indirect and direct consumption estimates are discussed in Chapters 4 and 5.

A description of marine communities is an essential prerequisite for understanding a marine system and the ecological effects of marine pollution and other human activities (Kaandorp, 1986). Understanding an ecosystem's composition and the fluxes running through it are essential if the consequences of man-induced changes to the environment are to be evaluated. With foci (e.g. Mossel Bay) on the Cape south coast destined for industrial development, decisions regarding effluent disposal will have to be made from a sound scientific base. Results from this project are intended to supply some of the necessary background as well as basic information with regard to the organic matter flow through the reef environment.

SECTION 1

CHAPTER 1: TEMPERATURE FLUCTUATIONS IN THE REEF ENVIRONMENT

Introduction

The aim of this project is to obtain a minimum consumption estimate for the reef fauna by measuring respiration and filtration rates of a dominant organism of the community. Physiological rates vary with temperature, which will ultimately affect the minimum consumption estimate. The effect of temperature on respiration rate is well documented and according to Edwards and Irving (1943), Armitage and Wall (1982) and De Mont and O'Dor (1984) the metabolic rate of poikilothermic animals is directly proportional to temperature. Temperature affects not only the ability of marine organisms to survive in particular environmental situations, but also has a profound effect on the rate of individual physiological functions (Newell and Branch, 1980). Therefore it is essential to measure the temporal and vertical temperature fluctuations the reef fauna are subjected to. It is necessary to establish the range, distribution and time scales in which these fluctuations occur as all these factors affect the reef community and would play a role in any adaptive strategies developed by the reef fauna.

Temperature measurements on the Agulhas Bank have been reported on by Shannon (1966), De Decker (1973), Lutjeharms, Bang and Valentine (1981), Lutjeharms and Valentine (1983), Swart (1983), Zoutendyk and Flemming (1983), Schumann and Beekman (1984) and Swart and Largier (1987). Of these studies that of De Decker was a report on the surface temperature distribution, while the majority were large-scale investigations based on single surveys of the thermal structure of the Agulhas Bank water. The spatial temperature distribution forms the main theme of these studies and data on the short-term temperature fluctuations in the Agulhas Bank nearshore regions are sparse. No longer term records are available comparable with the water temperature

measurements off the southern Cape Peninsula carried out by Velimirov et al. (1977), Dieckman (1980), Anderson and Bolton (1985) and Anderson and Hay (1986).

This chapter reports on an investigation of the subsurface temperature regime above the aeoleonite reef system on the Cape south coast. The vertical and temporal temperature fluctuations are measured on a seasonal and short-term basis while the frequency of these fluctuations are established.

Material and methods

Subsurface water temperature were recorded with the use of a temperature profile recorder (Aanderaa Type TR-2). This instrument consists of a thermistor string and a recording unit. The thermistor string consists of a hose with internal strain wire, and has eleven thermistors built in along its length. A built-in quartz clock triggers the recorder at regular intervals. When it is triggered, it records a reference number, then in sequence the temperature sensed by the eleven thermistors. This was done once every hour. An electro-mechanical encoder (analog to digital converter) samples and converts the measurements to binary digital signals which are recorded on 6,25 mm magnetic tape. Power is supplied by a battery capable of recording for six months using a 60-minute sampling interval and a temperature range of -0,34°C to 32,17°C can be detected.

The temperature profile recorder was deployed during the March 1986 cruise on board the RV Meiring Naudé. With the use of an echo-sounder, an obstruction-free area was located and buoyed in 30 m of water. An inflatable rubber boat was launched as a tender for the divers who used a marker buoy as a shot-line to investigate the suitability of the bottom for deploying the thermistor array. The temperature recorder was deployed (34'05"S; 22'14"E) after which a second team of divers checked its mooring.

The instrument was vertically moored with the use of an anchor weight and three subsurface non-compressible buoys (Figure 1.3). During the June cruise on board the RV Meiring Naudé the 20 m thermistor string was acoustically released and retrieved for servicing. The tape and batteries were replaced and the complete array serviced and redeployed in close proximity to the original site (34'04,08"S; 22'14,2"E). The thermistor string was acoustically released and retrieved on 14 November 1986. The temperature values were decoded and read onto magnetic tape. The maximum, minimum and average values for each thermistor were obtained with the aid of a Fortran program.

Results

The vertical temperature profile above the reef environment is presented graphically in Figure 1.4. Average values as well as the temperature ranges recorded by each thermistor are given over the seven-month period. The deployment took place in 30 m of water which means that the deepest thermistor at 27,5 m was approximately 2,5 m above the sea floor. The largest temperature range was recorded by the deepest thermistor. The erratic intrusion of the cold bottom water appears to be restricted to below 22 m depth at this specific position.

Temperature fluctuations due to seasonal variation, as recorded by the bottom thermistor, are presented in Figure 1.5. The lowest average temperatures were recorded in July and the highest in March. The seasonal variation was damped as the mean monthly values were affected by individual events, evidenced by the monthly minimum values recorded. The typical vertical temperature profiles presented in Figure 1.6 show the presence of a strong thermocline during summer and a well-mixed layer during winter.

The daily averages of the maximum, mean and minimum temperatures at 27,5 m, 17,5 m and 7,5 m respectively are presented graphically in Figures 1.7 to 1.9. The hourly water temperature, as

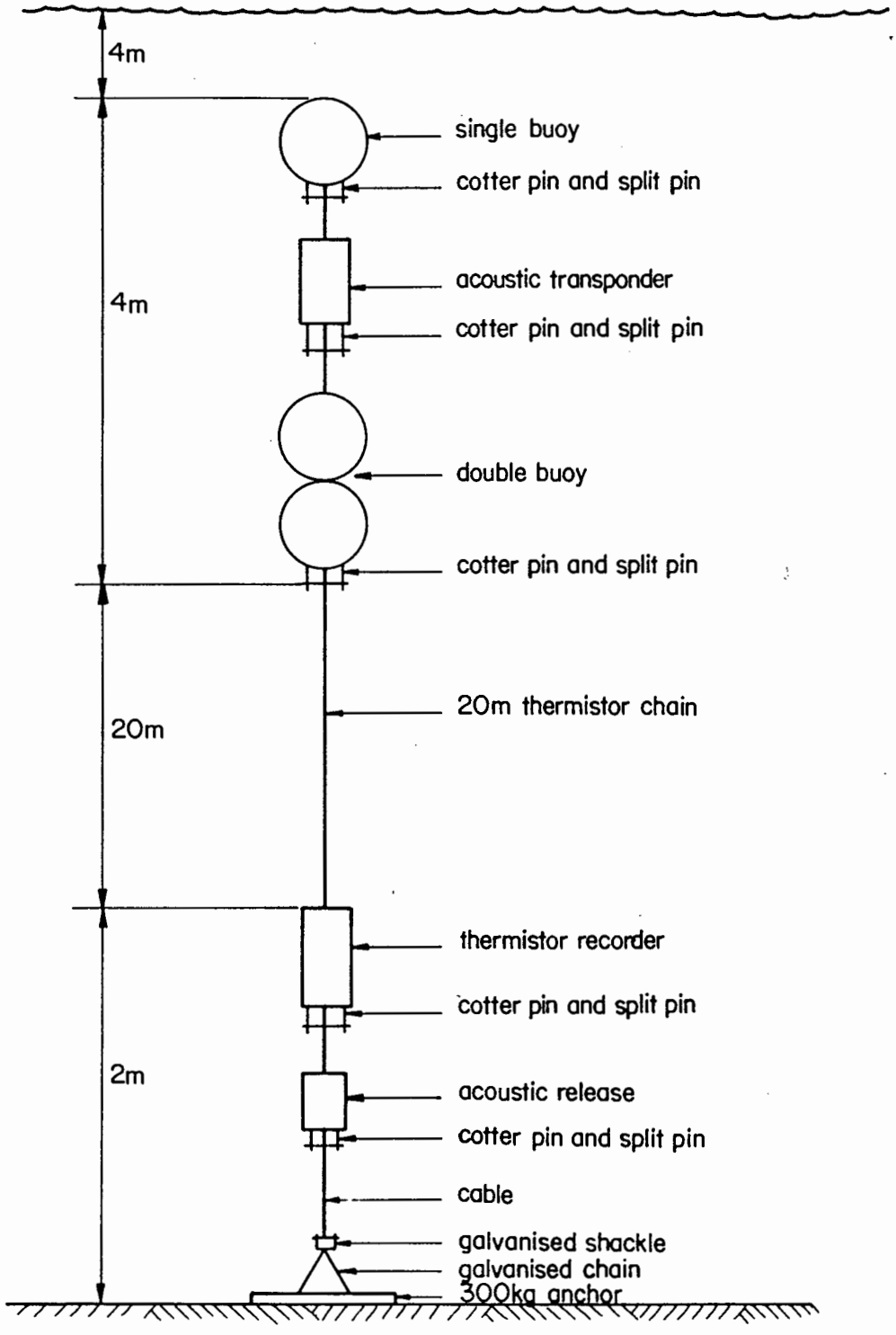

FIGURE 1.3: Schematic illustration of the temperature profile recorder deployment.

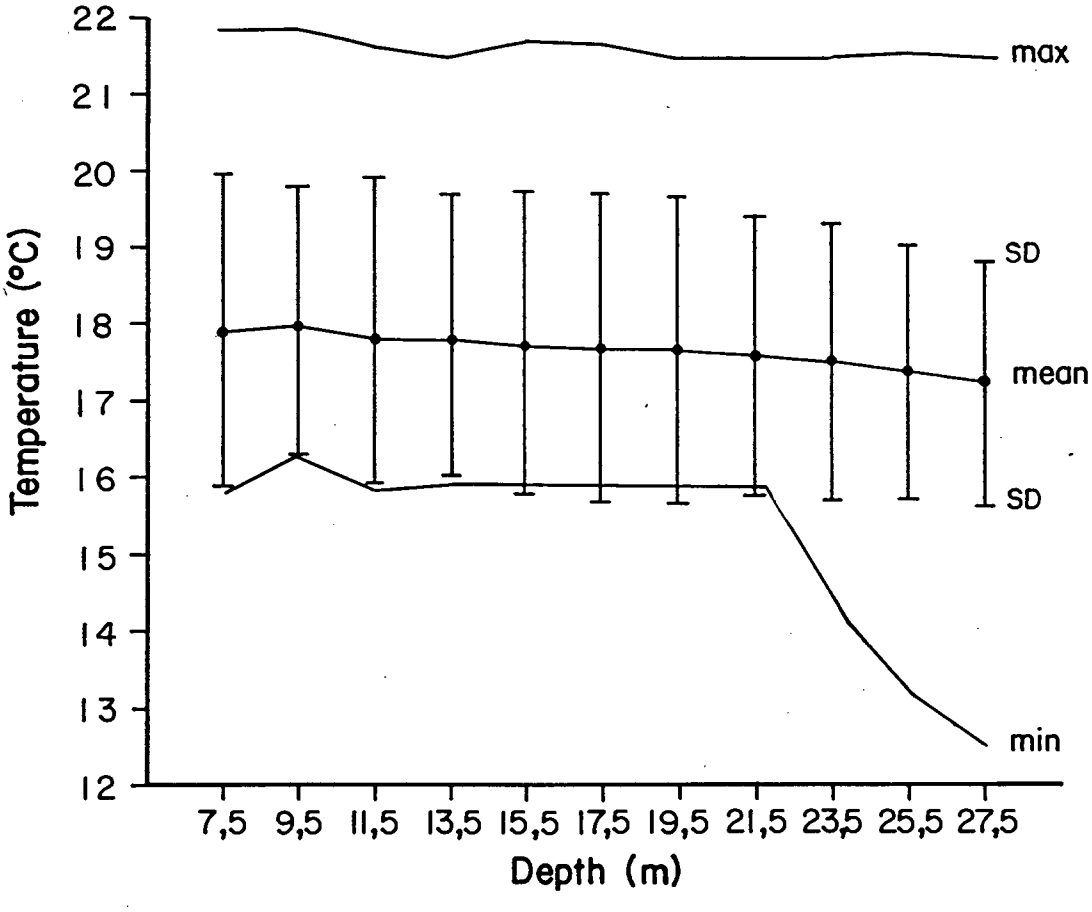

FIGURE 1.4: Minimum, maximum and average temperature values recorded by eleven thermistors over a seven-month period (34'05"S; 22'14"E - 13/3-3/10/1986).

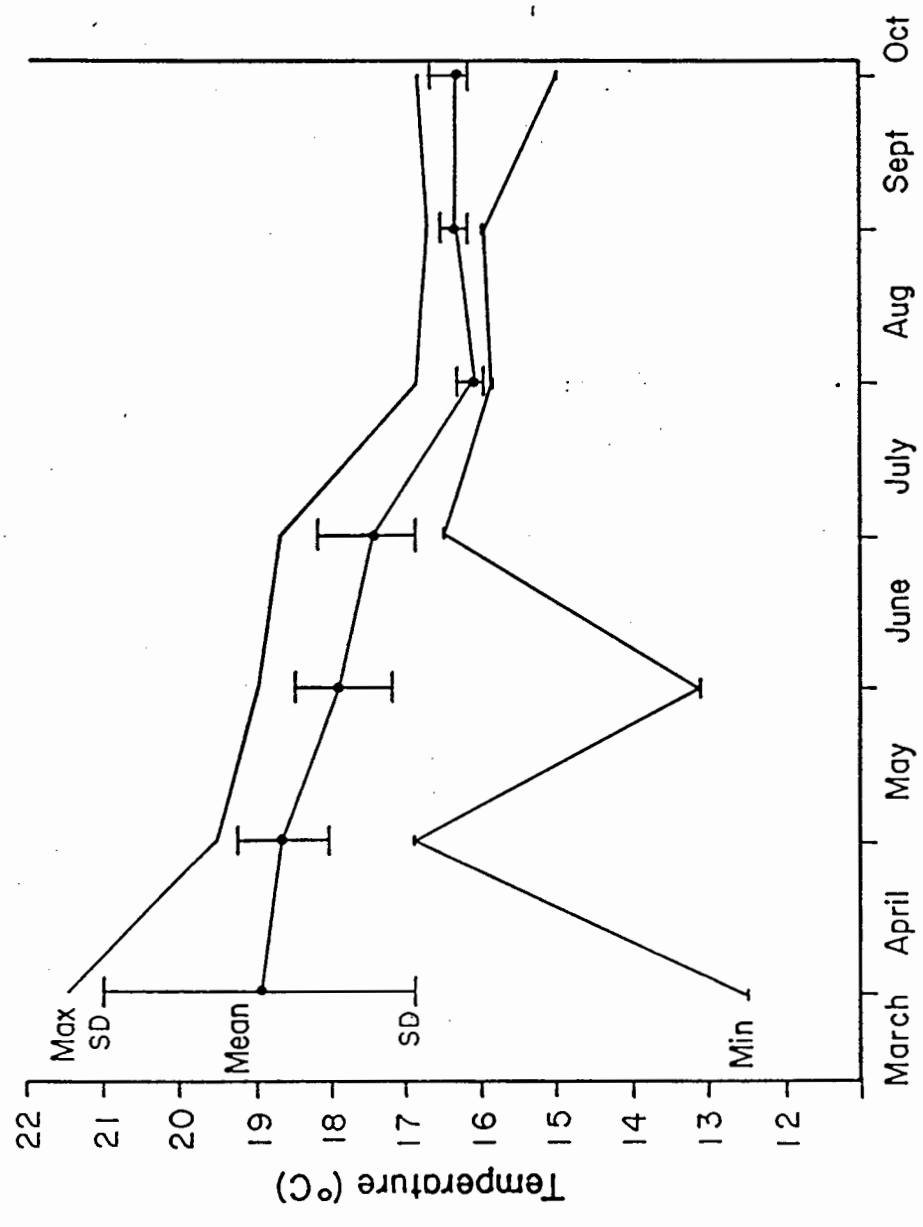

FIGURE 1.5: Monthly minimum, maximum and average temperature values with standard deviations recorded by the deepest thermistor (34'05"S; 22'14"E - 13/3-3/10/1986).

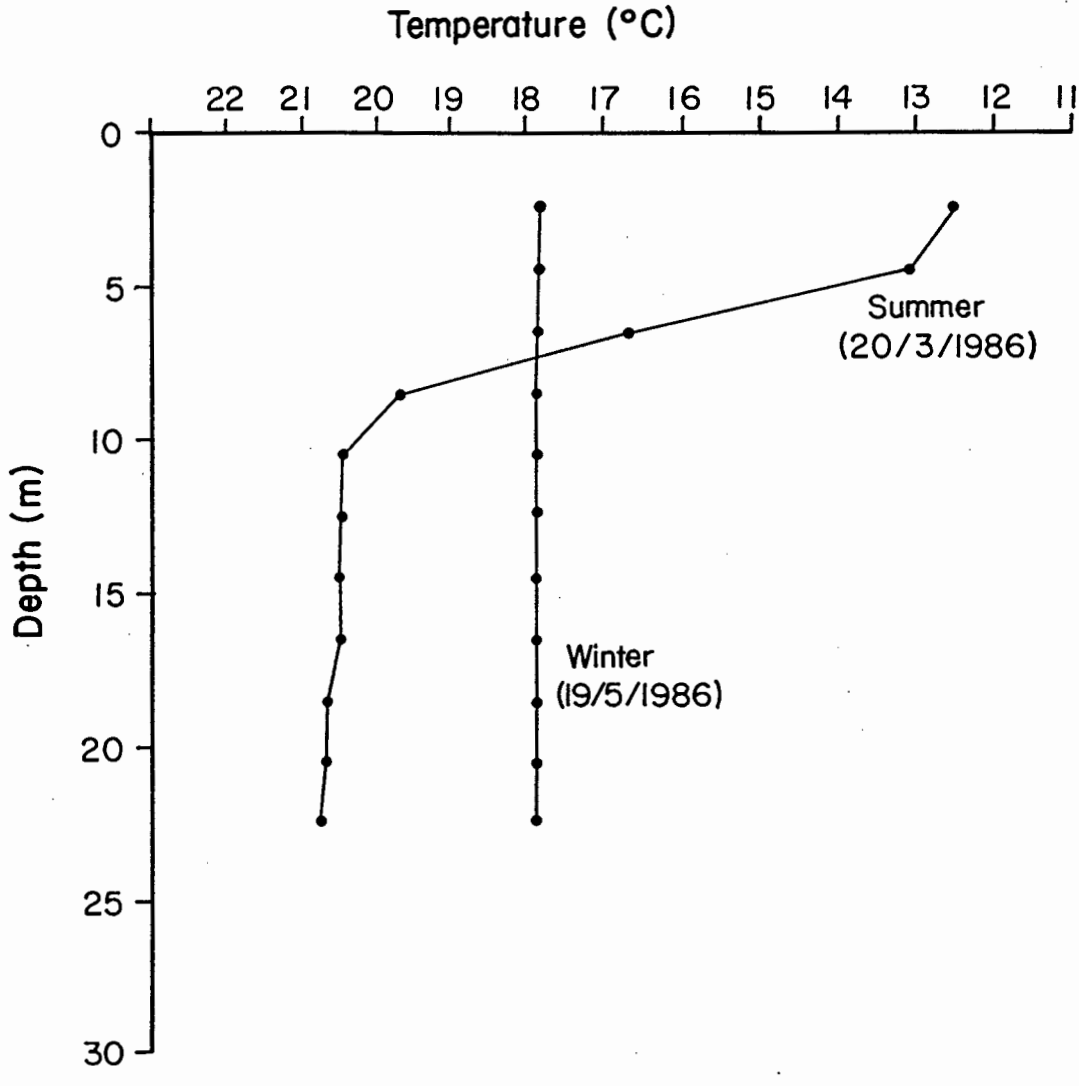

FIGURE 1.6: Typical vertical temperature profiles recorded by the eleven thermistors in summer and winter (34'05"S; 22'14"E).

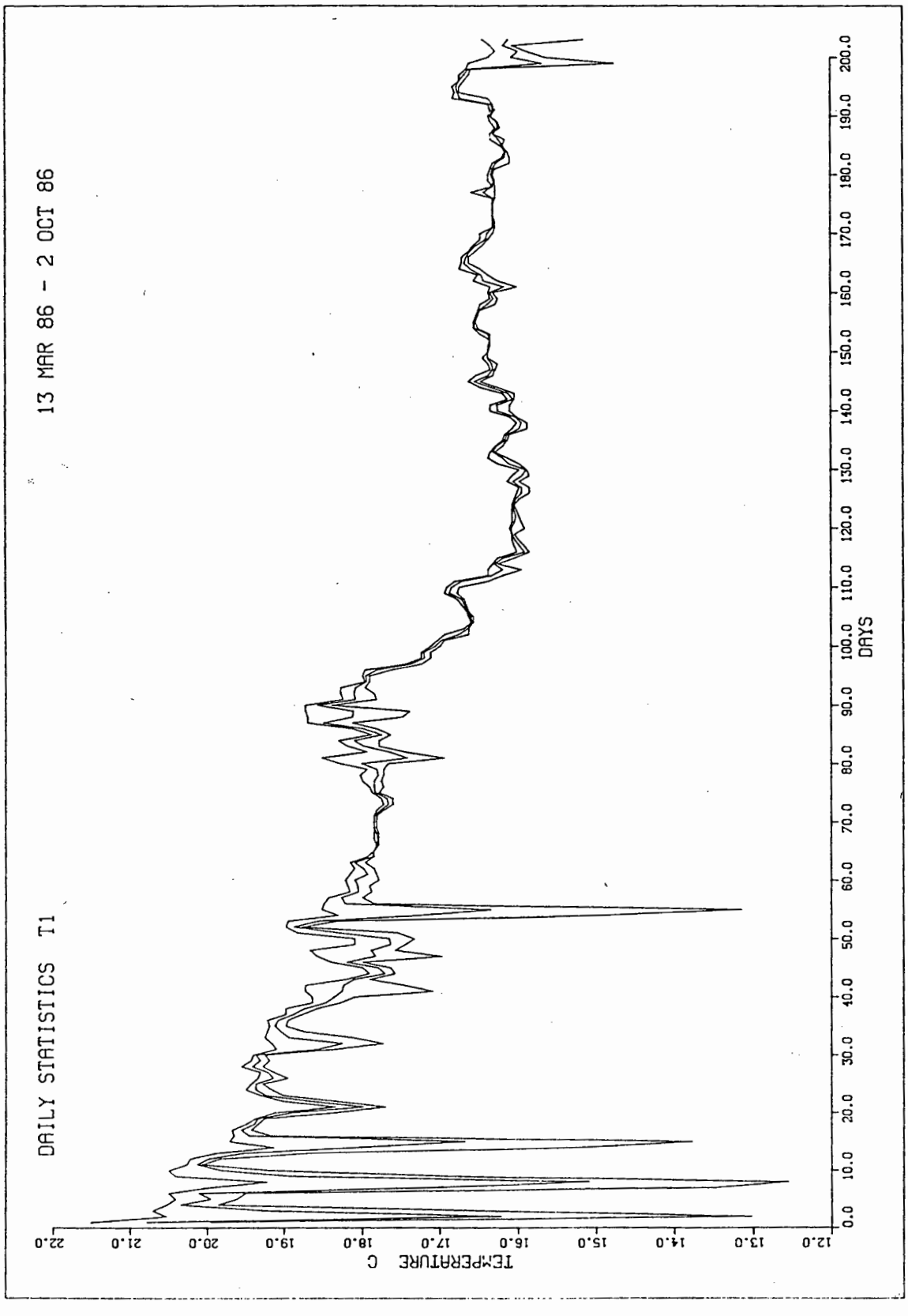

FIGURE 1.7: Maximum, mean and minimum temperatures at 27,5 m depth.

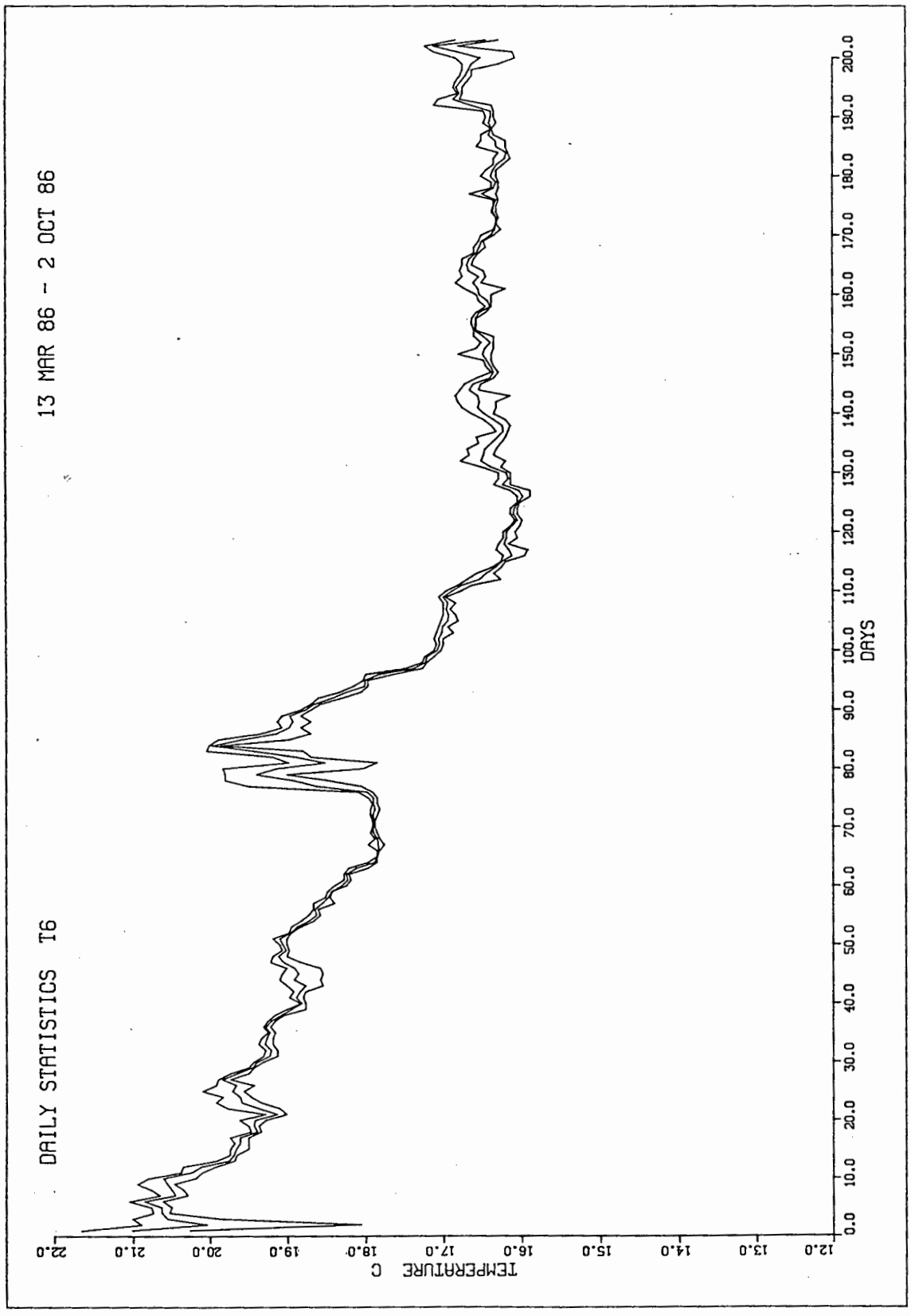

FIGURE 1.8: Maximum, mean and minimum temperatures at 17,5 m depth.

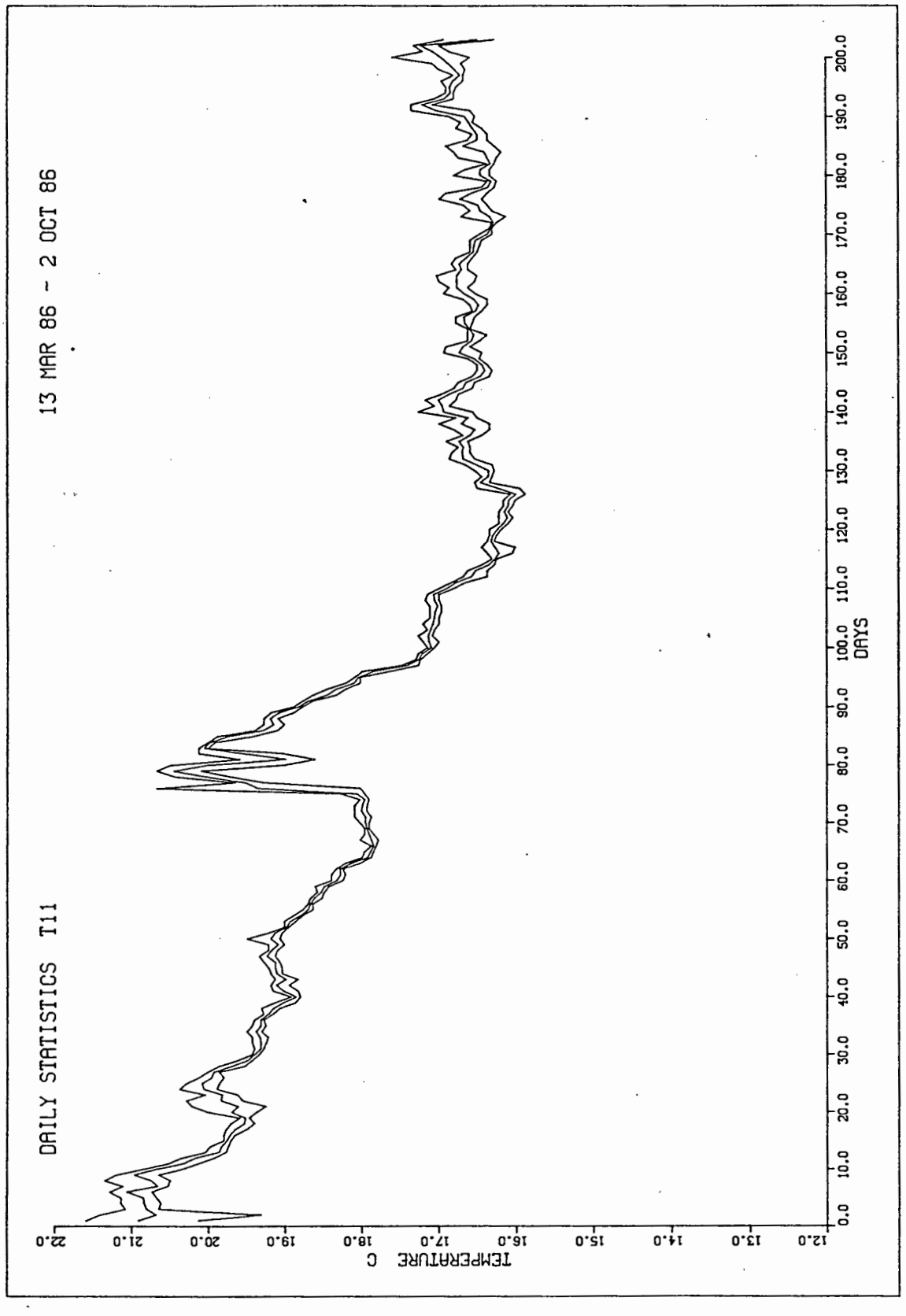

FIGURE 1.9: Maximum, mean and minimum temperatures at 7,5 m depth.

recorded by the deepest thermistor, was generally above 20°C until the end of March, after which the temperature decreased to below 20°C. On seven separate occasions, bottom water temperatures of 15°C and below were recorded; four times in March, twice in May and once in October. An example of the short-term temperature fluctuations to which the reef fauna are subjected, is presented graphically in Figure 1.10.

The frequency of the temperature fluctuations is illustrated by dividing the more than 63 000 measurements into smaller intervals. The temperature range measured by each thermistor was subdivided into 0,5°C intervals and the time corresponding to each specific interval was expressed as a percentage of the total time. The values calculated from measurements recorded by the three deepest thermistors are presented graphically in Figure 1.11 as they are of more specific importance to the reef fauna. The bimodal distribution about the mean is a prominent feature of the frequency of the temperature fluctuations.

Discussion

The vertical temperature profile (Figure 1.4) shows a well-mixed water column above the reef with the average temperature recorded by the eleven thermistors fairly constant between 17°C and 18°C. The temperature over the seven-month period varied between 16°C and 22°C, with the exception of the measurements recorded during the cold water intrusions. An important factor emerging from Figure 1.4 is the large temperature range recorded by the three deepest thermistors. It is obvious that the reef animals are subjected to a temperature range of at least 9°C and possibly more, as there were no temperature recordings during the summer months. The three deepest thermistors were at 2,5 m, 4,5 m and 6,5 m respectively, above the actual reef and this distance could not be reduced due to practical considerations such as possible damage to the array in the event of a storm. The minimum temperatures were due to occasional isolated events as this drastic decrease is not reflected in the average temperature values.

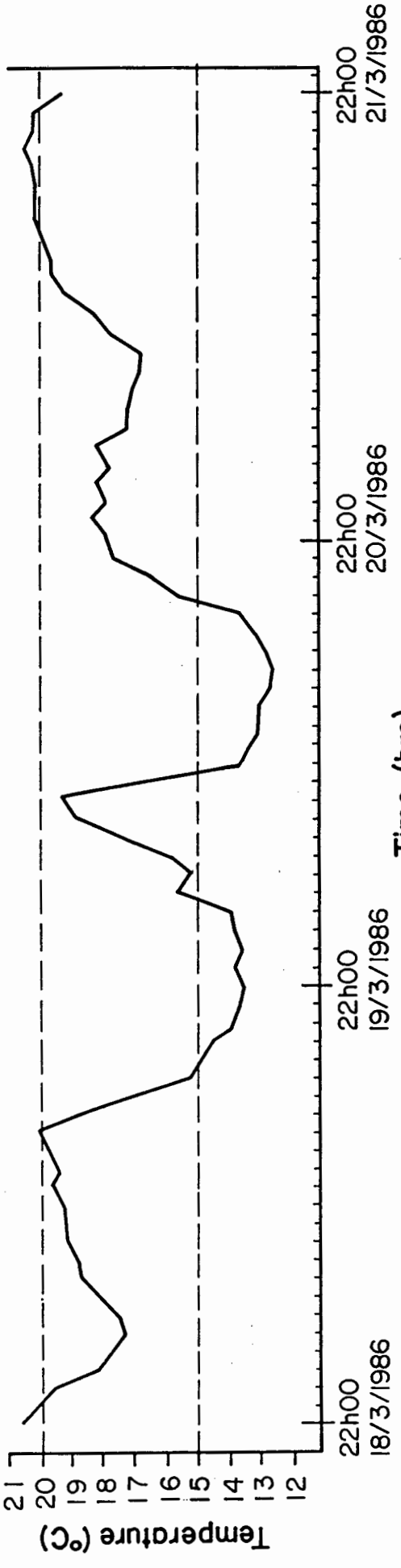

FIGURE 1.10: Temperature fluctuations recorded by the bottom thermistor over a three-day period (34'05"S; 22'14"E).

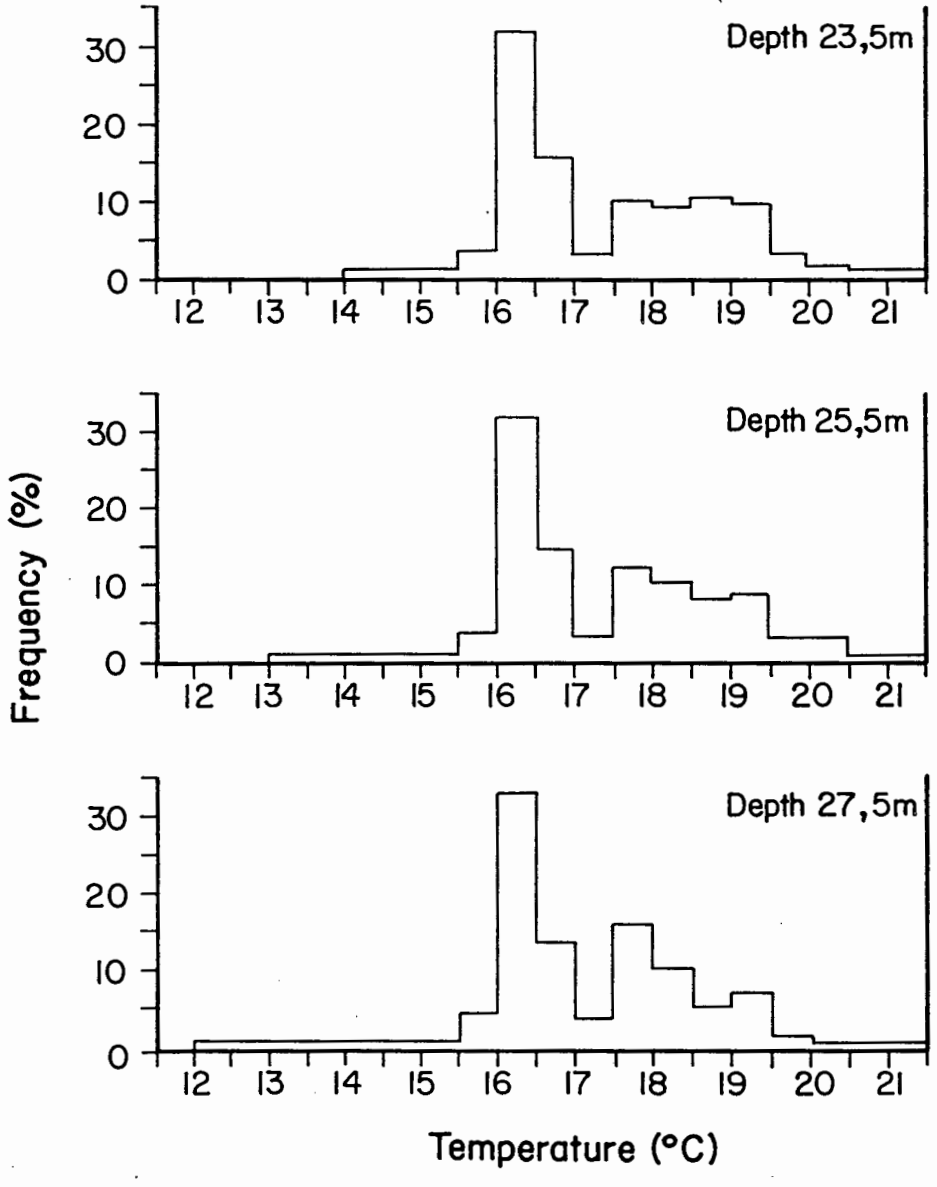

FIGURE 1.11: Frequency distribution of the temperature fluctuations recorded by the three deepest thermistors over a seven-month period (34'05"S; 22'14"E - 13/3-3/10/1986).

The monthly average temperatures in Figure 1.5 are taken to represent the mean bottom water temperatures for the reef and show a distinct seasonal cycle. Temperature fluctuations due to seasonal variations are even more pronounced if the consecutive presence and absence of cold bottom water in summer and winter, as can be seen from the monthly minimum values recorded, is taken into consideration. The associated decrease in standard deviation and temperature range of the monthly averages towards the winter months is further evidence of the temperature stratification occurring in summer and the presence of well-mixed water in winter (Figure 1.6). The cold water intrusions in the summer months are evident in Figure 1.7, while Figures 1.8 and 1.9 show the high temperatures measured in the surface water during June 1986.

Figure 1.10 illustrates the shorter time scales (e.g. tidal) over which recorded temperatures fluctuate significantly. A decrease of 6°C in bottom temperature over a two-hour period was recorded. These low values and sudden changes are symptomatic of the summer regime which according to Swart (1983) is characterized by pronounced stratification due to the intrusions of warm surface and cold bottom Agulhas Current water. A thermocline gradient of 8°C over a vertical distance of 8 m was recorded in March 1986. These cold water intrusions, which occurred in March, May and October were not recorded in winter. This is in accordance with evidence, presented by Swart (1983) that the winter regime is characterized by a well-mixed water column extending down to the bottom due to strong wind forcing in winter.

The same pattern was observed by various authors off the southern Cape Peninsula, although the temperature range was at least 5°C lower. South-easterly winds occurring late spring and summer caused pulses of upwelling while the maximum temperatures were recorded in winter (Velimirov et al., 1977; Dieckman, 1980; Anderson and Hay, 1986). Anderson and Bolton (1985) found that the mean tempeature was lower in winter than in summer at

Betty's Bay due to the orientation of the coast, with the result that summer south-easterly winds blow onshore, bringing warm oceanic water to the coast. A shallowing of the thermocline on the Agulhas Bank towards the east was recorded by Swart and Largier (1987), and the depth of the surface mixed layer was found to be approximately 10 m deep in the vicinity of the reef.

The difference between the winter and summer regimes is demonstrated by the presence of the two peaks in Figure 1.11. The first narrow peak between 16°C and 17°C is due to the well-mixed water during winter, whereas the second broader peak and the measurements to the left of the first peak are both due to the stratified water in summer. According to Swart and Largier (1987), cyclonic frontal eddies accompanying the meanders of the Agulhas Current along the south-eastern edge of the Agulhas Bank force both warm subtropical surface water and cold, less saline Indian Ocean central water onto the continental shelf. Cold water upwelled over the shelf-edge to form the basal layer on the shelf, has been described by Shannon (1966) and Bang (1972).

It is evident that the reef fauna are subjected not only to fluctuations within a large temperature range but also to sudden intrusions of cold bottom water over short-time periods and two entirely different temperature regimes. The dynamic nature of this physical feature of the reef environment will have a definite influence on the physiology of the reef fauna. The results of this study are thus useful and must be incorporated into the oxygen consumption measurements and ultimately the consumption estimate for the dominant reef organism.

CHAPTER 2: PARTICULATE MATTER AND DISSOLVED ORGANIC CARBON IN THE REEF ENVIRONMENT

Introduction

Quantitative measurements of the particulate matter and dissolved organic carbon present in the reef environment will establish the amount of organic matter available to meet the consumption requirement of the filter-feeding community. Such a measurement will also provide information on the organic matter flow through the reef environment, as the presence of organic matter in the immediate vicinity of the reef is a contributing and resulting factor of the organic matter flux.

Analyses of dissolved or particulate organic matter in South African coastal waters have been made by Cliff (1979; 1982) Field et al. (1980), Griffiths (1980), Berry and Schleyer (1983) and Stuart and Klumpp (1984). The studies by Cliff and Griffiths were carried out in False Bay. Berry and Schleyer determined the amount of organic matter in the extremely turbulent subtidal waters of Natal while the work by Field et al. and Stuart and Klumpp were done at Oudekraal on the west coast of the Cape Peninsula.

In estimating the amount of food available to the filter feeders it is necessary to know not only how much organic matter is present in the water but also its distribution according to particle size, because it is largely the particle size that determines whether a substance is effectively retained or not (Jorgensen, 1955; Mullin, 1965). The hypothesis that sponges may be able to utilize dissolved organic carbon was advanced by Pütter (1914) and reported on by Stephens and Schinske (1961), Reiswig (1971b), Smith and Tiffon (1979) and Wilkinson and Garrone (1980). For the purposes of this study it was therefore essential to obtain values for the dissolved organic carbon concentration as well as the total concentration and size distribution of particulate organic matter present in the bottom water above the aeoleonite reef system on the Agulhas Bank.

Material and Methods

Water samples were collected during the March and June 1986 and October 1987 cruises on board the RV Meiring Naudé. The water was obtained from 14 different stations at various depths (Figure 1.2). Ten stations were in the biomass study area while four were further offshore between 32 m and 44 m depth. All the water samples were collected approximately 1 m above the reef by SCUBA divers using 20 ℓ plastic containers.

Between 300 mℓ and 5 ℓ of reef water, depending on the density of the particulate load, were passed through a series of filters of six pore sizes. Particles were thus separated into fractions >150 µm, 50-150µm, 10-50 µm, 5-10 µm, 1,2-5 µm and 0,7-1,2µm. Each size fraction was rinsed using 3,033% isotonic ammonium formate solution to remove salt. This may reduce cell lysing and any subsequent loss of contents due to osmotic shock (Armstrong, 1958; Newell et al., 1982). Sieves were used for the 150, 50 and 10µm fractions, Nuclepore filter papers for the 5µm size fraction and Whatman GFC and GFF filter papers for the 1,2 and 0,7µm size fractions.

The particulate material collected on the sieves was backwashed with the ammonium formate solution onto pre-ashed (450°C), preweighed GFC filter papers. The 5µm Nuclepore polycarbonate membrane filter papers were rinsed in ammonium formate to remove particulate material, after which the water was filtered onto pre-ashed (450°C), preweighed GFC filter papers. Rinsing of the Nuclepore filter papers in the ammonium formate was not sufficient to remove all the particulate material from the paper. Therefore the filtrate from the 10µm sieve was directly filtered onto a GFC filter paper. The 5µm fraction were calculated by subtraction of the 1,2 µm size fraction from the GFC fraction. The filter papers were stored at -20°C. Five replicate samples of the final filtrate were taken and stored at -20°C for later dissolved organic carbon analysis.

All the GFC and GFF filter papers were dried at 60°C for 24 hours and the dry weights determined (Lovegrove, 1966). Each paper was then ground into powder form with the use of an agate mortar and pestle. The powder was divided into two halves. One half was placed in a numbered and preweighed porcelain crucible and the weight determined, while the other half was stored in a numbered glass vial. The filter paper in the crucible was ashed at 450°C for 4 hours after which the crucible was weighed and the contents transferred to a numbered glass vial. Organic matter was determined by weighing before and after ignition at 450°C. The aim of the division was the determination of total and inorganic carbon, and by subtraction, of organic carbon through CHN analysis.

Both halves of each filter paper was subjected to CHN analysis using a Carlo Erba elemental analyser standardized to acetanelide (Rosenthal, 1984). The dissolved organic carbon analysis was carried out using a Technicon auto analyser which employed the UV photo-oxidation process (Mostert, 1983). The total and dissolved inorganic carbon were measured and the dissolved organic carbon was obtained by subtraction.

Results

The total suspended particulate matter (TSPM) and particulate organic matter (POM) present in the reef water are expressed as milligrams dry weight of matter retained by each filter per litre of water filtered through the series of filters (Figure 2.1). The data are presented in Table 2.1 and the results obtained by other authors in Table 2.2. The concentration of the total suspended particulate matter ranged from 8,28 $mg\ell^{-1}$ to 34,8 $mg\ell^{-1}$ at the 14 stations, with a mean value of 20,6 $mg\ell^{-1}$. A mean value of 1,18 $mg\ell^{-1}$ was obtained for the organic content of the particles while the mean inorganic content was 19,42 mg ℓ^{-1}. The mean organic fraction comprised 5,7% of the total. The mean size fractioned data are presented in Figure 2.2.

TABLE 2.1: Concentration of TSPM and POM in milligrams of dry mass per litre at the 14 stations. Column a - POM, column b - TSPM

Stn no.	Depth (m)	Date	Visibility	TSPM and POM (mg/ℓ dry weight) (µm)													
				>0,7		>1,2		>5		>10		>50		>150		Total	
				a	b	a	b	a	b	a	b	a	b	a	b	a	b
1	13	10.03.86	3	0,03	2,70	0,08	3,60	0,08	3,60	0,04	3,40	0,26	1,18	0,00	0,00	0,49	14,48
2	17	16.03.86	0	0,04	1,80	0,42	7,80	0,40	3,00	0,16	5,40	0,40	8,20	0,04	1,60	1,46	27,80
3	25	17.03.86	10	0,15	1,80	0,10	1,70	0,26	2,04	0,28	2,02	0,01	0,46	0,02	0,26	0,82	8,28
4	20	17.03.86	3	0,25	3,60	0,04	0,53	0,06	2,70	0,63	4,00	0,02	0,88	0,00	0,00	1,00	11,71
5	40	18.03.86	0	0,22	3,86	0,20	2,14	0,01	0,45	0,45	7,71	0,01	0,62	0,01	0,40	0,90	15,18
6	14	18.03.86	0	0,03	1,63	0,03	1,13	0,02	1,12	0,49	13,10	0,08	0,30	0,004	0,26	0,65	21,54
7	29	18.03.86	5	0,05	4,30	0,04	1,57	0,25	11,25	0,03	2,70	0,07	0,60	0,00	0,20	0,43	20,62
8	44	19.03.86	0	0,08	5,25	0,03	3,00	0,08	2,60	0,65	9,40	0,32	4,80	0,09	1,58	1,25	26,63
9	32	10.06.86	0	0,03	1,90	0,12	3,40	0,59	6,50	0,28	3,80	0,66	0,36	0,14	2,66	1,82	27,62
10	19	15.06.86	0	0,99	9,40	0,68	6,80	0,64	5,20	0,87	8,40	0,56	5,80	0,20	1,80	3,94	38,40
11	18	16.06.86	1,5	0,05	1,45	0,34	10,30	0,30	8,50	0,07	1,98	0,04	1,20	0,23	2,40	1,03	25,83
12	35	17.06.86	3	0,001	0,03	0,10	1,17	0,17	5,87	0,05	1,21	0,02	1,16	0,00	0,00	0,34	9,44
13	18	31.10.87	-	0,40	1,90	0,80	2,90	0,20	1,80	0,20	0,60	0,20	0,60	0,10	0,80	1,90	8,60
14	18	31.10.87	-	0,80	2,00	0,50	1,20	0,80	3,40	0,40	1,00	0,20	0,60	0,10	0,80	2,80	9,00
Mean				0,16	3,14	0,18	3,60	0,24	4,40	0,33	5,26	0,20	2,90	0,06	1,01	1,18	20,60
Standard deviation				0,27	2,4	0,2	3,08	0,21	3,19	0,28	3,64	0,28	3,28	2,08	1,12	0,97	9,10

The dissolved organic carbon concentrations are presented in Table 2.3. The values are expressed as $mg\ell^{-1}$ and were obtained by subtraction of dissolved inorganic carbon values from dissolved total carbon. The values ranged from 0,23 to 3,58 $mg\ell^{-1}$ with a mean value of 1,29 $mg\ell^{-1}$.

TABLE 2.2: Total suspended particulate matter (TSPM); particulate organic matter (POM) and organic fraction of particulate matter in sea-water

TSPM ($mg\ell^{-1}$)	POM ($mg\ell^{-1}$)	Organic fraction (%)	Study area	Source
1-7	0,7-5,5	40-50	Oudekraal	Field et al. (1980)
25,68	4,80	10-30	Bailey's Cottage	Griffiths (1980)
3,80	1,50	39,00	Dalebrook	Cliff (1982)
3,28	1,59	49,00	Oudekraal	Stuart (1982)
23,59	5,80	19,20	ORI reef	Berry and Schleyer (1983)
20,60	1,18	5,70	South coast reef	Present study

Discussion

A mean value of 20,6 $mg\ell^{-1}$ was obtained for the total suspended particulate matter present in the reef water. The organic content averaged 1,18 $mg\ell^{-1}$ (5,7%) while the mean inorganic content was 19,2 $mg\ell^{-1}$ (94,3%). The amount of TSPM is in accordance with values recorded by Griffiths (1980) and Berry and Schleyer (1983). Griffiths recorded a mean annual value of 25,68 $mg\ell^{-1}$ and Berry and Schleyer a value of 23,59 $mg\ell^{-1}$ for the 2 to 200 µm size fraction. Cliff (1982) obtained a mean value of 3,8 $mg\ell^{-1}$ at Dalebrook and Stuart (1982) a mean value of 3,28 $mg\ell^{-1}$ at Oudekraal. The study by Field et al. (1980) showed that the value varies between 1 $mg\ell^{-1}$ and 7 $mg\ell^{-1}$. These low values could be attributed to the relatively sheltered

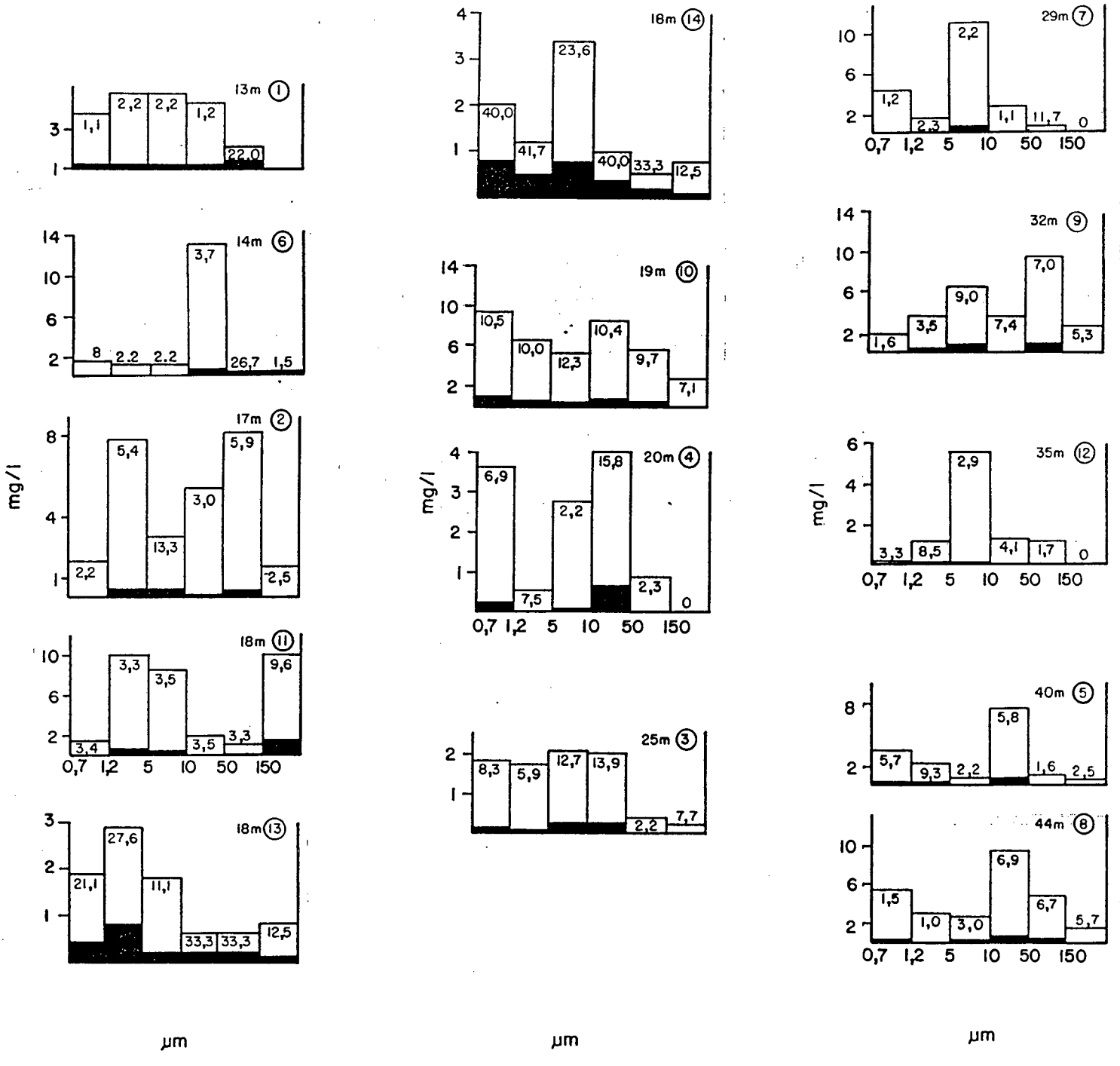

FIGURE 2.1: Concentration of total particulate matter and particulate organic matter in mg dry mass per litre at fourteen sampling stations. The POM (shaded) expressed as a percentage of TSPM are included for each size fraction.

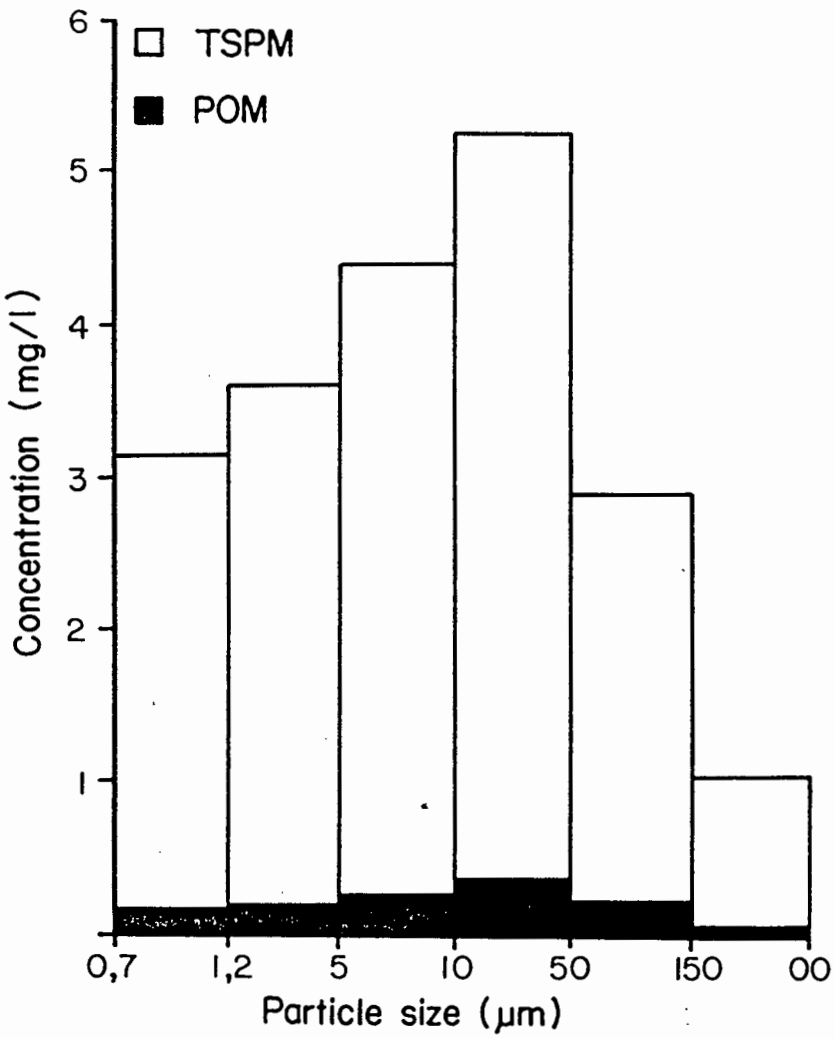

FIGURE 2.2: Average particle size distribution of TSPM and POM in the reef water.

positions of the Dalebrook and Oudekraal study sites as increased turbulence and the resulting increase in particulate inorganic matter is characteristic of the less sheltered areas. The proximity of fine sediments is another factor that would influence the amount of suspended matter present in the reef environment.

TABLE 2.3: Dissolved organic carbon recorded at the 12 stations

Station number	Depth (m)	Dissolved organic carbon (mgℓ) ±SD
1	13	3,58 (±0,30)
2	17	0,40 (±0,10)
3	25	0,23 (±0,17)
4	20	0,47 (±0,34)
5	40	0,46 (±0,36)
6	14	0,58 (±0,44)
7	29	0,60 (±0,45)
8	44	2,28 (±0,69)
9	32	1,43 (±0,58)
10	19	1,50 (±0,38)
11	18	1,74 (±0,36)
12	35	2,2 (±0,52)
	Mean	1,29 (±1,03)

The amount of particulate organic matter was lower than values obtained by the other authors. According to Field et al. (1980) the values ranged from 0,7 $mg\ell^{-1}$ to 5,5 $mg\ell^{-1}$ at Oudekraal. Scattered values for ash-free particulate organic matter determined elsewhere are found in the literature. Armstrong and Atkins (1950) found 1,62 $mg\ell^{-1}$ and 1,77 $mg\ell^{-1}$ in two samples from the English Channel while Riley (1939) measured values of 0,2 $mg\ell^{-1}$ to 0,5 $mg\ell^{-1}$ in the Northern Gulf of Mexico.

The products of primary production may become available to suspension feeders via fragmentation and heterotrophic biodegradation (Newell, 1979). The observed abrasive action of the

suspended sand grains on the macrophytes is probably a major contributing factor to the amount of POM available for utilization by the filter feeding community. The macrophyte: macrofauna ratio was small (Chapter 3) in comparison with the ratios obtained for the extensive kelp bed system on the west coast (Velimirov et al., 1977; Field et al., 1978). This would imply a relatively low POM production and a relatively high POM utilization which could account for the lower POM values recorded during this study.

The organic content of the particulate suspended matter was low in comparison with values obtained by the other authors. Widdows et al. (1979) found that organic material represented 6% to 25% of the particulate matter in the Lynher estuary and Verwey (1952) an average of 12% in the Wadden Sea. The small organic fraction of the TSPM was thus due to the slightly reduced POM values but more importantly to the increased particulate inorganic matter. This may be due to the presence of the nepheloid layer described by Zoutendyk (1971). This phenomenon of turbid water was observed at various sampling stations and could also be a limiting factor of the macrophyte distribution.

The variability in the concentrations measured is expected as the water samples were obtained at different stations at various depths. The spatial and temporal variability of POM has been reported by Armstrong (1958), Wangersky (1974), Cauwet (1981), Dawson and Duursema (1981) and Romankevich (1984). The spatial patchiness of organic matter is mostly due to variations in production and decomposition of organic matter and resuspension of the bottom sediment. The temperature fluctuations and intrusions of cold bottom water described in Chapter 1 together with the erratic presence of the nepheloid layer would also play a role in the variability of the measurements. These factors probably account for the high POM values recorded in October 1987.

Analyses of the data showed no association between either depth and POM or depth and TSPM, whereas a positive correlation (r=0,78) was found for the POM regression against TSPM. The mean values obtained from the size fractioned data are presented in Figure 2.2, and show a standard distribution.

Problems were experienced with carbon analyses of the particulate matter due to the variability and relatively high values of the carbon blanks as opposed to the amount of particulate carbon on the filter papers. This problem has been reported and discussed by Sharp (1974), Wangersky (1974) and MacKinnon (1981). Although the problem can be minimized by increasing the volume of water filtered, this may result in clogging of the filters which would lead to distorted values. An attempt can be made to estimate the particulate organic carbon present in the reef environment from the particulate organic matter values obtained. According to Lenz (1974) and Andrews and Hutchings (1980) particulate organic carbon constitutes 50% of the particulate organic matter. This would suggest a value of 0,59 $mgC\ell^{-1}$.

A mean value of 1,29 $mg\ell^{-1}$ was recorded for the dissolved organic carbon in the reef water (Table 2.2). The dissolved organic carbon thus constitutes 68% of the total sum of dissolved and particulate organic carbon. This is in accordance with values obtained by Williams (1967) and MacKinnon (1981). The relative proportions of POC:DOC:POM:TSPM present in the reef environment were calculated to be 1:2:2:33.

It is evident from the data presented that fluctuations in the concentration and particle-size distribution of the available food source are prominent features of the reef environment. The filter-feeding component is thus subjected to changes in the amount and composition of seston available for utilization. The amount and particle sizes utilized by a dominant organism of the filter-feeding community are investigated in Chapter 5. At this stage it was only necessary to estimate that the average amount of particulate organic carbon available for utilization is approximately 0,6 $mg\ell^{-1}$.

CHAPTER 3: BIOMASS DETERMINATION FOR A SUBTIDAL REEF COMMUNITY

Introduction

A proper understanding of aquatic ecosystems requires an exploration of the structure and functioning of its constituent components. Therefore an estimation of the minimum consumption requirement of the reef community and an investigation into the organic matter flow through the system necessitates determination of the biomass present. Apart from providing basic information concerning the ecology of a reef, a reproducible description of the subtidal reef community is an essential prerequisite for any investigation of the reef community.

A large number of studies on marine hard substratum communities only deal with a particular taxonomic group (e.g. Nienhuis, 1976; Weinberg, 1978b) while studies on these communities as a whole are often qualitative studies (e.g. Könnecker and Keegan, 1983). Analyses of the biomass and spatial distribution of kelp bed communities on the Cape west coast were made by Velimirov *et al*. (1977) and Field *et al*. (1980). Biomass measurements of filter-feeding detritivores on a littoral rocky reef on the Natal coast were carried out by Berry (1982).

The subtidal reefs of the study area consist of carbonate-cemented sands similar to those found onshore in the Wilderness area. Large-scale cross-bedding suggested an aeolian origin and the reefs therefore represent a succession of coastal dune belts, formed in the course of successive Pleistocene low stands of the sea and which were drowned and partially buried in the course of the Holocene transgression of the sea. There is considerable evidence for erosion by wave action in former surf zones. Rounded pebbles and cobbles of fluvial origin are common and extensive gullying and undercutting can be observed (Zoutendyk and Flemming, 1983). These irregularities of the rock surface provide a great variety of microhabitats, causing a wide diversity of forms among the reef fauna on the rocky bottom. A

high species diversity was observed on preliminary dives and all the major invertebrate phyla appeared to be well represented.

Apart from a general description by Tietz and Robinson (1974) and a comparative study by Zoutendyk and Flemming (1983) and Zoutendyk (unpublished), the distribution of the Cape south coast subtidal communities on the aeoleonite reefs have not previously been described. It was therefore necessary to determine the biomass and relative importance of the dominant taxa present in order to estimate the consumption requirement of the reef community.

Material and Methods

The biomass survey was carried out during March and June 1986 on board the RV Meiring Naudé. The 10 m to 30 m depth area of the aeoleonite reef system was subdivided into five depth sections for the purpose of this biomass survey. A station was selected in each section. Station A was in the 10 m to 14 m depth section, B in the 14 m to 18 m depth section, C in the 18 m to 22 m depth section, D in the 22 m to 26 m depth section and E in the 26 m to 30 m depth section.

Six SCUBA divers were grouped into three teams and each team dived at each station to clear two 1/10 m^2 quadrats and carry out a combined belt count. The depth of each station was determined with the use of sonar equipment and confirmed after deployment and retrieval of an anchor rope. Specimens of nine dominant species of the reef fauna were collected and divided into small, medium and large size ranges for belt count purposes. The specimens and their respective sizes were studied by the divers after which note pads with the relevant information were issued.

At each of the five stations the first team deployed a bottom line from the anchor point after confirmation of the depth range with a depth guage. The 25 m bottom line was equipped with

marked lead weights secured at 1 m intervals. After deployment of the line, two random 1/10 m^2 quadrats were cleared by the team on the way back to the anchor point. The contents of each quadrat was transferred to separate plastic bags which were tied to the anchor. The belt count (Quast, 1971) was carried out along the bottom line back to the end point. One diver counted all the predetermined species and noted down their respective sizes in a 1 m wide strip on one side of the line, while the second diver followed the same procedure on the other side of the line. The bottom line was rolled up and the deployment direction for the second team was indicated at the central anchor point. The new direction was 60° clockwise of the previous direction. The second and third team repeated the procedure after which the equipment was recovered.

The samples removed by the random quadrat method were preserved in a 10% formalin solution buffered by hexamine. Representative samples over a size range of the species noted in the belt count method were frozen at -20° C. In the laboratory the contents of each quadrat was subdivided according to species and the wet weight of each species in each quadrat determined after removal of the external water. No effort was made to compensate for potential weight loss caused by preservation as Leuven et al. (1985) concluded that preservation in formaldehyde did not cause significant changes in biomass. The dominant species were identified and the remainder grouped into the major taxa. Representative subsamples of the taxa constituting more than 1% of the total wet mass were dried to constant mass at 60°C and ashed at 450° C for 4 hours. The belt count numbers were converted to biomass by determining the mean wet mass for the size range of each species. The procedure of measuring wet mass, drying and ashing was conducted as above.

Results

The wet mass values obtained by the random quadrat method are summarized in Table 3.1. Each value represents the mean weight

of six quadrats removed in each depth zone. Porifera and Bryozoa accounted for 70% of the total wet mass. The total value in each depth zone ranged from 1248 g in the shallow area to 2775 g in the deepest zone. The determined interrelationships of wet, dry and ash-free dry weights are presented in Table 3.2 All values are equivalent to 1 g dry mass. The values in Table 3.3 were calculated with the use of these conversion factors. Porifera accounted for 33% of the total ash-free dry weight.

TABLE 3.1: Mean wet mass of major taxa from six 0,1 m^2 quadrats in each depth zone

		Wet mass (gm^{-2})						
Depth (m)		10-14	14-18	18-22	22-26	26-30	Mean	%
Porifera	$\bar{x}$	148,80	758,7	628,1	1305,8	1321,7	832,6	36,50
	±1 SD	128,50	597,0	364,2	1294,3	988,3		
Cnidaria	$\bar{x}$	212,80	192,5	278,7	272,6	273,4	246,0	10,80
	±1 SD	304,40	179,2	546,0	412,6	218,2		
Bryozoa	$\bar{x}$	272,60	634,4	1289,1	675,3	933,8	761,0	33,30
	±1 SD	281,20	548,9	1916,9	774,9	608,4		
Crustacea	$\bar{x}$	0,00	2,6	1,4	0,9	4,9	2,0	0,09
	±1 SD	0,00	4,6	2,3	2,1	4,6		
Annelida	$\bar{x}$	34,90	29,5	142,4	35,6	42,9	57,1	2,50
	±1 SD	25,20	45,4	196,2	52,6	35,2		
Mollusca	$\bar{x}$	5,00	26,8	20,8	8,2	9,1	14,0	0,60
	±1 SD	8,90	41,7	22,3	14,5	10,7		
Echinodermata	$\bar{x}$	61,34	15,1	11,5	5,8	18,6	22,4	0,98
	±1 SD	104,10	19,1	21,5	7,8	43,4		
Algae	$\bar{x}$	111,90	30,5	21,2	3,4	2,1	33,8	1,50
	±1 SD	102,50	29,8	33,1	7,8	5,1		
Miscellaneous	$\bar{x}$	1,70	39,9	5,0	14,8	32,0	18,7	0,80
	±1 SD	4,10	69,1	12,2	21,5	40,0		
TOTAL		1248,40	2483,1	2462,4	2441,1	2774,6	2282,0	100,00

The weights of each taxa expressed as a percentage of the total ash-free dry weight are presented for each depth zone (Figure 3.1). The combined contribution of Porifera and Bryozoa are directly proportional to depth while the ash-free weight of the algae decreased with depth. The dominance of the filter feeders (73%) is evident in all five depth zones while micropredators accounted for approximately 20% of the total ash-free dry weight. As expected the grazers and deposit feeders only made up a small percentage of the total.

The species numbers and their respective sizes obtained by the belt count method are summarized in Table 3.4. The sum of the species counted by all six divers is expressed in numbers per m^2. Wet weight values were assigned to each species after determination of the wet mass of collected specimens over a size range (Table 3.5). The values in Table 3.6 were calculated with the use of the conversion factors in Tables 3.2 and 3.5.

The random quadrat method was used to sample densely packed and slow-moving organisms while the density of large and widely scattered organisms was estimated by the belt count method. The ash-free dry weights obtained from the two methods were added to provide a total picture of the community structure (Table 3.7). It was done after exclusion from the quadrats of those species counted in the belt counts.

TABLE 3.2: Relationship between wet mass, dry mass and ash-free dry mass (AFDM) determined for selected taxa. All values are equivalent to 1g dry mass

Taxa	N	Wet mass (g)	AFDM (g)
Quadrats			
Porifera	8	4,34 (±1,12)	0,30 (±0,22)
Cnidaria	8	3,14 (±0,84)	0,49 (±0,32)
Bryozoa	12	3,76 (±1,08)	0,24 (±0,17)
Tunicata	9	5,86 (±0,94)	0,49 (±0,18)
Annelida	4	8,34 (±0,82)	0,46 (±0,12)
Algae	5	3,57 (±0,87	0,76 (±0,21)
Belt counts			
Spirastrella sp.	30	5,33 (±0,36)	0,30 (±0,09)
Wall Spronge	3	4,22 (±0,24)	0,36 (±0,11)
Porifera sp. C	3	4,09 (±0,27)	0,37 (±0,17)
Schizoretepora tesellata (Bryozoa)	3	3,94 (±0,18)	0,31 (±0,06)
Distapalia domuncula (Tunicata)	3	6,26 (±0,44)	0,54 (±0,07)
Marthasterias glacialis (Echinodermata)	3	3,06 (±0,22)	0,26 (±0,18)
Thecocarpus formosus (Cnidaria)	3	3,88 (±0,17)	0,46 (±0,17)
Lophogorgia flammea (Cnidaria)	3	4,26 (±0,36)	0,54 (±0,09)
Sea fan	3	3,29 (±0,42)	0,42 (±0,10)

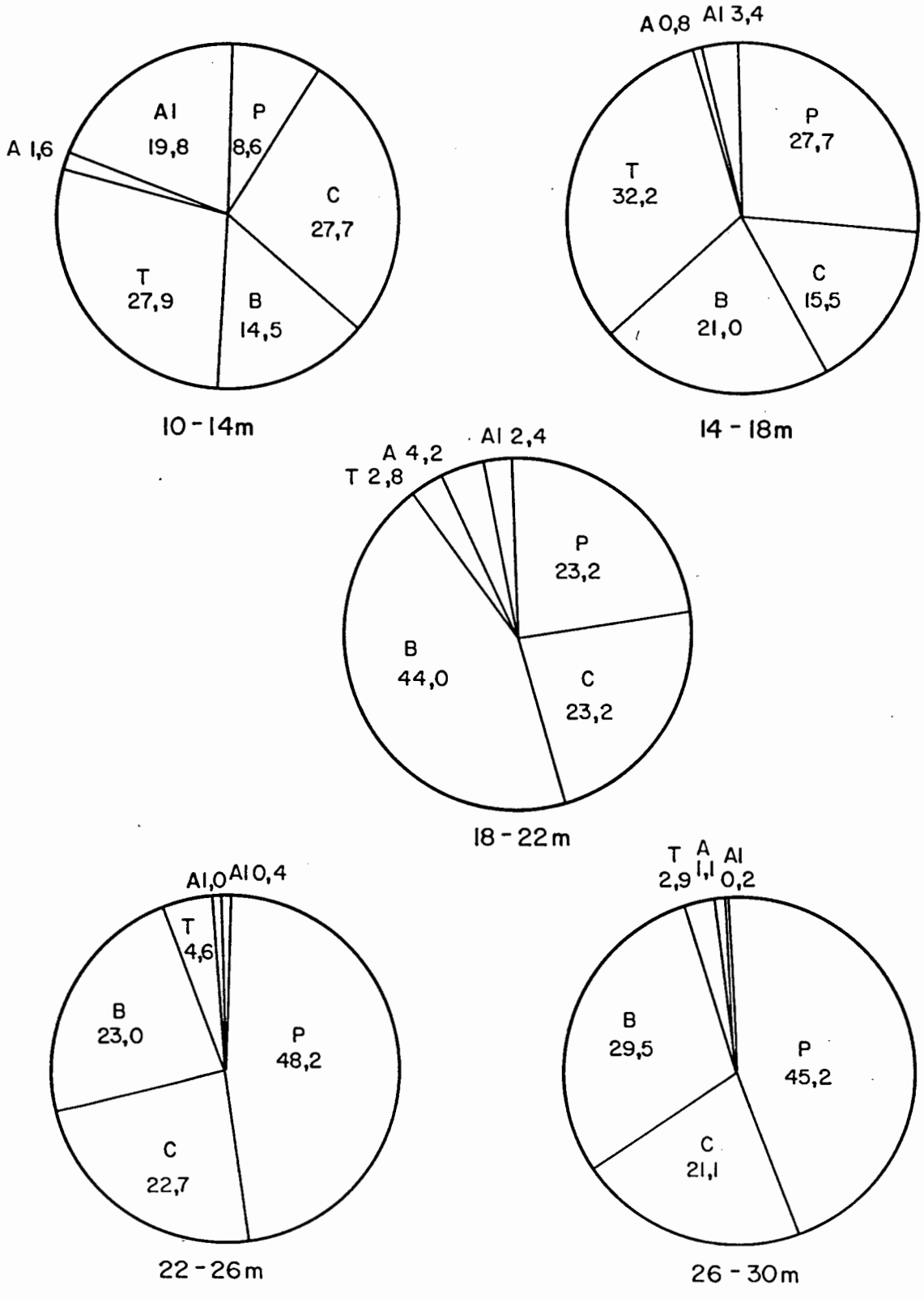

FIGURE 3.1: Ash-free dry weight of the major taxa expressed as a percentage of the total; P = Porifera; C = Cnidaria; B = Bryozoa; T = Tunicata; A = Annelida; Al = Algae.

TABLE 3.3: Dry and ash-free dry weight of the major taxa calculated from Table 3.1

Depth (m)	Weight	Weight (gm^{-2}) 10-14	14-18	18-22	22-26	26-30	Mean	%
Porifera	Dry	34,3	174,8	144,7	300,9	304,5	192,0	35,8
	AFD	10,3	52,4	43,4	90,3	91,4	57,6	32,6
Cnidaria	Dry	67,8	61,3	88,8	86,8	87,1	78,4	14,6
	AFD	33,2	30,0	43,5	42,5	42,7	38,4	19,3
Bryozoa	Dry	72,5	168,7	342,8	179,6	248,4	202,0	37,8
	AFD	17,4	40,5	82,3	43,1	59,6	48,6	27,3
Tunicata	Dry	68,1	126,7	10,9	17,5	11,9	47,0	8,8
	AFD	33,4	62,1	5,3	8,6	5,8	23,0	13,0
Annelida	Dry	4,2	3,5	17,1	4,3	5,1	6,8	1,3
	AFD	1,9	1,6	7,9	2,0	2,3	3,1	1,8
Algae	Dry	31,2	8,5	5,9	0,9	0,6	9,4	1,8
	AFD	23,7	6,5	4,5	0,7	0,5	7,2	4,0

TABLE 3.5: Mean wet mass values for selected species and respective size groups from collected specimens for the belt count method

Species	Small (g)	Medium (g)	Large (g)
Spirastrella sp.	15	40	70
Wall sponge	20	60	140
Porifera sp. C	2	6	10
Schizoretepora tesellata	15	40	80
Distapalia domuncula	10	40	60
Marthasterias glacialis	5	12	20
Thecocarpus formosus	1	7	14
Lophogorgia flammea	5	15	25
Sea fan	2	12	30

TABLE 3.4: Number of individuals of selected species for the belt count method recorded in each depth zone. S = small, M = medium, L = large

Depth (m)	10-14			14-18			18-22			22-26			26-30		
Area covered (m^2)	100			80			50			60			36		
	S	M	L	S	M	L	S	M	L	S	M	L	S	M	L
Spirastrella sp.	0,30	0,12	0,09	0,30	0,24	0,24	0,36	0,24	0,04	0,39	0,09	0,12	0,33	0,24	0,27
Wall sponge	0,07	0,01	0,00	0,06	0,15	0,02	0,50	0,30	0,06	0,50	0,90	0,10	0,47	0,59	0,28
Porifera sp. C	0,14	0,03	0,00	1,20	0,29	0,02	0,02	0,04	0,02	0,19	0,10	0,02	0,45	0,14	0,11
Schizoretepora tesellata	0,24	0,26	0,08	0,17	0,35	0,22	0,16	0,14	0,23	0,42	0,39	0,09	0,62	0,34	0,15
Distapalia domuncula	0,42	0,08	0,07	0,32	0,03	0,12	0,26	0,12	0,02	0,17	0,07	0,02	0,34	0,01	0,22
Marthasterias glacialis	0,01	0,00	0,00	0,00	0,00	0,00	0,02	0,00	0,00	0,00	0,04	0,00	0,00	0,03	0,00
Thecocarpus formosus	0,03	0,04	0,04	0,26	0,54	0,50	0,04	0,08	0,00	0,10	1,40	0,00	0,06	0,45	0,00
Lophogorgia flammea	0,23	0,17	0,16	0,24	0,50	0,62	0,31	0,24	0,33	0,14	0,08	0,16	0,22	0,43	0,47
Sea fan	0,11	0,17	0,01	0,40	0,50	0,04	1,20	0,08	0,02	0,85	0,62	0,02	0,50	0,50	0,20

TABLE 3.6: Wet, dry and ash-free dry mass of selected species for the belt count method in each depth zone. a = wet, b = dry mass, c = ash-free dry mass (gm^{-2})

Depth (m)	10-14			14-18			18-22			22-26			26-30			AFDW
Weight (g)	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	Mean
Spirastrella sp.	18,8	3,50	1,10	37,30	7,00	2,10	24,2	4,50	1,40	17,85	3,30	1,00	35,1	6,60	2,00	1,50
Wall sponge	2,0	0,47	0,17	13,00	3,10	1,10	30,8	7,30	2,63	78,00	18,50	6,67	84,0	19,9	7,16	3,50
Porifera sp. C	0,5	0,12	0,04	4,34	1,06	0,39	0,5	0,12	0,04	1,20	0,29	0,11	2,8	0,68	0,25	0,17
Schizoretepora tesellata	20,4	5,2	1,60	34,20	8,70	2,70	26,4	6,70	2,10	29,10	7,40	2,30	34,9	8,90	2,80	2,30
Distapalia domuncula	11,6	1,85	1,00	11,60	1,85	1,00	8,6	1,37	0,74	5,70	0,91	0,49	17,0	2,70	1,46	0,94
Marthasterias glacialis	0,1	0,03	0,01	0,00	0,00	0,00	0,2	0,07	0,02	1,60	0,52	0,14	1,2	0,39	0,10	0,05
Thecocarpus formosus	0,9	0,23	0,11	11,00	2,84	1,31	0,6	0,15	0,07	9,90	2,55	1,17	3,2	0,82	0,38	0,60
Lophogorgia flammea	7,7	1,80	1,00	24,20	5,70	3,10	30,5	7,20	3,90	5,90	1,40	0,80	19,3	4,50	2,40	2,24
Sea fan	2,6	0,79	0,32	8,00	2,43	1,00	4,0	1,22	0,50	9,70	2,95	1,21	13,0	3,95	1,62	0,93
TOTAL	128,0	30,90	11,05	223,00	5,40	21,30	234,0	57,00	20,90	257,00	62,70	23,60	396,0	96,80	34,60	12,30

TABLE 3.7: Ash-free dry weight of selected taxa in each depth zone

	Weight (gm^{-2})						
Depth (m)	10-14	14-18	18-22	22-26	26-30	Mean	%
Spirastrella sp.	1,10	2,10	1,40	1,00	2,00	1,52	0,89
Wall sponge	0,17	1,10	2,63	6,67	7,16	3,55	2,10
Porifera sp. C	0,04	0,39	0,04	0,11	0,25	0,17	0,10
Schizoretepora tesellata	1,60	2,70	2,10	2,30	2,80	2,30	1,35
Distapalia domuncula	1,00	1,00	0,74	0,49	1,46	0,94	0,55
Marthasterias glacialis	0,01	0,00	0,02	0,14	0,10	0,05	0,03
Thecocarpus formosus	0,11	1,31	0,07	1,17	0,38	0,61	0,36
Lophogorgia flammea	1,00	3,10	3,90	0,80	2,40	2,24	1,30
Sea fan	0,32	1,00	0,50	1,21	1,62	0,93	0,55
Porifera	8,85	36,40	34,20	80,60	74,40	48,90	28,70
Cnidaria	30,60	22,90	37,40	36,20	34,10	32,20	18,90
Bryozoa	15,40	36,20	78,60	39,80	55,50	45,10	26,50
Tunicata	29,80	57,40	4,90	9,10	5,20	21,30	12,50
Annelida	1,90	1,60	7,90	2,00	2,30	3,14	1,85
Algae	23,70	6,50	4,50	0,70	0,50	7,18	4,20
TOTAL	115,60	183,70	175,90	182,30	190,20	170,10	

Discussion

A prominent feature of the results obtained by the random quadrat method is the low algal biomass recorded. Algae accounted for only 4% of the total ash-free dry weight, which is much lower than the plant to animal ratio of 1,27:1 of the generally shallower kelp communities along the Cape west coast (Field *et al.*, 1980). These authors found a well-marked trend down the west coast with kelp extending much deeper in the south due to the clear water off the southern Cape Peninsula. The depth penetration increased from 9 m to 31 m down the west coast. Betty's Bay on the south coast did not continue the trend as the kelp depth penetration decreased to 20 m.

Available light is the main factor in macrophyte distribution and usually it is the water depth which regulates the light intensity at a particulate depth. The layer of high turbidity water observed at various sampling stations, appears to be another limiting factor and will tend to increase the effect of depth. Zoutendyk (unpublished) measured an algal cover of 80% at Dalgleish Bank (28 m depth) as opposed to 25% on the aeoleonite reef (1,8 km offshore) at the same depth. It is probably due to the fact that Dalgleish Bank lies further offshore (11 km) and is thus less affected by the nepheloid layer. The ash-free dry weight percentage of the algae decreased from 19,8% in the 10 m to 14 m depth section to 0,25% at the deepest sampling station. It appears that the fauna relies largely on nutritional sources other than attached algae, such as plankton or detritus.

This high turbidity layer could also be a contributing factor to the presence or absence of certain components of the filter feeders. The turbid water may be beneficial to some filter feeders in supplying suitable size and composition food particles, or the presence of inorganic food particles could adversely affect the filtering mechanism of others through clogging. According to Field et al. (1980) the standing crop of mussels decreased from north to south down the west coast with a decrease in water turbidity, while sponges showed the reverse trend since they tend to become clogged in very turbid water.

There is a distinct decline in algae as one passes from inshore to offshore and a corresponding increase in the faunal element. This was even more pronounced in the results of Velimirov et al. (1977) because of the dominance of kelp in the inshore areas. Tunicata and Cnidaria were the dominant taxa in the shallower zone while the biomass of Porifera and Bryozoa increased with depth. The wet mass of the quadrats is in accordance with the mean value of 2200 gm^{-2} obtained by Zoutendyk and Flemming (1983) on the aeoleonite reefs at 15 m and 30 m. Porifera was the dominant taxa and accounted for 35,8% of

the total ash-free dry weight. Zoutendyk (unpublished) measured 64% and 58% at two stations to the west of the study area on the same reef system. Filter feeders are the major primary consumers and made up 73% of the total biomass. A small biomass of grazers was present while the micropredators accounted for approximately 20% of the total ash-free dry weight. Newell et al. (1982) concluded that the filter feeders in a kelp bed community comprised 72% of the total standing stock. Berry (1982) measured a high biomass value of 3029 gm^{-2} dry weight on the Natal coast. The author points out that the high value is not a valid total estimate because it incorporates Pyura stolonifera which was only recorded in years when the settlement of Perna perna failed and thus these two species never co-existed at the standing crop levels recorded for each.

The results obtained from the belt counts also reflect the dominance of Porifera, Bryozoa and Cnidaria on the subtidal reefs. The average of the six counts in each depth zone was used to minimize any potential errors made by individual divers. Two Porifera species contributed 25,3 gm^{-2} while the ash-free dry weight of the Bryozoa species was estimated to be 11,5 gm^{-2}. The combined weight of the three Cnidaria species, which included two sea fans and a hydroid, was 18,9 gm^{-2}.

From the combined data it can be concluded that the filter feeding component is the major trophic group of the reef community and that Porifera (32%) and Bryozoa (28%) are the dominant taxa. A mean ash-free dry mass value of 170 gm^{-2} was determined for the subtidal reef community and attached algae appears to be a minor nutritional source. It is suggested that the high turbidity water analysed in Chapter 2 played a prominent role in establishing and maintaining the biomass distribution of the aeoleonite reef community.

SECTION 2

CHAPTER 4: ASPECTS OF *SPIRASTRELLA* RESPIRATION

Introduction

The aim of this study is to contribute to the investigation of the organic matter flow through an aeoleonite reef environment. In order to construct an organic matter budget, knowledge of the losses and the way in which they vary is essential (Lampert, 1984). Therefore the purpose of this section is to provide a respiration estimate for a dominant species of the filter-feeding community. The values can be related to field data using the biomass measurements obtained in Chapter 3, to arrive at energy expenditure per square metre.

Respiration represents the basic energy cost of maintenance to the organism and consequently respiration estimates provide minimum assimilation estimates, assuming that metabolism is aerobic and the energy balance positive (Newell, 1979). Aeoleonite reefs are characterized by high turbulence which ensures that high dissolved oxygen levels are maintained. For this reason metabolic processes of the filter-feeding community are considered to be aerobic and oxygen uptake is taken to be a reliable measure of respiratory rate.

From the data presented in Chapter 1 it is obvious that the reef fauna are subjected to sudden temperature fluctuations. The metabolic variations associated with these short- and long-term changes will be a major consideration in the overall budget of the species. This study aims to provide temperature coefficients for use in calculating the respiration rates which can be integrated into an overall bio-energetic model of the species.

Sponges are one of the major suspension-feeding invertebrate groups of hard-bottom, coastal marine habitats (Reiswig, 1974). In spite of this, little is known about their activities under

either laboratory or natural conditions. According to Reiswig (1974) it is therefore impossible to estimate the effect that local sponge populations exert upon the overlying water layers and the rates at which they convert suspended organic material into benthic biomass. Oxygen consumption measurements on sponges have been carried out by Pütter (1914), Hyman (1916; 1925), De Laubenfels (1932), Hazelhoff (1938), Pourbaix (1939), Von Buddenbrock (1938), Von Ledebur (1939), Gordon, Spiegel and Villee (1955), Ivlev (1963), Ivlev and Yakovleva (1964), Killian (1964) and Reiswig (1974). No documented oxygen consumption estimates for Spirastrella could be found. General concepts concerning the dependance of respiratory metabolic rate on body mass within the physiological range and the possible presence of a strict relationship between respiratory rate and temperature still remain abstract and controversial (Ivleva, 1980). It was therefore necessary to estimate the effect of body mass and temperature on the oxygen consumption of a dominant Porifera species on the Agulhas Bank aeoleonite reef system.

Experiments were carried out on specimens over a representative size range at three temperatures covering the environmental temperature range. Based on these measurements respiration rates per unit body weight were calculated at each of the experimental temperatures and these data were applied to the field biomass estimates to estimate population respiration rates. These were converted to carbon equivalents and 'minimum' consumption was calculated on the basis of a retention efficiency of 79% estimated by Reiswig (1971b).

Material and Methods

The oxygen consumption rate of Spirastrella (Plate 1) was measured by means of a closed respirometer system. Approximately 50 specimens were collected by SCUBA divers during the June 1986 cruise on board the RV Meiring Naudé. The sessile organisms were carefully scraped off the hard bottom and all damaged specimens were discarded. They were transported to the laboratory in holding tanks and were provided with a continuous supply

of air. The animals were transferred to separate tanks equipped with running sea-water at ambient temperature (16°C) and fed three times a week on a mixture of blended Choromytilus meridionalis and yeast. They were not fed during experiments.

The respirometers were made of cylindrical 'perspex' tubing onto which flat perspex caps, containing an 0-ring were placed (Plate 2). Two respirometer sizes were used; the smaller respirometer (600 mℓ) for specimens weighing less than 30 g and the larger respirometer (1900 mℓ) for organisms more than 30 g. On the top were openings made to take the oxygen temperature probes (Yellow Springs Instruments, Model 5739). Individuals were placed in the sealed cylinder and supported on a plastic mesh above a magnetic stirrer.

The respirometers were placed in a temperature controlled water bath and sea-water was provided from a separate tank whose level was maintained by an overflow. The water in this tank was aerated by an air-stone after the temperature was reduced to a constant level slightly below the experimental temperature by a temperature controller. Water flow to the constant temperature bath and the respirometers was via 4 mm silicone tubing (Plate 3). Before use the apparatus was thoroughly cleaned and tests without an animal in the chamber showed that a blank correction of respirometer oxygen consumption was not necessary. The water in the constant temperature bath was kept at the required temperature by means of a temperature sensor and heater.

The YSI probes were connected to a dissolved oxygen meter (Model 57 YSI) which was calibrated daily. The polarographic sensors were calibrated once a week by a two-point calibration method (Lampert, 1984). For adjustment of the zero-point a solution of sodium dithionite was used while saturated water was measured for the second reference point. A check of the calibration was done by Winkler titration. The dissolved oxygen meter was connected to a double-channel graph recorder and a

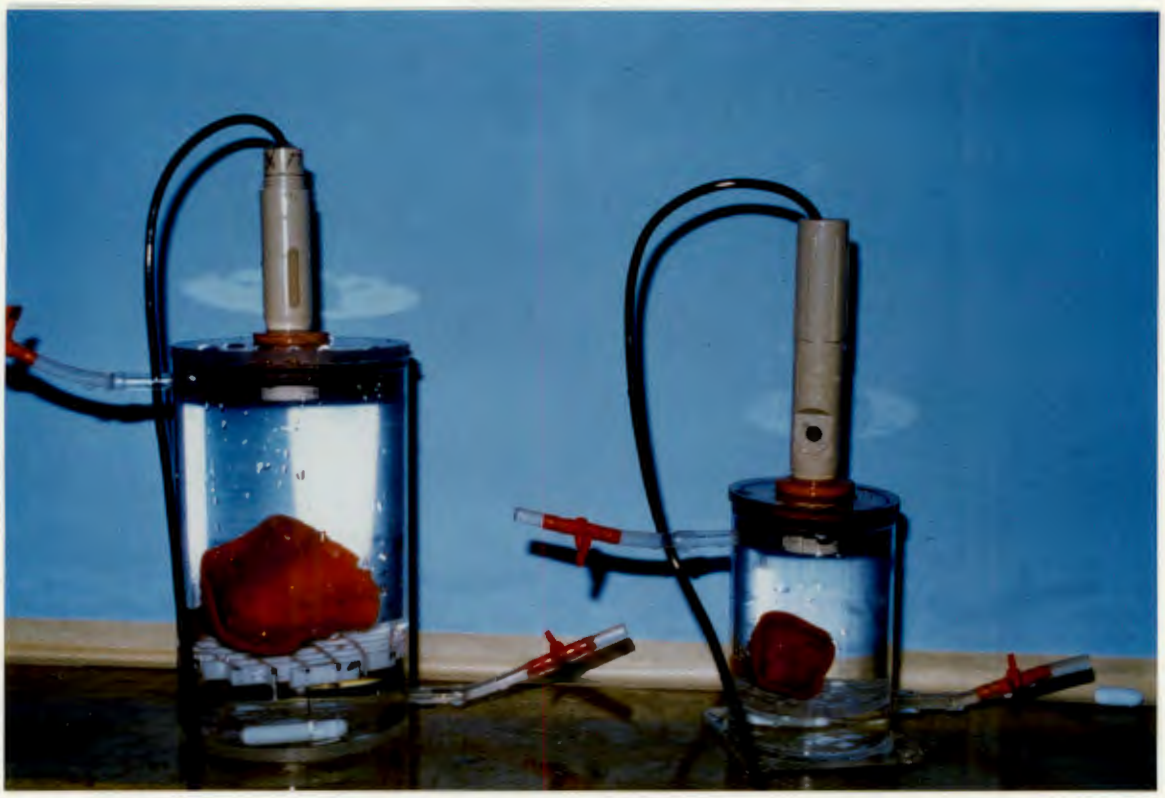

PLATE 2: Respirometer with oxygen temperature probes and *Spirastrella* specimens.

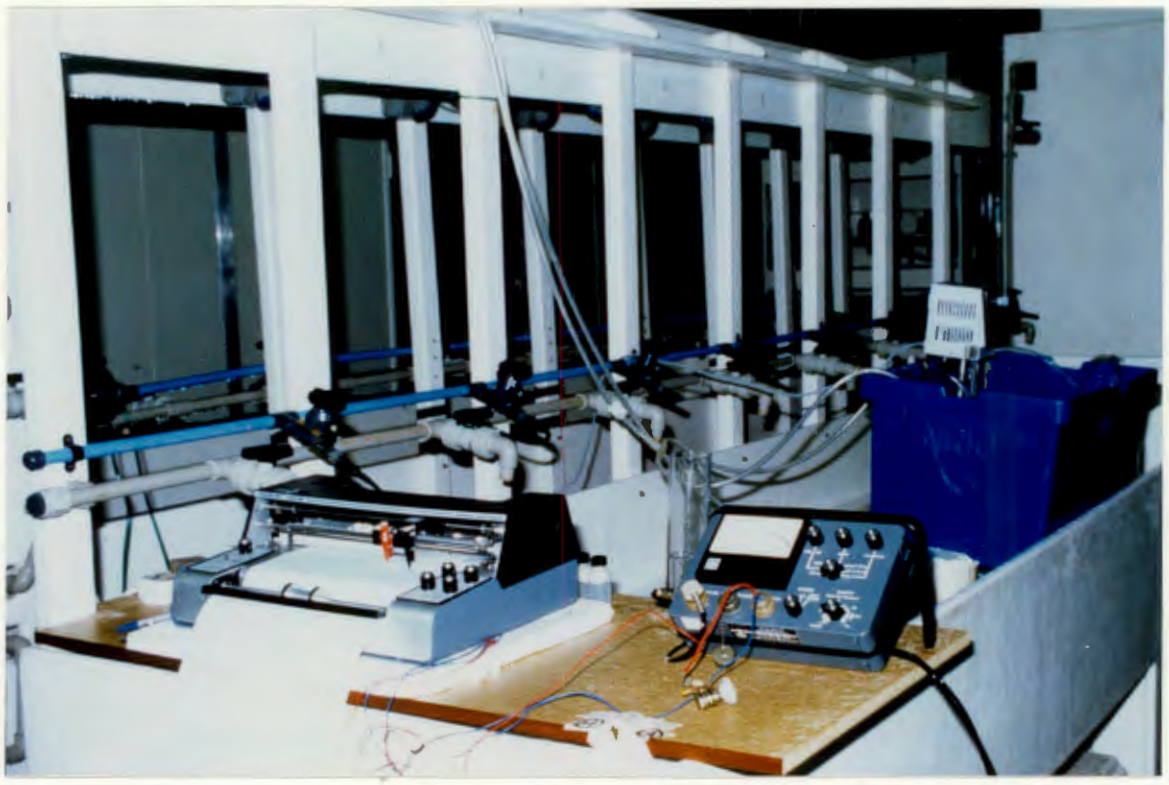

PLATE 3: Dissolved oxygen meter, double-channel graph recorder, constant temperature bath and temperature sensor and heater.

switch was built into the system to facilitate a change-over between the two respirometers without a loss of polarity. Aerated water was permitted to flow through the system until the oxygen level in the respirometers stabilized (1-2 hrs). The flow was stopped and by frequently changing over from one channel to the other, the dissolved oxygen decrease in both respirometers was recorded. The measurements were conducted for one hour and the oxygen tensions never fell to below 70% saturation. The lids were then opened and the chambers flushed with air-saturated sea-water before repeating the procedure. Five readings for each individual were obtained in this manner and averaged.

The animals were acclimatized for 48 hrs in running sea-water at the appropriate temperature before commencing the measurements at 12°C, 16°C and 20°C. The rate of oxygen consumption was calculated from the slope of the line showing oxygen depletion over time. Only oxygen uptake curves displaying linearity throughout the measurement were used in the analysis as a precaution against including rates responding to possible environmental changes, such as accumulating waste products or declining oxygen partial pressure. All values were converted to mg oxygen consumed per hour per gram (ash-free dry weight) of animal. Following removal from the respiration chamber, the sponges were blotted dry and weighed to yield the wet weight. Dry weights were determined after the animals were dried at 60°C to constant weight and the ash content was estimated following ignition at 450°C for 4 hours.

Results

Figure 4.1 depicts graphs of Spirastrella respiration rate (R) versus body weight at each of the experimental temperatures. The weight-specific respiration rates are presented graphically in Figure 4.2. The log transformed form of the allometric equation $R = aW^b$ and r values for each graph are included. Table 4.1 presents Porifera respiration rates obtained by other authors.

Most comparative studies have established that metabolism is proportional to a constant power of the body weight and is described by the allometric equation:

$$Y = a \cdot X^b$$

where

Y = metabolic rate (in oxygen consumption)
a = intercept
X = body mass
b = exponent

In its logarithmic form the equation becomes:

$$\log_{10} Y = \log_{10} a + b \cdot \log_{10} X$$

where a is the intercept when $\log_{10} X = 1$ and b is the slope of the regression line (Newell, 1979). The proportionality constant a and the exponent b of the above power function were calculated from the logarithmic transformed equation using the method of least squares.

Plotted on a double logarithmic grid, routine oxygen consumption increased linearly with weight with values of the exponent b ranging between 0,66 and 0,68. It is also convenient to compare the metabolic rate of organisms per unit of body weight. The weight-specific metabolic rate is then described by $Y/X = a \cdot Xb^{-1}$ and the negative slope so obtained ranged between -0,32 and -0,34.

TABLE 4.1: Porifera weight-specific respiration rates

Respiration rate $mgO_2 h^{-1} g^{-1}$ (AFDW)	Taxa	Source
0,39	Haliclona sp.	Jorgensen, 1966
0,07	-	Hyman, 1925
0,019	Siliceous sponge	Von Buddenbrock, 1938
0,49	-	Pütter, 1914
2,13	Mycale sp.	Reiswig, 1974
1,54	Verongia sp.	Reiswig, 1974
0,63	Tethya sp.	Reiswig, 1974
0,33	Spirastrella sp.	Present study
0,7 (mean) ±0,7 SD		

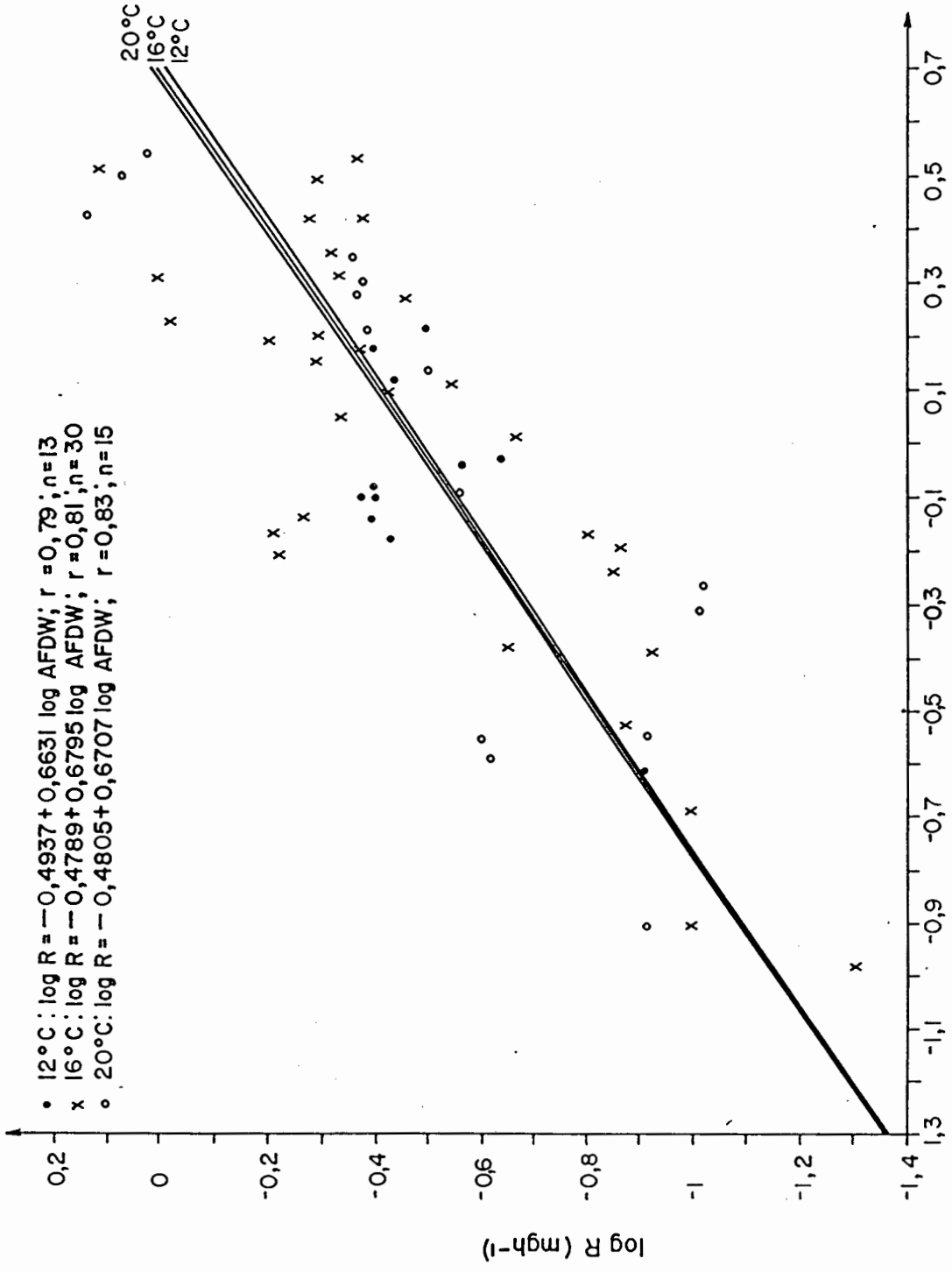

FIGURE 4.1: Spirastrella respiration rate versus body weight at 12°C, 16°C and 20°C.

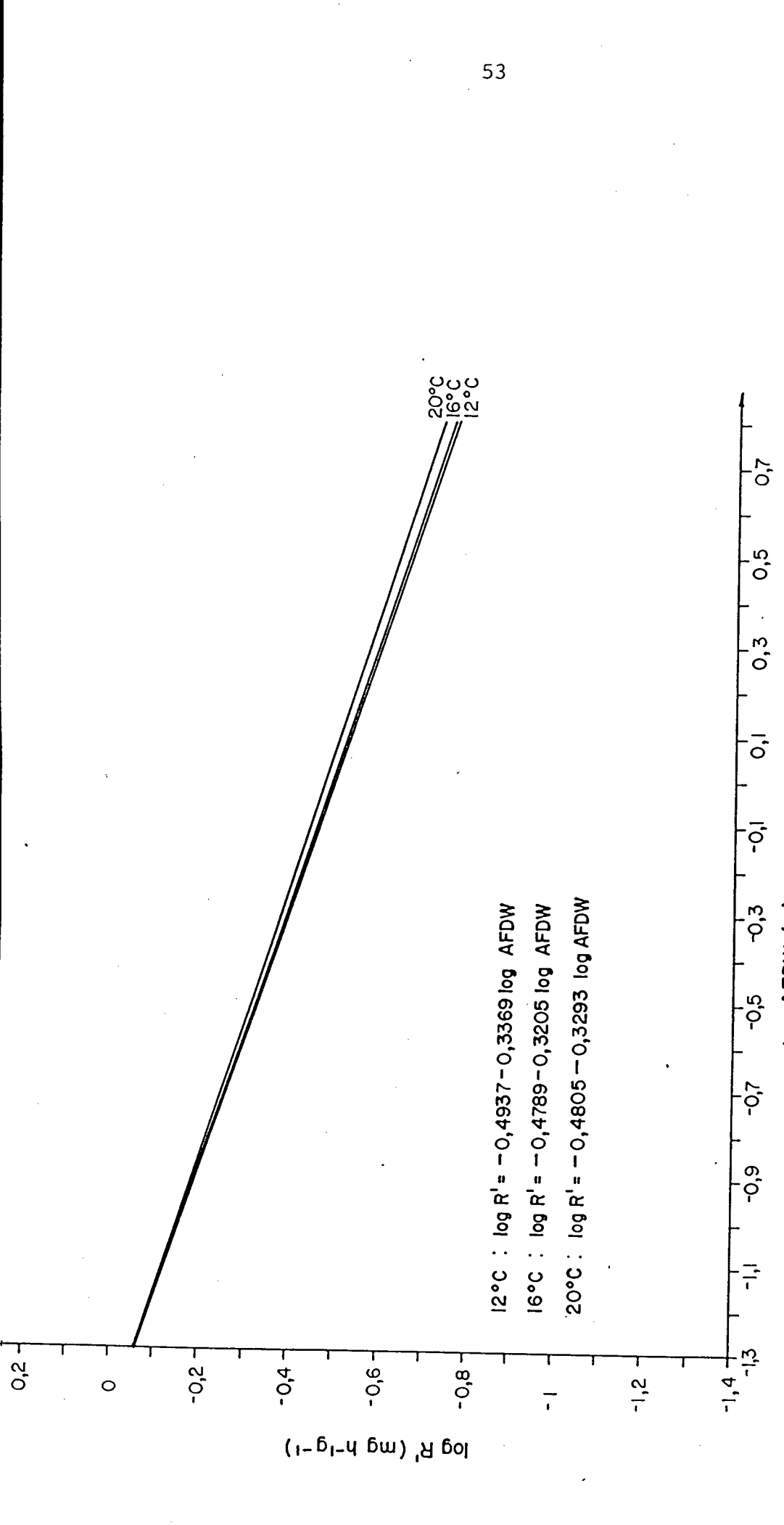

FIGURE 4.2: Spirastrella weight-specific respiration rate versus body weight at 12°C, 16°C and 20°C.

No significant differences could be detected between respiration rates measured at 12°C, 16°C or 20°C. The constant a has been termed the level of metabolism and b the metabolic rate by Dagg (1976) and Vidal (1980). According to Dagg (1976) variations in metabolism with changing temperature are due to varying metabolic level (a). The intercept on the Y-axis was 0,32 at 12°C; 0,33 at 16°C and 0,22 at 20°C.

Discussion

Larger individuals consumed more oxygen than smaller ones at all three temperatures, but the increase of the respiration rate is slower than the increase of the weight. Thus on a weight basis, the respiration rate decreases with increasing size of the animals. It is in accordance with results obtained by Zeuthen (1953; 1970) and as this phenomenon is well-known it need not be pursued further here.

Figure 4.1 shows that regressions of R on ash-free dry weight at 12°C, 16°C and 20°C are very similar. Many marine invertebrates are known to have a very flat rate: temperature curve while they are inactive, at least over part of the appropriate temperature range (Newell, 1967; Newell and Branch, 1980). It could be interpreted as indicative of thermal compensation of the metabolic rate, an adaption known to be widespread among poikilothermic invertebrates acclimatized to different temperatures (Precht, et al., 1973; Newell, 1979). The plateau in the middle range of the R:T curve is not only the expression of a homeostatic mechanism for keeping rates of metabolism constant in the face of fluctuating temperatures, but may also be regarded as an adaptation for conserving energy and is most frequently seen in animals which are subject to daily rapid fluctuations in temperature and have only periodic opportunities for the renewal of their energy resources (Brown, 1982b; Gee, 1985). It was shown in Chapter 1 that the animals are subjected to rapid temperature fluctuations and therefore the marked depression of metabolic responses to rising temperature are clearly advantageous to the subtidal reef community.

A weight specific respiration rate of 0,33 $mgO_2h^{-1}g^{-1}$ (AFDW) for Spirastrella was measured. This is within the range recorded by other authors. A mean value of 0,7 $mgO_2h^{-1}g^{-1}$ (AFDW) was calculated from the values measured by these authors. The high standard deviation thus obtained is probably due to a difference in metabolic level, characterized by the coefficient a, between species. Ivlev and Yakovleva (1964) recorded a value of 0,025 for the intercept a for the sponge Suberites domuncula. This is lower than the 0,33 obtained during the present study and demonstrates the difference in metabolic level between species. The higher rates estimated by Reiswig (1974) was obtained by analysing samples of ambient and exhalent water while the others were estimated by means of closed respiratory chambers. These lower specific rates could be attributable to the depressive effects of laboratory conditions and self-inhibition (repeated water cycling).

A mean biomass value (AFDW) of 1,52 gm^{-2} for Spirastrella was estimated in Chapter 3 while a weight specific respiration rate of 0,33 mg $O_2h^{-1}g^{-1}$ was measured. The respiration rate is applied to the field biomass estimates to estimate a population respiration rate of $12mgO_2m^{-2}d^{-1}$. The community respiration rate estimate can be converted to carbon equivalents by the relationship:

$$mgC\ utilized \cdot unit\ time^{-1} = m\ell O_2\ respired \cdot unit\ time^{-1} \cdot 12/22,4 \cdot RQ$$

where RQ = respiratory quotient (Parsons and Takahashi, 1973). The respiratory quotient was taken to be 1.

Using the community respiration rate data, consumption estimates can be made. These are derived from the energy budget equation:

$$P = A-R$$

where

P = production
A = assimilation
R = respiration

and assuming a retention efficientcy of 79% (Reiswig, 1971b). 'Minimum' consumption rates can be calculated by setting production at zero, that is,

'Minimum' consumption = 1,27R

where

C = consumption

In this way a minimum consumption of 5,7 $mgCm^{-2}d^{-1}$ was estimated for the Spirastrella community. Minimum consumption expressed as a fraction of biomass yields a value of 26,7%.

If the weight specific respiration rate estimated for Spirastrella is taken to be representative for the sponge population as a whole, a minimum consumption of 203,7 $mgCm^{-2}d^{-1}$ is estimated (biomass = 54 gm^{-2}). This value (0,33 $mgO_2h^{-1}g^{-1}$) could also be incorporated into a consumption estimate for the filter feeding community if it is assumed that weight-specific respiration rates are in the same order of magnitude for all filter feeders. This would give a minimum consumption requirement of 466,89 $mgCm^{-2}d^{-1}$ for the filter feeding community (biomass = 123 gm^{-2}).

CHAPTER 5: ASPECTS OF **SPIRASTRELLA** CONSUMPTION

Introduction

In many marine habitats Porifera are very abundant, both in terms of numbers of species and numbers of individuals. As a consequence of this abundance, they are also of considerable ecological significance. It is essential to investigate the feeding ecology of marine Porifera in order to gain knowledge of the organic matter flow through a subtidal reef environment. Marine sponges derive their nutrition by filtering ambient seawater and much of their nutrition is particulate organic matter which inludes intact cells (Jorgensen, 1966; 1976; Reiswig, 1971b). Data on Porifera filtration rates are important as they provide information on the degree of utilization of the available organic matter.

Several authors have studied the filtration activity of sponges. A summary of the early investigations can be found in Pourbaix (1933). Later measurements have been made by Jorgensen (1949; 1955), Van Weel (1949), Rasmont (1961; 1968), Claus et al. (1967), Reiswig (1971b; 1974), Frost (1978), Willenz (1980) and Willenz and Rasmont (1979). The earlier studies relied almost exclusively on the use of suspensions of inert non-digestible particles such as carmine and carbon. These investigations provide no quantitative information on Porifera filtration rates when fed digestible particles, unless the assumption is made that sponges do not discriminate between digestible and indigestible particles. Although this assumption has been made by most of the authors later studies proved that filter feeders do discriminate between particles (Reiswig, 1971b; Kiørboe, Møhlenberg and Nøhr, 1980; Stuart and Klumpp, 1984).

The studies by the other authors dealt mostly with Porifera filtration rates when fed bacteria while Reiswig (1971b) investigated the retention rate by measuring the concentration of particulates entering the ostia and their concentration in

the excurrent stream leaving the oscules. The clearance or filtration rate is an indirect measure of the removal of particulates and is determined by measuring the rate of decrease in concentration of particulates in a known, static volume of ambient water due to retention by the sponges. The clearance rate is thus of theoretical value which is very useful for the comparison of feeding activities. In sponges possessing small oscules, it is technically not feasible to sample the excurrent stream of water and thus determination of the clearance rate is the only means of assessing feeding (Frost, 1978). The rest of the studies lack applicability for ecological analysis of marine demosponges in that they were based on work with the specialized group of freshwater sponges. No documented consumption estimates for Spirastrella could be found.

The present study is therefore an attempt to provide a quantitative assessment of Spirastrella consumption. It was also necessary to estimate the effect of body size and temperature on the filtration rate in order to gain a better understanding of the consumption of this dominant Porifera species on the Agulhas Bank subtidal reef.

Material and Methods

Spirastrella specimens were collected from the aeoleonite reef system by SCUBA divers in December 1987. The animals were transported to the aquarium in holding tanks and were provided with a continuous supply of air. The sponges were transferred to separate tanks equipped with running sea-water.

The filtration rates were measured indirectly by recording the rate of decrease in algal concentration in a known, static volume of ambient water. The sponges were fed with a constant concentration (10×10^3 algal cells$\cdot m\ell^{-1}$) of Dunaliella primolecta (4-6,35µm diameter) to measure the effect of temperature and body weight on the filtration rate. The animals were acclimatized for 36 hours in running sea-water at the appropriate

temperature before commencing the experiments at 12°C, 16°C and 20°C. The sponges were held in filtered sea-water (0,45 µm) for at least 1 hour before they were transferred to new beakers.

Each animal was placed on a mesh-covered grid suspended in 1 ℓ 0,45 µm filtered sea-water circulated with a magnetic stirrer. Appropriate volumes of the suspended algal cells were added and samples were removed for Coulter Counter analyses after a few minutes. Successive samples were removed at one-hour intervals over a four-hour period and the decline in algal numbers recorded. Results were corrected for settling and division of cells using control beakers containing food only, while beakers containing animals in filtered sea-water were used to correct for any production of particles by the animals.

The algal cells in the sample were counted immediately after collection, using a Coulter Counter model TA II. An orifice tube 200 µm in diameter was used and cells were counted in three size classes from 4 to 6,35 µm equivalent spherical diamater (channels 3 to 5). The machine blank was filtered sea-water (0,45 µm membrane). Two samples were collected from each beaker and all samples were counted twice. The sponges were blotted dry and weighed to yield the wet weights. The values were converted to ash-free dry weights with the use of the conversion factors obtained from Chapter 3.

The filtration rates can be calculated from the decline in algal numbers with time, using the standard formula:

$$\text{Filtration rate } (\ell \cdot h^{-1}) = \frac{\log_e N_1 - \log_e N_2}{T_2 - T_1} \times V$$

where N_1 and N_2 are cell concentrations (ℓ^{-1}) at times T_1 and T_2 respectively; V is experimental volume.

Results

Figure 5.1 depicts graphs of Spirastrella filtration rates (R_f) versus body weight at each of the experimental temperatures. The weight-specific filtration rates are presented graphically in Figure 5.2. The log transformed form of the allometric equation $R_f = aW^b$ and r values for each graph are included.

The filtration rate (R_f) increases with increasing body size (W) in accordance with the general allometric equation:

$$R_f = a \cdot W^b$$

where

R_f = filtration rate
a = intercept
W = body mass
b = exponent

In its logarithmic form the equation becomes:

$$\log R_f = \log a + b \log W$$

where a is the intercept when log W = 1 and b is the slope of the regression line. The proportionality constant a and the exponent b of the above power function were calculated from the logarithmic transformed equation using the method of least squares.

Plotted on a double logarithmic grid, filtration rate increased linearly with weight with values of the exponent b ranging between 0,57 and 0,61. The weight-specific filtration rate is then described by $R_f/W = a \cdot b^{-1}$ and the negative slope so obtained ranged between -0,38 and -0,43. No significant differences could be detected between filtration rates at the three experimental temperatures.

Discussion

The filtration rate of the larger sponges were higher than the smaller ones at all three temperatures but the increase in filtration rate was relatively small in comparison to the weight

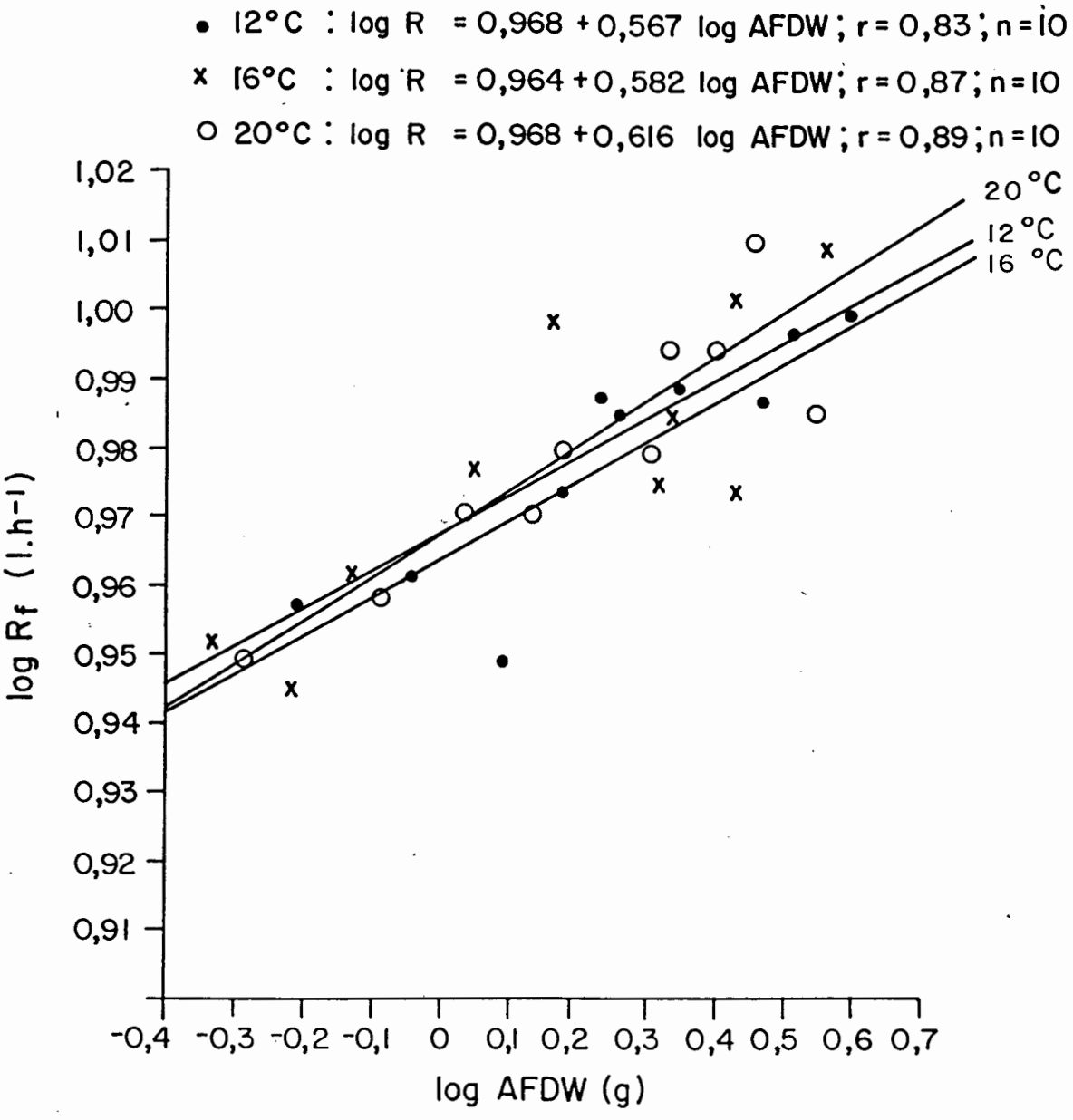

FIGURE 5.1: Spirastrella filtration rate versus body weight at 12°C, 16°C and 20°C.

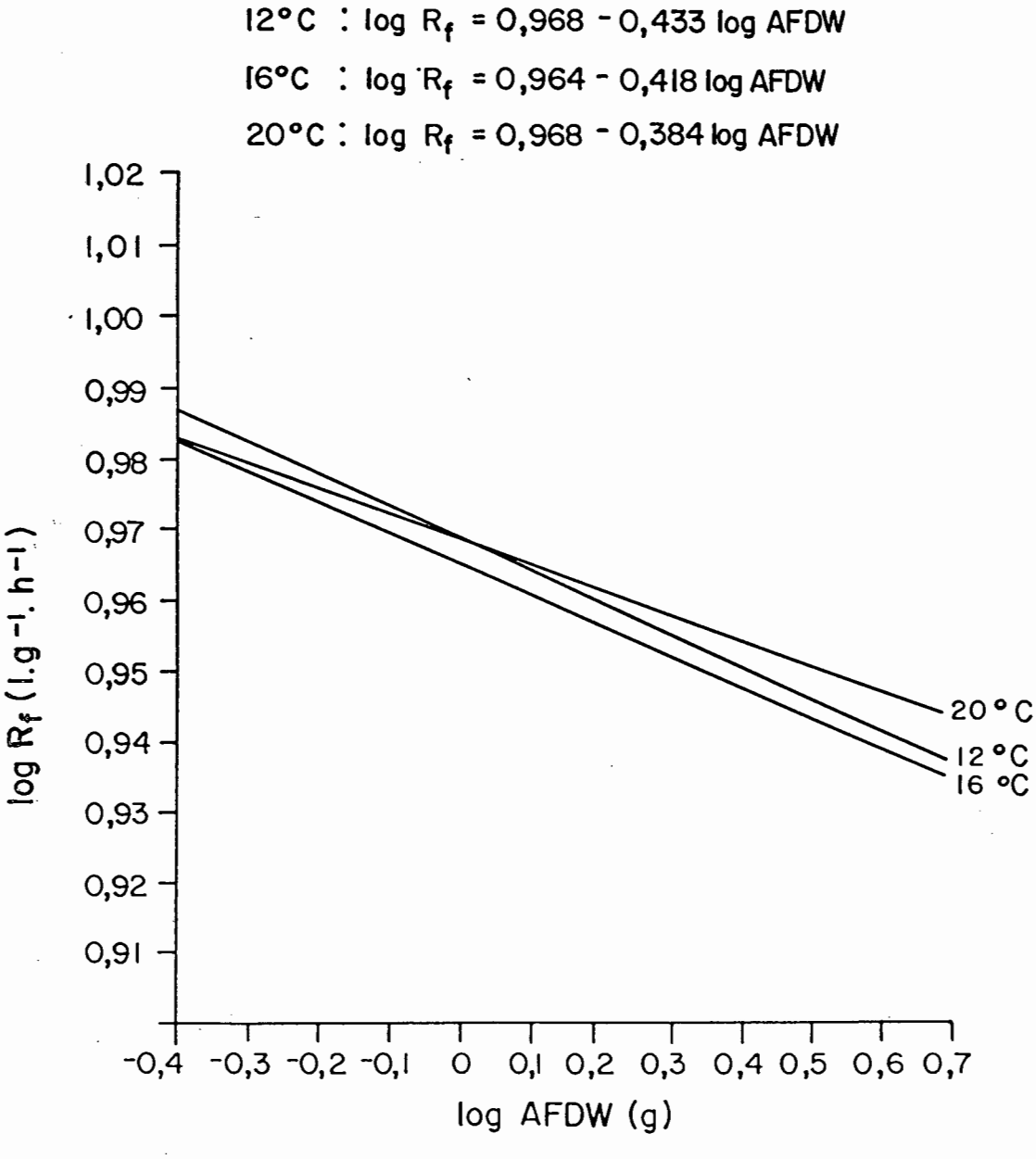

FIGURE 5.2: Spirastrella weight-specific filtration rate versus body weight at 12°C, 16°C and 20°C.

increase. Thus on a weight basis, the filtration rate decreases with an increase in weight. Although data on the effect of animal size on Porifera filtration rates are sparse it is in accordance with the results obtained by Frost (1978; 1980) on Spongilla lacustris and studies by various authors on several other metazoan phyla (Jorgensen, 1966; Vahl, 1973; Buhr and Winter, 1977; Widdows, 1978 and Winter, 1978).

The value of the weight exponent reflects the relative proportion of filtration area to body volume and because it is less than 1,0 it follows that the weight-specific filtration rate of large animals is less than that of small ones. The slope of the regression is then given by the value (b-1) yielding a mean of -0,25 for many organisms (Newell, 1979). The negative slope so obtained for Spirastrella ranged between -0,38 and -0,43. The decrease in weight-specific filtration rate is significant when the metabolic rate estimated in Chapter 4 is taken into account. The latter increased faster than the filtration rate in relation to body size. This implies that the net energy gain becomes progressively less as the animals increase in size and will thus act as a limiting factor of ultimate body size that can be attained (Barkai and Griffiths, 1987).

No significant differences could be detected between filtration rates measured at 12°C, 16°C and 20°C. Reports on the effect of temperature on Porifera filtration rates are scarce in the literature. Frost (1978; 1980) measured an increase in filtration rate with increasing temperature and the majority of studies on other metazoan phyla also showed an accelerated filtration rate with an increase in temperature with a few exceptions (Widdows, 1973; Conover, 1980). The ability to derive an energetic gain is dependent on the maintenance of the delicate balance between maximal energy gain from feeding, ingestion and assimilation and minimization of energy losses through respiration and excretion (Newell, 1979). Therefore the absence of compensatory adjustment in the filtration rate must be viewed in combination with the suppressed metabolic rate:

temperature curve obtained in Chapter 4. It is well-known that some marine invertebrates manipulate the components of the energy balance equation in order to maintain or improve the scope for growth and reproduction.

The relation between the gain and losses has been quantified through the balanced energy equation of Winberg (1956):

$$C = P + (R + F + U)$$

where

C = energy content of the food consumed
P = energy produced as growth or gametes
R = energy loss through metabolism
F = energy loss as faeces
U = energy loss as dissolved organic matter

The difference between the net energy gain from the assimilated ration and the energy losses from respiration may be regarded as the scope for growth (Warren and Davis, 1967; Bayne et al., 1973). The maintenance of a positive index of energy balance will therefore be beneficial to an organism.

According to Newell and Branch (1980) the potential energy gain or loss by filter feeding organisms can be calculated from the ratio of the clearance rate (V_W; litres of water cleared of particles) to oxygen consumption (V_{O2}; millilitres of oxygen consumed). The ability to maintain optimal values for the V_W/V_{O2} ratio over the range of environmental temperatures the organism is subjected to will ensure continued survival and growth. The net gain from the environment is thus a reflection not only of filtration rate but is also controlled to a large extent by food concentration and environmental temperature, as well as by the metabolic cost or losses associated with the feeding process, a factor which is governed by the body size of the organism concerned (Newell, 1979). It is possible that an increase in Spirastrella filtration rate with increasing temperature would result in a high energetic cost of filtration which in turn would imply a lower filtration efficiency and

V_W/V_{O2} ratio. An increase in absorption efficiency with an increase in temperature, as measured by Winter (1969; 1970) in combination with a decrease in filtration rate would also explain a flat filtration rate: temperature curve while ensuring an increase in energy flow into secondary production.

With a reduction in food availability, energy conservation is affected by a reduction in activity level and the rate of oxygen consumption may be then less affected by an increase in environmental temperature (Newell and Branch, 1980). It is thus possible that the cyclical and seasonal variations in food availability, due to the tidal effect and intrusions of cold and turbid bottom water shown in Chapter 1, would play a role in the suppressed filtration rate: temperature curve. According to Newell (1979) species which suffer food shortage, adopt a conservationist strategy which involves a delicate regulation between energetic gain and expenditure and the responses of animals to temperature may thus ultimately depend on the availability of food. It was shown in Chapter 1 that the reef fauna are subjected to large temperature fluctuations and according to Prosser (1973) genetic capacity for temperature acclimation may be greater in animals where temperature fluctuations are considerable. This factor would explain the presence of thermal compensation measured for Spirastrella.

CONCLUSION

The purpose of this study was to gain a better understanding of the biological structure on the subtidal aeoleonite reef system and to obtain a consumption estimate for a dominant species of the community. Although the project design might appear unconventional, this aim was achieved as part of an overall project investigating the organic matter flow through three subtidal environments.

Section 1 provided valuable insight into some of the physical features the reef fauna are subjected to. It was concluded that sudden, cold bottom water intrusions, large temperature fluctuations and two entirely different seasonal temperature regimes were dominant features of the subtidal reef. In Chapter 2 the variability in concentration and particle-size distribution of the available food source as well as the small organic fraction present in the water column were measured. The information obtained in this section was applied in the following chapters.

The combined results from the belt counts and random quadrat method reflected the dominance of the filter-feeding component and in particular, Porifera, in the reef community. Therefore the respiration and consumption measurements were carried out on a Spirastrella sp., a dominant Porifera species. It was concluded that neither consumption nor respiration increased with an increase in experimental temperature. The percentage of ingested energy respired (per 1 g AFDW of animal) varied between 3,45% (12°C and 20°C) and 3,49% (16°C). The value increased with an increase in animal size from 1,35% (0,4 g AFDW) to 9,88% (5 g AFDW).

The difference between the net energy gain from the assimilated ration and the energy losses from respiration may be regarded as the scope for growth. This energy which is available for incorporation into growth and reproduction is calculated on the basis of a Porifera retention efficiency of 79% (Reiswig, 1971b). The

scope for growth varied between 97,8% (0,4 g AFDW) and 87,8% (5 g AFDW). The P/B ratios ranged from 1,88:1 to 1,98:1 with an average of 1,93:1. This is slightly lower than the value of 2,5:1 used by Koop and Griffiths (1982) for macrofauna although this value could be an overestimate for slow-growing, long-lived species (Gibbons and Griffiths, 1986).

A pumping efficiency of 20 $\ell(m\ell O_2^{-1}$ consumed) was measured which is similar to the values obtained by Reiswig (1974) for three Porifera species (20-23 $\ell m\ell O_2^{-1}$). Reiswig (1974) concluded that, at pumping efficiencies significantly above those of other suspension feeders, sponges are able to maintain large dynamic populations in nutrient-poor waters by virtue of a high efficiency of energy cycling. The excess input over the basic need of water pumping will then determine the rate of growth and reproductive effort and will not necessarily influence the size of the standing crop of species density.

According to Jorgensen (1955) food requirements during optimal growth are three to four times greater than indicated by the metabolic rate. At a filtration rate of 20 $\ell(m\ell O_2^{-1}$ consumed), these 20 ℓ should contain at least 0,8 mg organic matter that can be retained and utilized be the sponge, or about 0,04 $mg\ell^{-1}$, since 1 $m\ell$ of oxygen is required to combust about 0,8 mg organic matter of mixed food (Jorgensen, 1955). An average value of 1,18 $mg\ell^{-1}$ was measured for the organic content of the total suspended particulate matter (Chapter 2). Although the lowest value recorded was 0,34 $mg\ell^{-1}$ this amount is not available for sponge utilization since sponges are only able to retain particles within a specific size range. In this respect it is possible that reproduction and growth of Spirastrella might be affected by the variability of particulate organic matter in the water column.

The carbon requirements of Spirastrella (1 g AFDW) can be calculated from the metabolic rate, multiplied by a factor of three for optimal growth and using a factor of 1 $m\ell O_2$ = 458 µg carbon

(Jorgensen, 1955). The value thus obtained is 453 $\mu gCh^{-1}g^{-1}$ while the average content present in the reef water was estimated to be 600 $\mu gC\ell^{-1}$.

If the weight-specific respiration rate estimated for Spirastrella is taken to be representative for the filter-feeding community, a minimum consumption requirement of 466,89 $mgCm^{-2}d^{-1}$ (biomass = 123 gm^{-2} AFDW) is estimated. In a similar way the filter-feeding community respiration and filtration rates are estimated to be 40,6 mgO_2h^{-1} m^{-2} and 1132,2 $\ell h^{-1}m^{-2}$ respectively.

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