Physiology and Ecology of *Stylophora pistillata* and *Echinopora gemmacea* From the Red Sea

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SUMMARY

1. Some aspects of the biology and nutritional physiology of the corals ***Stylophora pistillata*** and ***Echinopora gemmacea*** from the Red Sea are described in this thesis. The two species were selected on the basis of their differing growth form and nutritional strategies. The main objective was to compare their nutritional energy budgets and to examine the effects upon these of environmental factors associated with differing depths on the reef and with different seasons.

2. ***S. pistillata*** is a branching coral, with small polyps. In shallow water (1m) the coral has compact club-shaped branches, whereas at 10m it has an open growth form with slender branches. ***E. gemmacea*** has large polyps, and both encrusting and lightly branching growth forms. It was not found at depths of less than 3m.

4. Histological examination showed that the coenosarc of ***S. pistillata*** is characterised by holotrich nematocysts and mucus-gland cells containing neutral mucopolysaccharides. By contrast, the epidermis of ***E. gemmacea*** contains spirocysts and large numbers of mucus-gland cells secreting an acid mucopolysaccharide. The gastrodermis of the tentacles of ***S. pistillata***, which are expanded during the day time are packed with zooxanthellae. In ***E. gemmacea*** the tentacles are withdrawn during the day and are devoid of zooxanthellae. In both species, lipid stores are concentrated in the gastrodermal layers only, mainly in the lower half of the polyps.

4. Four types of nematocyst are present in both species : spirocysts, microbasic P-mastigophores, microbasic B-mastigophores and holotrichs. Spirocysts are most common on the oral discs and mainly at the tentacle tips. Microbasic P-mastigophores are more common in the tentacles of ***E. gemmacea*** suggesting a more important role for prey capture in this species. In both species the mesenterial filaments are armed with microbasic P-mastigophores and holotrichs, indicating that they are important for aggression and defence.

5. ***S. pistillata*** displays a weak ability to deal with particulate food when presented as *Artemia* nauplii or eggs. There is an extensive development of ciliary currents on the outers epidermis, but these appear to be used only for cleansing of the outer surface. ***E. gemmacea*** expands its tentacles at night and feeds on particulate organic matters trapped on the surface mucus net. Large particles, including fish faecal pellets, may be ingested.

The expansion of the tentacles of *S. pistillata* during the day time suggests a nutritional economy which is more dependent upon the symbiotic zooxanthellae.

6. Both species are hermaphrodite with protogynous gametogenesis. *S. pistillata* has an extended breeding cycle. Oogenesis began in May, whilst spermatogenesis was first detected in August. Fertilisation takes place in the coelenteron and the first planulae were observed in December. *E. gemmacea* has a short annual cycle of gametogenesis. Oogenesis was first observed in June and spermatogenesis in August. Broadcast-spawning occurred in November.

7. The distribution of the two species on a shallow fringing reef in Sharm Ubhur, a small creek to the north of Jeddah, is described from a transect survey. At the study site, the lowest mean water temperature of 25.5°C was reached in March whilst the maximum mean of 31°C occurred from July to October. Salinity varied only between 39‰ in winter to 40‰ in summer. At 3m depth the duration of sunlight was 13.75 hours in summer with an integrated daily irradiance of 30.12 $E.m^{-2}.d^{-1}$, whilst in winter the day length was 10.5 hours and the integrated daily irradiance 14.99 $E.m^{-2}.d^{-1}$. The light transmission decreased with depth and in winter and summer the daily integrated irradiance was about 47% and 41% respectively of that of the shallow site.

8. The two species show some variation in skeleton and biomass characteristics. The density of the skeleton is similar at 2.87 $g.cm^{-3}$. *S. pistillata* has a 28% lower biomass on a surface area basis, when compared with *E. gemmacea*. As a result, the tissue accounts for only 0.85% of the buoyant weight in the former compared with 1.25% in the latter.

9. The density of zooxanthellae in *S. pistillata* is 9.82×10^5 cm^{-2} of colony surface, compared with 6.27×10^5 cm^{-2} in *E. gemmacea*. The energy content of the tissue of shallow water *S. pistillata* (25.51 $J.mg^{-1}$) is 3.5% higher than in *E. gemmacea* whilst the energy content of the zooxanthellae at 10.135 $J.10^6$ zooxanthellae is identical in the two species.

10. The mean dark respiration rates of *S. pistillata* were 36% to 50% higher than *E. gemmacea*. The lower values of respiration in *E. gemmacea* were related to its larger polyp size and lower surface to volume ratio. The mean respiration values in winter were about 64% and 78% of that in summer at both depths in *S. pistillata* and *E. gemmacea* respectively. The seasonal variation in respiration

was a result of the 5.5°C seasonal difference in temperature. The respiration rate of corals from 10m. was approximately 81% and 86% of those at 1m. and 3m. in both summer and winter in *S. pistillata* and *E. gemmacea* respectively.

11. There was little variation in the respiration rates of the zooxanthellae between the two species, but in both cases the mean respiration rates of zooxanthellae declined with depths and season. The respiration rates at 10m. were 81% of that at 1m. and 3m. for the two species, whilst in winter the values were about 67% and 53% of that in summer for *S. pistillata* and *E. gemmacea* respectively. The mean maximum gross photosynthesis ($Pg_{max.}$) rates were higher in *S. pistillata* than *E. gemmacea* on the basis of both biomass and surface area. This was a result of the higher number of zooxanthellae in the former, but on the basis of zooxanthellae density, *E. gemmacea* showed higher values than *S. pistillata*. This was related to self-shading of zooxanthellae in the latter species.

12. Photosynthesis versus irradiance (P v I) curves were obtained and lines fitted to the data using the hyperbolic tangent function. The lower values of $Pg_{max.}$ for *S. pistillata* in winter than summer at both depths was related to the lower temperature in winter. Conversely, the $Pg_{max.}$ for *E. gemmacea* was higher in winter than summer at both depths, suggesting the possibility of compensatory processes for either the lower light-levels or the lower water temperature during winter. The two species displayed lower values of I_k and higher values of α in the winter than the summer months at both depths. Similar responses were seen when comparing corals from deep water with those from shallow water at both seasons, indicating a photoadaptation response as a function of decreased irradiance.

13. The growth rate of *S. pistillata* was lower in winter than in summer, and was lower at 10m. depth than at 1m. By contrast, *E. gemmacea* showed difference in growth rate with season and very little decrease with water depth between 3 and 10m.

14. Energy budgets were constructed from the data obtained on photosynthesis, respiration and growth. The budgets were balanced by assuming that the energy fixed in photosynthesis which was not used for respiration and growth was lost from the colony as mucus-lipids.

15. In both species the energy used in the respiration of the zooxanthellae was in the range of 13-24% of the daily energy fixed in photosynthesis, whilst the energy expended in the growth of the zooxanthellae was very low, ranging from 0.2% to

0.8% of energy fixation. The energy translocated to the host varied between 75% and 86%. The major use of daily photosynthetically fixed energy in the two species was for host respiration, with values ranging between 52% and 61% of energy fixation.

16. The host growth was a minor sink for fixed energy, ranging from 4% to 7%. The surplus energy after respiration and growth of both zooxanthellae and animal was predicted to be between 10% to 23% of energy fixed. However, the values fell into a deficit of 36.06% and 18.65% at 10m. during summer in *S. pistillata* and *E. gemmacea* respectively.

17. Comparison of the energy budget of the two species *S. pistillata* and *E. gemmacea* showed that the percentage of energy used in respiration of zooxanthellae, animal tissue respiration, growth of animal tissue and energy loss as mucus-lipid was remarkably similar, the only major difference being that the energy used in the growth of the zooxanthellae of *S. pistillata* was 2-4 times that of *E. gemmacea*.

18. Despite photoadaptation, the photosynthetic production in both species was lower at 10m. than in shallow water. This was partially offset by lower respiration with increasing depth. The surplus energy was lower at 10m., except in the case of *E. gemmacea* in winter, when it was higher.

19. In *S. pistillata*, the daily photosynthetic production in winter was only 58% of that in summer, as a result of the drop in water temperature and the lower duration and levels of irradiation. The rate of respiration and growth rate were also reduced by 50% and the surplus in the budget was lower by about the same amount. *E. gemmacea* seasonal trends were less clear. There was little difference in photosynthetic rates, growth rates or the rates of respiration of the host tissue. Respiration rate of zooxanthellae was however higher in the summer and this had the effect of creating a larger predicted surplus in winter than in the summer.

20. In order to determine whether errors could be introduced into energy budget calculations, possible variation in rates of respiration and photosynthesis during the course of a day were investigated. When kept in darkness during the day the respiration rate did not change. Similarly, there was no change in net photosynthesis at saturating light levels measured over intervals of 10mins alternating with periods of darkness. However, the dark respiration increased by 44% in *S. pistillata* and 66% in *E. gemmacea* following a cumulative exposure of 150 min to saturating light. Furthermore, the net photosynthesis was found to increase under continuous

light exposure, by factors of 38% and 22% in *S. pistillata* and *E. gemmacea* respectively.

21. Lipid reserves in corals are probably utilised on overcast days when photosynthetic production fails to meet the energy utilisation. The total lipid levels in *S. pistillata* varied between 28% and 40% of the dry weight, and in *E. gemmacea* between 21% and 27% of dry weight. There was a tendency for lipid levels to be lower in winter than in summer. In *S. pistillata* lipid levels were lower at 10m. than in shallow water, but in *E. gemmacea* there was no difference. It was calculated that in both species the energy stored as lipid would be sufficient to meet energy requirement for between 8 and 13 days in the absence of any other nutritional input.

CHAPTER I

1. GENERAL INTRODUCTION

Coral reefs are one of the most interesting environments due to their enormous species variety. Corals which are members of the phylum Cœlenterata, class Anthozoa, sub-class Hexacorallia and order Scleractinia (Scheer and Pillai, 1983) are the dominant species. The Scleractinia can be divided into hermatypic and ahermatypic. The terms are usually used by biologists to distinguish between corals with or without symbiotic algae (zooxanthellae) respectively (Wells, 1956). The majority of hermatypes contain symbionts, are reef-building, and live usually in shallow water, whilst the ahermatypes do not contain symbionts, are non reef-building, and are often found in deep water. However, there are asymbiotic and symbiotic genera with or without reef-building roles respectively (Sheppard, 1982). The hermatypes are the major reef builders, secreting a calcium carbonate skeleton which forms the major component of reef frameworks (Goreau, 1959). Other organisms play important secondary roles in reef construction (Goreau and Goreau, 1973). These include red coralline algae, the green alga Halimeda (Dahl, 1974); sponges (Wulff and Buss, 1979) and other organisms with internal calcium carbonate or siliceous skeletons (Nybakken, 1988).

Hermatypic corals are restricted to tropical and sub-tropical seas where the temperature is not lower than 18°C, with optimal reef development between 25° and 29°C (Wells, 1956). They live in shallow water being restricted to depths of less than 100m (Goreau ***et al,*** 1979 ; Fricke and Schumacher, 1983). The depth restriction is mainly due to light reduction with increasing depth, since light is very important for zooxanthellae photosynthesis (see later). Other factors such as water movement, sedimentation, predation and inter-specific competition which control coral distribution and zonation are reviewed by Sheppard (1982).

Each coral colony is made up from the contiguous skeletons of the polyps, or "corallites". Each corallite contains a series of vertical septa rising from the basal plate (Wells, 1956). The arrangement of these septa varies from one species to another and together with colony morphology, is used as a taxonomic tool (Veron, 1986). Since the morphology of colonies is subject to exogenous factors (Yonge, 1968; Lang, 1971 and Veron, 1986) taxonomists may need to use other criteria as the basis of classification (Gattuso ***et al***, 1991).

In shallow water, corals may modify the shape of the colony to be more compact with increasing wave action (Veron, 1986) or orientated to wave direction (Shinn, 1963). In deep water, colony shape may change in order to satisfy their nutritional requirements (Jaubert, 1977 a ; Dustan, 1979) . They may change from branching to flat plates (Yonge, 1968) or from hemispherical forms to encrusting sheets (Barnes, 1973) in response to light attenuation with increasing depth. Sediments may cause changes in growth form as will aggressive interaction between species (Lang, 1971).

The polyps of hermatypic corals have a cylindrical body with a mouth surrounded by simple tentacles. The mouth leads to a short tube, the pharynx, which opens into the gastrovascular cavity. The gastrovascular cavity is divided by vertical partitions, the mesenteries which alternate with the septa of the skeleton. The body wall is divided into three layers, the epidermis, gastrodermis and an intermediate layer the mesoglea. The epidermal layer is distinguished according to its location into the edge zone or cœnosarc layer and the calicoblast layer (Wells, 1956 ; Matthai, 1914). The former is the outer surface consisting of ciliated columnar supporting cells, sensory cells , mucus cells and cnidae cells. The calicoblast layer is attached to the corallum and secrets the organic matrix which acts as a template for calcification to form the skeleton (Goreau, 1959a). The mesoglea contains a homogeneous substance in which some cells and fibres are found. The gastrodermis has digestive, absorptive and secretory roles . The zooxanthellae are confined to this layer (Matthai, 1914 ; Yonge, 1968). So far no comparative studies on the histology of coral polyps have been made to relate cell type and size to their significance in feeding . Most of our knowledge on the feeding behaviour of the polyps has come from observations on ciliary activity and from the morphology of the coral polyps.

It seems likely that most of the cell types of the polyp are involved to some extent in feeding. For example, the mucus-gland cells of coral polyps usually occur in the epidermal layer and the mesenterial filaments of the gastrodermis. No experiments have been carried out to relate the composition of the mucus to its function . However early studies showed that the function of mucus is mainly in food capture, protection and cleansing (Duerden, 1906; Yonge, 1930; Abe, 1937 ; Lewis and Price, 1975). Some of these studies provided interesting information about the mucus and its significance in the feeding of corals . Yonge (1930) showed

that corals with small tentacles, such as Agariciidae, rely mainly on mucus to entangle and trap prey and food materials which are then carried to the mouth by ciliary currents . Lewis and Price (1975) reported that corals which contract only during the day, such as Agariciidae, depend on the mucus net for suspension feeding, whilst the small polyp corals such as Poritidae and Pocilloporidae, which expand during both the day and the night, use only their tentacles to capture their prey. By contrast, families which have large polyps, expand during the night and use both the mucus net and the tentacles to catch their prey , usually as large zooplankton.

Another mucus function has been reported by Sorokin (1973), who suggested that coral mucus on the surface of the epidermis stimulates growth of bacteria which provides another food source for the corals.

All corals possess cnidae in their epidermal surface (Matthai, 1914). There are two major groups of cnidae : spirocysts, which capture zooplankton by attaching to the surface of the prey, and nematocysts, which are used to capture prey by injection of a toxic substance (Mariscal, 1974). The discharge of the cnidae has been reported to be controlled by appropriate mechanical and chemical stimuli mainly from the bodies of the prey (Thorington and Hessinger, 1988 ; Watson and Hessinger, 1988).

A further feeding mechanism is the direct uptake of dissolved nutrients from the seawater . It has been shown that the epidermal cells are adapted to take up organic compounds such as glucose and amino acids by active transport (Mariscal, 1974 ; Stephens, 1962)

The role of the mesenterial filaments was mentioned by Yonge (1930), who showed that some polyps depend on their mesenterial filamentes to capture and digest large food extra-coelenterically on the coenosarc surface.

In addition to the above observations of heterotrophic feeding mechanisms, corals can also obtain autotrophic nutrition from their zooxanthellae. Zooxanthellae have been reported to occur in a wide variety of marine invertebrates (Smith and Douglas, 1987). These dinoflagellate algae, which live symbiotically inside vacuoles within the cells of the gastrodermis, were originally grouped with the single species ***Symbiodinium microadriaticum*** (Fruedenthal, 1962). However,

there is now some evidence that zooxanthellae from different hosts may be genetically different (Blank and Trench, 1985). In symbiosis, zooxanthellae are single cells, spherical in shape and about 7-10μm in diameter (Wilkerson ***et al***, 1988) They contain a chloroplast, pyrenoid, starch (Trench, 1987) and lipid droplets (Patton and Burris, 1983). The population size may be controlled by the coral host by regulating the availability of nutrients, such as nitrogen and phosphorus (Rees, 1991)(see also Davies, 1991b).

The role of zooxanthellae in determining the calcification rate of corals was shown by Goreau (1959b), by measuring the incorporation rate of ^{45}Ca into the skeleton at different regions of the colony in the light and darkness . He assumed that the calcification began on the organic matrix , which is secreted by the calicoblastic epidermal cells , by the combination of calcium (Ca^{2+}) from seawater and bicarbonate (HCO_3^-) from animal metabolism to give calcium bicarbonate [$Ca(HCO_3)_2$] which would be rapidly converted to calcium carbonate and carbonic acid (H_2CO_3). The carbonic acid would be catalysed by carbonic anhydrase to give carbon dioxide and water.

$$Ca^{2+} + 2HCO_3^- \longleftrightarrow Ca(HCO_3)_2 \longleftrightarrow CaCO_3 + H_2CO_3 \xleftrightarrow[\text{anhydrase}]{\text{carbonic}} CO_2 + H_2O$$

So the removal of CO_2 during photosynthesis enhances the rate of calcification by shifting the reaction from left to right.

Zooxanthellae have an important role in recycling and conserving nutrients (Yonge and Nicholls, 1931) in an environment of low inorganic nutrients (Muscatine, 1980b). In addition, these nutrients may be absorbed from the surrounding water e.g., phosphorus (D'Elia, 1977), nitrate (Webb and Wiebe, 1978), and ammonium (Muscatine, 1980b), or by eating zooplankton (Johannes, ***et al***, 1970) . For more information on the mechanism or factors which stimulate the uptake of nutrients, see Davies (1991b) for a review.

The role of zooxanthellae in coral nutrition was a matter of debate for many years. An early study showed that corals eat zooplankton (Murray, 1889). Later it was suggested that the mesenterial filaments are capable of digesting zooxanthellae which would thereby provide a food source for the corals (Boschma, 1925). The results of Boschma were rejected by Yonge (1930) who demonstrated that corals have no capability for digesting cellulose , and concluded that they are specialised for a

carnivorous diet using their tentacles, armed with stinging cells, to capture zooplankton. Furthermore, Yonge and Nicholls (1931) provided evidence that corals can remain well in darkness for 228 days in the presence of food, but corals starved in the light died.

Goreau and Goreau (1960) and Yonge (1963) continued to argue that the main role of zooxanthellae was the removal of waste products of host metabolism, with the possibility of trace amounts of vitamin-like substances.

However in 1958 Muscatine and Hand revealed the first evidence of the translocation of photosynthetic products from the zooxanthellae to their host in the sea anemone, ***Anthopleura elegantissima***, using $Na_2{}^{14}CO_3$ as a label . Similar observations were made in corals (Muscatine, 1967 ; Muscatine and Cernichiari, 1969 ; Trench, 1971 a,b). Subsequently it was shown that corals can grow in filtered seawater in sun light (Franzisket, 1970 ; Johannes ***et al***, 1974), thus confirming the nutritional role of the zooxanthellae. Johannes (1970) showed that in ***Porites*** sp zooplankton intake was insufficient to meet the corals requirements . He suggested that the zooplankton may nevertheless supply corals with essential nutrients. It is clear that the zooxanthellae play a very important role in the nutrition of corals.

The major photosynthetic products which were released from freshly isolated zooxanthellae of corals were mainly glycerol and other small organic compounds such as glucose and alanine (Muscatine, 1967 ; Muscatine and Cernichiari, 1969 ; Trench, 1971b). They also showed that the release was stimulated by the presence of host tissue homogenate. Muscatine and Cernichiari (1969) showed that about 35-50% of photosynthetic products were recovered from the coral tissue of ***Pocillopora damicornis*** as lipid and protein. They also suggested that glycerol was synthesised into lipid, since the labelled lipid in the host appeared to be associated with the glycerol moiety. A later study by Patton ***et al***, (1977, 1983) indicated that the photosynthetic product appears in the host as lipids, mainly wax ester and triglyceride, and that wax ester synthesis took place in the animal tissue (Patton and Burris, 1983). Subsequently Crossland ***et al***, (1980b) and Kellogg and Patton (1983), confirmed that the zooxanthellae are the major sites of lipid synthesis, and droplets of lipid could be seen in electron micrographs and phase contrast light micrographs beneath the algal plasmalemma . It now appears

likely that the photosyntheticaly fixed carbon is synthesized into lipid mainly as triglyceride and glycerol. The glycerol is thought to be used as a substrate for respiration by the host cells, whilst translocated lipid is metabolised and stored chiefly as wax ester (Battey and Patton, 1987).

The amount of carbon products translocated to the host was estimated to be less than 50% of that fixed in photosynthesis (Muscatine and Cernichiari, 1969 ; Trench, 1971a). Later it was shown that the amount translocated was more than 90% of carbon fixation (Davies, 1984 ; Muscatine, ***et al***, 1984). Recent work showed that the percentage translocation varies with the light level , ranging from 54% on an overcast day to 91% on an ideal cloudless day (Davies, 1991a). These studies also suggested that corals could meet all of their energy requirements for growth, respiration and reproduction from the translocated carbon during cloud-free days and that there would be an excess production which would have to be excreted probably as muco-lipids (see also Edmunds and Davies, 1986). Light-adapted corals were shown to fix more carbon and release less dissolved organic material to the sea water than shade-adapted corals . This was a result of photoadaptation which increased photosynthesis whilst growth and respiration rate decreased (Muscatine, ***et. al***, 1984 ; Edmunds and Davies, 1986). Davies (1991a) showed variation in the surplus with a variation in light levels. These data were all obtained using branching corals which have small polyps . Porter (1976) concluded that branching corals with a high surface to volume ratio may be totally dependent upon light for their nutrition, whilst corals with large polyps and a low surface to volume ratio may depend more on zooplankton capture.

The main purpose of this Ph.D. study is to investigate the biology and the physiology of two Red Sea corals with different colony morphologies : ***Stylophora pistillata*** has a much branched morphology , with small polyps whilst ***Echinopora gemmacea*** has an encrusting or lightly branched growth form and large polyps. The ecology , and histology of the two species were investigated and a detailed comparison made of their energy budgets at different depths on the reef and at different seasons.

CHAPTER II

2. BIOLOGY AND HISTOLOGY OF *STYLOPHORA PISTILLATA* AND *ECHINOPORA GEMMACEA*

2.1 SYSTEMATIC POSITION AND GENERAL DESCRIPTION

2.1.1 INTRODUCTION

Identification of hermatypic scleractinians has been principally based on the morphology of their skeleton (Wells, 1956). However a wide range of variations in the skeletal characteristics of corals has been related to environmental factors (Richmond and Jokiel, 1984 ; Veron, 1986). Very recently both morphological and physiological characters have been used in the taxonomy of scleractinian corals (Gattuso ***et al***, 1991).

The aim of this section is to describe the morphological characteristics of the two corals of ***Stylophora pistillata*** and ***Echinopora gemmacea.***

A) ***Stylophora pistillata*** (Esper, 1792)

This is a member of the Family Pocilloporidae (Gray, 1842) and is widespread in the Indo-Pacific (Scheer and Pillai, 1983 ; Veron, 1986). There is some confusion over the taxonomic status of the species when it occurs in shallow water of less than 5 m depth. Here the colonies comprise thick club-like branches (Fig. 2.1.1B). However in deeper water the branches are very much thinner and more widely spaced (Fig. 2.1.1A). This change in growth form has been attributed to differences in wave action (Schumacher and Plewka, 1981) and as an adaptive response to maximise light utilisation with increasing depth (Frick and Schumacher, 1983). However Gattuso ***et al*** (1991) have suggested that the shallow water form is not an ecomorph of ***S. pistillata***, but is a separate species ***S. mordax*** (Dana, 1846). However, Scheer and Pillai (1983) did not recognise this species and grouped both forms into the single species ***S. pistillata.*** Since the taxonomic status is not yet resolved, the shallow water form will continue to be referred to as ***S. pistillata*** in this thesis.

S. pistillata has small corallites approx 1.0 mm diameter and 1.6 mm deep. The corallites are cerioid in form, and sunk below the general colony surface. The perithecal wall rises from one half of the corallite, forming an over-arching hood.

Fig.2.1.1. Types of colony growth form in the two species

S. pistillata

A) 10m. deep branches are thin and widely spaced branches (flat-branched)

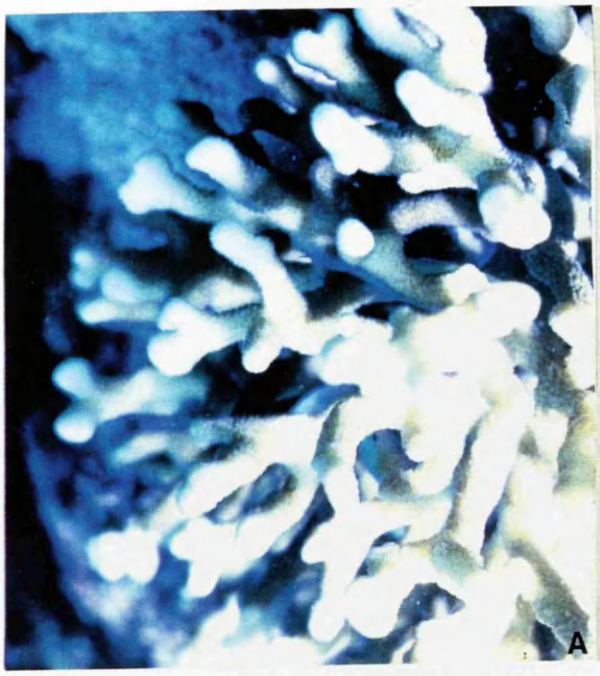
B) Shallow water, branches are thick and closely spaced

E. gemmacea

This species shows two growth forms in both shallow and deep water.

C) An encrusted form

D) An irregular branched form.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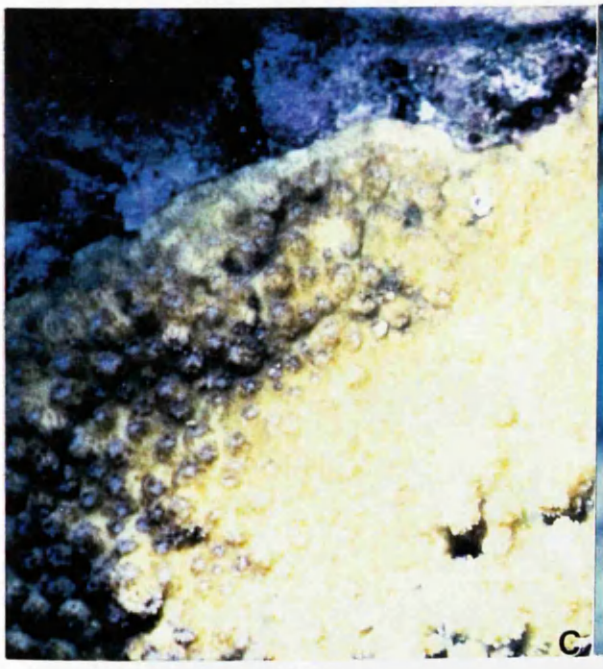
B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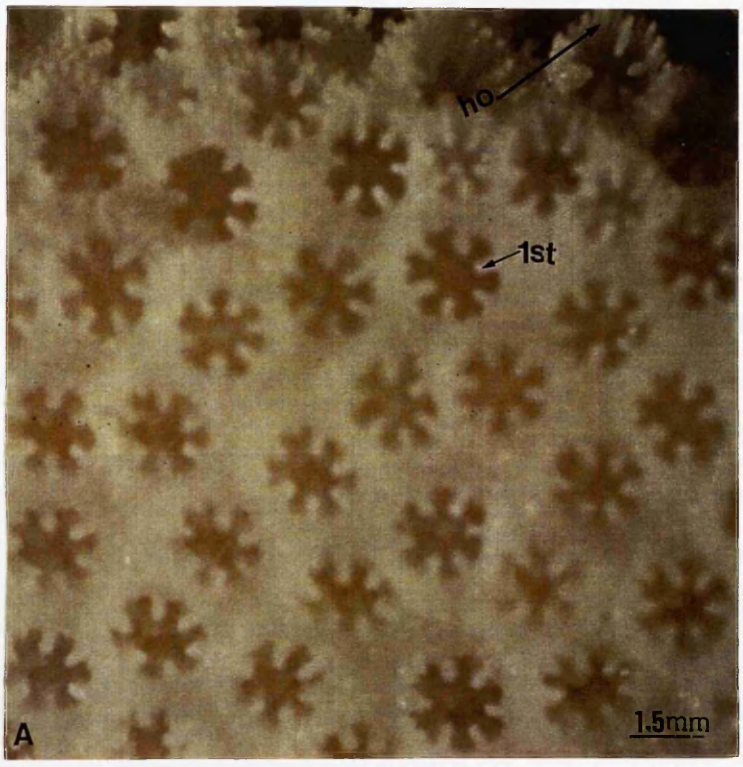
D

Fig.2.1.2. Corallites of both species, showing the main features and septal cycle of each corallite.
A) Corallites of ***S. pistillata*** are hooded (ho.) with six primary (1st) septa, and six short secondary septa, poorly developed.
B) Corallites of ***E. gemmacea*** have three cycles of septa (1st., 2nd .and 3rd.) and spongy (co.) columella. The first and second septa are fused with the columella.cr.,costal ridge ; pa, paliform lobes .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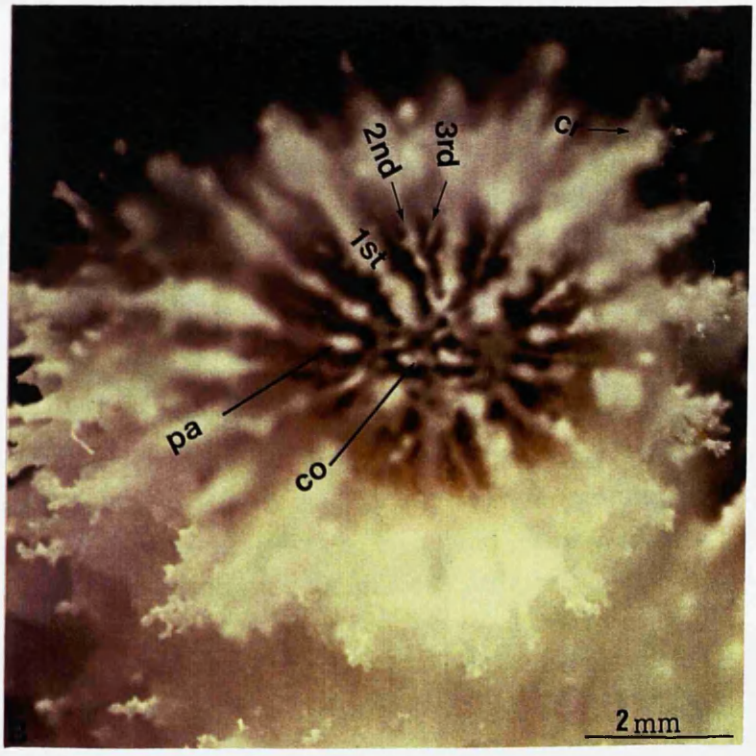

2nd
3rd
c
1st
pa
co
2 mm

(Fig. 2.1.2A). On average there are 76 polyps per cm^2. Each corallite has two cycles of septa. The first cycle of six septa is connected to the styliform columella in the base. The secondary septa are very short and do not extend to the base.

Living colonies show a variety of colours from dark or light brown to pink or brown-green. The polyps are extended during both day and night. Expanded polyps are 1 mm in diameter and up to 2 mm in length, with 12 short (0.5 -0.7 mm) white tipped tentacles (Fig. 2.1.3A).

B) *Echinopora gemmacea*

This species occurs from the Red Sea to New Caledonia, East Australia and the East Indies (Scheer and Pillai, 1983 ; Veron, 1986).

E. gemmacea is common in the Red Sea, especially in lagoons (see Veron, 1986). The colonies show both branching and encrusting growth forms (Fig. 2.1.1.C.D). Corallites are well separated (plocoid) and are 2-3 mm above the level of the colony surface. They are circular averaging 5.6 mm in diameter and 8.8 mm in depth. Each corallite has a spongy columella at its centre. The first and second cycle of septa are highly exserted over the colony surface forming costae. The costae run from one corallite to the next forming costal ridges with coarse spines. The primary and secondary cycles develop paliform lobes (Fig. 2.1.2.B). The colour of the colony is light or dark brown. The polyps which have 24 white tipped tentacles, are expanded only at night (Fig. 2.1.3.B).

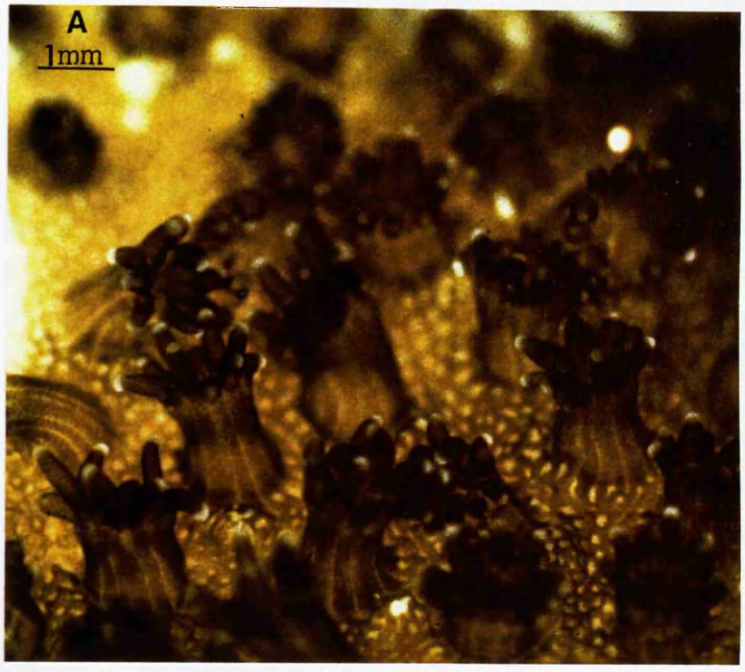
2.2. HISTOLOGY

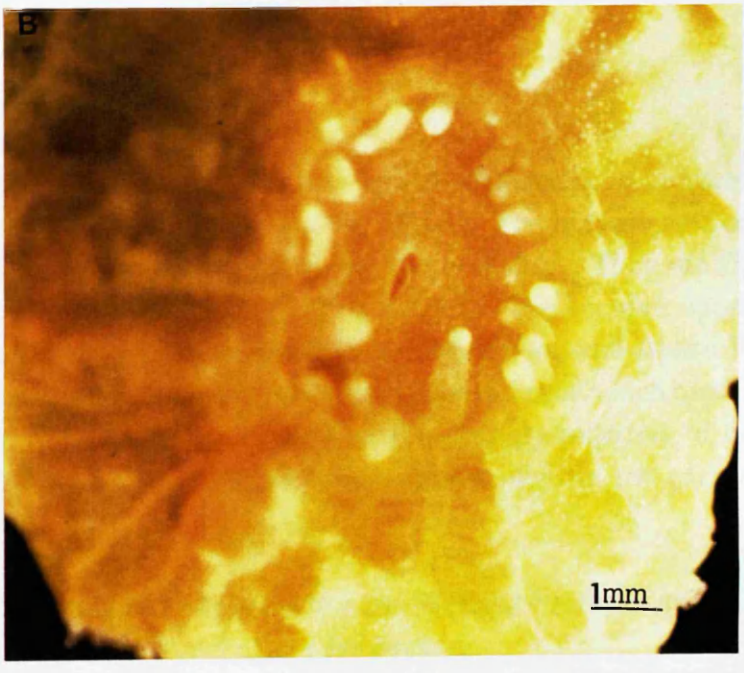
2.2.1 Introduction

The essential features of the body structure of cnidarians are that their body wall is divided into three layers : epidermis, gastrodermis and an intermediate layer, the mesoglea (Matthai, 1914; Wells, 1956). In this section, the histology of ***S. pistillata*** and ***E. gemmacea*** will be compared , with reference to the cells which are most involved in feeding i.e the mucous cells and cnidae , and the storage of lipids.

Fig. 2.1.3. The basic features of coral polyps of both species.
A) Extended polyps of ***S. pistillata*** at both day and night with 12 extended tentacles.

B) Polyp of ***E. gemmacea*** with 24 extended tentacles at night only.


A
1mm


B
1mm

2.2.2 METHODS

Samples for histological study were taken every month from March 1988 to January 1990. They were relaxed for six hours in a solution of 3.5% $MgSO_4$ and then placed in 7% sea water formalin for at least three days. Thereafter, they were transferred to a 7% solution of nitric acid to decalcify the skeletons. The decalcified polyps were washed with distilled water and preserved in 70% ethanol for further histological study. Parts of the decalcified specimens which were to be examined for lipid were post-fixed in potassium dichromate-osmium tetroxide solution (50 mls 2% osmium tetroxide and 50 mls 5% potassium dichromate) for eight hours. Thereafter, the post-fixed samples were washed in running water for two hours and preserved in 70% ethanol.

The preserved specimens were dehydrated in a series of strengths of ethyl alcohol, then cleared in xylene. The cleared specimens were infiltrated and embedded in paraffin wax.

Serial sections, 7 μm in thickness were cut, and then stained with Haematoxylin and Eosin. Those sections that were to be used for visualisation of mucus-glands were stained with Alcian Blue at pH 1.0 for 30 minutes and neutral red stain for two minutes. The stained sections were cleared with xylene and mounted in canada balsam.

2.2.3. RESULTS

A) *S. pistillata*

The epidermis consists of elongated columnar cells, nematocysts (holotrich type) and a few mucus-gland cells (Fig. 2.2.1A). The mucus-gland cells are present in small numbers in all tissues except the oral disc. They are flask-shaped or elongated, about 12 μm in length (Fig. 2.2.2C). The contents appear to be either transparent or finely granular and stain reddish-brown with Alcian Blue at pH 1.0. The gastrodermis contains large numbers of zooxanthellae which mask the animal cell nuclei. No mucus-gland cells were seen in the gastrodermis of the tentacles or coenosarc (Fig. 2.2.2A & B), but they were evident in the gastrodermis of the mesenteries.

The tentacle tip consists of a concentrated battery of cnidae. Below the tip neither mucus-gland cells nor cnidae are present.

Fig. 2.2.1. Longitudinal section through coenosarc and the tentacles of both species, showing details of the cell types occuring in each part. (A and B) The coenosarc and the tentacle of ***S. pistillata*** (C and D) The coenosarc and the tentacle of ***E. gemmacea*** epi., epidermis ; gas., gastrodermis ; gr. muc. g., granular mucus-gland ; hol., holotrich nematocyst ; mg., mesoglea ; muc. g., mucus-gland cell ; muc.g. l., mucus-gland like cell ; spr., spirocyst ; P-mast., P-mastigophore ; zox., zooxanthella.

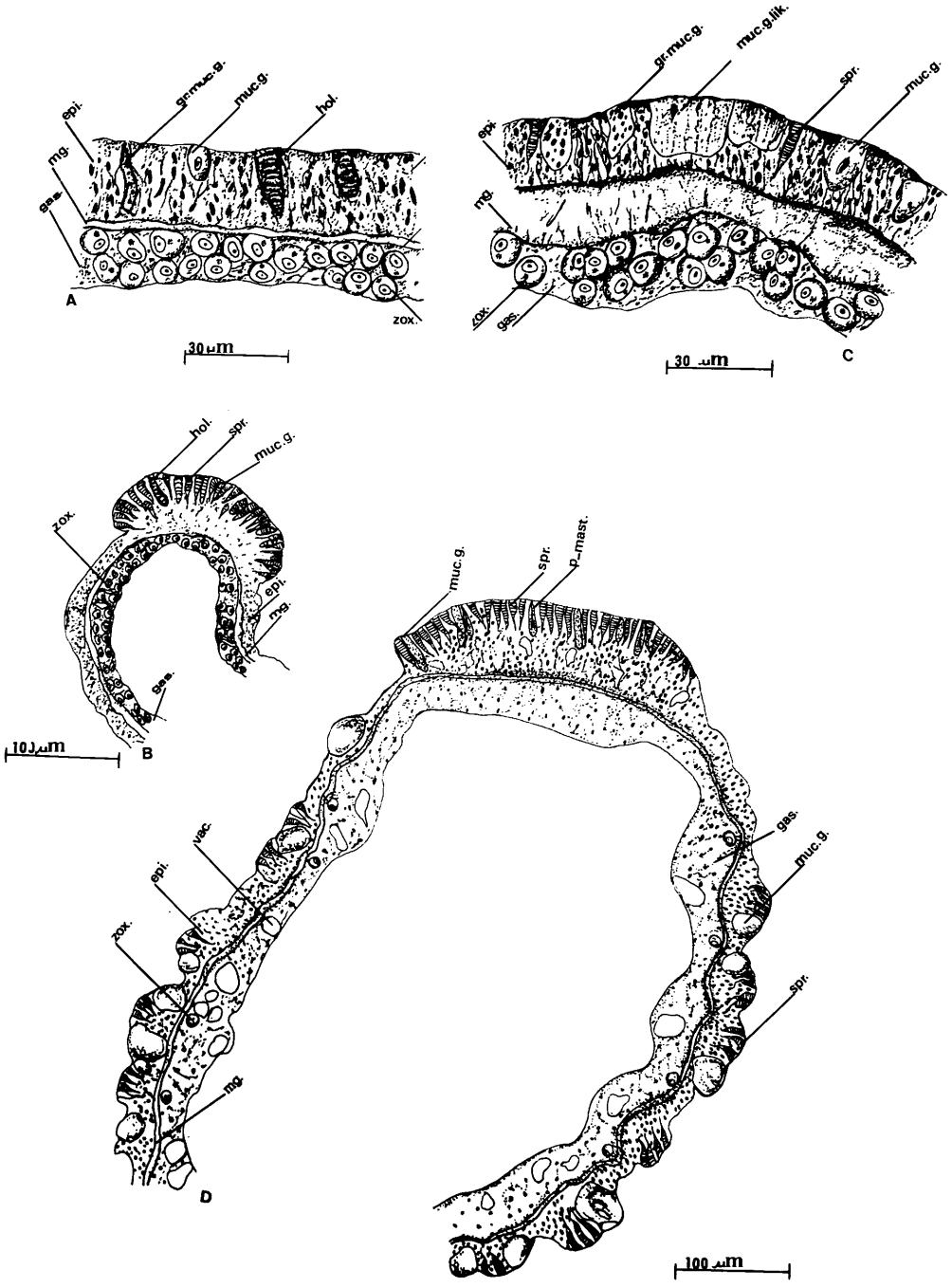
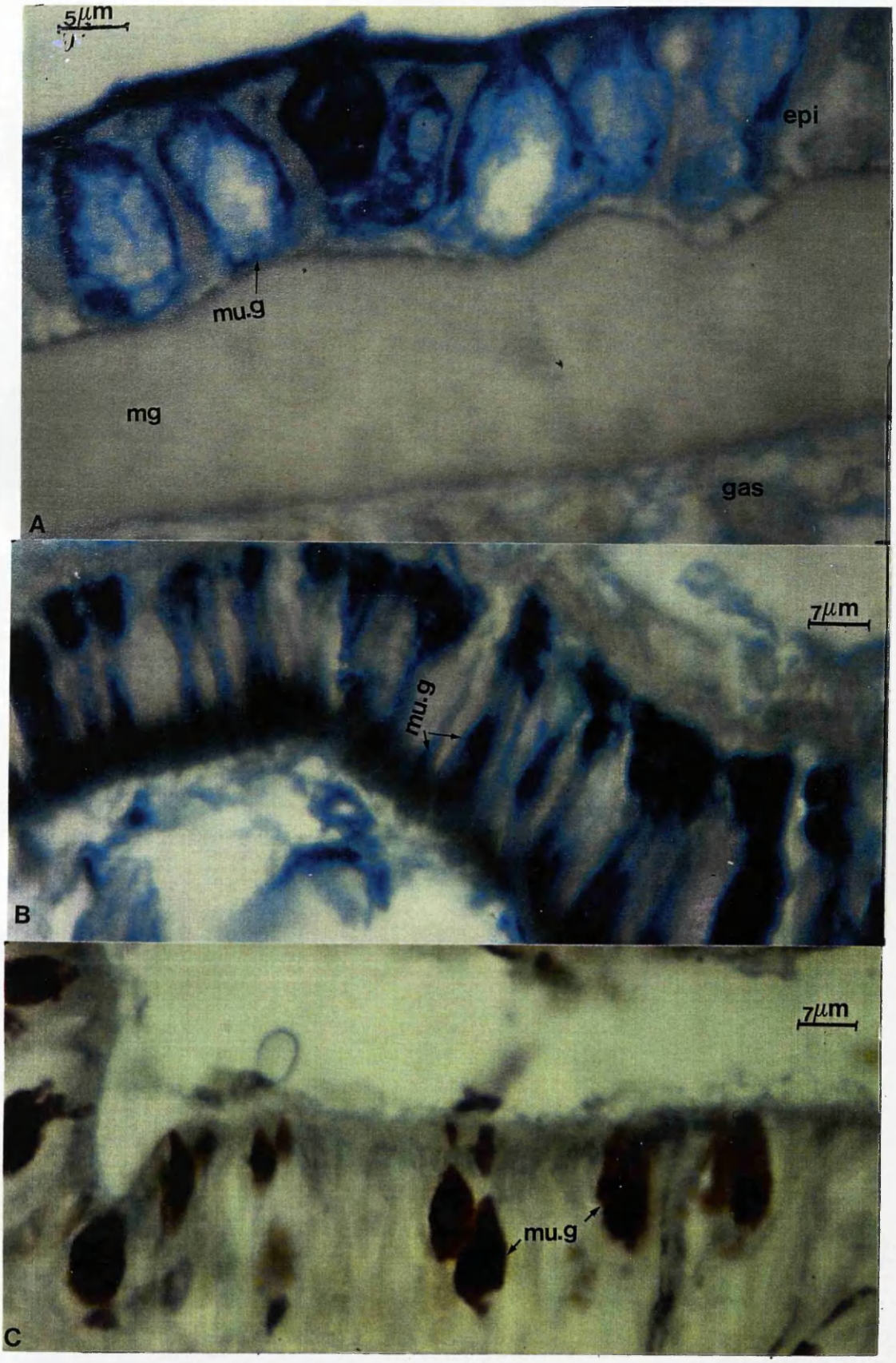
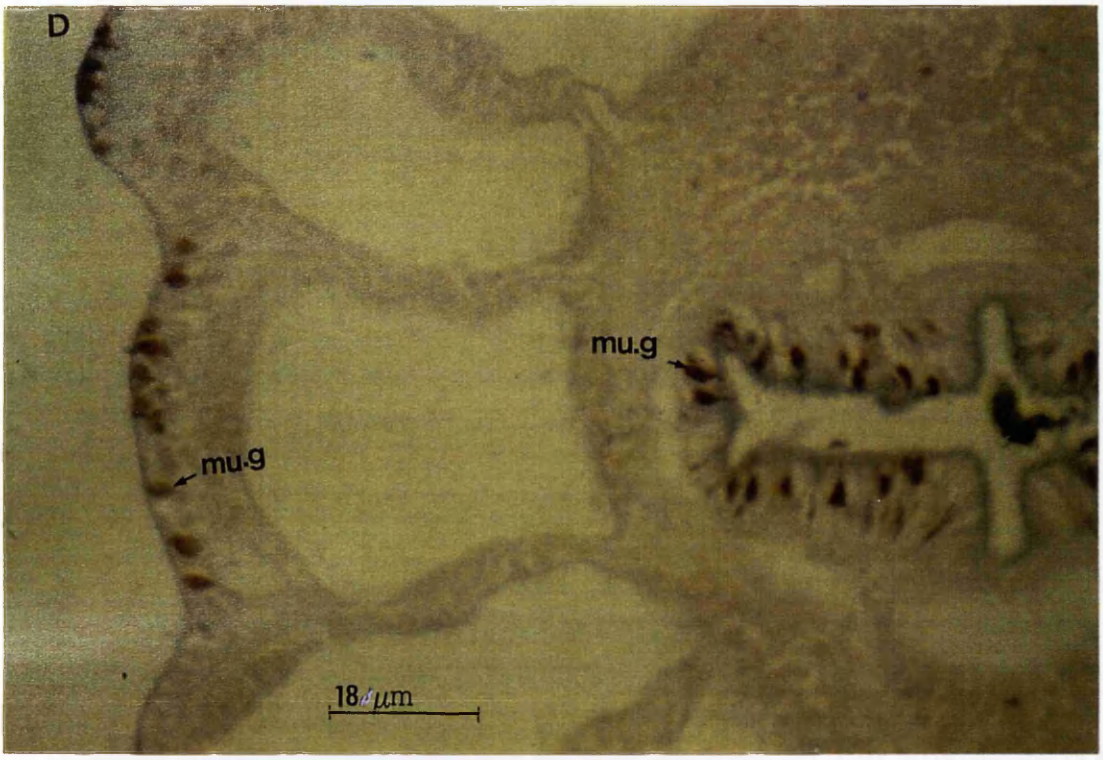
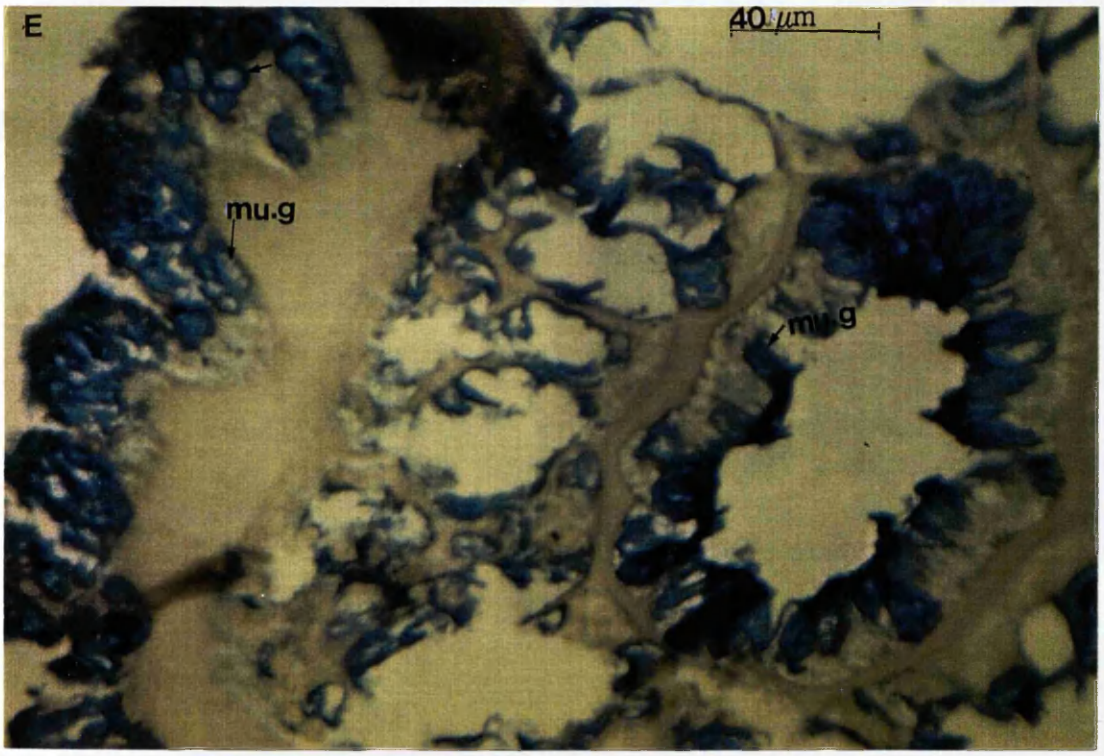

epi.
gr.muc.g.
muc.g.
hol.
mg.
gas.
zox.
A
30 µm
gr.muc.g.
muc.g.lik.
spr.
muc.g.
epi.
mg.
zox.
gas.
30 µm
C
hol.
spr.
muc.g.
zox.
epi.
mg.
gas.
100 µm
B
muc.g.
spr.
p-mast.
gas.
muc.g.
spr.
vac.
epi.
zox.
mg.
D
100 µm

Fig.2.2.2. Cross-section through the coenosarc (A) and the stomodaeum (B) of ***E gemmacea*** and the stomodaeum of ***S. pistillata*** (C): Note the shape and the colour of mucus-gland cells when stained with Alcian Blue at pH 1.0.
mu.g; mucus-gland cell ; epi., epidermis ; gas., gastrodermis.
In the following page, cross-section through the polyp mouth of ***S. pistillata*** (D) and ***E gemmacea*** (E), showing the distribution of mucus-gland cells in each species.


5μm
epi
mu.g
mg
gas
A
7μm
mu.g
B
7μm
mu.g
C


D
mu.g
mu.g
18 µm


E
40 µm
mu.g
mu.g

The gastrodermis of the tentacles is densely packed with zooxanthellae (Fig. 2.2.2B).

Lipid was stained black in osmium-tetroxide-fixed tissue. It was observed as black particles 4-6 μm diameter between the zooxanthellae (Fig. 2.2.3A), in the gastrodermis of the lower half of the polyp (Fig. 2.2.4A), in the mesoglea and in the eggs. (Fig. 2.2.3B). Lipid was never observed in the epidermal layer. Occasional `fat bodies' similar to those described by Stimson (1987), were found occluding the lumen of a tentacle.

B) ***E. gemmacea***

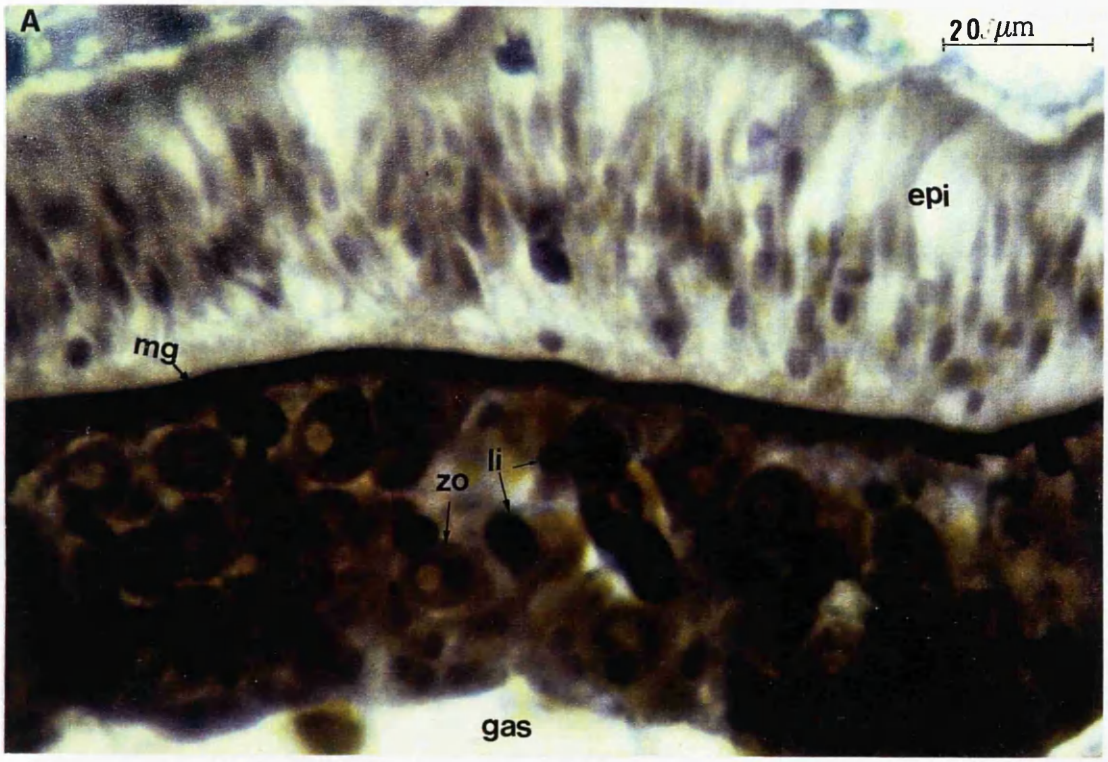
The epidermis of the coenosarc and polyp wall comprises columnar epithelial cells, together with spirocysts, a large number of mucus-gland cells and structures which resemble larger mucus-gland cells (Fig. 2.2.1C). The mucus-gland cells vary in number and size according to their location. They occur in large numbers in the coenosarc, oral disc and stomodaeum. They are flask-shaped in the coenosarc region and about 16 μm in length, whilst in the stomodaeum they are narrow and about 30 μm in length. (Fig. 2.2.3. A,B.). The mucus-gland cells appeared to contain a clear mucus substance, sometimes finely granular. All the mucus-gland cells of ***E. gemmacea*** were stained blue by Alcian Blue stain at pH 1.0.

The gastrodermal cells are again crowded with zooxanthellae and cell detail cannot be seen. Mucus-gland cells are scarce in the gastrodermis. The mesoglea of ***E. gemmacea*** is thicker than that of ***S. pistillata*** and again stained black with osmium tetroxide.

The tips of the tentacles are formed into knobs containing batteries of spirocysts and p-mastigophores, nematocysts being scarce. Lower down the tentacle, the cnidae are grouped together forming small protuberances. Mucus-gland cells are associated with each group of cnidae, which mainly comprise spirocysts. The gastrodermis of the tentacles appeared vacuolated in places and is almost devoid of zooxanthellae (Fig. 2.2.1D).

Lipid was again concentrated in the gastrodermal layer, particularly in the lower half of the polyp (Fig. 2.2.4B).

Fig.2.2.3. Transverse section through the coenosarc (A) and an oocyte (B) of *S. **pistillata*** to show distribution of lipid. Note that in the coenosarc lipid appears as droplets in the gastrodermis, the mesoglea stains uniformly for lipid, whilst there is no lipid evident in the epidermis. .li., lipid droplet ; epi., epidermis ; gas., gastrodermis ; zo., zooxanthella ; mg., mesoglea ; mf, mesenterial filament ; o, oocyte.


A
20 µm
epi
mg
li
zo
gas

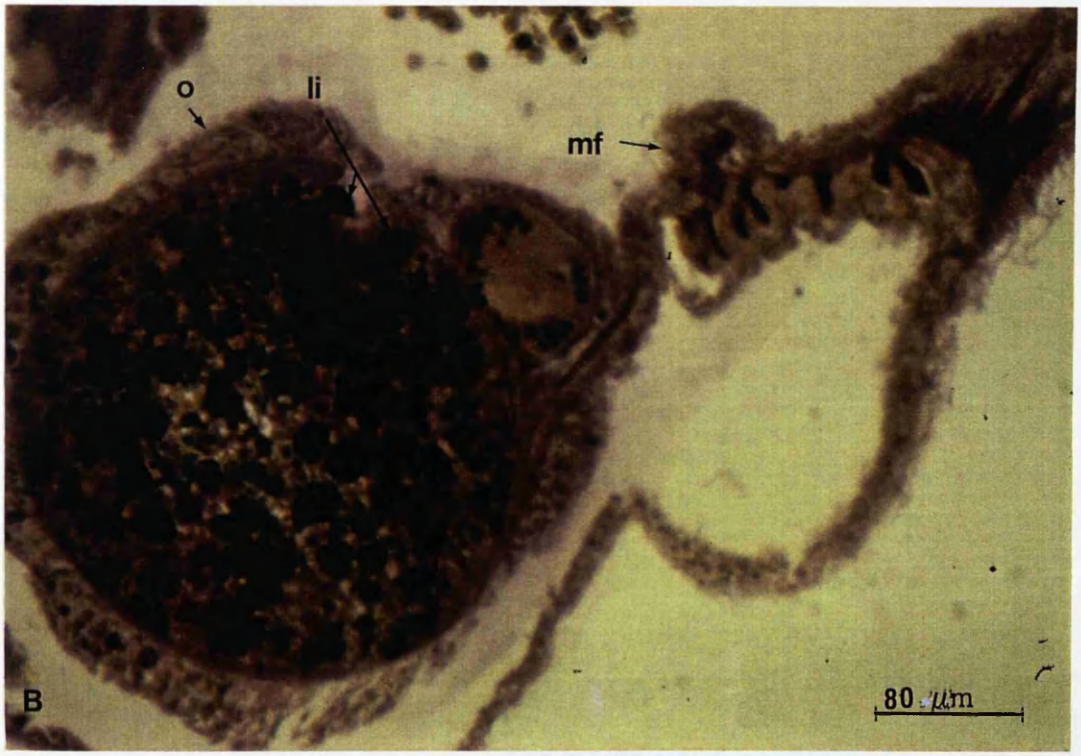
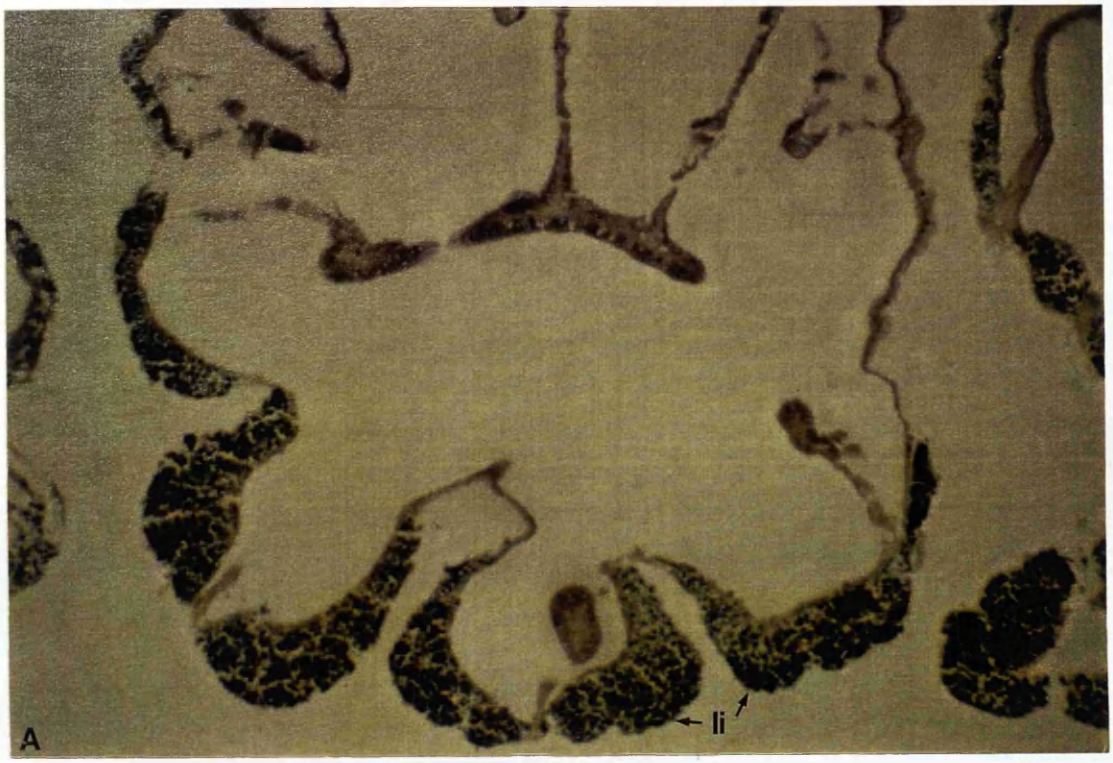

o
li
mf
B
80 µm

Fig.2.2.4. Longitudinal section through the polyp of ***S. pistillata***(A) and ***E. gemmacea*** (B) , showing black-stained lipid ,li. in the end part of the column wall of the polyp.


li
A


li
B

2.2.4 DISCUSSION

The structure of the outer layer of the coenosarc in both species was similar, with epidermal cells, containing mucus-gland cells and cnidae separated by the mesoglea from the gastrodermis. The gastrodermis contained large numbers of zooxanthellae but no mucus cells and no cnidae. The structure of the tentacles however is different in the two species. ***S. pistillata*** has small polyps and the tentacles which are expanded during the day, are packed with zooxanthellae. This is common in corals which are expanded in daytime (Muscatine, 1973). Conversely ***E. gemmacea,*** which has a large diameter polyp expands only at night for feeding and the tentacles which would not be exposed to light are devoid of zooxanthellae (see Wainwright, 1967).

The mucus-gland cells of the two species reacted differently to the Alcian Blue stain. This stain reacts with acid mucopolysaccharides to yield a blue colour, whilst neutral mucopolysaccharides are stained a reddish colour (Wallington and Drury, 1980; Harry, 1990). Previous reports of the composition of anthozoan mucus indicated the presence of acid mucopolysaccharide (Goreau, 1956; Richards ***et al,*** 1983) and mucopolysaccharides combined with lipids, especially wax esters (Benson and Muscatine, 1974). In neither ***S. pistillata*** nor ***E. gemmacea*** did the epidermal mucus-gland cells stain black with osmium tetroxide. Coral mucus has been reported to function in food capture (Duerden, 1906, Lewis and Price, 1975), sediment capture and cleansing (Ducklow and Mitchell, 1979b) and settlement attachment and recognition (Tidball, 1984). In addition Crossland ***et al*** (1980a) and Crossland (1987) showed that excess carbon fixed during photosynthesis of corals in daylight leaves the colony as muco-lipid. In view of the absence of lipid from the epidermal mucus-gland cells, it seems likely that this would be released from the coelenteron.

The distribution of lipid in the gastrodermal cells, particularly those in the lower part of the polyp, is very similar to that described for Hawaiian corals by Stimson (1990). The 'fat bodies' which Stimson described associated with the stomodaeum of ***Pocillopora damicornis*** were not present at all in ***E. gemmacea*** whilst ***S. pistillata*** occasionally displayed a similar body within the tentacles.

2.3. CNIDAE

2.3.1. INTRODUCTION

Cnidae serve a variety of functions : prey capture, adhesion, defence and aggression (Thorington and Hessinger, 1990 ; Purcell and Mills, 1988; Mariscal, 1974 and Muscatine, 1973). The aim of this study is to determine their type and number in both species and to relate their relative proportions of number and types in different parts of the polyp to the mode of feeding of the corals.

2.3.2. METHODS

Small branches from each species were narcotised in 3.5% Mg SO_4 for 6 hours, then fixed in 7% seawater formalin for 3 days before decalcifying with a 7% solution of nitric acid. The decalcified polyps were washed with distilled water and preserved in 70% ethanol. Samples of tentacle tips, mesenterial filament and oral disc were dissected from the polyps and placed in a solution of 5% potassium hydroxide overnight at a temperature of 5 ^{o}C. Pieces of tissue were then mounted on a slide and squashed beneath a coverslip. The number, type and size of cnidae were recorded using a microscope with a x 1000 oil-immersion objective. The oral disc was divided into 4 pieces before counting, and the mesenterial filaments divided into 2 pieces. Estimates of the total population of cnidae were then made.

2.3.3 RESULTS

Cnidae were separated into spirocysts and nematocysts following the classification of Cutress (1955) and Mariscal (1974). Three types of nematocysts were identified: microbasic P-mastigophores, microbasic B-mastigophores and holotrichs. The features used to distinguish these were:

1. SPIROCYSTS: Capsules thin with single wall; contents positive to acid stains; thread uniform in diameter with no spines (Fig. 2.3.1A).

2. NEMATOCYSTS: Capsules with thick double wall: contents positive to basic stains.
   (a) Microbasic P-mastigophore: Shaft with V-shaped notch at its base; shaft reducing abruptly in diameter to form the thread (Fig. 2.3.1B).

Fig. 2.3.1. Type of cnidae found in both species under phase contrast.
(A) Spirocyst from the tentacles of ***S. pistillata.***
(B) P-mastigophore from the mesenterial filament of ***E. gemmacea.***
(C) Holotrich from the oral disc of ***E. gemmacea.***
(D) B-mastigophore from the oral disc of ***S. pistillata.***

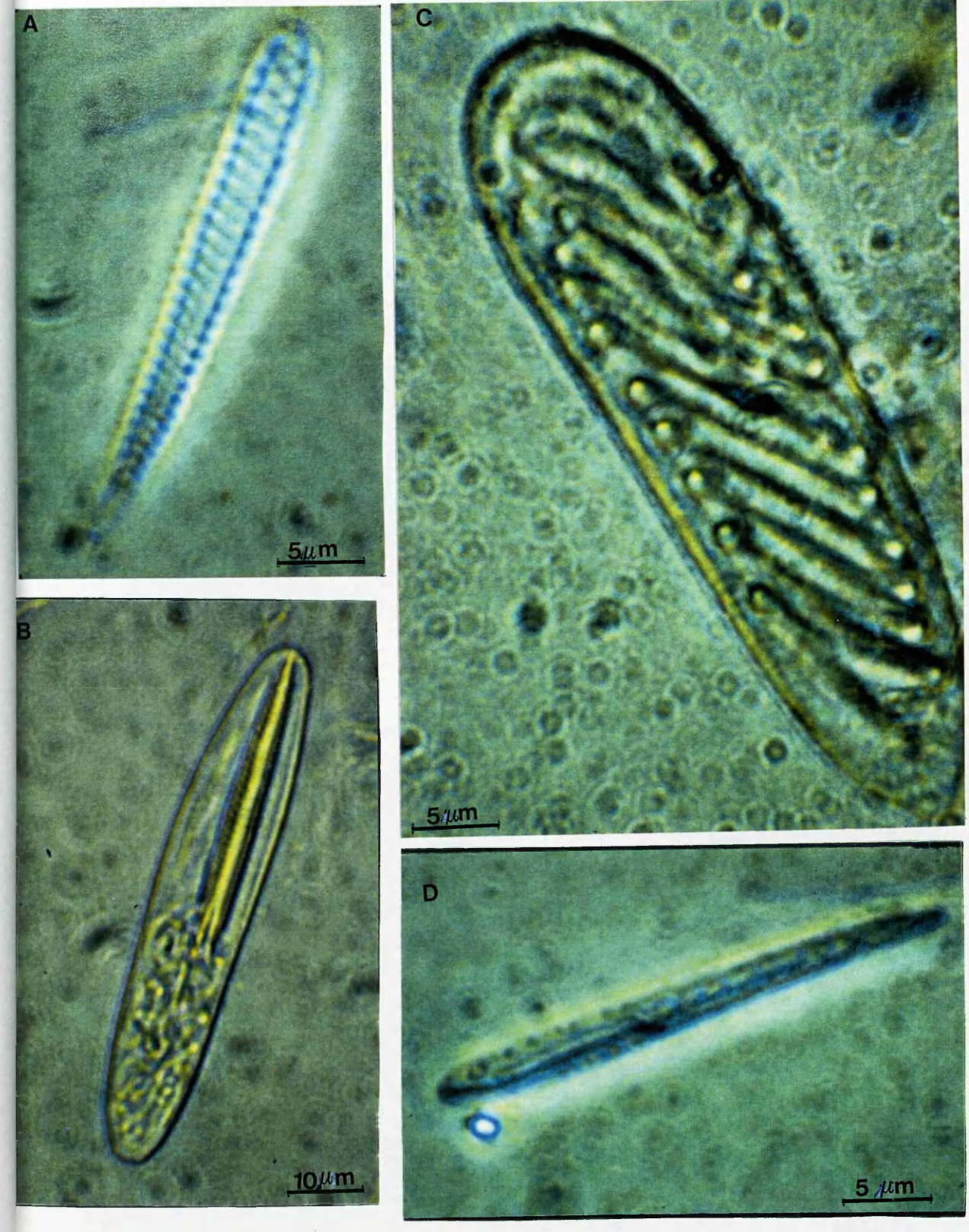

A
5μm
B
10μm
C
5μm
D
5 μm

Table 2.3.1. Average number and size of cnidae type per polyp in each tissue type in ***S. pistillata*** and ***E. gemmacea*** (means ± standard deviations and sample size). Where size was uniform no standard deviation is given.

Cnidae	Spirocysts		Nematocysts					
	Spirocysts		P-mastigophores		B-mastigophores		Holotrichs	
	Size	No.	Size	No.	Size	No.	Size	No.
S. pistillata								
Tissue								
Tentacle	21	15150.0	-	-	-	-	36	1804.5
s.d. (n)	- (11)	1447.32 (8)	-	-	-	-	- (10)	269.2 (8)
Oral disc	21	184.86	45.0	6.2	13.0	53.25	45	8.4
s.d. (n)	- (10)	42.52 (7)	- (10)	2.48 (7)	- (10)	13.87 (7)	- (10)	3.2 (7)
Filament	-	-	36.0	835.5	-	-	30	915.0
s.d. (n)	-	-	- (10)	195.6 (8)	-	-	- (10)	224.2 (8)
E. gemmacea								
Tissue								
Tentacle	45.75	62913.12	49.29	1572.0	-	-	-	-
s.d. (n)	1.39(10)	5231.28 (8)	1.6	(10)	331.92 (8)	-	-	-
Oral disc	21	1480.75	-	-	27.0	607.14	45	330.6
s.d. (n)	- (10)	128.78 (8)	-	-	- (10)	134.75 (8)	- (10)	108.4 (8)
Filament	-	-	59.67	6843.0	-	-	72	16518.0
s.d. (n)	-	-	1.0 (10)	1267.68 (8)	-	-	- (10)	3976.8 (8)

Table 2.3.2 Percentage distribution of cnidae within different tissue types.

Cnidae	Spirocysts	P-mastigophores	B-mastigophores	Holotrichs
S. pistillata				
Tissue				
Tentacle	89.36	-	-	10.64
Oral disc	73.15	2.45	21.07	3.32
Filament	-	47.73	-	52.27
E. gemmacea				
Tissue				
Tentacle	97.56	2.44	-	-
Oral disc	61.23	-	25.10	13.67
Filament	-	29.29	-	70.71

(b) Microbasic B-mastigophore: Shaft appears as a straight-axial rod throughout the centre of the capsule, then gradually reducing in diameter to form the thread (Fig. 2.3.1 D).

(c) Holotrichs: No shaft; thread is of uniform diameter, with well developed spines along its whole length (Fig. 2.3.1 C).

In ***S. pistillata***, the predominant cnidae in the tentacles were spirocysts, no P-mastigophores or B-mastigophores being present and only relatively few holotrichs (Tables 2.3.1. and 2.3.2). The total number on the oral disc was considerably smaller and again spirocysts were most common, with small numbers of P-mastigophores and B-mastigophores. By contrast spirocysts were absent from the mesenterial filaments as were B-mastigophores, whilst P-mastigophores and holotrichs were present in about equal proportions.

In ***E. gemmacea*** spirocysts were again predominant in the tentacles, P-mastigophores were present, but there were no B-mastigophores or holotrichs. On the oral disc spirocysts were again most common, P-mastigophores were not present but B-mastigophores and holotrichs were found. The pattern in the mesenterial filaments followed that of ***S. pistillata***, in that spirocysts and B-mastigophores were both absent, but in this species the holotrichs predominated over the P-mastigophores.

2.3.4. DISCUSSION

All four types of cnidae that are found in the Scleractinia (Mariscal, 1974 ; Thomasson and Brown, 1986) are present in both species of corals. The functions which each type is thought to perform is related to the location within the polyp and to the mode of feeding. Thus spirocysts which have a long thread composed of fine hollow tubules which are thought to fan out after discharge probably have a function in adhesion. The P-mastigophores and B-mastigophores are used in defence and prey capture, since they are thought to be involved in the injection of toxins. Holotrichs are thought to participate in aggressive interactions (Mariscal, 1974).

In the tentacles of both species, the predominant form is the spirocyst. In ***S. pistillata*** there was a small percentage of holotrichs but no venom-injecting nematocysts. It seems very unlikely therefore that this species uses the tentacles for

prey-capture during feeding. In ***E. gemmacea*** 2.4% of the cnidae on the tentacles comprised P-mastigophores suggesting that tentacular prey-capture would be more significant in this species. However, in both species, the pattern of appearance of cnidae has led to the tentacles being classified as feeding tentacles (Hidaka and Yamazato, 1984 ; Bigger, 1988; Thorington and Hessinger, 1990; Goldberg ***et. al.***, 1990). In this way they would contrast with the sweeper tentacles of ***Montastrea cavernosa*** which are composed of 63% of holotrichs and only 3.5% of spirocysts (Den Hartog, 1977).

The oral disc of both species was still dominated by spirocysts, although B-mastigophores were present to the extent of 21% in ***S. pistillata*** and 25% in ***E. gemmacea***, again indicating the important role played in feeding.

Spirocysts were absent from the mesenterial filaments, their place being taken by P-mastigophores and holotrichs, the latter being slightly more prevalent in ***E. gemmacea*** than in ***S. pistillata***. Both of these types of cnidae are important in aggression and defence (Thorington and Hessinger, 1990; Purcell and Mills, 1988; Muscatine, 1973; Mariscal, 1974 ; Den Hartog, 1977).

2.4. FEEDING

2.4.1. INTRODUCTION

Corals have the ability to obtain their nutrition from different sources (Johannes, 1974). They were described as carnivores, using their tentacles to capture zooplankton (Yonge, 1930). Others concluded that corals also feed on bacteria (Sorokin, 1973). They may also feed on organic particulate matter (Lewis, 1977). In this section investigations into the feeding behaviour and food type from both laboratory and field observations will be described.

2.4.2. Methods

A) Prey capture

Nubbins of ***S. pistillata*** and ***E. gemmacea*** were placed in a glass aquarium containing 90 litres of running seawater for 2 days. They were then transferred separately into a small tank (150 ml) filled with aerated seawater. *Artemia*

nauplii and eggs were offered as food. The feeding behaviour of each species was observed under a binocular microscope during the daytime under normal laboratory lighting conditions.

In a second experiment to determine the number of prey items captured at night when the tentacles of ***E. gemmacea*** would be expanded, small colonies of each species were fed with eggs and newly hatched nauplii of *Artemia* shortly after darkness. One hour later, branch tips were removed at random and fixed in 10% formalin. The fixed specimens were decalcified in 10% nitric acid, washed in water and preserved in 70% ethanol. Finally, the coelenteron of each polyp was dissected under a binocular microscope.

B) Ciliary current feeding

In order to visualise the ciliary currents on the coenosarc and tentacles, a suspension of colloidal graphite was carefully dropped on to the surface of the nubbins with a pipette. The experiment was carried out under daytime laboratory lighting conditions and observations were made under a binocular dissecting microscope. In order to test the ability of the coral surface to discriminate between different organic particles, the experiment was repeated using finely ground dried fish meat and cultures of the algae *Tetraselmis, Chlorella* and *Chaetoceros.*

C) Field observations

Direct observation on the feeding behaviour of the two species in the field was made using SCUBA equipment . Close-up photographs were taken with a Nikonos V camera fitted with a flash attachment.

2.4.3. RESULTS

A) Prey capture

The polyps of ***S. pistillata*** were expanded at all times. *Artemia* nauplii were caught by contact with the tentacle tips, but these were not successfully transferred to the mouth. Usually they dropped off on to the coenosarc and were rejected. *Artemia* which contacted the oral surface of the tentacles were captured, probably by the cooperative activity of other tentacles. The mouth was then opened and attempts were made to swallow the *Artemia.* Few of the polyps were successful in this. Eggs which settled on the oral disc were carried by cilia to the mouth and swallowed.

Table 2.4.1 Total number of *Artemia* eggs and nauplii obtained from the coelenteron of each polyp after one hour of feeding.

Polyp No.	*E. gemmacea*		*S. pistillata*	
	Eggs	Nauplii	Eggs	Nauplii
1.	67	-	1	-
2.	27	-	2	-
3.	51	-	1	1
4.	45	1	2	-
5.	70	1	2	1
6.	60	5	2	-
7.	29	1	1	-
8.	45	2	1	1
9.	15	5	1	-
10.	78	-	1	-
11.	23	6	-	1
12.	57	1	2	-
13.	113	-	-	1
14.	12	-	1	-
15.	76	-	1	-
16.	8	-	1	-
17.	60	2	-	1
18.	36	-	2	-
19.	69	1	1	-
20.	45	-	-	1
Mean	49.30	1.25	1.10	0.35
S.D. ±	26.28	1.88	0.71	0.48

In ***E. gemmacea*** it was not possible to make direct observations on prey capture at night when the tentacles were expanded, since it was found that tentacle retraction took place at the lowest levels of light at which observation could occur. During the daytime, with tentacles retracted, *Artemia* nauplii were not caught. At times, *Artemia* were observed to be trapped by mucus and probably by the spirocysts on the surface. Eggs on the other hand were bound together in mucus strands on the coenosarc, carried between the costal ridges to the oral disc and were drawn into the opened mouth.

The contents of the coelenterons (Table 2.4) of twenty polyps of each species, which were examined after 1 hour of feeding in darkness revealed that neither species was particularly successful at prey capture. Ten of the polyps of ***E. gemmacea*** had captured one or more *Artemia* nauplii, the maximum capture being 6 nauplii and the total number captured was 25. By contrast in ***S. pistillata*** only seven polyps had managed to capture a single nauplius, so that the total ingested was 7.

A similar pattern emerged with the capture of eggs. The 20 polyps of ***E. gemmacea*** had managed to ingest a total of 986 eggs, with a range from 8 to 113 eggs per polyp. In ***S. pistillata***, 4 polyps contained no eggs, the total ingested was only 22 and the range was from 0 to 2.

B) Ciliary Feeding

S. pistillata

Experiments with colloidal graphite showed that on the oral disc ciliary currents flowed in two different directions. Around the mouth cone, particles moved towards the mouth. Elsewhere, the currents passed between the bases of the tentacles, carrying particles to the edge of the oral disc where they were rejected (Fig 2.4.1A). On the tentacles the ciliary current was towards the tip, except at the lower part on the outerside where the current passed downwards to meet the upward current generated on the polyp wall (Fig. 2.4.1, B). On the coenosarc between polyps particles were carried upwards towards the `hood' to be rejected (Fig. 2.4.1., C, A)

No feeding response was observed with suspensions of algae. However, when finely ground fish meat was added to the surface of the colony, the mouth opened widely and mesenterial filaments were extruded both through the mouth and body wall. The direction of the ciliary currents did not change.

Fig.2.4.1. Ciliary currents in both species, showing the direction of the ciliary currents as indicated by arrows.

S. pistillata

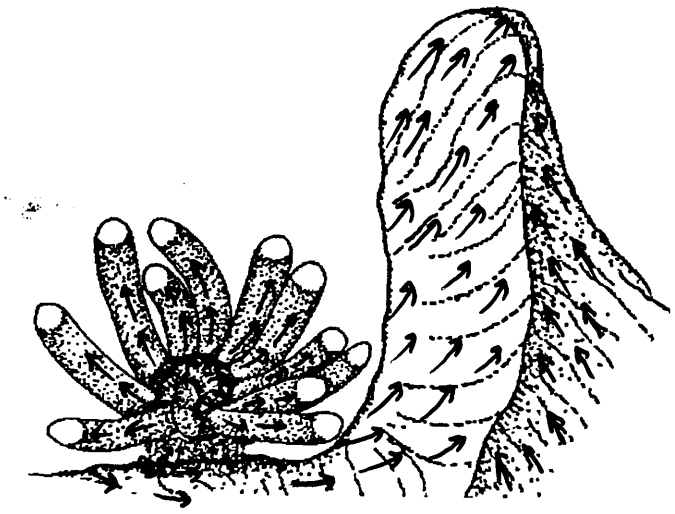
(A) Ciliary currents on the oral disc, and the internal surface of tentacles and hood .

(B) Ciliary pattterns on the column wall of the polyp and on the outer surface of the tentacles and the hood

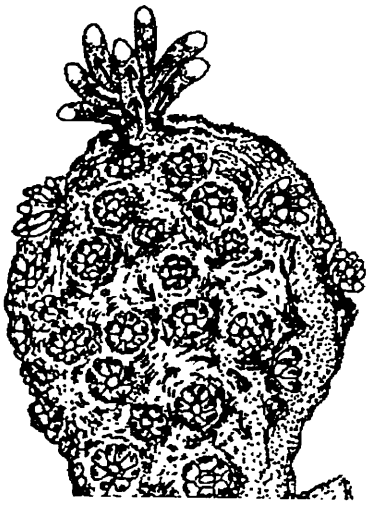
(C) General ciliary direction on the colony surface.

E. gemmacea

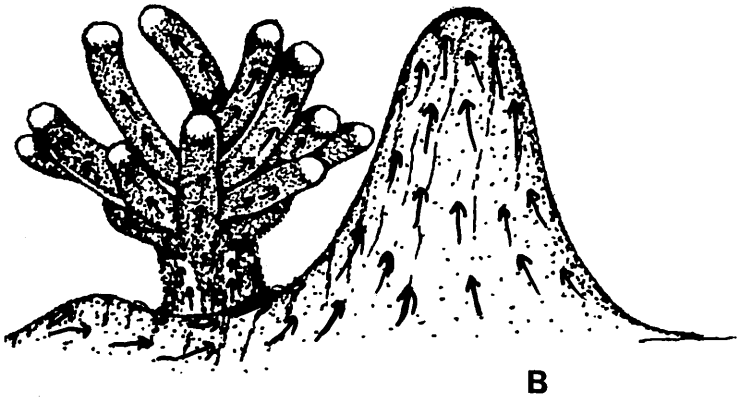
(D) Ciliary current on the polyps surface and on the oral disc. Note : the ciliary direction along the shallow grooves, and three stages of the opening of the mouths of the polyps when stimulated with organic particles.



A

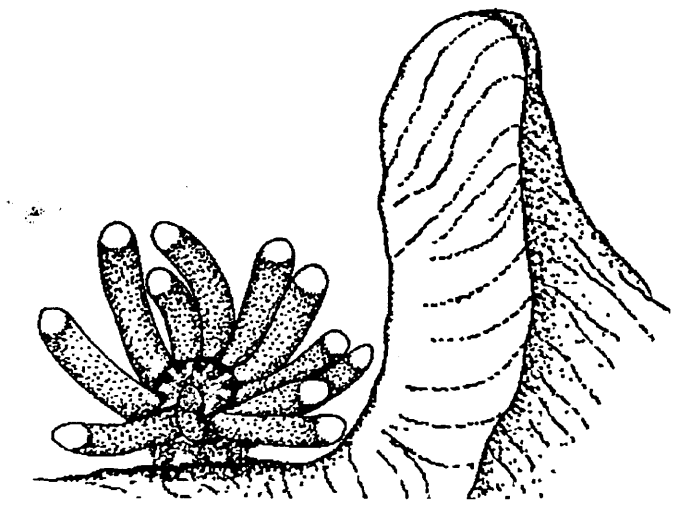


C

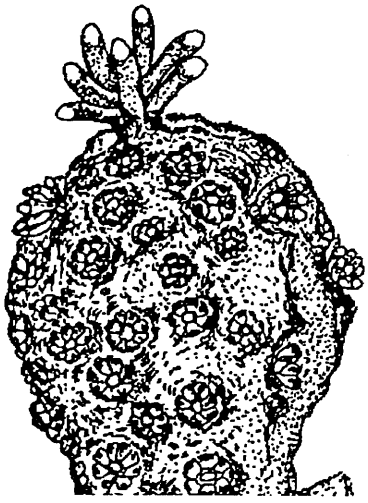


B

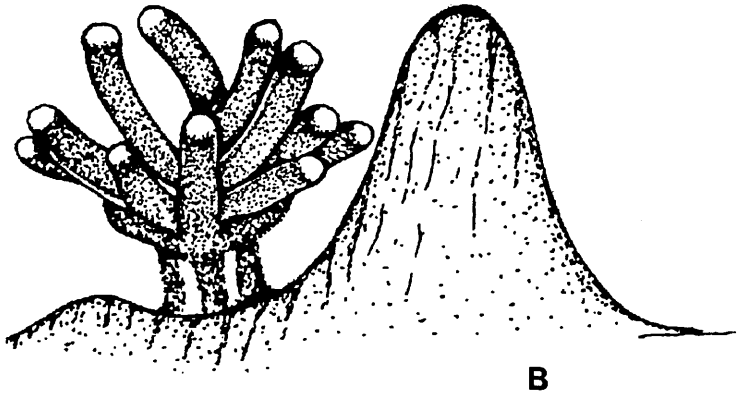
D



A



C



B

D

E. gemmacea.

On the oral disc, ciliary currents again moved towards the mouth whilst on the remainder of the surface the currents carried particles outwards to be rejected. On the coenosarc ciliary currents moved particles along shallow grooves. However when these reached the septal ridges of the corallites they were deflected upwards (Fig. 2.4.1., D).

The algal suspensions were trapped in mucus strings on the surface of the coenosarc, carried to the mouth and ingested, to be quickly egested again. When finely ground fish meat was added , the mouth opened widely and the outward ciliary current around the periphery of the oral disc was less pronounced. The particles were trapped in mucus strands on the coenosarc, and passed along the shallow grooves to the mouth where they were drawn downwards into the coelenteron.

C) Field Observations.

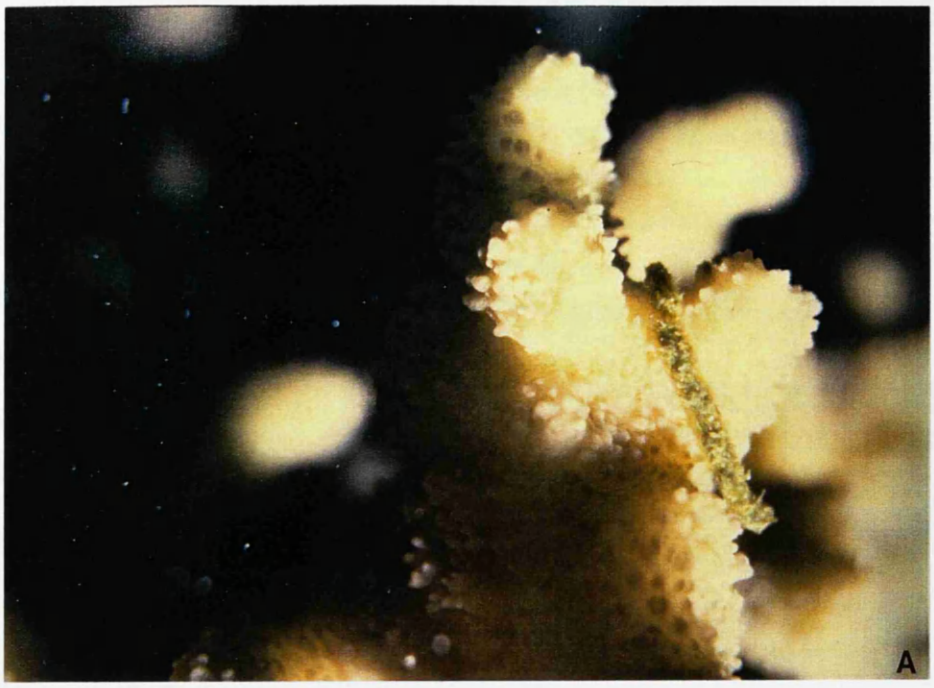
No feeding activity either by tentacles or by mesenterial filaments was observed in ***S. pistillata*** in the field. In ***E. gemmacea***, on several occasions feeding on fish faecal pellets was observed. These were trapped in mucus on the coenosarc and transmitted to the mouth, as observed in the laboratory feeding experiments (Fig. 2.4.2).

2.4.4 DISCUSSION

Stylophora pistillata uses both tentacles and mesenterial filaments when feeding. Despite this the success at ingestion of both *Artemia* nauplii and *Artemia* eggs was very low. Part of this may have resulted from the size of the nauplii since difficulty was apparent when the polyps attempted to swallow those which had been caught. It is possible that a higher success might have been achieved with smaller zooplankton. In addition, feeding by entrapment in mucus strands on the coenosarc was not observed. It seems likely that the ciliary currents in this species are used primarily for clearing the surface of the colony of falling particulate matter. Similar patterns were observed in other Atlantic and Pacific species (Yonge, 1930; Lewis and Price , 1976). The apparent lack of feeding specialisation was corroborated by the histological data, notably the relatively small number of mucus cells present and the absence of the venom-containing mastigophore nematocysts on the tentacles.

In a study of feeding mechanisms of Atlantic corals, Lewis and Price

Fig. 2.4.2. Underwater photograph showing fish faecal pellets caught on the colony surface of ***E. gemmacea*** by mucus (A) . Ingestion of the faecal pellet by the mouth of the polyp is shown in (B)


A


B

(1975) and Lewis (1977) concluded that those corals whose tentacles were expanded during the day (e.g. Pocilloporidae and Poritidae) used the tentacles for feeding. Conversely those species which expanded only at night-time feed on particulate matter caught on the mucus net, or by a combination of mucus net and tentacles. They did not observe the role of mesenterial filaments in feeding, although this was described by other workers (Yonge, 1930 ; Abe, 1937 ; Goreau ***et al***, 1971; Muscatine, 1973).

E. gemmacea was more successful than ***S. pistillata*** in capturing *Artemia* nauplii during darkness when the tentacles were expanded. No direct observation could be made of the feeding behaviour and so the role of the tentacles in feeding could not be evaluated. However, observations made during the daytime clearly showed that this species is adapted primarily as a mucus net particulate feeder. This is borne out by the histological study which demonstrated the large number of mucus-gland cells in the epidermis.

The apparent inability of ***S. pistillata*** to feed successfully by either zooplankton capture or by mucus nets, suggests that it may obtain relatively more of its nutrition from autotrophy from its zooxanthellae. The expansion of the tentacles which are densely packed with the symbionts is probably an adaptation for this.

2.5 REPRODUCTION

2.5.1. INTRODUCTION

Some Scleractinian corals exhibit internal fertilisation of the eggs within the coelenteron and "brooding" of the planula larva, whilst other species liberate eggs and sperm. The mode and time of reproduction of reef building corals has been reviewed by many workers (Rinkevich and Loya, 1979a,b ; Kojis and Quinn, 1981 and 1982; Fadlallah, 1983; Jokiel, 1985 and Willis ***et al***, 1985). There are few studies on the reproductive cycle of Red Sea corals. The aim of this study was to compare the mode and timing of reproduction in ***S. pistillata*** and ***E. gemmacea.***

2.5.2. METHODS

Specimens of ***S. pistillata*** were sampled at the study site (see page 45) at monthly intervals from January to December 1989. ***E. gemmacea*** was sampled

from February to December 1988. Specimens were anaesthetized, fixed, decalcified and histological preparations made for staining in Haematoxylin and Eosin as described in section 2.3.

In an attempt to quantify the state of gonad development, the maximum and minimum dimensions of a transverse section through a single testis and ovary of six or seven specimens was measured with a calibrated eye-piece micrometer on a compound light microscope. An approximation of gonad size was then obtained from the mean of the maximum and minimum dimensions.

*S. **pistillata*** were found to readily release planulae in the laboratory. Observations were made upon their histology, behaviour, and settlement.

2.5.3. RESULTS

Both species are hermaphrodite with protogynous gametogenesis. In *S. **pistillata*** the ovaries are carried on short thick outgrowths of the polyp wall, into the coelenteron, each ovary containing a single egg (Fig.2.5.1A). The ovaries are present throughout the year. The reproductive cycle begins in May when immature oocytes with a mean diameter of 45.6 μm may be seen. These increase in size until December, when they reach their maximum size of 214.5 μm. In January and February eggs of a smaller size, 111.5 μm and 82.3 μm are found and these increase to a maximum of 169.8 μm in April (Table 2.5.1 and Fig. 2.5.2,A).

The bilobed testes are not present in the months of May to July, appearing first in the month of August and increasing in size until December. In January their size appears to diminish, probably coinciding with the first release of male gametes, and thereafter they increase to a second maximum in April (Table 2.5.1 and Fig. 2.5.2A).

Fertilisation of the eggs takes place within the coelenteron (Fig. 2.5.1B) and thereafter embryogenesis gives rise to a planula which is brooded in the coelenteron, beneath the pharynx (Fig. 2.5.3A). Planulae were observed from December to March, reaching a maximum size of 485.3 μm in February. During this period differentiation of the planula takes place and mesenteries may be seen within the developing coelenteron, in longitudonal sections F (Fig. 2.5.3B)

Newly liberated planulae were 1.5 mm in length and 0.5 mm in diameter.

Fig.2.5.1. *S. **pistillata*** cross-section through polyp , showing male and female gonads (A) , note : the oocyte on short stalks. t., testes ; o , oocyte ; mf., mesenterial filament ; st., stalk.

(B) A mature oocyte , note : the thickness of egg envelope. gas., gastrodermal layer.

(C) A male gonad, showing two lobes of testes. sp. , sperm cells.

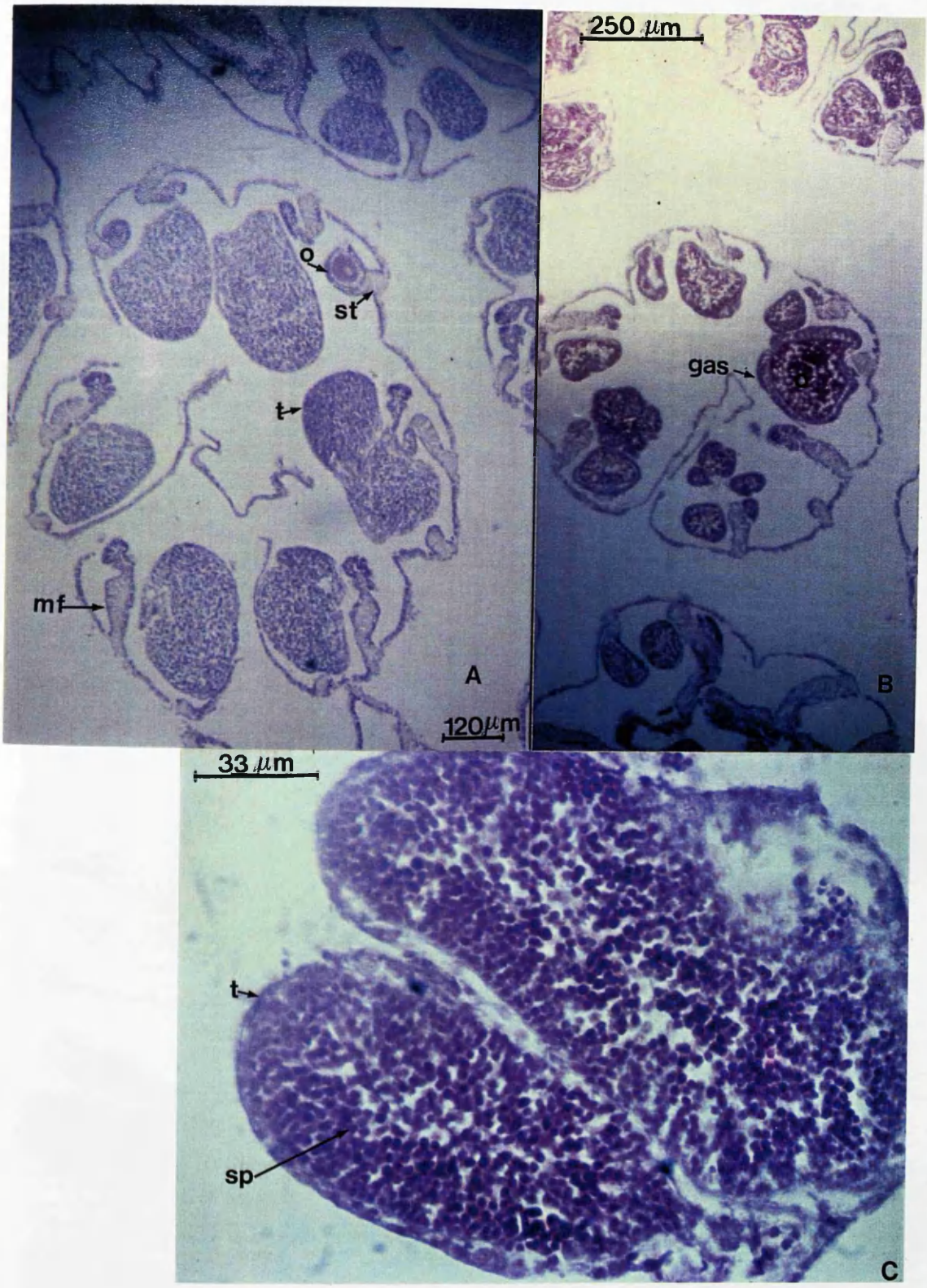

o
st
t
mf
A
120 µm
250 µm
gas
B
33 µm
t
sp
C

Table 2.5.1 Mean size of eggs and testes (μm) ± s.d. (n) each month for *S . pistillata* at the study site from January 1989 to December

Month	Egg size	Testes size
January	111.5 ± 7.6 (2)	151.5 ± 21.2 (6)
February	82.3 ± 16.6 (14)	161.9 ± 20.3 (17)
March	164.2 ± 46.6 (17)	171.5 ± 31.7 (12)
April	169.8 ± 41.3 (22)	184.4 ± 37.6 (12)
May	45.6 ± 3.5 (7)	-
June	58.3 ± 5.4 (10)	-
July	74.3 ± 14.9 (21)	-
August	127.7 ± 29.0 (16)	133.2 ± 41.4 (2)
September	185.3 ± 30.2 (19)	138.8 ± 37.8 (22)
October	192.6 ± 30.6 (14)	159.5 ± 24.7 (14)
November	208.8 ± 38.6 (10)	171.8 ± 20.5 (10)
December	214.5 ± 38.8 (6)	183.8 ± 16.4 (10)

Table 2.5.2 Mean size of eggs and testes (μm) ± s.d. (n) each month for ***E. gemmacea*** at the study site from June 1988 to November 1988.

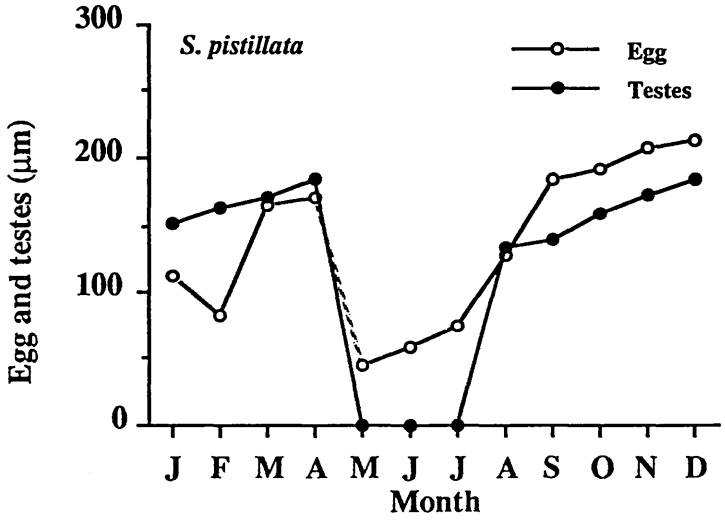
Month	Egg size	Testes size
June	50.1 ± 10.5 (70)	-
July	58.9 ± 8.3 (12)	-
August	126.3 ± 27.4 (12)	121.7 ± 16.3 (11)
September	156.6 ± 21.1 (22)	144.7 ± 24.5 (13)
October	159.0 ± 14.4 (18)	152.5 ± 26.2 (5)
November	186.7 ± 14.0 (9)	145.0 ± 21.5 (9)

Fig.2.5.2.

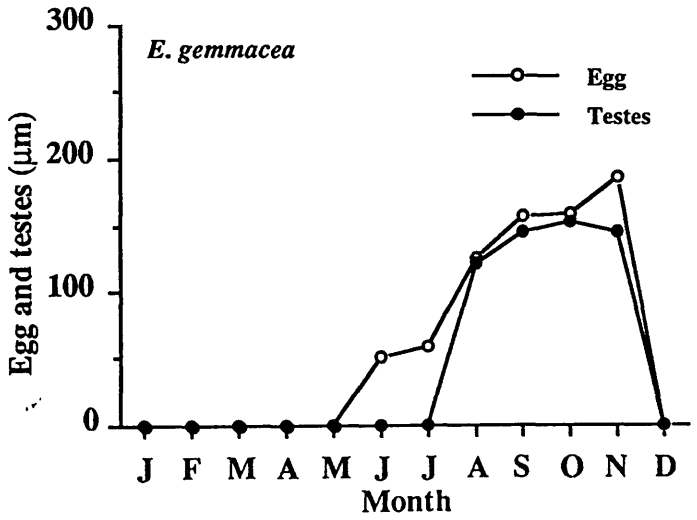
(A) Mean size of oocytes and testes in ***S. pistillata*** from January 1989 to December1 1989.

(B) Mean size of oocytes and testes in ***E. gemmacea*** from June 1988 to November 1988.

Error bars have been ommited for clarity. Data derived from table 2.5.1 and 2.5.2.


S. pistillata
Egg
Testes
Egg and testes (µm)
300
200
100
0
J F M A M J J A S O N D
Month

A


E. gemmacea
Egg
Testes
Egg and testes (µm)
300
200
100
0
J F M A M J J A S O N D
Month

B

Attachment to the bottom of the aquarium tank took place within 2-3 days of liberation and skeletal elements were observed 6 days later (Fig. 2.5.4).

E. gemmacea is again a protogynous hermaphrodite (Fig. 2.5.5). It has a very short reproductive season (Table 2.5.2; Fig. 2.5.2B). Small eggs of 50 μm diameter were first observed in June, and these increased to a maximum of 186 μm in November. Partial spawning was observed at the end of October and presumably continued into November , since by December the ovaries were absent.
Development of the testes began in August, and these increased progressively in size until November. By December the testes were absent. No planulae of this species were observed.

2.5.4 DISCUSSION

In ***S. pistillata*** gonads are found in the polyps throughout the year at the study site. Similar results were obtained for this species at Yanbu to the north of Jeddah (Fadlallah and Lindo, 1988) where there were 2 cycles of oogenesis and one cycle of spermatogenesis. At Eilat at the North of the Red Sea, gonads were only present in the months of July to January. (Rinkevich and Loya, 1979 a,b).

In the Red Sea, north-south gradients in temperature appear to influence the timing of the reproductive cycle. Thus at Jizan, in the south, ***S. pistillata*** began oogenesis in April (Sofyani, 1987) whilst at Eilat in the north, oogenesis did not begin until July.

The onset of oogenesis in May at the study site coincided with an increase in seawater temperature (Fig.3.4.1). Mature eggs were found in November and December, and planulae were first observed in December. The reduction in the size of the eggs observed in January and February (Fig.2.5.2A) is probably due to the fertilisation of the first maturing eggs, leaving the slower or later maturing eggs to continue in growth until April. Planulae were only observed in December and January and so it is possible that the eggs observed after this were later reabsorbed. In the northern Red Sea, Rinkevich and Loya (1979b) observed that planulation lasted from January to July. Harriott (1985) pointed out that winter planulation was common in pocilloporid corals and correlated this with lower light levels in the surface waters.

The maximum swimming phase of the planulae lasted only three days,

whereas Rinkevich and Loya (1979b) found that they would defer settlement for up to 35 days, enabling the species to be distributed over long distances (Jokiel 1985 ; Richmond and Jokiel, 1984).

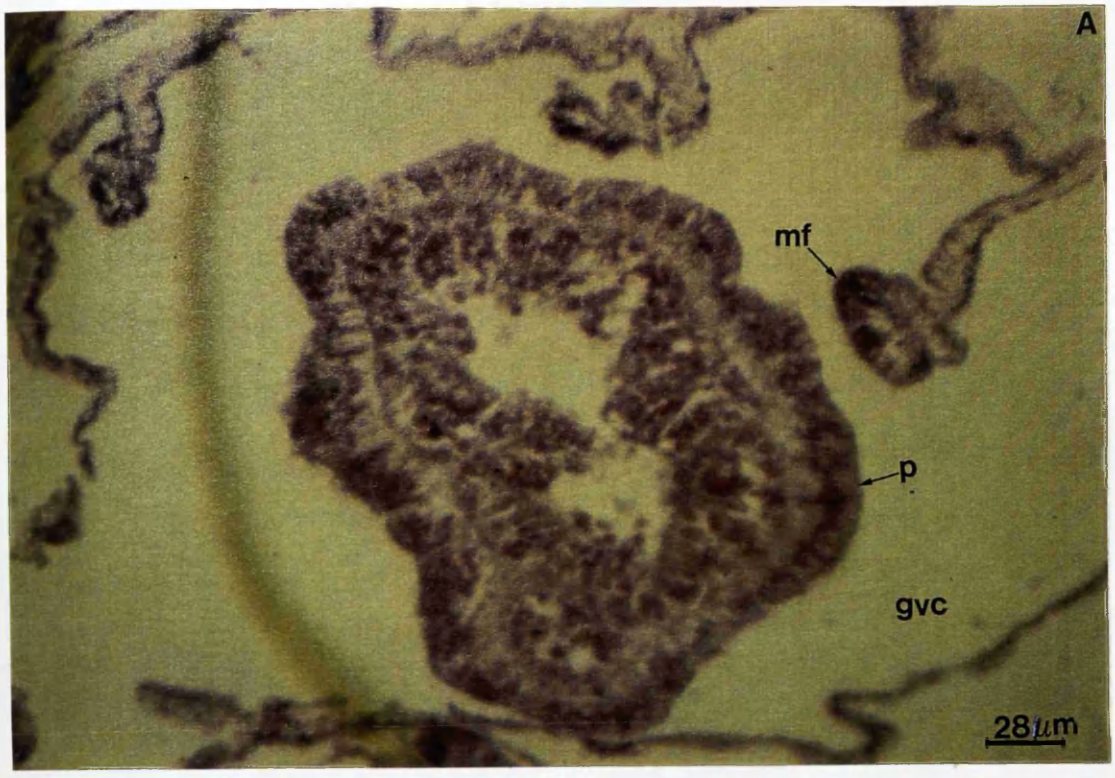
E. gemmacea has a much reduced reproductive season. However gonad development again began in early Summer associated with the increase in seawater temperature with maturation being reached in November. All species of faviid corals appear to share similar patterns of reproduction (Kojis and Quinn, 1981 and 1982; Wyers, 1985; Willis ***et al,*** 1985).

Fig. 2.5.3.

S. pistillata

(A) Cross- section through the polyp showing early stage of planula (p) in the gastrovascular cavity (gvc.); mf., mesenterial filament.

(B) Longitudinal section of coral polyp during December 1989, showing mature planula (p) with mesenterial filament (mf).. Note : the planula occupies most of the central cavity and was about to leave through the mouth (mo).


A
mf
p
gvc
28µm

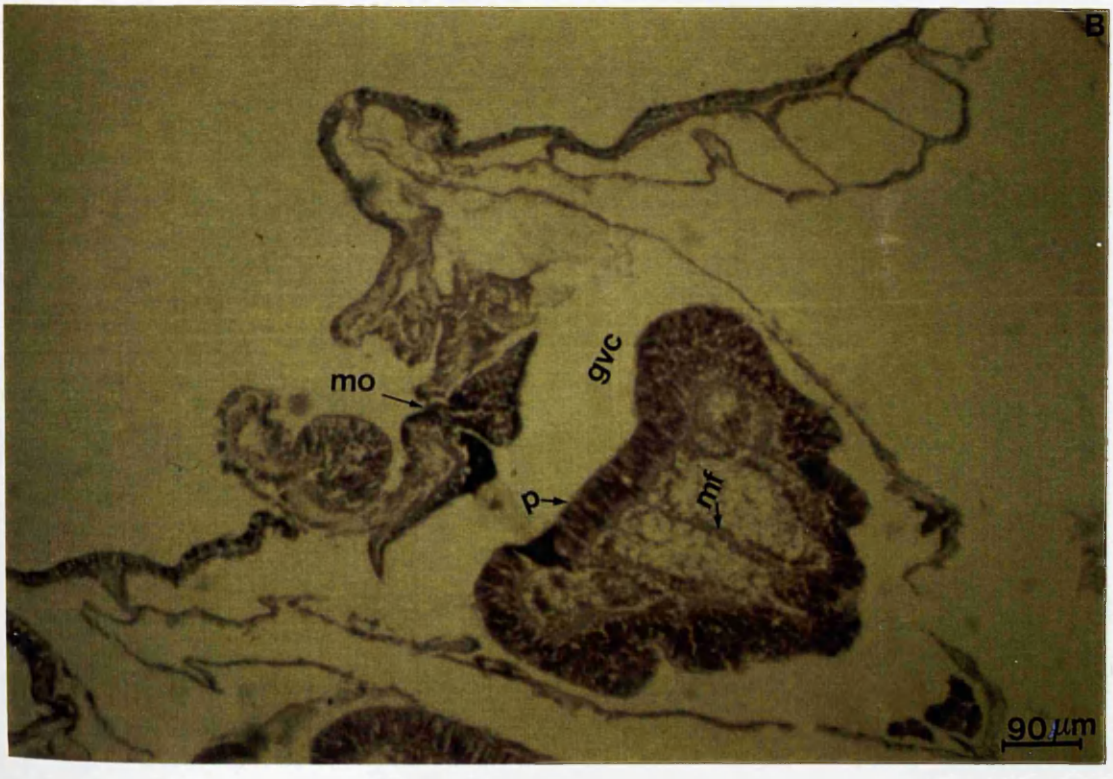

B
mo
gvc
p
mf
90µm

Fig. 2.5.4. Newly settled planula on the bottom of the aquarium, showing primary and secondary septa.

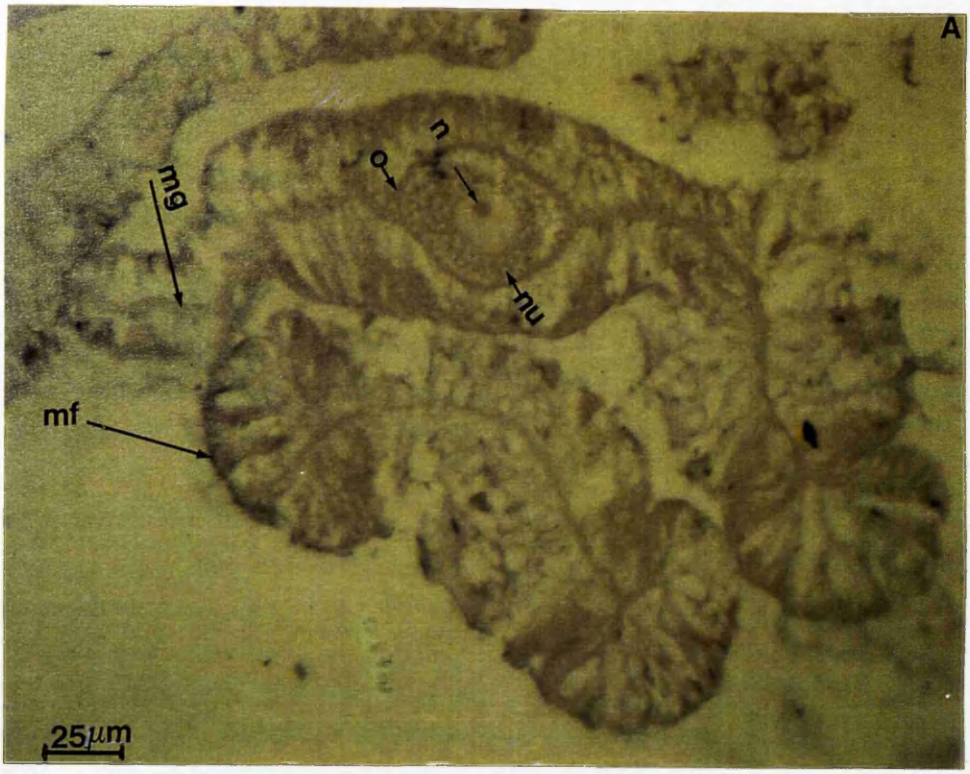

mo
sep

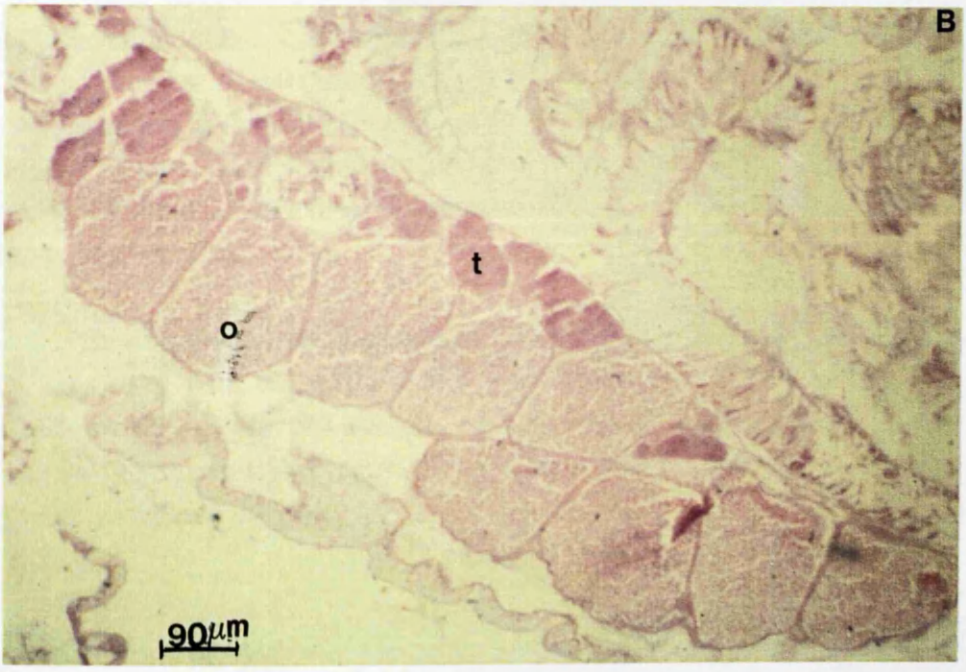
Fig. 2.5.5.

E. gemmacea

(A) Oocyte during June 1988 in a cross-section of polyp, showing the location of oocyte(o) in the mesoglea (mg) of the mesenterial filament (mf.) nu., nucleus ; n.;. nucleolus.

(B) Gonad during October 1988 in longitudinal section , showing ovaries (o) and testes (t).


A
mg
o
n
mu
mf
25μm


B
t
o
90μm

CHAPTER III

3. DISTRIBUTION OF *STYLOPHORA PISTILLATA* AND *ECHINOPORA GEMMACEA* AT JEDDAH.

3.1 INTRODUCTION

Many different ecological factors affect the biology and distribution of corals. With increase in temperature there is an increase in the rate of respiration, of photosynthesis by the zooxanthellae and the rate of calcification of the skeleton (Jacques ***et al***, 1983). The ratio of photosynthesis to respiration (P/R ratio), in Hawaiian corals decreases as temperature increases (Coles and Jokiel, 1977). At temperatures above environmental norms corals expel their zooxanthellae and become bleached (Marcus and Thorhaugh, 1981).

Salinity has a direct effect on the rate of coral growth (Squires, 1962). At salinities below 20‰ and above 40‰ ***Porites*** spp. expel their zooxanthellae and die (Marcus and Thorhaugh, 1981), an observation corroborated by field observations of coral bleaching following post-hurricane decrease in salinity resulting from fresh water runoff from the land (Goreau, 1964).

Water turbidity due to suspended sediments decreases light penetration, reducing the depth of the photic zone. This in turn results in an increase in respiration rate and a reduction of the rate of photosynthesis (Abdel-Salam and Porter, 1988), causing bleaching and death of corals, particularly in deeper water (Rogers, 1979). Deposition of suspended sediments also prevents the settlement of planula larvae (Fadlallah, 1983), decreases the growth rate (Dodge ***et al***, 1974) and increases coral mortality (Brown ***et al***, 1990).

Environmental factors such as temperature, salinity, turbidity and light might also vary with depth on a reef and with season. For this reason, the distribution of ***S. pistillata*** and ***E. gemmacea*** was investigated on a shallow fringing reef at Sharm Ubhur, near Jeddah and the main environmental factors were monitored throughout the year.

3.2. GENERAL DESCRIPTION OF THE RED SEA INSHORE ENVIRONMENT

The Red Sea is a long narrow basin extending for 1932 km in a NNW to SSE direction from the Sinai Peninsula at the north to Perim Island, (Fig. 3.1). The surface water temperature increases from north to south. The extreme ranges are from 22°C in winter in the north to 31°C in summer in the south (Edwards, 1987). The mean annual surface temperature in the north varies from 24.5 to 25.5°C and in the south from 28.4 to 28.7°C (Tunnell, 1963).

The salinity is generally higher than in other open oceans, increasing from the south to the north. Values of 38‰ at 17°N, 39‰ at 22°N and 40.5‰ at the entrance to the northern gulfs were recorded by Edwards (1987). These high salinities result from evaporation, upwelling and the extremely limited freshwater runoff from the land (Dubach, 1964).

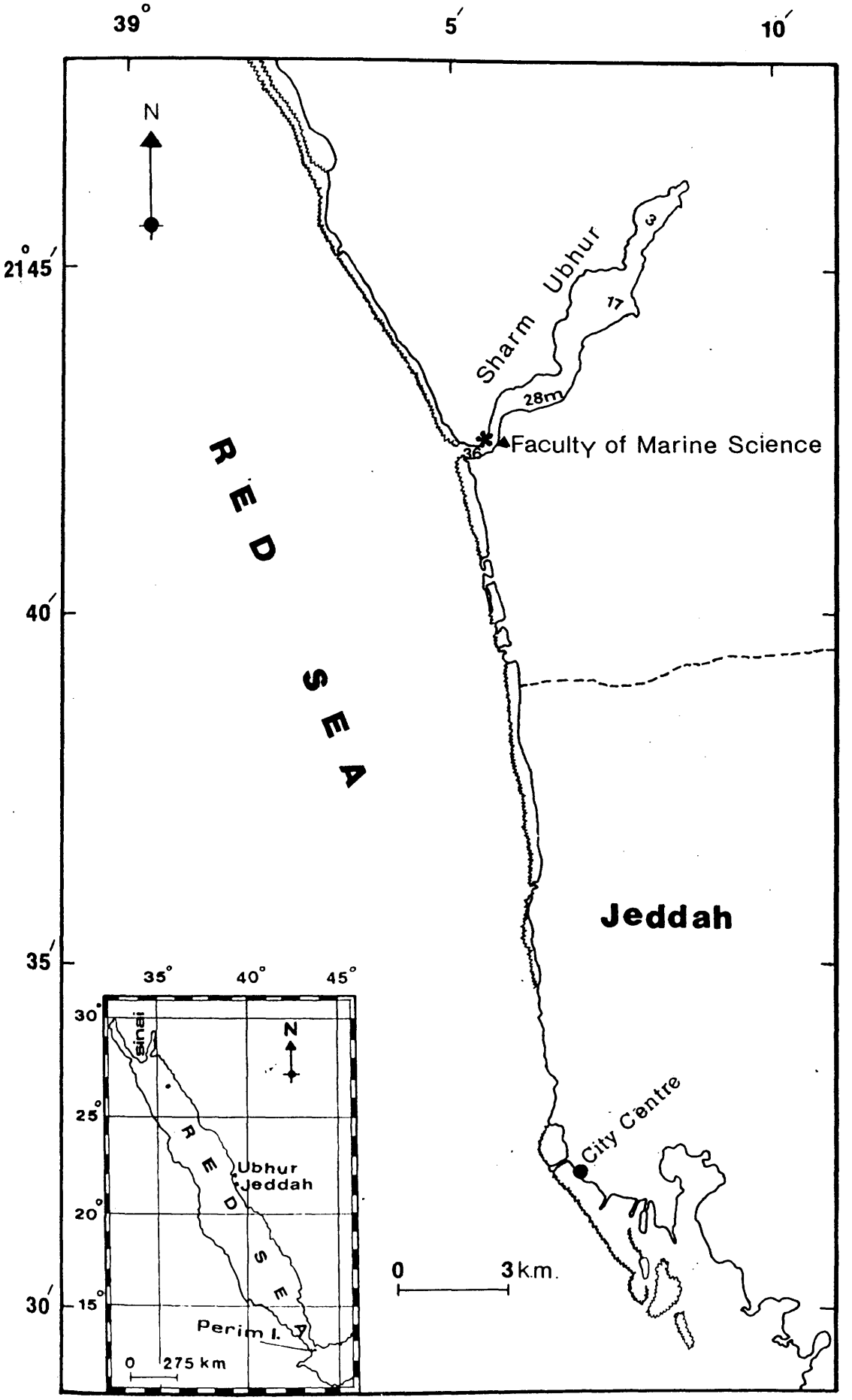
Because the Red Sea is partially enclosed, the tides are not affected by the tides of the Indian Ocean. High tide at the north coincides with low tide in the south, and vice versa. The mean tide range is from approx. 0.6 m near the entrance to the northern gulfs to approx. 0.9 m in the south. (Edwards, 1987).

The wind system is relatively simple. During the summer months, the wind blows from a N or NW direction throughout the length of the Red Sea. In the winter months, they blow from the same direction in the northern half, whilst they blow from the opposite direction in the southern half (Edwards, 1987; Morcos, 1970).

Generally, the water is well illuminated from high solar radiation coupled with very little cloud cover (Edwards 1987). In addition light penetration is high because of low suspended sediment loads (Bemert and Ormond, 1981).

Shallow inshore areas show development of coral reefs along the full length of the Red Sea, typically as fringing reefs, which are occasionally interrupted by creeks (sharm) or bays, or as offshore patch-reefs.

Fig.3.3.1. Red Sea map and location of Sharm Ubhur which is north of Jeddah city. The study site is marked as (*) at the entrance of Sharm Ubhur.


39°
5′
10′
N
21°45′
Sharm Ubhur
3
7
28m
36
Faculty of Marine Science
RED SEA
40′
Jeddah
35′
35°
40°
45°
30°
25°
20°
15°
Sinai
N
RED SEA
Ubhur
Jeddah
Perim I.
0 275 km
City Centre
0 3 km.
30′

3.3 STUDY SITE

The study site selected was within the creek of Sharm Ubhur, 35 km north of Jeddah. The Sharm runs in a SW-NE direction for about 9.3 km and has an average width of about 500 m (Fig. 3.1). The entrance to the Sharm is about 36 m deep and the depth decreases gradually to 3 m at it northernmost extremity. The lower reaches have relatively undisturbed fringing reefs. An area of reef was chosen for study on the northern side, just within the entrance to the Sharm (Fig. 3.2.). Here, the reef edge occurs in about 1 m of water and the reef front descends steeply to the sand at the base of the channel. The distribution of ***S. pistillata*** and ***E. gemmacea*** was determined from a transect line laid from the shore to a depth of 10 m.

3.3.1 METHODS

A transect line 10 m in length and marked at intervals of 2 m was used and laid out across the reef normal to the shoreline. Quadrats made from aluminium and with a side of 2 m were placed sequentially on either side of the line at intervals of 2 m. Water depth was measured with a SCUBA divers depth gauge. The number of coral species in each quadrat and the percentage bottom cover was recorded on a plastic board whilst underwater.

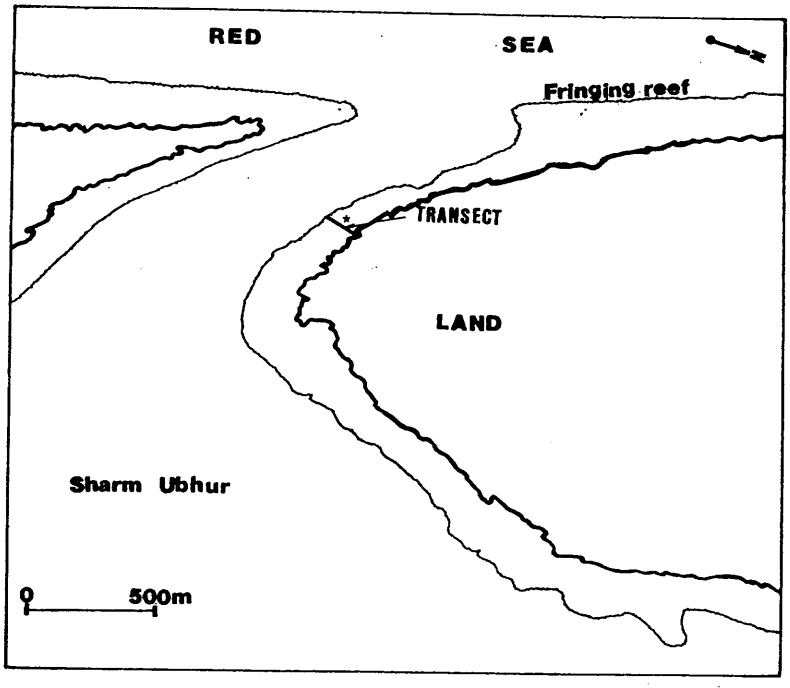
3.3.2 RESULTS

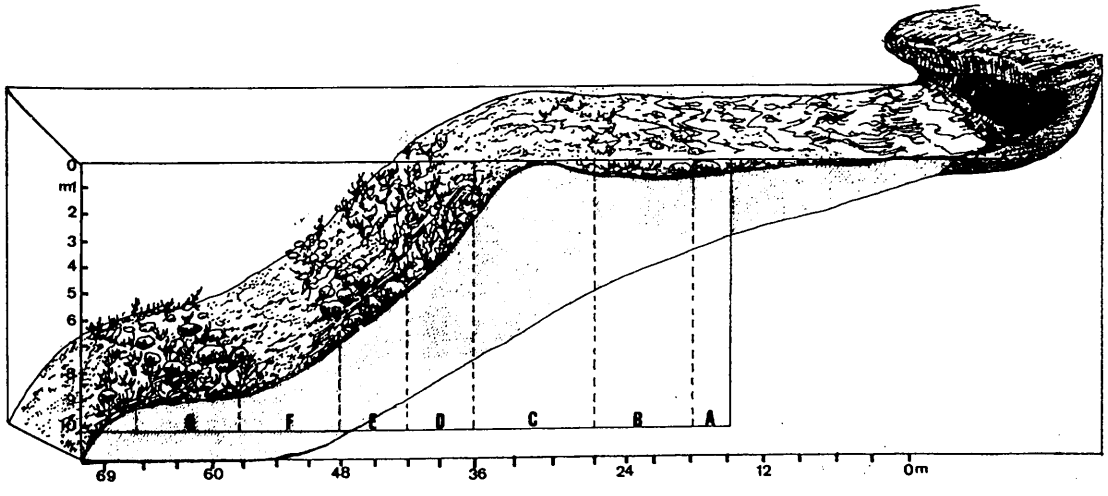
Reef Flat

The inshore zone occupying the first 15 m from the shore line was characterised by bare rock and dead coral fragments (Fig. 3.3). The next zone, Zone A was dominated by ***Stylophora pistillata*** with a percentage cover of approximately 35%. The colonies of this species were round with clustered thick branches. Other genera were represented by ***Porites*** spp. ***Goniastrea*** spp. and ***Pocillopora*** spp. each occupying about 17% of the bottom cover. Zone B which ran to the reef edge, which was about 33 m from shore, was dominated by mixed corals including ***Pocillopora*** spp. ***Goniastrea*** spp. and ***Platygyra*** spp. ***Stylophora pistillata*** was less common, accounting for about 12% of bottom cover. ***Echinopora gemmacea*** was not recorded on the reef flat. Zone C was the reef edge. This was devoid of living corals and was characterised by coral skeletons overgrown by algae.

Fig. 3.3.2. Study site at the entrance of sharm Ubhur, showing the study area (*) and the transect location.

Fig.3.3.3. North-East section through fringing reef at the study site,showing details of the bottom characteristics from 1m. to 10m. depth.


RED
SEA
Fringing reef
TRANSECT
LAND
Sharm Ubhur
0
500m


0
m
2
3
4
5
6
G
F
E
D
C
B
A
69
60
48
36
24
12
0m

Reef Slope

Zone D at a depth of between 2 and 5 m was the richest area of living coral, dominated by ***Pocillopora*** spp. (25%), ***Acropora*** spp. (11%) and ***Fungia*** spp. (11%). ***S. pistillata*** accounted for only 2% whilst ***E. gemmacea*** accounted for 5%.

Zone E at a depth of 5 to 7.5 m was characterised by sand patches with few coral genera. ***Pocillopora*** spp. accounted for 30%, ***Favites*** spp. 17%, ***S. pistillata*** 8% and ***E. gemmacea*** 4%.

At Zone F , from 7.5 to 9 m depth, the gradient was more gentle and the floor was of sand with no coral colonies. Zone G is a terrace-like reef at a depth of 9 to 10 m. This reef area was dominated by ***E. gemmacea*** which increased from 8% at the uppermost part to 27% at its lowermost end. ***S. pistillata*** accounted for only 5% cover at this zone and was represented by open-branched colonies with slender finger-like branches. (Fig 2.1.A). Below zone G coral growth terminates and there is a sand slope to a bottom depth of 30 m.

3.4 ENVIRONMENTAL FACTORS AT THE STUDY SITE

3.4.1 METHODS

A) Temperature:

Water temperature was measured using two maximum/minimum thermometers. These were attached to a piece of iron bar and hidden between coral colonies at a depth of 3 m. Readings were taken at intervals of one month, from April 1988 to January 1990. In addition summer and winter measurements of temperature at 10m were made in the months of July 1989 and January 1990. The mean monthly temperature was calculated as the average between the mean maximum and minimum temperature for each month.

B) Salinity:

Salinity of the seawater was measured monthly on samples of surface water, from February 1989 to January 1990, using a hand-held salinity refractometer (Atago Co. Ltd) which could be read to the nearest 1.0‰.

C) Sedimentation:

A set of three sediment traps was set-up at a depth of 3 m on the study site. The traps comprised plastic tubes with an internal diameter of 8 cm. They were secured with rubber bands to vertical iron rods driven into the coral rock. The traps were removed monthly from April 1988 to January 1990. After removal of macroscopic organisms, the seawater was decanted and the sediments washed with distilled water. The sediments from the 3 traps at 3m were combined and dried at 60°C for 48 hours before weighing to the nearest 0.1 mg on a Precisa 120A balance.

Grain size analysis was carried out in the department of Marine Geology, Faculty of Marine Science, King Adbulaziz University, using one-phi (Ø) interval sieves. (A total of 6 sieves with a mesh size from 1 mm to 0.063 mm). The fractions in each size grade were weighed. Then the cumulative percentages were calculated and plotted on probability scale graph paper. The phi values for 16Ø, 50Ø and 84Ø were read off the curve, added together and divided by 3 to obtain the mean grain size following the method of Folk and Word (1957).

D) Light

Underwater Light: Underwater down-dwelling irradiance was measured with a quantum sensor with cosine collector (Skye Instruments type SKP200) mounted vertically on a concrete block connected by underwater cable to a hand held meter (Skye Instruments, SKP215) on a moored boat. The output from the meter was recorded on a Teckman Model TE850 battery-operated chart recorder, set to a chart speed of 2 $cm.h^{-1}$. A variable capacitor was connected across the input leads to the recorder to dampen out some of the high frequency oscillation in light input caused by surface movement of the water. The quantum sensor measures Photosynthetically Active Radiation (P.A.R.) with wavelengths between 400 and 700 nm.

Light was measured over a complete day at monthly intervals from August 1989 to July 1990. On the day before measurements were taken, the output on the chart recorder was calibrated using a surface light reading. On the following day at 5.00 am, before sunrise, a small boat was moored adjacent to the concrete block in a position which ensured that its shadow would not fall upon the sensor below. The sensor was then attached to the concrete block, and the chart recorder switched on. Recordings of underwater light were made until sunset.

The monthly readings were taken with the sensor at a water depth of 3 m.

In addition light recordings were made at a depth of 1 m and 10 m in July 1989 (summer) and January 1990 (winter). Because of the climatic conditions at Jeddah, the majority of the readings were made on days in which the sky was free of clouds. In order to evaluate the effect of cloud cover on underwater light, a recording was also made at a depth of 3 m on 10th December 1989 when the sky was overcast.

3.4.2 RESULTS

A) Temperature.

The mean monthly temperature together with the mean maximum and minimum temperatures for each month are shown in Table 3.4.1 and Fig. 3.4.1. The lowest minimum temperature was 24.8°C in March 1989 and the highest maximum was 32.0°C in July to September 1989 and August to October 1990.

The lowest monthly average was 25.5°C in March 1989 and the highest was 31.0°C in July and August 1989. The mean difference between the maximum and minimum readings was 1.9°C, with no seasonal trend. The annual range of monthly mean temperature was between 25.5 and 31.0°C, a difference of 5.5°C. The mean temperature at 10 m was 30.0°C and 25.0°C in July 1989 and in January 1990 respectively.

B) Salinity

Salinity values ranged from a minimum of 39.0‰ to a maximum of 40.5‰ (Table 3.4.1; Fig. 3.4.2.), the lowest values occurring in the first half of the year and the slightly higher values in the second half.

C) Sedimentation

The average monthly sedimentation rates and mean grain size of the sediments are shown in Table 3.4.1 and Figs. 3.4.3 and 3.4.4). The rates of sedimentation were very variable ranging from 0.55 to 20.81 mg. $cm^{-2}.d^{-1}$. Exceptionally high rates of from 7.73 to 20.81 $mg.cm^{-2}.d^{-1}$ were recorded in the months of July, November and December 1988, and September 1989. In the remaining months sedimentation rates ranged only from 0.55 to 3.33 $mg.cm^{-2}.d^{-1}$, with a mean for these months of 1.63 ± 0.80 (s.d.)

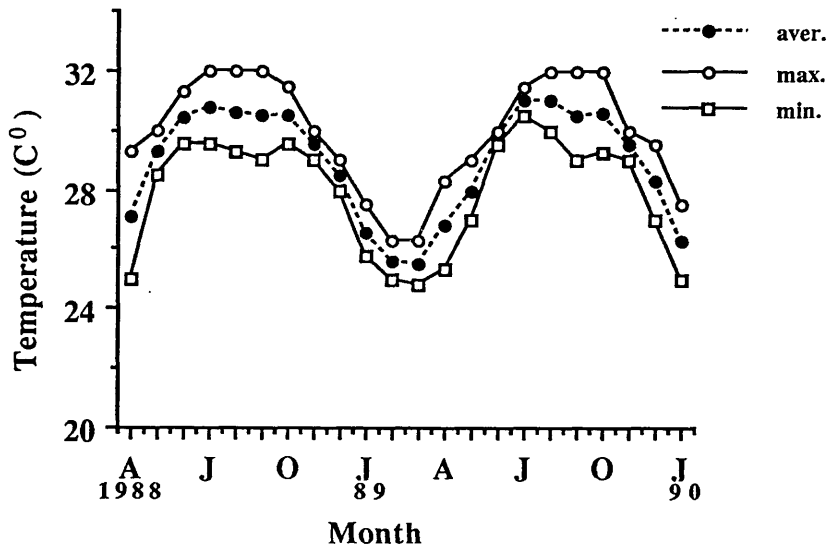
Mean grain size varied very little during the sampling period, ranging from 2.1 to 3.3 Ø, all falling within the fine and medium sand classification.

Table 3.4.1 Physical parameters from April 1988 to January 1990, at study site.

Month	Temperature °C			Sediments		Salinity
	Ave	Max	Min	Rate $mg.cm^{-2}.d^{-1}$	Grain Size Ø	‰
1988						
April	27.1	29.3	25.0	3.33	2.5	no record
May	29.3	30.0	28.5	2.29	2.8	"
June	30.4	31.3	29.5	1.44	2.6	"
July	30.8	32.0	29.5	20.81	2.6	"
August	30.6	32.0	29.3	2.13	2.3	"
September	30.5	32.0	29.0	2.57	2.5	"
October	30.5	31.5	29.5	2.74	2.9	"
November	29.5	30.0	28.0	10.52	2.5	"
December	28.5	29.0	28.0	10.52	2.5	"
1989						
January	26.6	27.5	25.8	1.68	2.3	"
February	25.6	26.3	25.0	1.0	2.1	39.5
March	25.5	26.3	24.8	0.77	2.3	39.5
April	26.8	28.3	25.3	1.23	2.5	39.0
May	28.0	29.0	27.0	no record	-	39.0
June	29.8	30.0	29.5	1.87	2.6	39.5
July	31.0	31.0	30.5	1.0	2.4	40.0
August	31.0	32.0	30.0	1.48	3.2	40.5
September	30.5	32.0	29.0	11.47	3.2	39.5
October	30.6	32.0	29.3	0.55	3.0	40.0
November	29.5	30.0	29.0	1.33	3.1	40.0
December	28.3	29.0	27.0	0.68	3.3	40.0
1990						
January	26.2	27.0	25.0	1.19	2.7	40.0

Fig. 3.4.1. Variation of mean monthly max.-min. and average sea water temperature(^{0}C) at study station in Sharm Ubhur at 3m depth , measured with max.-min. thermometer from August 1988 to January 1990.

Fig. 3.4.2. Monthly variation of surface sea water salinity (‰) at study station in Sharm Ubhur , from February 1989 to January 1990


aver.
max.
min.
Temperature (C⁰)
32
28
24
20
A
1988
J
O
J
89
A
J
O
J
90
Month

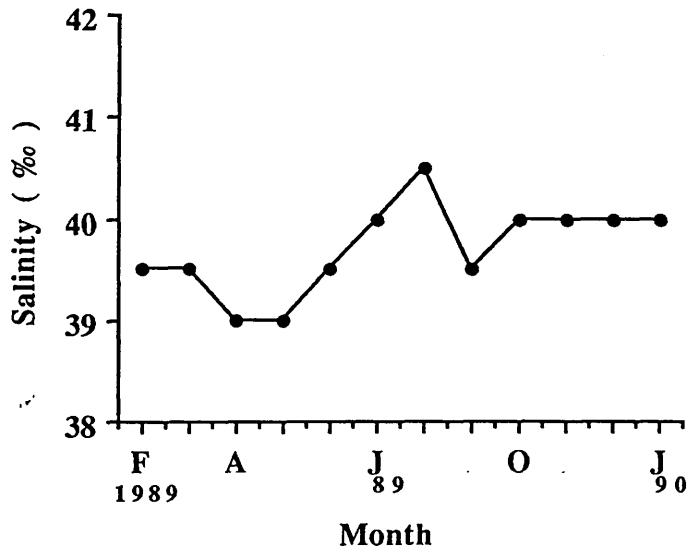
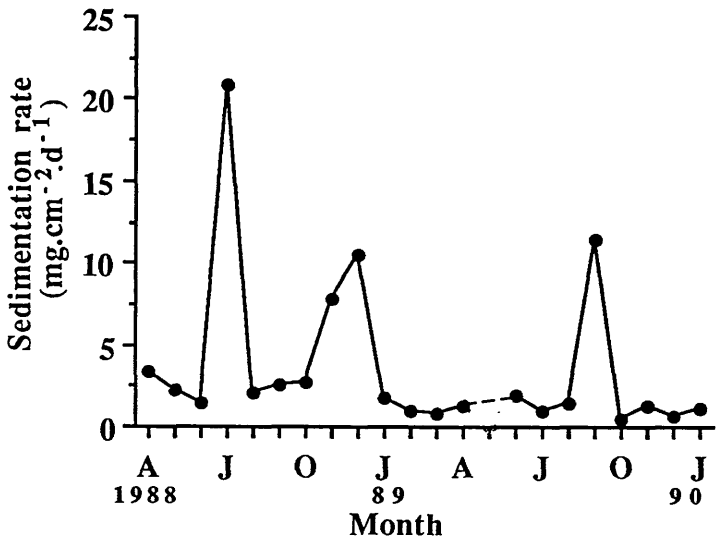
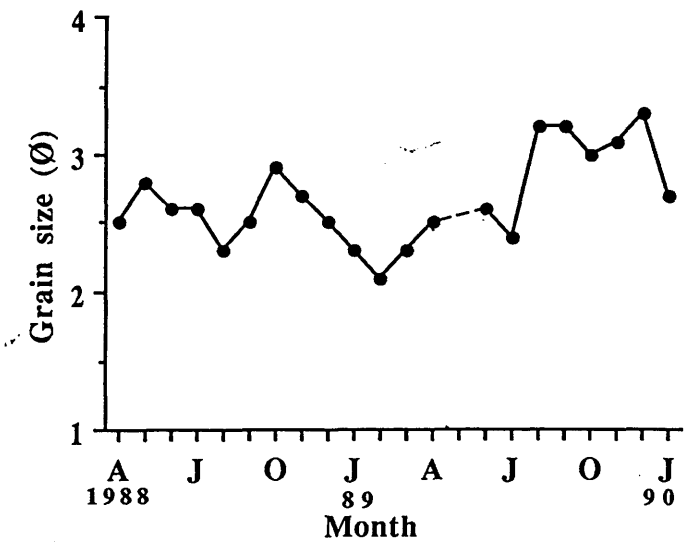

Salinity (‰)
42
41
40
39
38
F
1989
A
J
89
O
J
90
Month

Fig.3.4.3. Average monthly variation of sedimentation rate (mg. $cm^{-2}.d^{-1}$.) from three traps at 3m depth at the study site in Sharm Ubhur, from April 1988 to January 1990. No record in May 1989.

Fig.3.4.4. Monthly variation of the mean grain size (Ø) for the sediments collected from traps at 3m. depth at the study site in Sharm Ubhur, from April, 1988 to January 1990 . No record for May 1989.


Sedimentation rate
(mg.cm-2.d-1)
25
20
15
10
5
0
A
J
O
J
A
J
O
J
1988
89
90
Month


Grain size (Ø)
4
3
2
1
A
J
O
J
A
J
O
J
1988
89
90
Month

D) Light

An example of the chart recorder trace of a daily light curve at 3m is shown in Fig. 3.4.5. Wind action between approx. 8.00 hours and 16.00 hours produced high frequency oscillations in irradiance, despite damping by the capacitor. An eyefitted curve was drawn through the centre points of the noise on the trace and used to determine light levels at 15 min intervals during the day. By summing these values a value for the integrated daily irradiance was obtained . The record shown in Fig. 3.4.5 is typical of the majority of those obtained and shows the regular sine wave curve characteristic of light transmission from a cloud-free sky. All recordings, with the exception of that made on 10 December 1989, were made under similar cloudless conditions.

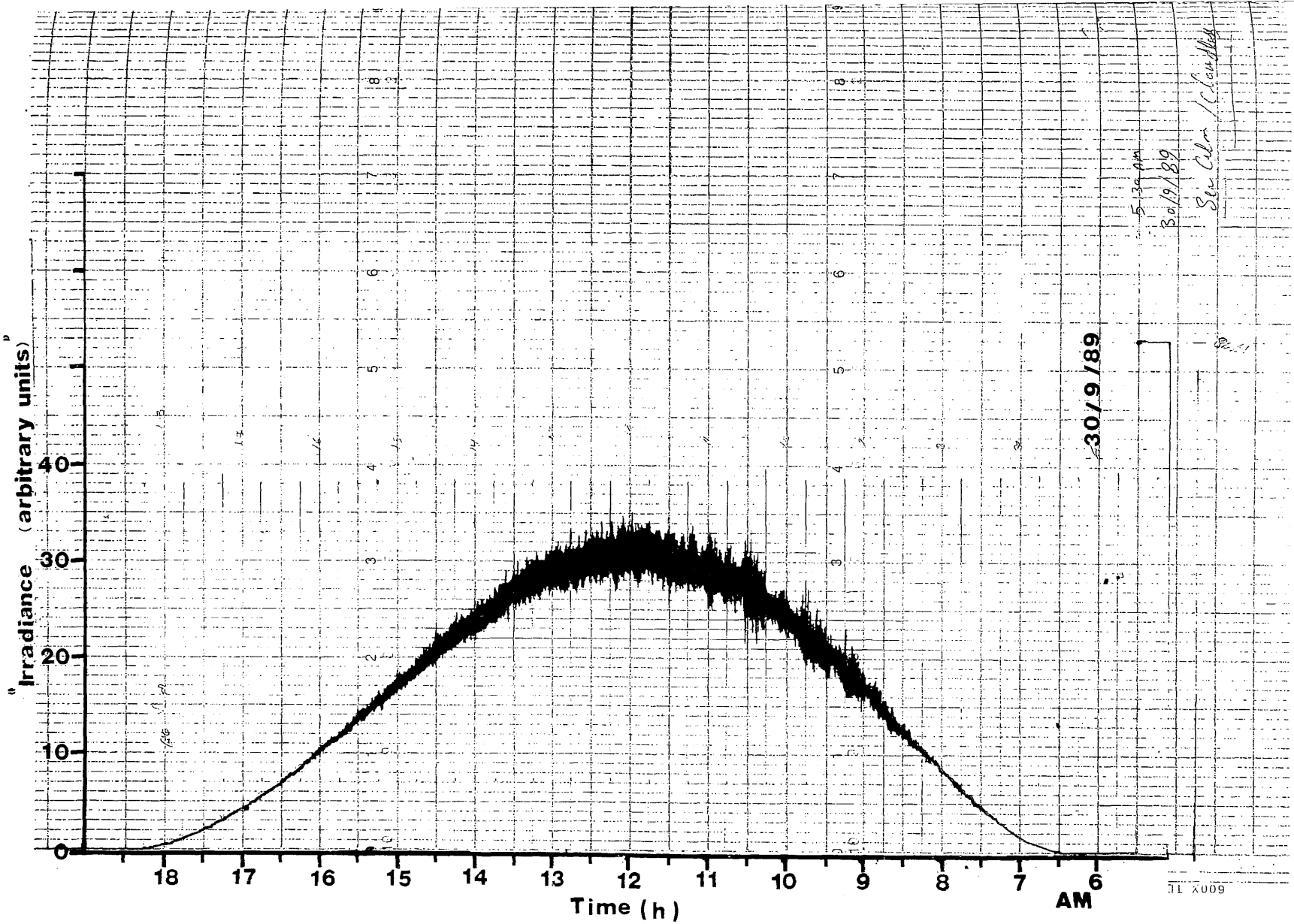
Annual variation in irradiance at 3 m on cloudless days.

The annual cycle of variation in daily integrated light, maximum P.A.R. and no. of hours of light recorded are shown in Table 3.4.2 and Figs 3.4.6 - 3.4.8. The number of hours of sunlight reached a minimum of 10.5 in December 1989 and a maximum of 13.75 in June 1990. The P.A.R. of the daily light curve was at a maximum in June 1990 with a value of 1212 μE. m.$^{-2}$s^{-1} and at a minimum at the end of November 1989 when the value was 727 μE. m.$^{-2}$s^{-1} . The integrated daily P.A.R., resulting from variations in both hours of sunlight and maximum daily P.A.R., was at a minimum at the end of November 1989 with a value of 14.99 E .$^{-}$ m.$^{-2}$d^{-1}. The maximum value observed was in June 1990 when it was over double that of the November value, at 30.12 E.m.$^{-2}$d^{-1}.

Effect of depth on irradiance levels

Irradiance levels were measured at 1m, 3m and 10m in `winter' (end January 1990) and summer (end July 1990) (Table 3.4.3 Figs. 3.4.9 and 3.4.10). In winter the maximum P.A.R. recorded was 970 μE. m.$^{-2}$s^{-1} at 1 m, falling to 430 μE. m.$^{-2}$s^{-1} at 10m. In summer the value at 1 m was 1292 μE. m.$^{-2}$s^{-1}, compared with only 455 μE. m.$^{-2}$s^{-1} at 10m. Similarly the integrated P.A.R. was 21.55 E. m.$^{-2}$d^{-1} at 1 m in winter, falling to 8.43 E.m.$^{-2}$d^{-1} at 10m. In summer, integrated daily P.A.R. fell from 32.56 E.m.$^{-2}$d^{-1} at 1 m to 10.94 E.m.$^{-2}$d^{-1} at 10 m.

Fig.3.4.5. An example of the chart recorder trace of a daily light curve at 3m at the study site in Sharm Ubhur , measured during a cloudless day from 5:30 am to 6.30 pm. on 30th of August 1989. Notice a high frequency oscillation in an irradiance due to the wind action between 8h and 16h.


"Irradiance (arbitrary units)"
0
10
20
30
40
18
17
16
15
14
13
12
11
10
9
8
7
6
AM
Time (h)
30/9/89
5.13 pm
30/9/89
Sun Calm / Cloudless

Winter/Summer differences in P.A.R.

A comparison of the daily light curves at 3m depth between summer and winter is shown in Fig 3.4.11. Higher maximum P.A.R. values were recorded at all 3 depths in summer than in winter (Table 3.4.3). Similarly, the integrated daily P.A.R. in winter is seen to be between approx 25% and 50% lower than in summer.

Effect of overcast sky conditions on underwater light

Underwater light was measured at 3 m on 10 December 1989, an overcast day, and can be compared with the closest date on which light was recorded under cloudless conditions, (Table 3.4.2; Fig. 3.4.12). The maximum P.A.R. recorded was only 297 $\mu E.\ m.^{-2}s^{-1}$ compared with a value of 727 $\mu E.m.^{-2}s^{-1}$ on the cloud-free day of 30 November. Similarly the daily integrated P.A.R. at 6.98 $E.m.^{-2}d^{-1}$ was only about 46% of the value of 14.99 $E.m.^{-2}d^{-1}$ on the cloudless day.

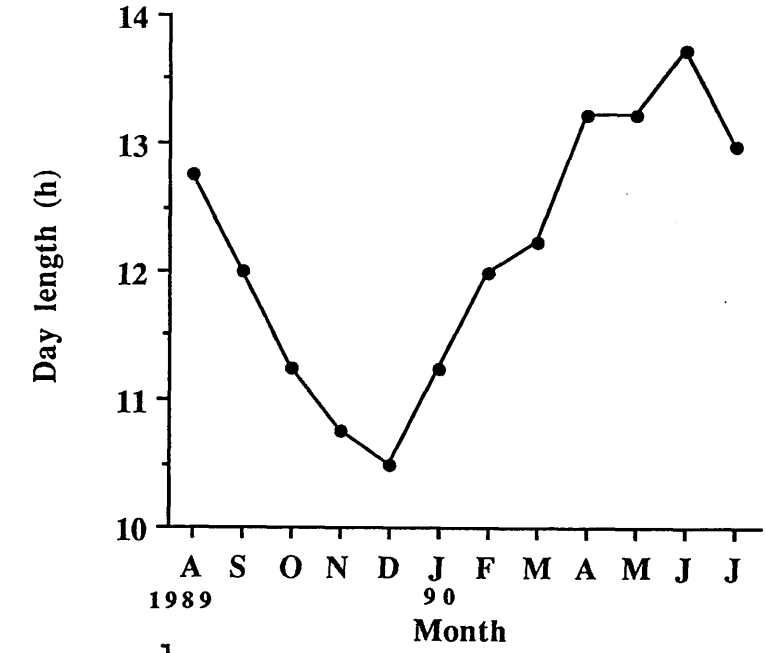
Table 3.4.2 Daily integrated values of photosynthetically active radiation P.A.R., daily maximum P.A.R. values and number of hours of daylight at the study site, recorded at 3 metre depth from August 1989 to July 1990.

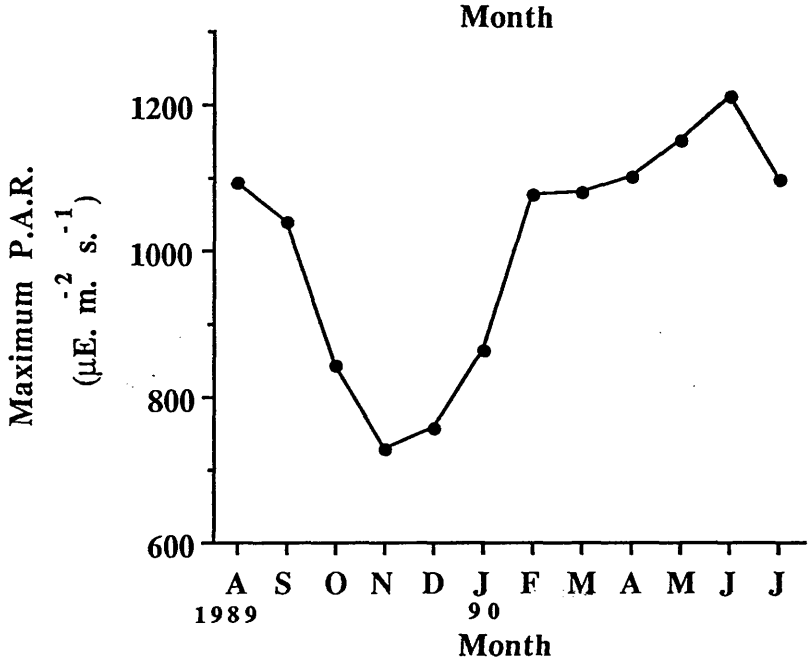
Date	Hours of sunlight (h)	Max P.A.R. ($\mu E.m.^{-2}.s^{-1}$)	Integrated daily (P.A.R. $E.m.^{-2}.d^{-1}$)
Cloudless days			
1989			
30 August	12.75	1093	26.25
30 September	12.0	1040	23.53
30 October	11.25	843	18.93
30 November	10.75	726	14.99
28 December	10.5	756	15.5
1990			
26 January	11.25	864	18.06
28 February	12.0	1080	24.67
30 March	12.25	1081	25.85
30 April	13.25	1104	26.45
30 May	13.25	1152	28.3
28 June	13.75	1212	30.12
30 July	13.0	1101	26.72
Overcast day			
1989			
10 December	10.75	297	6.98

Fig. 3.4.6. Annual cycle of variation in the number of sunlight hours, recorded at 3m. depth in Sharm Ubhur from August 1989 to July 1990.

Fig.3.4.7. Annual variation of maximum photosynthetically active radiation $\mu E.m^{-2}.s^{-1}$. (P.A.R.) of the daily light, recorded at noon time (12h) at 3m. depth in the Sharm Ubhur from August 1989 to July 1990.

Fig.3.4.8. Variation of daily integrated photosynthetically active radiation $E.m^{-2}.d^{-1}$ at 3m. depth, recorded at the sampling site in Sharm Ubhur from August, 1989 to July, 1990.


Day length (h)
14
13
12
11
10
A S O N D J F M A M J J
1989
90
Month


Maximum P.A.R.
(µE. m.-2 s.-1)
1200
1000
800
600
A S O N D J F M A M J J
1989
90
Month

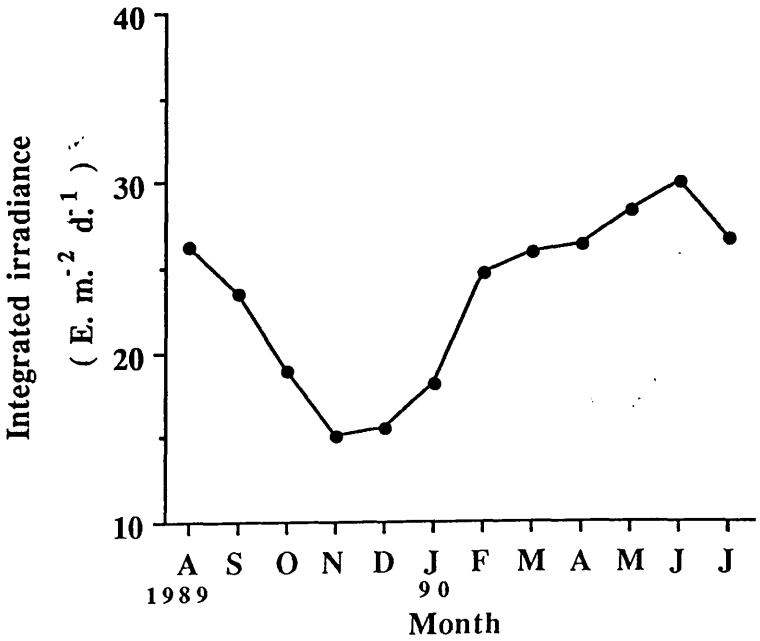

Integrated irradiance
(E. m.-2 d.-1)
40
30
20
10
A S O N D J F M A M J J
1989
90
Month

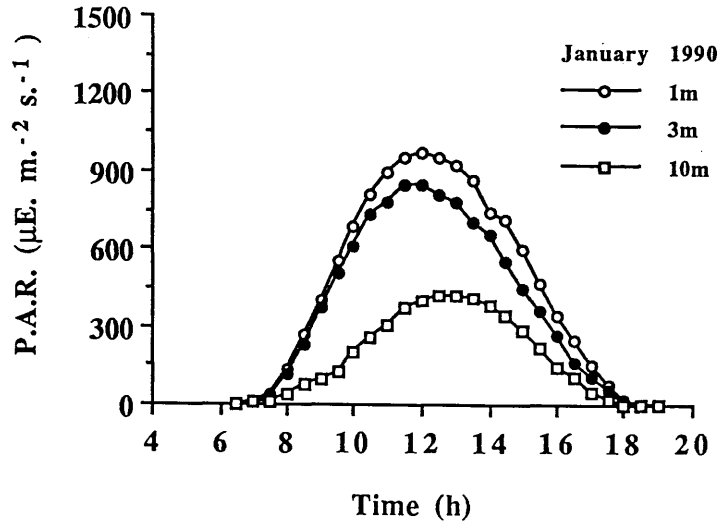
Table 3.4.3 Underwater irradiance values at the study site in Sharm Ubhur measured at depths of 1 metre, 3 metres and 10 metres in winter and summer 1990.

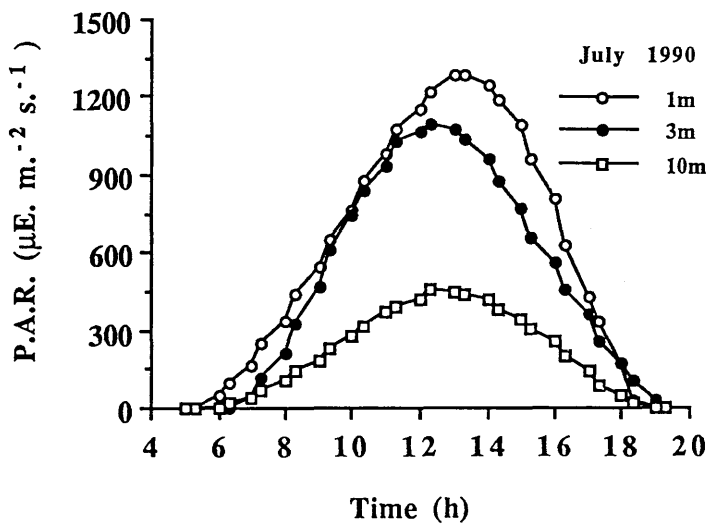
Date	Depth (m)	Hours of daylight	Max P.A.R. ($\mu E.m.^{-2}.s^{-1}$)	Integrated daily (P.A.R. $E.m.^{-2}.d^{-1}$)
Winter 1990				
25 January	1	11.25	970	21.55
26 January	3	11.25	864	18.06
24 January	10	11.0	430	8.43
Summer 1990				
1 August	1	13.25	1292	32.56
30 July	3	13.25	1101	26.72
31 July	10	12.5	455	10.94

Fig.3.4.9. Variation of photosynthetically active radiation (P A.R.) in January 1990, recorded at 1, 3 and 10 m. depth at the study area in Sharm Ubhur, showing the effect of depth on irradiance intensity.

Fig.3.4.10. Photosynthetically active radiation $\mu E.m^{-2}.s^{-1}$, measured at three different depths 1, 3 and 10m. at the study area in Sharm Ubhur during July 1990 displaying variations on light intensity with depth at the study area.

Fig.3.4.11. Differences in photosynthetically active radiation $\mu E.m^{-2}.s^{-1}$ at 3m depth, between January and July 1990 for the study station in Sharm Ubhur.


1500
1200
900
600
300
0
P.A.R. (µE. m.-2 s.-1)
4
6
8
10
12
14
16
18
20
Time (h)
January 1990
1m
3m
10m


1500
1200
900
600
300
0
P.A.R. (µE. m.-2 s.-1)
4
6
8
10
12
14
16
18
20
Time (h)
July 1990
1m
3m
10m

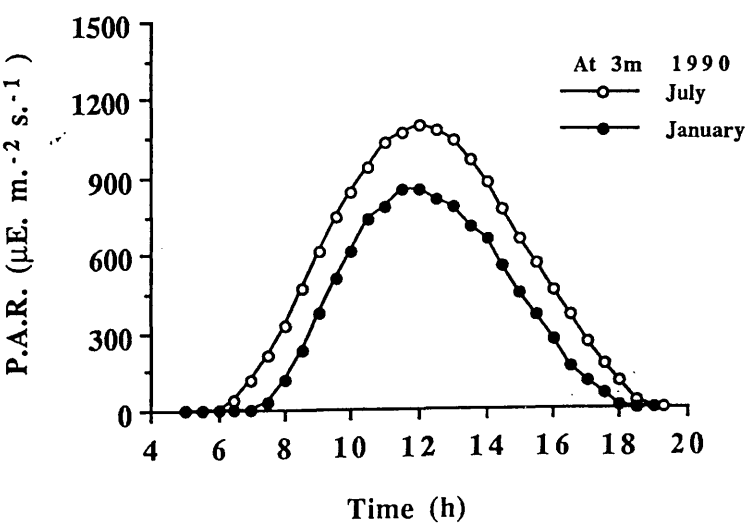
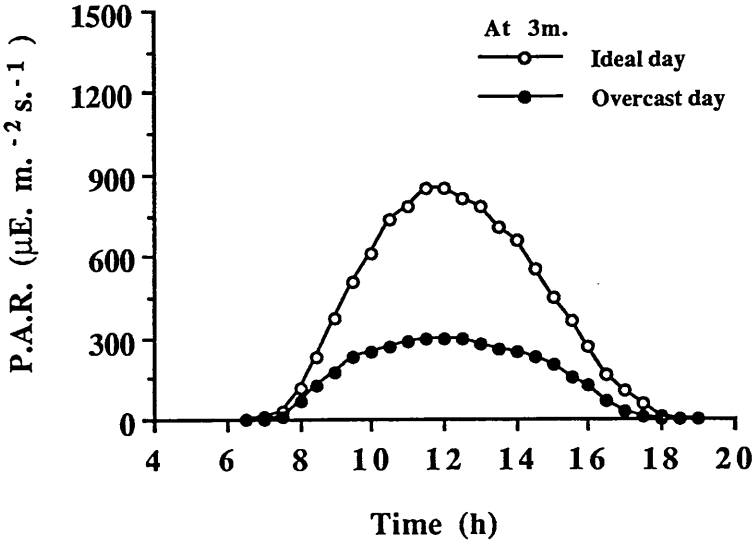

1500
1200
900
600
300
0
P.A.R. (µE. m.-2 s.-1)
4
6
8
10
12
14
16
18
20
Time (h)
At 3m 1990
July
January

Fig. 3.4.12. Variation in photosynthetically active radiation $\mu E.m^{-2}.s^{-1}$ measured at 3m. depth for the study site in Sharm Ubhur , showing the effect of sky conditions on underwater light. An ideal day and an overcast day were recorded during 30th November 1989 and 10th December 1989 respectively.


At 3m.
Ideal day
Overcast day
P.A.R. (μE. m.-2 s.-1)
1500
1200
900
600
300
0
4
6
8
10
12
14
16
18
20
Time (h)

3.5 DISCUSSION

3.5.1 DISTRIBUTION OF *S. PISTILLATA* AND *E. GEMMACEA.*

Stylophora pistillata is a common species in the shallow waters of fringing reefs and patch reefs (Loya, 1972, Scheer and Pillai, 1983 ; Rinkevich and Loya, 1984 ; Fadlallah and Lindo, 1988). In the transect at Sharm Ubhur, it was found that the compact club-branched form of ***S. pistillata*** was very common on the reef flat, at a water depth of 1 m, where it accounted for up to 35% of the coral cover. ***S. pistillata*** gradually declined in abundance with increasing depth on the transect, and at 10 m only accounted for 5% of coral cover.

In contrast ***E. gemmacea*** was not present on the reef flat and was not encountered until the reef slope where it accounted for only about 5% of coral at a depth of 3 m. It increased in abundance to the deepest point on the transect at 10 m. At Eilat in the northern Red Sea, Loya (1972) recorded the main zone of ***E. gemmacea*** between 8 and 12 m, whilst Frick and Schumacher (1983) and Head (1987) in Sudan showed that the overall bathymetric distribution of this species was from 1 m to 85 m. Both encrusting and branching growth forms were observed . The reason for the differences in growth form in the one species is not known (Veron, 1986).

3.5.2 ENVIRONMENTAL FACTORS

The pattern of annual seawater temperature change at Sharm Ubhur is for the lowest mean temperatures (25.5°C) to occur in March whilst the maximum mean temperature of about 31°C lasts over a broad period of 3 months within the months of July to October. Edwards (1987) recorded lowest temperatures in January and February (21°C) and highest temperatures in August and September (27°C) in Eilat, whilst Fadlallah recorded similar temperatures to those at Sharm Ubhur, at Yanbu, the coldest month being February and the warmest month was September.

There is little annual variation in salinity. The increase from 39‰ to 40‰ in the summer months is probably due to surface evaporation and to the action of the north westerly winds driving the more saline water from the northern Red Sea to more southerly latitudes (Edwards 1987).

The mean sedimentation rate of 1.63 mg. $cm.^{-2}.d^{-1}$ was low and

interrupted by episodes of high sedimentation, up to 20.81 mg. $cm.^{-2}.d^{-1}$ at times of strong wind action. These values compare with 1.9 mg. $cm.^{-2}.d^{-1}$ on an open coast patch reef 15 km north of Jeddah (Sofyani, 1987). Equivalent values were recorded by Edmunds (1986) in Jamaica where the sedimentation rate was 2.45 mg. $cm.^{-2}.d^{-1}$ on the West Fore Reef and 3.39 mg. mg. $cm.^{-2}.d^{-1}$ in the lagoon site of Columbus Park.

The underwater P.A.R. data presented are the first set of in situ measurements to be made over an annual cycle. The closest data set available for comparison of those of Porter (1985) who made predictions of in situ P.A.R. from annual records of surface irradiance and occasional determinations of percentage transmission of light through the water column.

In summer the longest duration of sunlight was 13.75 hours with integrated daily irradiation at 3 m of 30.12 E. $m^{-2}.d^{-1}$, whereas in winter the day length had shortened to 10.5 hours and the integrated daily irradiation was 14.99 E. $m^{-2}.d^{-1}$. In Hawaii, and in the turbid water of the fringing reef of Coconut Island, Oahu, Davies (1991a) recorded an integrated daily irradiance value of 14.39 E. $m^{-2}.d^{-1}$ at 3 m depth.

Incident P.A.R. decreases with depth. The daily integrated P.A.R. in January 1990 at 10 m depth was only 39% of that at 1 m and in July it was only 33%. Head (1987) recorded average light levels of about 45% of surface irradiance at a depth of 10 m in other areas of the Red Sea. At Davies Reef, Australia, Oliver ***et. al.***, (1983) recorded transmission of 65% and 28% of surface light to depths of 3 m and 10 m respectively. Edmunds (1986) recorded 26.9 and 19.4% transmission of surface light to 10 m in clear water and turbid water respectively in Discovery Bay, Jamaica.

All except one of the underwater irradiance measurements were made on days which were cloudless. On the one day in December when the sky was overcast, the daily integrated P.A.R. at 3m fell to only 6.98 E. $m^{-2}.d^{-1}$, a fall of approximately 45% from values recorded on a cloud-free day. This compares with a fall to a level of 43% of cloudless day levels on an overcast day in water of 3 m depth at Oahu, Hawaii, recorded by Davies (1991a).

CHAPTER IV

4. ENERGY BUDGET : METHODS

4.1 INTRODUCTION

One of the earliest studies on coral physiology was made by Yonge and Nicholls (1932) during the Great Barrier Reef expedition. These authors reported that corals produce more oxygen than their respiration demands. However, they did not appreciate the nutritional significance of this observation. Muscatine and Hand (1958) showed that the labelled materials of photosynthetically fixed carbon were translocated from the algae to their host sea anemone ***Anthopleura elegantissima.*** Similar results were found in corals (Muscatine, 1967; Muscatine and Cernichiari, 1969,Trench, 1971b ; Crossland ***et al,*** 1980a). Kanwisher & Wainwright (1967) and Roffman (1968) in observing that the ratio of photosynthesis to respiration was greater than 1 suggested that corals may be autotrophic. Further evidence was suggested from the observation of Franzisket (1970) that corals would continue to grow in water which had been filltered to remove particulate matter, if they were exposed to sunlight.

The major photosynthetic products which were translocated, were found to be mainly glycerol and other compounds such as glucose and fumaric acid (Muscatine, 1967; Muscatine and Cernichiari, 1969; Smith ***et al,*** 1969 and Trench, 1971b).

Early studies reported that the amount of product translocated to the host was less than 50% of the total carbon fixed in photosynthesis (Muscatine and Cernichiari, 1969 ; Trench, 1971a). More recently, the translocated amount was found to be between 90 to 95% (Davies, 1984 ; Muscatine ***et al,*** 1984). These studies confirmed also that corals could meet all their energy requirements from the translocated fixed carbon and the excess would pass to the surrounding water, probably as mucolipids (Crossland ***et al,*** 1980a ; Edmunds and Davies, 1986). However, these results came from branching corals with small polyps, and it has been suggested that corals with small polyps and a high surface area to volume ratio (s:v) may be totally autotrophic whilst corals with large polyps and a low surface area to volume ratio mass depend more on zooplankton feeding (Porter, 1976). The first purpose of the present study is to construct energy budgets of the small polyp coral ***S. pistillata*** and to compare this with that of coral ***E. gemmacea***, following the methods of Davies (1984 and 1991a) and Edmunds and Davies (1986) and to make comparisons with those of previous studies. Since there are seasonal variations in sea

water temperature and light intensity (Chapter III), the second aim was to compare the energy budgets for the two species during summer and winter. Furthermore, since corals living in deeper water may have a lower photosynthetic carbon fixation rate resulting from light absorption in the water column, a further aim was to compare energy budgets of the two species living at 1 and 3 m water depth with those living at lower irradiance level at 10 m.

The methods adopted for determining the energy budget were based upon those of Davies (1984) and Edmunds and Davies (1986) . However modification and improvements to the methodology were made in the course of the study. In this chapter the complete methodology, incorporating changes to the techniques for measuring the skeletal weight of the corals, and the tissue energy contents, will be described.

4.2 METHODS

4.2.1 Nubbins preparation

All determinations were made using branch tips or "nubbins" (Birkeland 1976; Davies, 1984; Edmunds and Davies, 1986). Specimens from both species were collected from the study area. ***S. pistillata*** colonies were obtained from a depth of 1 metre, whilst ***E. gemmacea*** colonies were collected from depths of 3 metres and 10 metres. Samples were transported in shaded buckets to the laboratory. A group of 20 branch tips from each depth were cut from the colonies using an electric diamond saw (Makita model 9501B). Thereafter their bases were smoothed with a rotary grindstone and then glued onto pre-marked and weighed (30 x 30 mm) perspex tiles using cyanoacrylate glue (super glue). The tiles bearing nubbins were kept for two days in an outdoor aquarium for recovery to take place.

Finally, the tiles bearing nubbins were inserted on to perspex racks and returned to the reef to the depth at which the nubbins had been collected. On the reef the perspex racks were screwed onto cement blocks. Another shallow-water group of ***S. pistillata*** was transferred to a 10 metre site. Usually nubbins living at their collection site were left for one week, whereas the nubbins transferred to a new depth were kept for three weeks to adapt to the new habitat before measuring the individual components of the energy budget.

4.2.2 GROWTH

4.2.2.1 Buoyant Weighing Procedure

A Precisa model 120A balance was used for the buoyant weighing of the nubbins. The balance was placed on stable wooden box 39 x 25 x 30 cm with a sliding transparent door at the front. The weighing pan was a watchglass suspended directly from a hook on the bottom of the balance using 0.05 mm diameter tungsten wire. A perspex bath 8 x 33 x 25 cm was placed on the floor of the box. In order to maintain a constant water temperature in the bath, it was lined with coiled plastic tubing which was connected to a constant temperature water bath (Grant Instruments).

4.2.2.2 Principle of the Measurements.

The unit reference of each component of the energy budget was dry skeletal weight which was calculated from the buoyant weight equations of Davies (1989). The technique involves weighing the living nubbins in sea water and converting the buoyant weight to the dry weight of skeleton by the following equations.

$$\text{Dry weight of object} = \text{weight in water} \div \left(\frac{\text{density of water}}{1 - \text{density of object}} \right) \quad (1)$$

$$\text{Buoyant weight of object} = \text{weight in air} \times \left(\frac{\text{density of water}}{1 - \text{density of object}} \right) \quad (2)$$

$$\text{Density of water} = \frac{\text{weight in air - weight in water}}{\frac{\text{weight in air}}{\text{density of object}}} \quad (3)$$

$$\text{Density of object} = \frac{\text{weight in air} \times \text{density of water}}{\text{weight in air} \times \text{weight in water}} \quad (4)$$

In order to measure the density of sea water, the density of a reference weight (a piece of glass rod) must be calculated after weighing it in distilled water, using equation (4). In equation (4), the density of distilled water was obtained from Table F5-6 and FM of the CRC Handbook of Chemistry and Physics (1984). The density of sea water can be calculated from equation (3). The density of sea water can be monitored during weighings by re-weighing the reference weight.

The skeleton density of ***S. pistillata*** and ***E. gemmacea*** was obtained by removing the tissue from the skeleton. A group of ten nubbins from each species was left in a 10% solution of chlorox and sea water for two days. The skeleton was then cleaned with a water jet to remove any residual tissue. Their buoyant weights were recorded in sea water whose density was measured immediately before buoyant weighing the skeletons. Thereafter, the skeletons were rinsed in distilled water and dried to a constant weight at 60°C. The skeleton density was then calculated from equation (4). The density of the tiles was also obtained using equation (4). Since the buoyant weight of tissue affects the buoyant weight of skeleton (Davies, 1989), a correction factor was calculated for each species as follows :

The buoyant weight of a group of ten nubbins from each species was measured. Their tissue was cleaned as before with a 10% solution of chlorox and sea water. The cleaned skeleton was then buoyant weighed. The buoyant weight of cleaned skeleton was subtracted from the buoyant weight of uncleaned skeleton to obtain the buoyant weight of tissue which was then used to calculate the correction factor.

Having calculated the foregoing factors for the application of the equations in growth studies, the buoyant weights of nubbins-bearing tiles were obtained every one to two weeks during winter and summer 1989 and winter 1990. The buoyant weight of tiles can be predicted from equation (2) and subtracted from the measured buoyant weight of the nubbin-bearing tile to obtain the buoyant weight of the nubbin alone. Thereafter, the buoyant weight of the nubbin was corrected for tissue weight and converted to dry weight of skeleton using equation (1).

4.2.3 BIOMASS RELATIONSHIPS

4.2.3.1 Skeletal Weight and Dry Tissue Weight

A group of 30 nubbins from each species was buoyant weighed and then fixed in 7% formalin for 24 hours. Thereafter, the nubbins were decalcified in a 10% solution of HNO_3 and sea water. The decalcified tissue was rinsed in distilled water after all the organic matrix had been removed from the tissue with fine forceps. Finally, the tissue was dried in a pre-weighed boat at 60°C and cooled over SiO_3. The dry tissue weight was related to dry skeletal weight and expressied as mg dry tissue wt/g skeletal wt.

4.2.3.2 Skeletal Weight and Number of Zooxanthellae

10 nubbins from each species were fixed in 4% formalin for 24 hours, decalcified in a 10% solution of HNO_3 and sea water and rinsed in distilled water. The decalcified tissue was homogenised with a hand-held Potter homogeniser until the tissue was completely broken down. The contents of the homogeniser tube were centrifuged for three minutes at 4000x g. The supernatant was carefully poured off and re-centrifugated at 10 minutes at 4000x g. Thereafter, the pellet of zooxanthellae and the pellet of supernatant were combined and re-suspended in a known volume of filtered sea water.

The total number of zooxanthellae from 10 replicate counts was calculated using a haemocytometer. The relationship was then obtained between the number of zooxanthellae and dry skeletal weight (g).

Having calculated the relationship between the skeletal weight and dry tissue weight and total number of zooxanthellae, the relationship between the zooxanthellae number and the dry tissue weight can be estimated indirectly.

4.2.3.3 Skeletal Weight and Surface Area

The dry weight of the skeleton of 10 nubbins from each species was calculated from their buoyant weight. Their tissue was removed by immersing them in a 10% solution of commercial chlorox and sea water. The skeleton was then rinsed with distilled water and dried at 60^{o}C. Aluminium foil was fitted carefully on to the surface of each nubbin. The fitted foil was then weighed and a value for surface area derived, in order to obtain a relationship between surface area and skeletal weight. The number of polyps per cm^2 was obtained from the number of calices per cm^2.

4.2.3.4 Number of Zooxanthellae and Dry Zooxanthellae Weight

Early attempts to separate zooxanthellae for counting encountered problems due to the clumping of the algae, which would not separate even when homogenized in a hand-held Potter homogeniser. It was suspected that this may be due to freshly extruded lipid on their surfaces. To combat this, nubbins were held in darkness for 48h before sampling. In this way complete separation was achieved. Tissue was removed with a Water Pik (Johannes and Wiebe, 1970), using 0.45µm filtered sea water. The tissue slurry was centrifuged at 2000 x g for one minute. The pellet was homogenized with 3-5 strokes in a hand-held Potter homogeniser and re-centrifuged

and re-suspended three times.

The final resuspension was in filtered sea water of known volume and five replicate counts were carried out with a haemocytometer. The remaining sample was re-pelleted for three minutes at 4000 x g. The supernatant was carefully poured off and re-centrifuged for 10 minutes at full speed. The two pellets were combined together and washed briefly in distilled water. The final pellet was dried in a pre-weighed weighing boat at 60°C, cooled and weighed to the nearest 0.1 mg.

4.2.4 ENERGY VALUE OF BIOMASS

4.2.4.1 Energy Value of Tissue

Freshly collected nubbins were fixed in Zenker's fixative (acid-free). The fixed samples were then decalcified in a 7% solution of nitric acid and sea water. The decalcified tissue was rinsed in distilled water, dried at 60°C, cooled and stored in a desiccator over SiO_2. Finally, approximately 15 mg samples from both groups were burned in a Model AH12/EF/2 microbomb calorimeter in order to determine their energy contents.

4.2.4.2 Energy Value of Zooxanthellae

The zooxanthellae which were isolated counted and dried as described in Section 4.2.3.4 were used to determine their energy content in the microbomb calorimeter.

4.2.4.3 Energy Value of Planulae

Planulae of *S. pistillata* were collected in January 1989 and counted. They were then rinsed in distilled water, dried at 60°C, cooled and weighed. The dry planulae were then burned in the bomb calorimeter to measure their energy content.

4.2.4.4 Energy Value of Heterotrophic Source

The fish faeces which were about to be ingested by ***E. gemmacea*** (Chapter III), were collected from the mouth of each polyp, rinsed in distilled water, dried at 60°C and weighed. The energy value was obtained using the microbomb calorimeter.

4.2.5. OXYGEN MEASUREMENT

4.2.5.1 Experimental Apparatus

The respirometer consisted of a clear perspex jacket (9.5 x 8 x 9 cm) surrounding a cylindrical perspex respirometer chamber 5 cm in diameter and 128 ml. volume. The respirometer chamber was fitted with an oxygen electrode (a Radiometer Copenhagen E-5046) which entered through the side of the chamber.

The jacket was connected to a constant temperature water bath (Grant Instruments Ltd). The chamber contained a Teflon covered magnetic stirring bar 2.5 cm in length, driven by an electronic stirrer (Rank Brothers Ltd., model 100). The oxygen electrode was connected to an oxygen meter (Strathkelvin Instruments 781 b), whose output was plotted on a 27 cm chart recorder (Tekman TE 850). The respirometer was located beneath a hood (L 69 cm x H 53 cm) whose interior was lined with aluminium foil and was illuminated by an over-head bank of six daylight fluorescent tubes (20W). The light intensity was increased or decreased by increasing or decreasing the voltage to the tubes using a variable transformer (Zenith). The irradiance was measured with a quantum sensor (Skye Instruments SKP200) connected to a light meter (Skye Instruments SKP215).

4.2.5.2 Experimental Procedures

The nubbins from each collection depth were collected and transported to the laboratory in shaded buckets. Any debris or fouling organisms that had settled on the tiles bearing the nubbins were carefully scraped off. The nubbins were then placed in the running sea water tank overnight.

The following day nubbins were placed individually in the chamber which was filled with 0.45μm filtered seawater. Respiration rate of each nubbin was measured in darkness, until the percentage saturation of oxygen had fallen to 50%. Thereafter, the light was switched on at an irradiance of 25 $\mu E.m^{-2}.sec^{-1}$. The irradiance was increased by 25 $\mu E.m^{-2}.sec^{-1}$ every 10 minutes, until saturation irradiance was obtained (370 $\mu E.m^{-2}.sec^{-1}$ for ***S. pistillata*** and 270 $\mu E.m^{-2}.sec^{-1}$ for ***E. gemmacea***. At the end of each experiment the nubbin was buoyant weighed in order to predict its skeletal weight..

The rate of oxygen consumption and rate of net photosynthesis at each irradiance were calculated in units of $\mu lO_2.h^{-1}$.

4.2.5.3 Analysis of Respiration and Photosynthesis Data.

The respiration value was converted to energy units (Joules) by multiplying by a conversion factor of 19.63 (Elliott and Davison, 1975), assuming that lipid is being metabolised (Davies, 1984; Edmunds and Davies, 1986 and Davies, 1991a), and normalised to a 10 g dry skeletal weight. The net photosynthesis data were plotted against irradiance and a best-fitting line was fitted, using the following equation of the hyperbolic tangent function curve (Chalker, 1981).

$$P_{net} = {}^{g}P_{max.} \tanh (I/I_k) - R$$

Where P_{net} = net photosynthesis ; ${}^{g}P_{max.}$ = maximum gross photosynthesis which is the sum of the net photosynthesis and the respiration rate ; R= rate of dark respiration ; I = irradiance ($\mu E.m.^{-2}sec.^{-1}$) , and I_k= the irradiance corresponding to the point of intersection between the extrapolated linear part of the curve and the horizontal asymptote line of maximum photosynthesis. The irradiance corresponding to 95% of the maximum photosynthesis was calculated with the following formula (Chalker and Dunlap, 1983).

$$I_{0.95} = 1.832 \times I_k$$

The compensation point was also calculated from the equation of Chalker ***et al*** (1983) .

$$I_c = I_k \tanh^{-1}(-R/ {}^{g}P_{max.})$$

Daily productivity of each species in situ on the reef was predicted using a daily in situ light curve (Chapter III). The light for the purpose of the energy budget was recorded continuously for one day during 1989 (summer) and 1990 (winter) at three depths 1, 3, 10 metres. The light intensity values ($\mu E.m.^{-2}sec.^{-1}$) were read from the light curve at 15 minute intervals, and substituted into the hyperbolic tangent

function formula using a computer programme. The programme summed the values of the net photosynthesis at each of these irradiance values from the curve and calculated values for the integrated daily net photosynthesis (mls O_2) in situ on the reef for that day. Gross productivity for each nubbin was calculated by adding the estimated total respiration during the period of photosynthesis. This value was then converted into Joules, using the oxy-joule equivalent of 21.831 (Davies, 1991a) on the assumption that lipid is the primary product of photosynthesis in corals.

The daily gross photosynthesis values were expressed as J. $24h^{-1}$. Subsequently, the values were normalized to a standard size nubbin of 10 g skeleton weight.

4.2.5.4 Zooxanthellae Respiration

Respiration of zooxanthellae of the two species from different depths (***S. pistillata*** from 1, 10 m and ***E. gemmacea*** from 3 and 10 m) was measured in a RC300 respiration cell (Strathkelvin Instruments) using a 1302 oxygen electrode, connected to a Strathkelvin Instruments oxygen meter.

A clean suspension of zooxanthellae was obtained by the Water Pik technique described earlier (see 4.2.3.4). The zooxanthellae were re-suspended in a suitable volume of 0.45 μm filtered sea water at the temperature of the experiment. One ml of the zooxanthellae suspension was placed in the respiration cell and respiration rate measured in darkness. At the end of each run the number of zooxanthellae in the chamber was calculated from ten replicate samples counted on a haemocytometer. The rate of respiration of the zooxanthellae was calculated as ml O_2 10^6 $zoox^{-1}$ $24h^{-1}$ and converted to Joules using the conversion factor of 19.63. The final results were normalized to 10 g skeletal weight nubbin, using the relationship between number of zooxanthellae and skeletal weight (see section 4.2.3.2).

CHAPTER V

5. COMPONENTS OF THE ENERGY BUDGET

5.1 INTRODUCTION

In chapter four the methods used to determine the different components of the energy budgets were described. Because of the necessity of normalising the budgets to a standard size of coral nubbin, characteristics of the biomass of both whole association and of the zooxanthellae were investigated. However the major components comprise the energy input from photosynthesis by zooxanthellae and energy expenditure from the respiration and growth of both zooxanthellae and animal tissue. Details of these components will be presented in this chapter and the integration of these into a 24 hour budget will be dealt with in chapter six. In addition the effects of change in light intensity, both with depth on the reef and with season on photosynthesis , which are expressed as photoadaptation , will be discussed in the present chapter .

5.2 RESULTS

5.2.1 Skeletal and Biomass Characteristics

The skeleton and biomass characteristics of both species are shown in table (5.1)

The mean density of the skeleton of both species is identical at 2.78 ± 0.01 (12) g. cm^{-3} . The mean surface area per g. skeleton is higher in ***S. pistillata*** 2.92 ± 0.39 (10) cm^2. g^{-1} skeleton than ***E. gemmacea*** 2.62 ± 0.45 (10) cm^2. g^{-1} skeleton and is significantly different (t-test $P<0.001$). The correction factor for use in converting buoyant weight of nubbins to skeletal weight due to the buoyant weight of tissue (Davies, 1989) is significantly lower 0.85 ± 0.19% (15) for ***S. pistillata*** than 1.25 ± 0.25% (15) for ***E. gemmacea***, because ***E. gemmacea*** has a higher tissue biomass 12.86 ± 2.54 (35) mg dry tissue wt.g^{-1} skeleton as compared with a value of 10.3 ± 1.49 (24) mg dry tissue wt.g^{-1} skeleton for ***S. pistillata***. There is a significant difference in

Table 5.1. The mean skeletal and tissue characteristics of *S. pistillata* and *E. gemmacea* at the study site . The mean values were compared by Student's t-test. Tests were not carried out on energy values because of the small size of sample available, nor in cases where the values given are derived values.

Characteristic	*S. pistillata*	*E. gemmacea*	t	Significance
Skeleton				
Skeletal density				
$g.cm^{-3}$	2.78 ± 0.01 (12)	2.78 ± 0.009 (11)	0.14	N.S.
Correction factor (%)	0.85 ± 0.19 (15)	1.25 ± 0.25 (15)	-	
Biomass				
Colony				
mg.d.t. g^{-1} skeleton	10.30 ± 1.49 (24)	12.86 ± 2.54 (35)	3.60	P <0.001
$cm^2.g^{-1}$ skeleton	2.92 ± 0.39 (10)	2.62 ± 0.45 (10)	-	
mg.d.t. cm^{-2}	3.53 ± 0.58 (10)	4.91 ± 1.14 (10)	-	
no. polyps cm^{-2}	75.60 ± 6.90 (10)	2.34 ± 0.62 (10)	-	
Zooxanthellae				
No.10^6.g^{-1} skeleton	2.87 ± 0.36 (10)	1.63 ± 0.38 (11)	7.55	P <0.001
No.10^5.mg^{-1} d. t.	2.78 ± 0.54 (10)	1.27 ± 0.96 (11)	-	
No.10^5.cm^{-2}	9.82 ± 0.14 (10)	6.27 ± 0.17 (11)	-	
mg.d.wt.10^6 zoox.	0.44 ± 0.03 (10)	0.42 ± 0.06 (10)	0.77	N.S.
Energy content				
Tissue				
$J.mg^{-1}$	25.51 ± 3.45 (2)	24.60 ± 0.26 (4)	-	
Zooxanthellae				
$J.mg^{-1}$	23.10 ± 3.45 (3)	24.06 ± 0.26 (4)		
$J.10^6$ zoox	10.14 ± 0.01 (3)	10.13 ± 0.14 (4)	-	
Planulae				
mg planula $^{-1}$	0.09 ± 0.05 (5)	-	-	
$J.mg^{-1}$	29.47 ± 1.60 (2)	-	-	
$J.planula^{-1}$	2.75 ± 0.14 (5)	-	-	
Fish waste				
$J.mg^{-1}$	-	13.92 (2)	-	

relative biomass between the two species (t-test P<0.001). The values remain different when they are expressed on a surface area basis, i.e. 4.91 and 3.53 mg dry tissue wt.cm^{-2} respectively.

S. pistillata has a higher number of zooxanthellae 2.78x10^5 mg^{-1} dry tissue wt. or 9.82x 10^5 cm^{-2} than the number of zooxanthellae in *E.gemmacea* 1.27x10^5 mg^{-1} dry tissue wt. or 6.27x10^5 cm^{-2}. There is a very highly significant difference in the number of zooxanthellae between the two species on the basis of biomass or surface area (t-test p<0.001).

There is no significant difference in the relative dry weight of zooxanthellae between the species, 0.44 ± 0.03 (10) and 0.42 ± 0.06 (10) mg. dry wt. 10^6 zoox^{-1} for *S. pistillata* and *E. gemmacea* respectively.

5.2.2 ENERGY VALUE

The energy contents of the tissues *S. pistillata* and *E. gemmacea* are 25.51 ± 3.45 (2) and 24.6 ± 0.26 (4) J.mg^{-1} dry tissue respectively, whilst the energy values of zooxanthellae are 23.10 ± 3.45 (3) and 24.06 ± 0.26 (4) J.mg^{-1} dry tissue. On a unit basis the values are 10.14 ± 0.01 (3) and 10.13 ± 0.14 (4) J. 10^6 zoox. for *S. pistillata* and *E. gemmacea* respectively. Planulae of *S. pistillata* contain 29.47±1.60(2) J.mg^{-1} planula or 2.75 J. planula^1.

The energy value of heterotrophic sources "fish faeces", which was collected from the polyps mouth of *E. gemmacea* is 13.95 J.mg^{-1} fish faeces.

5.2.3 DARK RESPIRATION

A) COLONY

The mean values of colony respiration for both species are expressed on a tissue biomass and surface area basis and given in table 5.2. and fig. 5.1

a) SPECIES VARIATIONS

The mean rate of respiration of whole colonies of *S. pistillata* is higher than that of *E. gemmacea* when compared at the same depth in both summer of 1989 and winter of 1990. The difference is significant in all cases (Table 5.3) . No significant difference was found when making similar comparisons on the rate of

respiration of freshly isolated zooxanthellae at ($P > 0.05$), except during summer at each depth (Table 5.3) .

b) SEASONAL VARIATIONS

S. pistillata

The average rate of respiration is lower 1.77± 0.52 (22) μlO_2 mg^{-1} dry tissue $wt.h^{-1}$ during winter time (26°C) than summer (30°C) 2.76± 0.45 (27) at 1 m . It is also higher in summer at 10 m 2.24± 0.34 (20) than winter at the same depth 1.44±0.22 (13) μlO_2 mg^{-1} dry tissue $wt.h^{-1}$. The difference is significant at each depth (t-test $P<0.001$).

E. gemmacea

There are slight variations in the mean values of respiration between summer 1.38 ± 0.16 (20) μlO_2 mg^{-1} dry tissue $wt.h^{-1}$ and winter 1.21 ± 0.52 (21) at 3 m whilst the differences at 10 m are obviously clear 1.29 ± 0.19 (20) and 0.91 ± 0.32 (20) μlO_2 mg^{-1} dry tissue $wt.h^{-1}$ during summer and winter respectively. There is a significant difference between seasons at 10 m (t-test $P<0.001$) but no significant difference at 3 m ($P<0.05$).

c) DEPTH VARIATIONS

S. pistillata

The mean rate of dark respiration is significantly higher at 1 m 2.76 (summer) and 1.77 (winter) μlO_2 mg^{-1} $d.t.wt.h^{-1}$ than at 10 m 2.24 (summer) and 1.44 (winter) μlO_2 mg^{-1} d.t. wt. h^{-1} (t-test $P < 0.001$ summer and $P < 0.05$ in winter).

E. gemmacea

The mean value of oxygen consumption decreases with increasing depth 1.38±0.16 (20) during summer at 3 m and 1.29 ± 0.19 (20) μlO_2 mg^{-1} $d.t.wt.h^{-1}$at 10 m, and 1.21 ± 0.52 (21) and 0.91 ± 0.32 (20) at 3 and 10 m during winter respectively. There is no significant difference during summer whilst during winter it is significantly lower at 10 m ($P < 0.03$).

Table 5.2. The mean dark respiration of the whole colony and freshly isolated zooxanthellae of ***S. pistillata*** and ***E. gemmacea*** at different depths (1, 3, and 10m) and seasons (summer and winter) with standard deviations (S.D.) and the number of measurements (n) in parenthesis. d.t. = dry tissue weight . The values expressed on a surface area basis were calculated from the ratio between the surface area and the dry tissue weight (5.1). Student's t-tests were used to compare the mean values of respiration between seasons at one depth and between depths in each season.

N.S = not significantly different at P = 0.05

Symbols of t-tests

(0) between seasons at one depth

(*) between depths in summer

(**) between depths in winter.

Note : Symbols do not refer to the probability level of t-test.

Dark Respiration	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	t	Significance	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90	t	Significance
Colony									
$\mu lO_2\ mg^{-1}d.t.h.^{-1}$	1	2.76	1.77	7.09^{0}	P <0.001				
S.D		0.45 (27)	0.52 (22)	4.21^{*}	P <0.001				
$\mu lO_2\ cm^{-2}h.^{-1}$		9.84	6.31						
S.D.		1.61 (27)	1.85 (22)						
$\mu lO_2\ mg^{-1}d.t.h.^{-1}$	3					1.38	1.21	1.37^{0}	N.S.
S.D.						0.16 (20)	0.52 (21)	1.56^{*}	N.S.
$\mu lO_2\ cm^{-2}h.^{-1}$						6.91	6.07		
S.D.						0.85 (20)	2.60 (21)		
$\mu lO_2\ mg^{-1}d.t.h.^{-1}$	10	2.24	1.44	7.49^{0}	P <0.001	1.29	0.91	4.53^{0}	P <0.001
S.D.		0.34 (20)	0.22 (13)	1.95^{**}	P <0.05	0.19 (20)	0.32 (20)	2.24^{**}	P <0.03
$\mu lO_2\ cm^{-2}h.^{-1}$		7.99	5.13			6.46	4.55		
S.D.		1.21 (20)	0.78 (13)			0.95 (20)	1.60 (20)		
Zooxanthellae									
$\mu lO_2\ 10^{6}zoox.^{-1}h^{-1}$	1	2.51	1.79	2.94^{0}	P <0.008				
S.D		0.58 (11)	0.24 (9)	1.21^{*}	N.S.				
$\mu lO_2\ 10^{6}zoox.^{-1}h^{-1}$	3					3.1	1.72	5.97^{0}	P <0.001
S.D						0.41 (12)	0.53 (9)	2.63^{*}	P <0.01
$\mu lO_2\ 10^{6}zoox.^{-1}h^{-1}$	10	2.15	1.38	5.54^{0}	P <0.001	2.63	1.37	7.78^{0}	P <0.001
S.D		0.33 (12)	0.13 (8)	4.21^{**}	P <0.001	0.41 (13)	0.25 (10)	1.66^{**}	N.S.

Table 5.3 Comparison between species of dark respiration and maximum gross photosynthesis ($P^g_{max.}$) rates of nubbins ($\mu lO_2.mg^{-1}.d.t.h^{-1}$) and respiration rates of freshly isolated zooxanthellae ($\mu lO_2 .10^6$ zoox.h^{-1}) of *S. pistillata* and *E. gemmacea* using Student's t-test.

Nubbins	*S. pistillata*	*E. gemmacea*	*t*	*Significance*
RESPIRATION				
Summer 89				
1m v 3m	2.76	1.38	1.285	P <0.001
10m v 10m	2.24	1.29	1.079	P <0.001
Winter 90				
1m v 3m	1.77	1.21	3.26	P <0.002
10m v 10m	1.44	0.91	2.913	P <0.006
PHOTOSYNTHESIS				
Summer 89				
1m v 3m	8.81	3.83	1.180	P <0.001
10m v 10m	5.23	3.39	5.387	P <0.001
Winter 90				
1m v 3m	5.68	4.76	1.341	N.S.
10m v 10m	4.72	3.46	1.70	N.S.
ZOOXANTHELLAE				
Summer 89				
1m v 3m	2.51	3.1	3.119	P <0.005
10m v 10m	2.15	2.63	2.850	P <0.009
Winter 90				
1m v 3m	1.79	1.72	3.470	N.S.
10m v 10m	1.38	1.37	1.208	N.S.

B) ZOOXANTHELLAE .

The mean respiration rates per 10^6 zooxanthellae are shown in table 5.2

a) SEASONAL VARIATIONS-

S. pistillata

The zooxanthellae respiration rate is significantly lower in winter 1.79 ± 0.24 (9) than in summer 2.51 ± 0.58 (11) $\mu l O_2$ 10^6 $zoox^{-1}$ h^{-1} at 1 m and also lower at 10 m, 1.38 ± 0.13 (8) during winter than summer, 2.15 ± 0.33 (12).

E. gemmacea

The mean values of respiration rates are lower in winter, 1.72 ± 0.53 (9) at 3 m and 1.37 ± 0.25 (10) $\mu l O_2$ 10^6 $zoox^{-1}$ h^{-1} at 10 m than summer, 3.1 ± 0.41 (12) and 2.63 $\mu l O_2$ 10^6 $zoox^{-1}$ h^{-1} at 3 and 10 m respectively. There is a significant difference between seasons at both depths .

b) DEPTH VARIATIONS

S. pistillata

The mean respiration rates decrease with increasing depth. In summer the value is higher at 1 m, 2.51 than at 10 m, 2.15 $\mu l O_2$ 10^6 $zoox^{-1}$ $h.^{-1}$, but it is not significantly different, whilst it is significantly lower at 10 m, 1.38 than at 1 m, 1.79 $\mu l O_2$ 10^6 $zoox^{-1}$ h^{-1} during winter ($P< 0.03$).

E. gemmacea

The zooxanthellae of this species show the same pattern of respiration rates which decrease with increasing depths, the rates being higher at 3 m during both seasons 3.1 and 1.72,. and lower at 10 m, 2.63 and 1.37 $\mu l O_2$ 10^6 $zoox^{-1}$ h^{-1} during summer and winter respectively. There is a significant difference between the two depths during summer but no significant difference in winter.

5.2.4 PHOTOSYNTHESIS

Mean photosynthesis v irradiance curves for ***S. pistillata*** and ***E. gemmacea*** plotted to the hyperbolic tangent function (Chalker, 1981) in summer 1989 and winter 1990 at 3 depths are shown in Fig. 5.1 The photosynthesis characteristics of

these curves are summarised in Table 5.4

a) SPECIES VARIATIONS-

S. pistillata has a higher maximum gross photosynthesis (Pg_{max}), ranging from 4.72 ± 0.88 (13) to 8.81 ± 1.78 (27) $\mu lO_2\, mg^{-1}$ dry tissue wt. h^{-1} as compared to the range of 3.39 ± 0.72 (20) to 4.76 ± 2.33 (21) $\mu lO_2\, mg^{-1}$ dry tissue wt. h^{-1} for *E . gemmacea*. The difference is significant between both species at each depth during summer (t-test $P < 0.001$), but not during winter at $P = 0.05$ (Table 5.3).

b) SEASONAL VARIATIONS

S. pistillata

The mean maximum gross photosynthesis (Pg_{max}) rates during summer are higher 8.81 ± 1.78 (27) than Pg_{max} in winter 5.68 ± 2.14 (22) $\mu lO_2\, mg^{-1}$ dry tissue wt. h^{-1} at 1 m and are significantly different. At 10 m, the values are also higher in summer 5.23 ± 1.33 (20) than in winter 4.72 ± 0.88 (13) but they are not significantly different.

E. gemmacea

The mean Pg_{max} is higher during winter 4.76 ± 2.33 (21) $\mu lO_2\, mg^{-1}$ dry tissue wt. h^{-1} as compared to 3.83 ± 0.69 $\mu lO_2\, mg^{-1}$ dry tissue wt. h^{-1} at 3m in summer, but it is not significantly higher during winter than summer

At 10m the average maximum gross photosynthesis rate in summer, 3.39±0.072 (20) is not significantly different from the winter value of 3.46 ± 1.03 (20).

c) DEPTH VARIATIONS

S. pistillata

The mean Pg_{max} is significantly higher at 1m, 8.81 ± 1.78 (27) when compared to 5.23 ± 1.33 (20) $\mu lO_2\, mg^{-1}$ dry tissue wt. h^{-1} at 10 m during summer, whilst Pg_{max} at 1m during winter 5.68 ± 2.14 (22), is not significantly different from 4.72 ± 0.88 (13) at 10m.

E. gemmacea

The mean maximum gross photosynthesis values 3.83 ± 0.69 (20) and 3.39 ± 0.72 (20) μlO_2 mg^{-1} dry tissue wt. h^{-1} during summer at 3, 10 m respectively are not significantly different, whilst in winter time the 3 m value, 4.76± 2.33 (21) is significantly higher than 3.46 ± 1.03 (20) at 10m.

5.2.5 CHARACTERISTICS OF THE (P v I) CURVE

The mean parameters of the P v I curve for the two species are shown in Appendix 1 to 6, Table 5.5 and Figs. 5.1.

A) The initial Slope (α)

S. pistillata

The mean values for α indicate that zooxanthellae of ***S. pistillata*** can utilize light slightly more efficiently during winter with α values of 0.0295 ± 0.01 (22) at 1 m and 0.03 ± 0.009 (13) at 10 m compared with summer 0.0271 ± 0.005 (27) at 1 m and 0.0274 ± 0.004 (27) μlO_2 mg^{-1} dry tissue wt. h^{-1} $\mu E.m^{-2}$ s^{-1} at 10 m.

The differences are not significantly different. The values are also slightly higher at 10 m than 1 m water depth during summer and winter time and the values are also not significantly different.

E. gemmacea

The mean values of α are significantly lower during summer at 3 m (0.021 ± 0.003 (20) and at 10 m (0.018 ± 0.003 (20) than winter (0.027 ± 0.009 (21) at 3 m and 0.028 ± 0.009 (20) at 10 m). The values increase slightly with depth during winter, but it is not significantly different. During summer, the value decreases with depth from 0.021 at 3m to 0.018 μlO_2 mg^{-1} d.t wt. h^{-1} $\mu E.m^{-2}$ s^{-1} at 10m, the difference being significant .

B) I_k

S. pistillata

The mean values of minimal light intensity which is sufficient to saturate photosynthesis are significantly higher during summer (343.44 ± 115.97 (27) and 194.4 ± 53.22 (20) $\mu E.m^{-2}$ s^{-1}) at 1 and 10 m water depth than winter at the same

Table 5.4 The mean maximum gross photosynthesis (Pg_{max}) of whole nubbins and of freshly isolated zooxanthellae of ***S. pistillata*** and ***E.gemmacea*** recorded from different depths (1, 3,.10m) and seasons (summer and winter). The whole nubbins values are expressed on the basis of the dry tissue weight (d.t.) and surface area (cm^{-2}). The standard deviation and the number of measurements for each period are shown as S.D ± (n) . The means are also compared between seasons at one depth and between depths in each season, using the Student's t-tests.

N.S = not significantly different at P = 0.05

Symbols of t-tests

(0) between seasons at one depth

(*) between depths in summer

(**) between depths in winter.

Note : Symbols do not refer to the probability level of t-test.

Photosynthesis	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	t	Significance	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90	t	Significance
$\mu lO_2\ mg^{-1}d.t.h.^{-1}$	1	8.81	5.68	5.57^{0}	P <0.001				
S.D		1.78 (27)	2.14 (22)	7.53^{*}	P <0.001				
$\mu lO_2\ cm^{-2}h.^{-1}$		31.46	20.29						
S.D.		6.35 (27)	7.64 (22)						
$\mu lO_2\ 10^{6}zoox.^{-1}h^{-1}$		31.7	20.44						
S.D		6.39 (27)	7.69 (22)						
$\mu lO_2\ mg^{-1}d.t.h.^{-1}$	3					3.83	4.76	1.72^{0}	N.S.
S.D.						0.69 (20)	2.33 (21)	1.92^{*}	N.S.
$\mu lO_2\ cm^{-2}h.^{-1}$						19.15	23.82		
S.D.						3.45 (20)	11.65 (21)		
$\mu lO_2\ 10^{6}zoox.^{-1}h^{-1}$						30.18	37.55		
S.D						5.43 (20)	18.36 (21)		
$\mu lO_2\ mg^{-1}d.t.h.^{-1}$	10	5.23	4.72	1.22^{0}	N.S.	3.39	3.46	0.24^{0}	N.S.
S.D.		1.33 (20)	0.88 (13)	1.54^{**}	N.S.	0.72 (20)	1.03 (20)	2.29^{**}	P <0.02
$\mu lO_2\ cm^{-2}h.^{-1}$		18.67	16.86			16.97	17.32		
S.D.		4.75 (20)	3.14 (13)			3.60 (20)	5.15 (20)		
$\mu lO_2\ 10^{6}zoox.^{-1}h^{-1}$		18.82	16.97			26.75	27.30		
S.D		4.77 (20)	3.15 (13)			5.65 (20)	8.10 (20)		

Table 5.5 The mean values of photosynthetic parameters (α, I_k, Ic and I0.95) calculated from the net photosynthesis vs irradiance, using the hyperbolic tangent function curve (see chapter four section 4.2, 5.3 for ***S. pistillata*** and ***E. gemmace***a recorded from different depths (1, 3, and 10m) and seasons (summer and winter). Student's t-test was used to compare the means between seasons and depths.

N.S = not significantly different at P = 0.05

Symbols of t-tests

(0) between seasons at one depth

(*) between depths in summer

(**) between depths in winter.

Note : Symbols do not refer to the probability level of t-test.

Photosynthetic parameter	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	t	Significance	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90	t	Significance
α									
$\mu lO_2\ mg^{-1}d.t.$									
$\mu E.m^{-2}.s^{-1}$	1	0.0271	0.0295	0.8^{0}	N.S.				
S.D		0.005 (27)	0.010 (22)	0.15^{*}	N.S.				
$\mu lO_2 cm^{-2}.\mu E.m^{-2}.s^{-1}$		0.096	0.110						
S.D		0.017 (27)	0.03 (22)						
$\mu lO_2\ mg^{-1}d.t.$									
$\mu E.m^{-2}.s^{-1}$	3					0.021	0.027	2.62^{0}	P <0.01
S.D						0.003 (20)	0.009 (21)	2.25^{*}	P <0.03
$\mu lO_2 cm^{-2}.\mu E.m^{-2}.s^{-1}$						0.100	0.130		
S.D						0.014 (20)	0.04 (21)		
$\mu lO_2\ mg^{-1}d.t.$									
$\mu E.m^{-2}.s^{-1}$	10	0.0274	0.030	1.39^{0}	N.S.	0.018	0.028	4.2^{0}	P <0.001
S.D		0.004 (20)	0.009 (13)	0.24^{**}	N.S.	0.003 (20)	0.009 (20)	0.32^{**}	N.S.
$\mu lO_2 cm^{-2}.\mu E.m^{-2}.s^{-1}$		0.097	0.11			0.088	0.140		
S.D		0.014 (20)	0.030 (13)			0.014 (20)	0.04 (20)		

Photosynthetic parameter	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	t	Significance	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90	t	Significance
I_k									
$\mu E.m^{-2}.s^{-1}$	1	343.44	233.73	2.68^{0}	P <0.01				
S.D		115.97 (27)	169.59 (22)	5.34^{*}	P < 0.001				
$\mu E.m^{-2}.s^{-1}$	3					183.5	171.57	1.12^{0}	N.S.
S.D						31.69 (20)	36.39 (21)	0.16^{*}	N.S.
$\mu E.m^{-2}.s^{-1}$	10	194.40	157.69	2.33^{0}	P <0.02	185.00	127.15	6.56^{0}	P <0.001
S.D		53.22 (20)	23.83 (13)	1.59^{**}	N.S.	28.57 (20)	27.17 (20)	4.41^{**}	P <0.001
I_c									
$\mu E.m^{-2}.s^{-1}$	1	110.90	73.27	4.38^{0}	P <0.001				
S.D		25.20 (27)	34.91 (22)	3.09^{*}	P < 0.003				
$\mu E.m^{-2}.s^{-1}$	3					70.00	45.19	8.85^{0}	P <0.001
S.D						11.01 (20)	6.45 (21)	1.25^{*}	N.S.
$\mu E.m^{-2}.s^{-1}$	10	90.6	51.00	6.92^{0}	P <0.001	74.90	33.25	12.61^{0}	P <0.001
S.D		17.36 (20)	13.74 (13)	2.19^{**}	P < 0.03	13.5 (20)	5.99 (20)	6.13^{**}	P <0.001

Photosynthetic parameter	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	t	Significance	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90	t	Significance
$I_{0.95}$									
$\mu E.m^{-2}.s^{-1}$	1	629.19	428.19	2.68^{0}	P <0.01				
S.D		212.46 (27)	310.00 (22)	5.34^{*}	P < 0.001				
$\mu E.m^{-2}.s^{-1}$	3					336.17	314.32	1.12^{0}	N.S.
S.D						58.07 (20)	66.68 (21)	0.15^{*}	N.S.
$\mu E.m^{-2}.s^{-1}$	10	356.14	288.89	2.33^{0}	P <0.02	338.92	232.94	6.50^{0}	P <0.001
S.D		97.5 (20)	43.65 (13)	1.59^{**}	N.S.	52.35 (20)	49.78 (20)	4.41^{**}	P <0.001

depth respectively (233.73 ± 169.59 (22) and 157.69 ± 23.83 (13) $\mu E.m^{-2} s^{-1}$. These values are also higher at 1 m than 10 m and the values are significantly lower at 10 m during summer but are not significantly different between depth during winter time.

E. gemmacea

The values of I_k , 183.5 ± 31.69 (20) at 3 m during summer are lower than 185.0± 28.57 (20) $\mu E.m^{-2} s^{-1}$ at 10 m, but are not significantly different, whilst the values during winter are significantly lower at 10 m 127.15 ± 27.17 (20) as compared to 171.57 ± 36.39 (21) $\mu E.m^{-2} s^{-1}$ at 3 m during winter.

The values show the same pattern as ***S. pistillata*** being higher during summer than winter time at both depths.

C) I_c

S. pistillata

The mean values of compensation point are significantly higher during summer 110.9 ± 25.2 (27) and 90.6 ± 17.36 (20) $\mu E.m^{-2} s^{-1}$ at 1 and 10 m water depth respectively than winter months 73.27± 34.91 (22) and 51.0 ± 13.74 (13) at 1 and 10 m respectively. The values also decrease with increasing depth and are significantly different.

E. gemmacea

The average values of I_c are lower during winter 45.19 ± 6.45 (20) at 3 m and 33.25 ± 5.99 (20) $\mu E.m^{-2} s^{-1}$ at 10 m than during the summer months 70.0 ± 11.01 (20) at 3 m and 74.9 ± 13.5 (20) at 10 m water depth. They are significantly different. During winter the values are significantly lower at 10 m but are not significantly different between depths during summer.

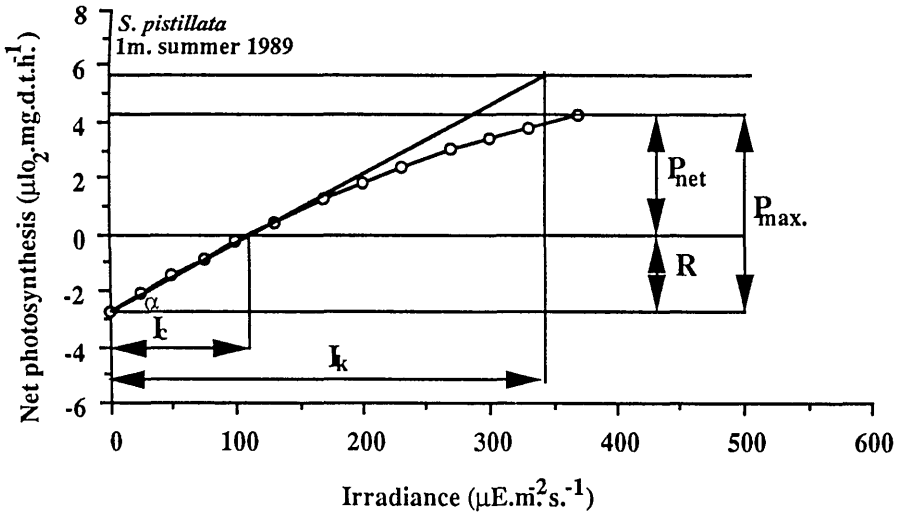
5.2.6 GROWTH

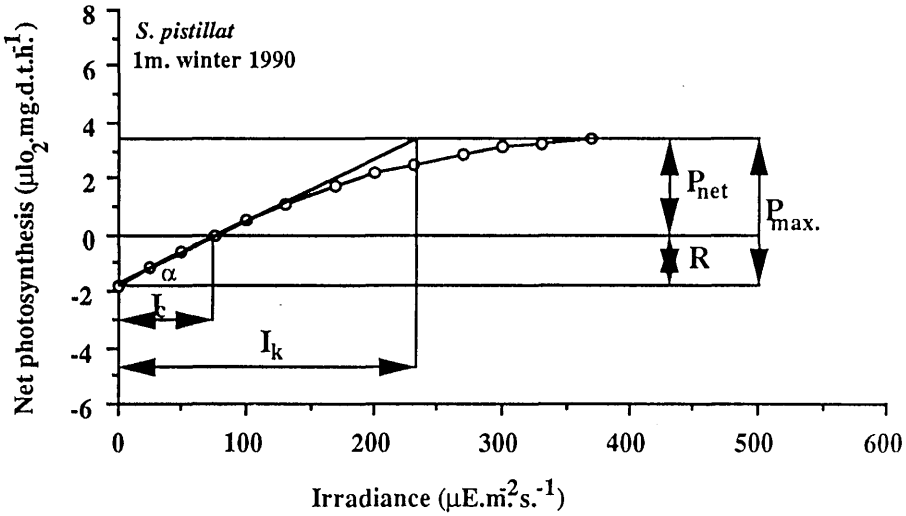
A) Skeleton

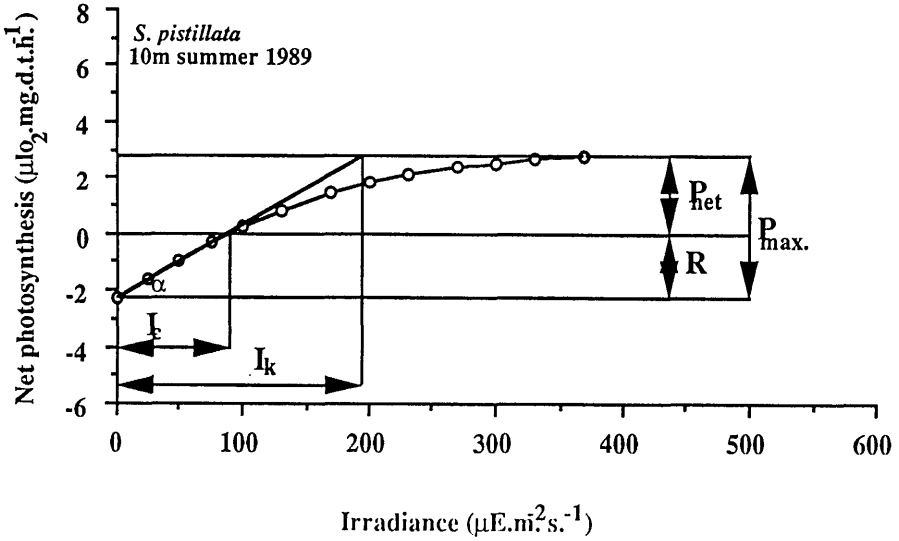
The mean daily growth rates of skeleton and tissue of both ***S. pistillata*** and ***E. gemmacea*** at different seasons and depths are shown in Appendix 9-16, Table 5.6 and Figs. 5.2.

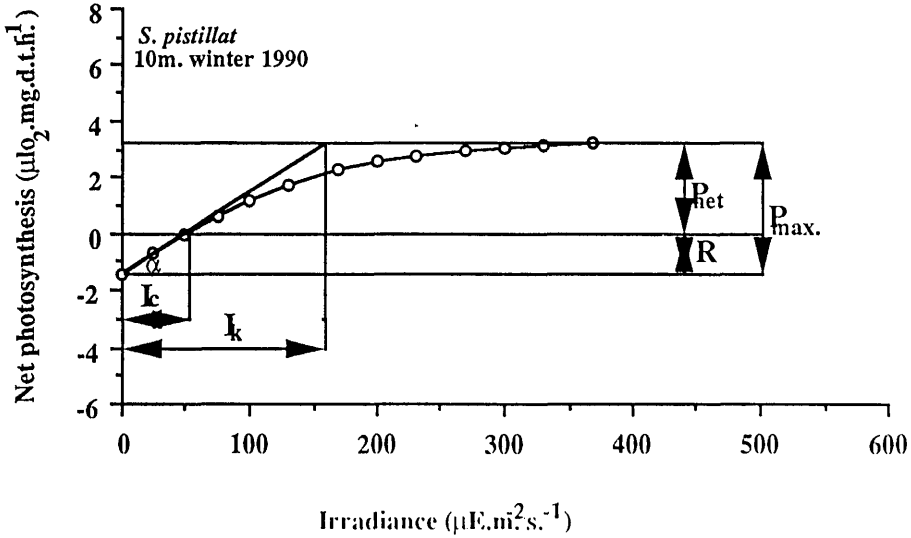
Fig. 5.1 Relationship between light intensity (I) and photosynthesis (P) for ***S. pistillata*** and ***E. gemmacea*** at each depth and season. The curves were derived from the mean values of photosynthetic parameters (see appendix , 1 to 6) , using the following equations :

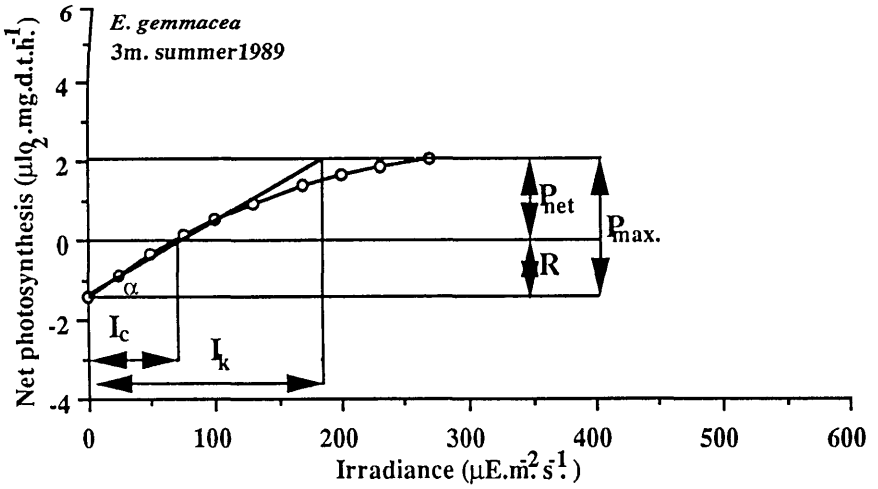
$\mathbf{P_{net} = p^{g}_{max.} \tanh (I/I_k) - R}$	Chalker (1981)
S. pistillata	
$P_{net} = 8.81 \tanh (I/343) - 2.76$	1m summer 1989
$P_{net} = 5.23 \tanh (I/194) - 2.24$	10m summer 1989
$P_{net} = 5.68 \tanh (I/233) - 1.77$	1m winter 1990
$P_{net} = 4.72 \tanh (I/157) - 1.44$	10m winter 1990
E. gemmacea	
$P_{net} = 3.83 \tanh (I/183) - 1.38$	3m summer 1989
$P_{net} = 3.39 \tanh (I/185) - 1.21$	10m summer 1989
$P_{net} = 4.76 \tanh (I/171) - 1.17$	3m winter 1990
$P_{net} = 3.46 \tanh (I/127) - 0.91$	10m winter 1990

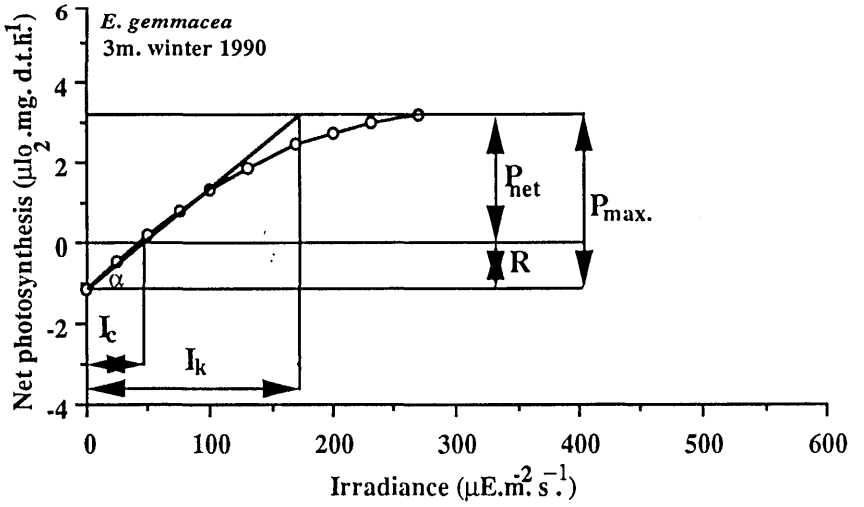

S. pistillata
1m. summer 1989
Net photosynthesis (µlo2.mg.d.t.h.-1)
Irradiance (µE.m-2s.-1)
Pnet
Pmax.
R
α
Ic
Ik

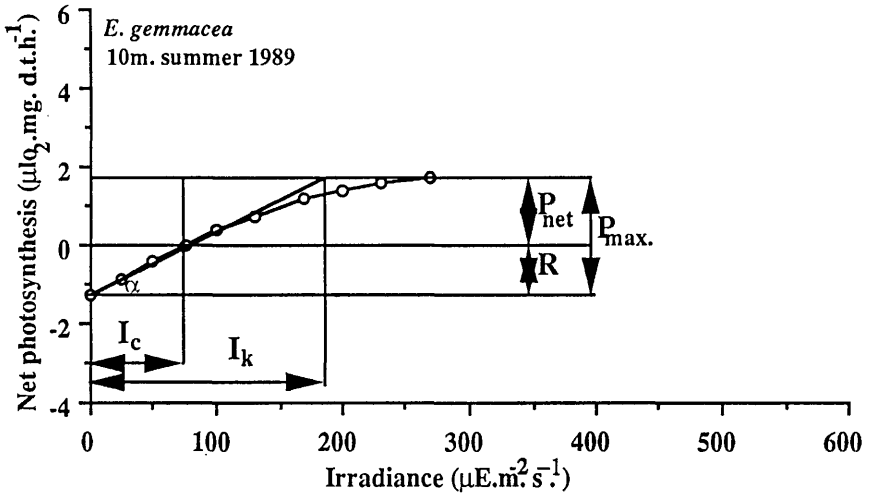

S. pistillat
1m. winter 1990
Net photosynthesis (µlo2.mg.d.t.h.-1)
Irradiance (µE.m-2s.-1)
Pnet
Pmax.
R
α
Ic
Ik

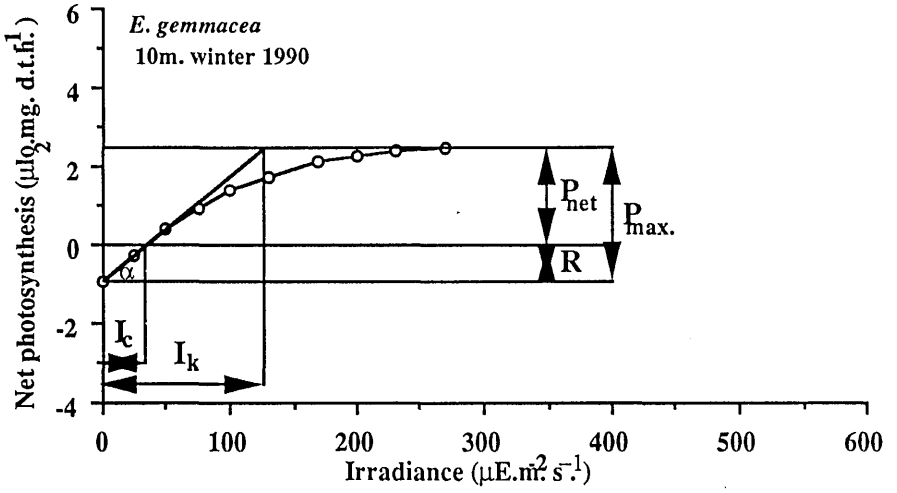

S. pistillata
10m summer 1989
Net photosynthesis (µlo2.mg.d.t.h.-1)
Irradiance (µE.m-2s.-1)
Pnet
Pmax.
R
α
Ic
Ik


S. pistillat
10m. winter 1990
Net photosynthesis (µlo2.mg.d.t.h.-1)
Irradiance (µE.m-2s.-1)
Pnet
Pmax.
R
α
Ic
Ik


E. gemmacea
3m. summer1989
Net photosynthesis (µlO2.mg.d.t.h.-1)
Irradiance (µE.m-2 s-1)
Pnet
Pmax.
R
α
Ic
Ik


E. gemmacea
3m. winter 1990
Net photosynthesis (µlO2.mg. d.t.h.-1)
Irradiance (µE.m-2 s-1)
Pnet
Pmax.
R
α
Ic
Ik


E. gemmacea
10m. summer 1989
Net photosynthesis (µlO2.mg. d.t.h.-1)
Irradiance (µE.m-2 s-1)
Pnet
Pmax.
R
α
Ic
Ik


E. gemmacea
10m. winter 1990
Net photosynthesis (µlO2.mg. d.t.h.-1)
Irradiance (µE.m-2 s-1)
Pnet
Pmax.
R
α
Ic
Ik

a) SEASONAL VARIATION IN DAILY GROWTH RATE.

S. pistillata

The growth rate was approximately linear during each period of measurement (fig. 5.2.). The highest mean daily skeletal growth rate was 56.03 ± 15.76 (51) mg. skel . d^{-1} at 1 m and 13.58 ± 3.73 (58) mg. skel . d^{-1} at 10 m during summer 1989. The lowest was 21.55 ± 7.21 (51) mg. skel . d^{-1} at 1 m and 9.26 ± 2.47 (46) mg. skel . d^{-1} at 10 m during winter 1990. Statistical comparison between winter 1990 and summer 1989 in the mean daily growth rate of skeleton and tissue at each depth indicates that there are very highly significant differences.

E. gemmacea

The growth rate of this species is also approximately linear during the period of each measurement (fig. 5.2) ***E. gemmacea*** shows less seasonal variation at 3m in the mean daily growth of skeleton (Table 5.6). The values range from 13.46± 4.0 (40) in summer to 13.55± 6.0 (41) in winter at 3 m and there is no significant difference. At 10 m, the mean growth of skeleton is higher in summer 12.46 ± 4.14 (64) than in winter 10.23 ± 5.0 (43) and there is a significant difference.

b) VARIATION IN DAILY GROWTH RATE WITH DEPTH.

S. pistillata

In general, the highest mean daily growth rate of skeleton and tissue was greater at 1 m than that at 10 m during both summer 1989 and winter 1990.

The t-test shows a very high significant difference in the mean daily growth rate between depths (t-test $P<0.001$).

E. gemmacea

During summer 1989 and winter 1990, the mean daily growth rate of both skeleton and tissue at 3 m is higher than that at 10 m and significantly different (t-test $P<0.005$) during winter 1990. There is no significant difference between the depths during summer 1989.

Table 5.6 Mean daily growth rate of skeleton and tissue of ***S. pistillata*** and ***E. gemmacea*** for each season and depth. The mean growth for each species was compared between seasons at each depth and between depths in each season. S.D ± (n) .

N.S = not significantly different at P = 0.05

Symbols of t-tests

(0) between seasons at one depth

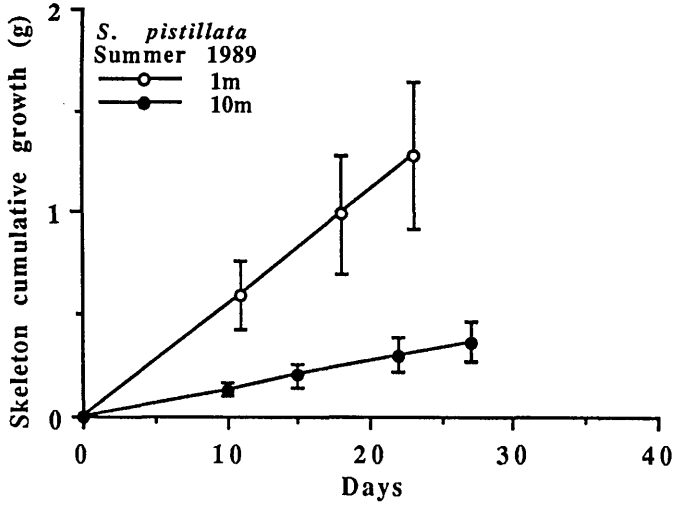
(*) between depths in summer

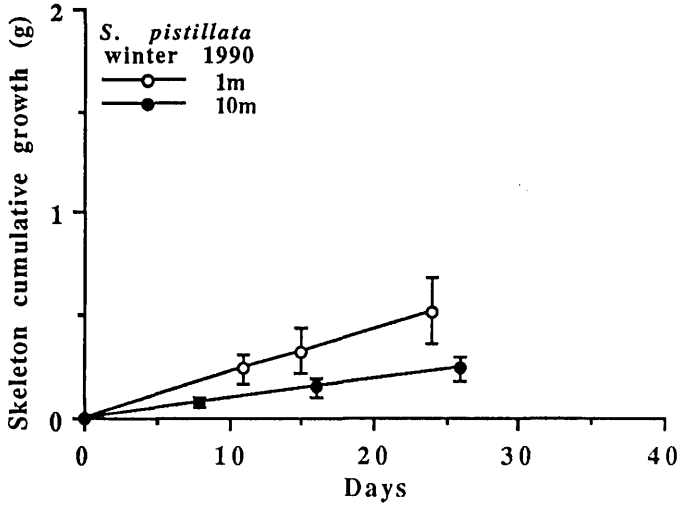
(**) between depths in winter.

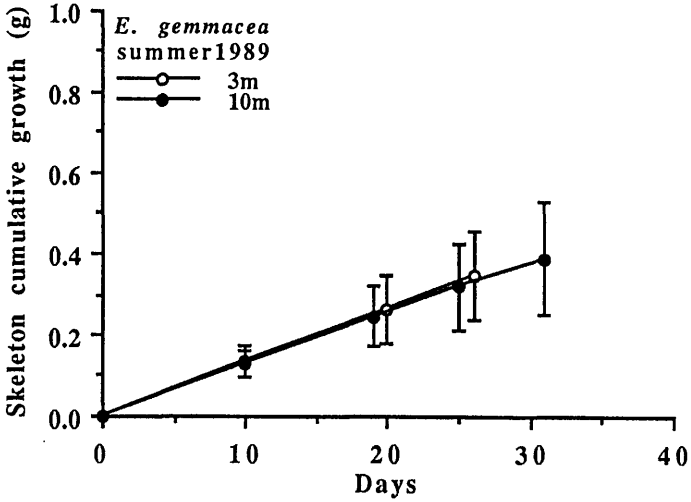
Note : Symbols do not refer to the probability level of t-test.

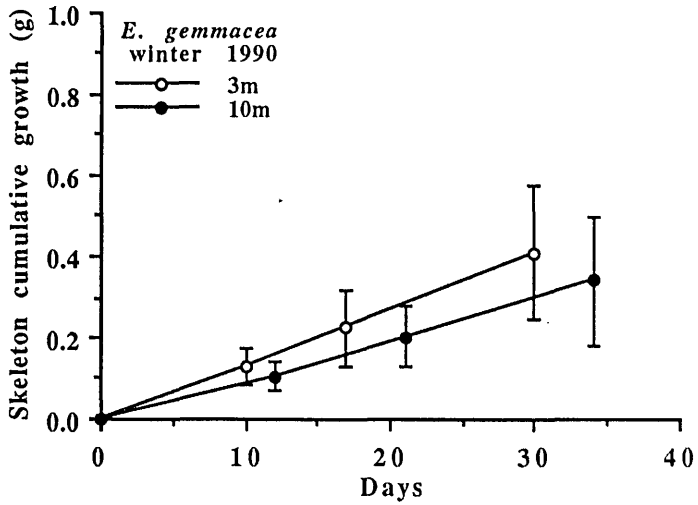
Growth rate	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	t	Significance	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90	t	Significance
Skeleton									
mg skeleton.d^{-1}	1	56.03	21.55	14.12^{0}	P <0.001				
S.D		15.76 (51)	7.21 (51)	10.9^{*}	P <0.001				
	3					13.46	13.55	0.1^{0}	N.S.
						4.00 (40)	6.00 (41)	1.21^{*}	N.S.
	10	13.58	9.26	6.69^{0}	P <0.01	12.46	10.23	2.5^{0}	P <0.01
		3.73 (58)	2.47 (46)	19.9^{**}	P <0.001	4.14 (64)	5.00 (43)	2.85^{**}	P <0.005
Tissue									
mg.d.t.d^{-1}	1	0.577	0.222						
S.D		0.16 (51)	0.07 (51)						
	3					0.173	0.174		
						0.05 (40)	0.07 (41)		
	10	0.140	0.095			0.160	0.132		
		0.03 (58)	0.02 (46)			0.05 (64)	0.06 (43)		

Fig 5.2. Cumulative growth of the skeleton of nubbins grown in situ at the study site at Sharm Ubhur at two depths in summer 1989 and winter 1990 .


S. pistillata
Summer 1989
1m
10m
Skeleton cumulative growth (g)
Days
0
1
2
0
10
20
30
40


S. pistillata
winter 1990
1m
10m
Skeleton cumulative growth (g)
Days
0
1
2
0
10
20
30
40


E. gemmacea
summer1989
3m
10m
Skeleton cumulative growth (g)
Days
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40


E. gemmacea
winter 1990
3m
10m
Skeleton cumulative growth (g)
Days
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40

5.3 DISCUSSION

5.3.1 SKELETAL AND BIOMASS CHARACTERISTICS

Skeletal densities for both ***S. pistillata*** and ***E. gemmacea*** are identical, 2.78 $g.cm^{-3}$ which is comparable to 2.783 and 2.785 $g.cm^{-3}$ recorded for ***Pocillopora eydouxi*** and ***Pocillopora verrucosa*** (Davies 1984, 1989) and lower than 2.822 for ***Porites porites*** (Edmunds and Davies, 1986).

The variations in the skeletal density among the species may be due to the difference in amount of organic matrix in the skeleton (Davies 1984, 1989). The similarity of the skeletal density of both species in the present study may reflect a similar percentage of the organic matrix in their skeleton.

S. pistillata has a 28% lower biomass of tissue per surface area when compared to ***E. gemmacea***. This may result from differences in the growth form and also the tissue location within the skeleton (Davies, 1984 and Davies, 1991a). ***S. pistillata*** has a shallow tissue depth (1.6mm) whereas in ***E. gemmacea*** the tissues penetrate to a depth of 8.8mm below the surface.

The relatively lower amount of tissue in ***S. pistillata*** in comparison with ***E. gemmacea*** is reflected in the differing contributions of the buoyant weight of tissue in the total buoyant weight 0.85 % and 1.25% respectively. Davies (1989) showed that the tissue biomass accounted for 1% of the total amount of the buoyant weight in ***Pocillopora verrucosa*** compared with 5% in ***Acropora humilis***. On a unit skeleton weight basis, ***S. pistillata*** has a 10% higher surface area than ***E. gemmacea*** due to the difference in the growth form of the two species (see chapter 11, section 2.2).

The tissue biomass, 10.30 $mg.d.t.g^{-1}$skel. for ***S. pistillata*** and 12.86 $mg.d.t.g^{-1}$skel for ***E. gemmacea*** are higher than the values of 4.73 for ***Pocillopora eydouxi*** at 5m (Davies, 1984) and lower than 18.56, 45.02 and 44.29 for ***P. damicornis***, ***Montipora verrucosa*** and ***Porites lobata*** at 3m respectively (Davies, 1991a). However, on a unit area basis ($mg.d.t.cm^{-2}$), the values of 3.52 for ***S. pistillata*** and 4.91 for ***E. gemmacea*** are lower than 6.56 and 9.65 for ***Montastrea annularis*** at 2 and 10m respectively (Davies, 1980), and much lower than 18.59 for ***P. porites*** at 10m (Edmunds and Davies, 1986) and close to the range of 2.8 to 12.5 for six species at 2.5m from Barbados, West Indies (Lewis and Post, 1982).

The number of polyps per cm^2 of ***S. pistillata*** is higher than ***E. gemmacea*** which has an approximately 82% larger polyp diameter than ***S. pistillata.***

The density of zooxanthellae is approximately 54% and 36% higher in ***S. pistillata*** at 1m when compared with the number of zooxanthellae in ***E. gemmacea*** at 3m on the basis of biomass unit and surface area respectively. This may be partly related to the number of zooxanthellae in the tentacles of the two species. The tentacles of ***S. pistillata*** are packed with zooxanthellae whilst the tentacles of ***E. gemmacea***, which are withdrawn in the day time, are devoid of zooxanthellae.

Comparing the values in the present study (Table 5.1) with other published data shows that the density of zooxanthellae in shallow water ***S. pistillata*** $9.82x10^5$ $.cm^{-2}$ is comparable with $10.0x10^5.cm^{-2}$. recorded from light-adapted ***S. pistillata*** from shallow water (Porter ***et al***, 1984) and lower than $16x10^5$ cm^{-2} for light-adapted ***S. pistillata*** (Falkowski and Dubinsky, 1981), $15.6 x10^5$ $.cm^{-2}$ for ***S. pistillata*** at 3-5 m depth (Drew, 1972), and much lower than $48.8x10^5$ cm^{-2} for ***S. mordax*** (cf. ***pistillata***) at 1m (Gattuso ***et al,*** 1991) or $24.5x10^3$ $polyp^{-1}$ for ***S. mordax*** at 13-15 m (Titlyanov ***et al,*** 1980). Some of these differences may result from differences in the methods used for measuring surface area.

Drew (1972) and Porter ***et al*** (1984) reported that the density of zooxanthellae per area unit are the same at different depths and among coral genera, although Dustan (1979) showed in ***Montastrea annularis*** the number of zooxanthellae decreases with increasing depth and the zooxanthellae appear to photoadapt to lower light intensity by increasing the size of the photosynthetic units (Dustan, 1982).

The energy content of tissue per mg. for ***S. pistillata*** 25.51 $J.mg^{-1}$ is 3.5% higher than the value of 24.6 $J.mg^{-1}$ for ***E. gemmacea*** tissue. This is probably due to the lower mean lipid content in the tissue of ***E. gemmacea*** as compared to ***S. pistillata*** (Chapter VII). The tissue energy content of both species is comparable to the mean value of five species of Gorgonacea 27.41 $J.mg^{-1}$ ash free dry weight (Lewis and Post, 1982), and higher than the 18.05 $J.mg^{-1}$ recorded for the tentacles of ***Heliofungia spp.*** (Davies, 1984) and 16.18 $J.mg^{-1}$ dry tissue for ***Porites porites***

(Edmunds and Davies, 1986). The low tissue energy content of tentacles of ***Heliofungia spp*** compared to ***S. pistillata*** and ***E. gemmacea*** may be related to the observation that lipid is stored in the lower half of the polyps (Fig. 2.2.4). The low value obtained for ***Porites porites*** was obtained using the wet oxidation technique, rather than by direct calorimetry.

The energy values of zooxanthellae are similar in both ***S. pistillata*** and ***E. gemmacea*** The values in the present study are comparable with 11.69 $J.10^6$ $zoox^{-1}$ recorded for ***Porites porites*** (Edmunds and Davies, 1986) and higher than 6.43 $J.10^6$ $zoox^{-1}$ for the temperate anemone, ***Anemonia sulcata*** reported by Tytler (1982) in Davies (1984).

The energy content of the planulae of ***S. pistillata*** 2.75 J. compares favourably with 2.6 J. $planula^{-1}$ recorded for ***Pocillopora damicornis*** (Richmond, 1981) and lower than 0.27 J. $planula^{-1}$ from ***Porites porites*** (Edmunds and Davies, 1986). On a unit weight basis the planula of ***S. pistillata*** has a high value of 29.47 J. mg., suggesting that it has a high level of stored lipid. This will favour its survival in the planktonic phase for a long period (Rinkevich and Loya, 1979a).

5.3.2 DARK RESPIRATION

The mean dark respiration rates vary between the two species. The values are 36% to 50% higher in ***S. pistillata*** when compared with ***E. gemmacea*** (Table 5.3). Kawaguti (1937) reported that corals with large polyps which are contracted in day time respire at a lower rate than corals with small and expanded polyps. Furthermore, Davies (1980) showed that corals with lower surface to volume ratios consume less oxygen than corals with higher surface to volume ratios. Finally, the lower value of respiration in ***E. gemmacea*** may result from the relatively greater proportion of the tissue extending deep into the skeleton which may be metabolically less active (Edmunds and Davies, 1986).

Comparing the mean rate of respiration on the basis of surface area in the present study with other published values shows that the mean dark respiration of ***S. pistillata*** at 1m during summer (9.84 μlO_2 $cm^{-2} h^{-1}$) is very similar to

9.7 μlO_2 cm^{-2} h^{-1} recorded for ***S. pistillata*** at 2 m from the Red Sea (Porter ***et al,*** 1984) and 8.1 μlO_2 cm^{-2} h^{-1} for ***Pocillopora eydouxi*** at 5 m from Guam (Davies, 1984). The respiration rates in the present study are within the range of 3.5-8.76 μlO_2 cm^{-2} h^{-1} for six species of coral at 2-5 m from Barbados, West Indies (Lewis, 1981) and lower than 11.38 μlO_2 cm^{-2} h^{-1} at 7 m for ***Porites lobata*** (Johannes and Tepley, 1974) and 11.91 μlO_2 cm^{-2} h^{-1} for ***Porites porites*** at 10 m (Edmunds and Davies, 1986).

The respiration rate for ***E. gemmacea*** of 1.38 μlO_2 mg^{-1} dry tissue h^{-1} at 3 m during summer is comparable with 1.65 and 1.19 μlO_2 mg^{-1} dry tissue wt.h^{-1} for ***Montipora verrucosa*** and ***Porites lobata*** at 3 m in Hawaii (Davies, 1991a) which also have a high relative biomass.

In ***S. pistillata***, the respiration rate in winter is about 64% of that in summer at both 1m and 10m depth, as a result of the 5.5 °C seasonal difference in temperature. ***E. gemmacea*** also shows lower winter values, the respiration rate being 87% (at 3m) and 70% (at 10m) of the rates in summer. There does not appear to be any information in the literature on equivalent measurements of seasonal variation in respiration rate for other coral species.

Respiration rates of ***S. pistillata*** at 10m are approximately 81% of those at 1m during both summer and winter whilst in ***E. gemmacea*** the respiration rates at 10m are 93% and 79% of the rates at 3m during summer and winter respectively.

It has been shown that the respiration rates of corals decrease with increasing depth (Davies 1977, 1980; McCloskey and Muscatine, 1984 ; Gattuso ***et al,*** 1991). Furthermore, shade-adapted corals respire less oxygen than light-adapted corals (Wethey and Porter, 1976; Falkowski ***et al,*** 1984 ; Porter ***et al,*** 1984).

In ***Montastrea annularis*** from Discovery Bay, Jamaica, the dark respiration rate at 10m is 46% of that at 3m (Davies, 1980) whilst, in shade-adapted ***S. pistillata*** the oxygen consumption is 54% of that in a light-adapted one (Muscatine ***et al,*** 1984). The reduction in coral respiration rates with depth or shade may be related to a reduction in translocation of organic material from the algae (Davies, 1980; Edmunds, 1986) which in turn is a function of decreased irradiance.

There is very little difference in the rates of respiration of the zooxanthellae between the two species. The values recorded, ranging from 1.37 to 3.1 $\mu lO_2 .10^6$ $zoox^{-1}$ h^{-1} are comparable with 2.61 μlO_2 10^6 $zoox^{-1}$ h^{-1} recorded for the zooxanthellae of ***Montastrea cavernosa*** at 5m (Davies, 1984), 1.84 μlO_2 10^6 $zoox^{-1}$ h^{-1} from ***Porites porites*** at 10m (Edmunds and Davies, 1986) 3.34 to 3.0 μlO_2 10^6 $zoox^{-1}$ h^{-1} for ***Montastrea annularis*** at 1m to 10m respectively (Dustan, 1982). The mean respiration rates of zooxanthellae decline with depths and seasons. The mean rates of zooxanthellae respiration at 10m are approximately 81% of that at 1m and 3m for ***S. pistillata*** and ***E. gemmacea***.. The values in winter are about 67% and 53% of that in summer for ***S. pistillata*** and ***E. gemmacea*** respectively, again reflecting the seasonal differences in water temperature.

5.3.3 PHOTOSYNTHESIS

The mean maximum gross photosynthesis (Pg_{max}) rates on the basis of both biomass and surface area are higher in ***S. pistillata*** than ***E. gemmacea***. This may be explained by the higher number of zooxanthellae when expressed on both biomass and surface area basis (Table 5.1.). When the values are expressed on the basis of zooxanthellae density, ***E. gemmacea*** shows higher values than ***S. pistillata*** (Table 5.4) suggesting that self-shading of zooxanthellae may occur in the latter species (Crossland and Barnes, 1977; Davies, 1991a).

In ***S. pistillata*** during the summer, the value of Pg_{max} on the basis of surface area (31.46 $\mu lO_2\,cm^{-2}\,h^{-1}$ at 1m) is higher than 22.9 $\mu lO_2\,cm^{-2}\,h^{-1}$ recorded for light-adapted ***S. pistillata*** at 2m (Porter ***et al***, 1984) but the value of 18.67 at 10m is comparable to 20.24 and 21.34 $\mu lO_2 cm^{-2} h^{-1}$ for shade-adapted specimens of the same species (Porter ***et al***, 1984 and Dubinsky ***et al***, 1984). The Pg_{max} for ***S. pistillata*** at 1m during summer is similar to 36.1μlO_2 cm^{-2} h^{-1} at 5m for ***Pocillopora eydoux***i (Davies, 1984).

However, the maximum gross photosynthesis values (ranging from 3.39 to 4.76 $\mu lO_2 mg^{-1}$ dry tissue wt.h^{-1}) for ***E. gemmacea*** fit quite well with 4.43 and 4.26 $\mu lO_2\,mg^{-1}$ dry tissue wt.h^{-1} for ***Porites porites*** at 10m and ***Porites lobata*** at

3m respectively, both of which species also have a large biomass of tissue (Edmunds and Davies, 1986 ; Davies, 1991a).

The Pg_{max} for ***S. pistillata*** is lower in winter than in summer and this can probably be attributed to the lower water temperature in winter. However, by contrast, at both 3m and 10m the maximum rate of photosynthesis of ***E. gemmacea*** is higher in winter than in summer, despite the temperature difference. No explanation is yet available for this, but the possibility of a compensatory process for either the lower light-levels and / or the lower water temperature of winter exist.

The values of Pg_{max} in the present study for both species decline with decreasing depth whilst the value of α increases with depth. These results have been shown to be associated with processes of photoadaptation in corals (Wethey and Porter, 1976; Chalker, 1981; Porter ***et al***, 1984; Gattuso, 1985, 1991 ; Wyman ***et. al***, 1987), although Chalker ***et al***, (1983) and Falkowski and Dubinsky, (1981) showed an increase in Pg_{max} with increases in depth .

The I_k values of the P v I curve are an indication of the relative efficiency of photosynthesis at low light-levels, a lower value of I_k indicating a higher efficiency.

The I_k values for ***S. pistillata*** decline from 343 $\mu E. m^{-2}.s^{-1}$ at 1m to194 $\mu E. m^{-2}.s^{-1}$ at 10m in summer and from 233 $\mu E. m^{-2}.s^{-1}$ at 1m to 157 $\mu E. m^{-2}.s^{-1}$ at10m in winter, as a result of photoadaptation by the zooxanthellae. Gattuso (1985) working with ***S. pistillata*** reported similar values of 318 $\mu E. m^{-2}.s^{-1}$ at 1m and 158.3 $\mu E. m^{-2}.s^{-1}$ at 10 m , whilst Porter ***et. al.*** (1984) found values of 273 and 60 $\mu E. m^{-2}.s^{-1}$ for light and dark adapted ***S. pistillata*** respectively. The I_k values for ***E. gemmacea*** show less variation with depth and the values are comparable to the values of 176 and 177 $\mu E. m^{-2}.s^{-1}$ for ***Montipora verrucosa*** and ***Porites lobata*** at 3m (Davies, 1991a).

Both ***S. pistillata*** and ***E. gemmacea*** display lower values of I_k in the winter than the summer at both depths, indicating photoadaption to the lower light levels prevailing during these months (see section 3.4.2). This appears to be the first report

of a seasonal photoadaption response in corals.

5.3.4 GROWTH

The linear growth rates in the two species can be interpreted as suggesting that growth increases rapidly at the tip of the nubbin rather than laterally (Goreau, 1959 ; Rinkevich and Loya, 1984 ; Davies, 1984). However, the growth rate of hermatypic corals is influenced by light, temperature and sedimentation (Goreau, 1959 ; Shinn, 1966; Dodge *et al*, 1974 ; Buddemeier and Kinzie, 1976; Houck and Buddemeier, 1977 ; Buskirk *et al*, 1981 ; Wellington and Glynn, 1983). Other factors such as reproduction and production of mucus tunics by species of ***Porites*** also reduce the growth rate of the skeleton (Loya, 1985 ; Davies, 1989). The seasonal and depth variation in the mean growth rate of the skeleton in ***S. pistillata*** and ***E. gemmacea*** in the present study are explained as being mainly due to the difference in the light intensity, temperature and day length with season and depth (see section 3.4.2.), since reduction in light intensity reduces the rate of calcification as a result of the reduction of the rate of photosynthesis by the zooxanthellae (Barnes and Crossland, 1980 ; Abdel-Salam and Porter, 1988). The rate of sedimentation in the present study is unlikely to affect the growth of the two species, whilst reproduction of ***S. pistillata*** during the period of measurement in winter might influnce its growth rate. However, ***S. pistillata*** seems to be more sensitive to exogenous and endogenous factors (Loya, 1985) than ***E. gemmacea*** which shows little variation in its growth rate with season and depth. This characteristic is shared with ***Porites lutea*** and ***Porites porites*** which also appear to be insensitive to environmental influence (Hudson *et al*, 1982 and Davies, 1990). The mean daily skeletal growth rates recorded for ***S. pistillata*** and ***E. gemmacea*** (Table 5.6) fall within the range of 12.5 to 51.6 mg skeleton d^{-1} measured for several other coral species from 2 to 10 m water depth (Davies, 1984; Edmunds and Davies, 1986 and Davies, 1989, 1990 and 1991a).

The daily tissue growth rate (Table 5.6) which was predicted from the ratio of the dry tissue weight to the skeletal weight is proportional to the skeletal growth. The mean daily tissue growth rate of ***S. pistillata*** at 1 m during summer is closely similar to 0.76 mg. d. t. d^{-1} for ***Pocillopora damicornis*** at 3 m (Davies, 1991a), but it is much higher than 0.122 mg. d. $t.d^{-1}$ measured for ***Pocillopora eydouxi*** at 5 m

(Davies, 1989).

When comparing the values of tissue growth rate in the two species (except ***S. pistillata*** at 1 m in summer) with other published values, those in the present study are much lower than 0.95 $mg.d^{-1}$ for ***Porites porites*** at 10 m, 1.2 and 2.26 $mg.d^{-1}$ recorded for ***Montipora verrucosa*** and ***Porites lobata*** at 3 m respectively (Davies, 1991a) .

CHAPTER VI

6. THE 24 HOUR ENERGY BUDGET

6.1. INTRODUCTION

Determination of the energy budget of corals involves measurement of the individual components of photosynthesis, respiration and growth of both zooxanthellae and animal tissue components. Results for these have been given and discussed in chapter five. In this chapter, the separate components are brought together, to create 24-hour energy budgets at different depths and seasons for the two species of coral.

6.2 RESULTS

The daily energy budget components of ***S. pistillata*** and ***E. gemmacea*** at 1, 3 and 10 m water depth during summer 1989 and winter 1990 are shown in Table (6.1). These values were calculated from the previous chapter (V) and normalized to a 10g skeleton weight nubbin. The 10g nubbin of ***S. pistillata*** contains a mean of 103 mg dry tissue, whilst the 10g nubbin ***E. gemmacea*** has a mean of 128.6 mg dry tissue.

6.2.1 ENERGY INPUT

A) Daily Productivity

The daily productivity of the two species at the study site was predicted using the daily in situ light curves (Fig. 3.4.9 and 3.4.10). The light curves at three depths 1, 3 and 10 m were measured on cloudless days during summer 1989 and winter 1990 (see Chapter III). In summer 1989 (from 30 July to 1August), the integrated daily P.A.R was 32.56, 26.72 and 10.94 $E.m^{-2}.d^{-1}$ at 1, 3 and 10 m respectively over approximately 13.25 hours, whilst in winter 1990, the values were 21.55, 18.06 and 8.43 $E.m^{-2}.d^{-1}$ at the same depths respectively over approximately 11.25 hours. Light readings at intervals of 15 minutes (Fig. 3..4.5) were read from these curves and substituted into the hyperbolic tangent function formula, using a computer programme to produce a value for daily productivity. This value was then

converted into Joules using the oxy-joule equivalent of 21.831 (Davies, 1991a) and then the values were normalized to a 10g skeleton weight nubbin (Table 6.1).

In ***S. pistillata*** the energy input from the zooxanthellae in summer at 10 m water depth was 42.8% (82.66J) of that at 1m (193.1J), and in winter it was 73.5% (82.81J) at 10 m of that at 1m (112.72J). The value in winter at 1m was 58.3% of that in summer at the same depth and at 10 m, it was not much different between winter and summer, despite the higher water temperature and the higher light-levels.

In ***E. gemmacea***, there was a similar pattern, although there was no significant difference between summer and winter for corals at 3m. The most significant feature was that photosynthesis at 10 m was lower in summer than in winter, as was noted previously with ***S. pistillata***. In summer 1989 (69.17J) and winter 1990 (75.9J) at 10 m, the values were 70.6% and 76.7% of that at 3m (98.01 J and 99.13J) respectively whilst in winter at 3m and 10 m, the values were 1.1% and 8.9% higher than that in summer respectively.

6.2.2 ENERGY EXPENDITURE

A) RESPIRATION

The mean dark respiration (μlO_2 mg^{-1} dry tissue $wt.h^{-1}$) of the colony of both species was extrapolated to 24h, assuming that the respiration during the day is the same as in the night. The values were then converted to energy units, using the oxy-joule equivalent of 19.63 (Elliot and Davison, 1975) and finally the values were normalized to a 10g skeleton weight nubbin (Table 6.1).

The dark zooxanthellae respiration (μlO_2 10^6 $zoox^{-1}.$ h^{-1}) from the previous chapter (Table 5.3) was also extrapolated to 24h and the values converted to Joules and normalized to a 10g nubbin for both species using data from Table 5.1 (Table 6.1).

a) Animal Tissue

The 24h energy expenditure of the animal tissue in each species was obtained by subtracting the 24h energy expenditure of zooxanthellae respiration from the 24h energy expenditure of the colony (Table 6.2).

In ***S. pistillata***, the energy used in respiration of the animal tissue decreases with depth in both summer and winter. Thus in summer a 10g nubbin uses 99.75J at a depth of 1m and 79.87J at a depth of 10 m. In winter the corresponding values are 61.62J at 1 m and 50.97J at 10 m.

As expected from the lower water temperatures in winter, the respiration rate of the animal tissue from corals at 1m decreases from 99.75J in summer to 61.62J in winter. Likewise in corals from 10m the fall is from 79.87J in summer 50.97J in winter.

Respiration of the animal tissues is a major energy sink, accounting for between 51.66% and 61.55% of energy fixed. This rises to 96.62% in the case of ***S. pistillata*** at 10m in summer where the photosynthetic fixation is only slightly higher than the 24h animal respiration demand.

In ***E. gemmacea*** there is very little difference in respiration with depth in summer, with values of 59.85J at 1m and 57.97J at 10m. In winter however, the 10m corals have a lower energy utilisation for animal respiration, 44.65J as against 60.05J at 3m.

The shallow corals do not show any seasonal difference: the summer value is 59.85J compared with 60.05 in winter. The corals at 10m however have a lower value in winter as expected, 44.65J compared with 57.97J in summer.

The animal tissue respiration in ***E. gemmacea*** accounts for between 58.83% and 61.07% of energy fixed except for the low depth corals in summer where, as a result of a low photosynthesis value, it is 83.8% of energy fixed.

b) Zooxanthellae

In ***S. pistillata*** the respiration of the zooxanthellae was lower for corals at 10m than 1m in both summer and winter. The values were 33.93J and 29.02J at 1 and 10m respectively in summer, and 24.16J and 18.66J respectively in winter. Winter values were lower at both depths, being 33.93J and 24.16J in summer and winter at 1m and 29.02J and 18.66J respectively at 10m. These represent between 17.57% and 22.53% of energy fixed except for the 10m corals in summer where it was 35.11%.

Table 6.1 Summary of 24h energy budget components of 10g nubbin of ***S. pistillata*** and ***E. gemmacea*** at 1, 3, and 10m water depth during summer 1989 and winter 1990 .

	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90
Photosynthesis					
ml $O_2.d^{-1}$	1	8.81 ± 1.32 (20)	5.163 ± 1.54 (22)		
$J.d^{-1}$		193.104 ± 28.84	112.722 ± 33.78		
ml $O_2.d^{-1}$	3			4.49 ± 0.58 (20)	4.54 ± 1.0 (18)
$J.d^{-1}$				98.01 ± 12.86	99.13 ± 21.90
ml $O_2.d^{-1}$	10	3.79 ± 0.66 (20)	3.79 ± 0.61 (12)	3.169 ± 0.62 (20)	3.48 ± 0.7 (20)
$J.d^{-1}$		82.66 ± 14.42	82.81 ± 13.39	69.17 ± 13.63	75.90 ± 15.17
Respiration					
Colony					
ml $O_2.d^{-1}$	1	6.81 ± 1.11 (27)	4.37 ± 1.28 (22)		
$J.d^{-1}$		133.687 ± 21.84	85.78 ± 25.12		
ml $O_2.d^{-1}$	3			4.26 ± 0.49 (20)	3.73 ± 1.6 (21)
$J.d^{-1}$				83.62 ± 9.61 (20)	73.22 ± 31.41
ml $O_2.d^{-1}$	10	5.55 ± 0.84 (20)	3.55 ± 0.54 (13)	3.98 ± 0.58 (20)	2.81 ± 0.98 (20)
$J.d^{-1}$		108.89 ± 16.49	69.63 ± 10.67	78.13 ± 11.38	55.16 ± 19.23

	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90
Respiration					
Zooxanthellae					
ml O_2.d^{-1}	1	1.728 ± 0.39 (11)	1.231 ± 0.16 (9)		
J.d^{-1}		33.93 ± 7.83	24.16 ± 3.23		
ml O_2.d^{-1}	3			1.212 ± 0.15 (12)	0.671± 0.20 (9)
J.d^{-1}				23.769 ± 3.14	13.17 ± 4.06
ml O_2.d^{-1}	10	1.48 ± 0.22 (12)	0.95 ± 0.04 (8)	1.03 ± 0.15 (13)	0.54 ± 0.09 (10)
J.d^{-1}		29.022 ± 4.45	18.655 ± 1.75	20.163 ± 3.14	10.51 ± 1.91
Growth rate					
Tissue					
mg.d^{-1}	1	0.577 ± 0.16 (51)	0.222 ± 0.07 (51)		
J.d^{-1}		14.72 ± 4.13	5.66 ± 1.78		
mg.d^{-1}	3			0.173 ± 0.05 (40)	0.174 ± 0.072 (41)
J.d^{-1}				4.256 ± 1.23	4.28 ± 1.77
mg.d^{-1}	10	0.14 ± 0.03 (58)	0.095 ± 0.02 (46)	0.16 ± 0.05 (64)	0.132 ± 0.06 (43)
J.d^{-1}		3.572 ± 0.96	2.424 ± 0.63	3.940 ± 1.30	3.250 ± 1.50

	Depth (m)	*S. pistillata* Summer 89	*S. pistillata* Winter 90	*E. gemmacea* Summer 89	*E. gemmacea* Winter 90
Growth rate					
Zooxanthellae					
10^5 zoox.d^{-1}	1	1.60 ± 0.45 (51)	0.62 ± 0.20 (51)		
J.d^{-1}		1.62 ± 0.45	0.63 ± 0.20		
10^5 zoox.d^{-1}	3			0.22 ± 0.065 (40)	0.22 ± 0.09 (41)
J.d^{-1}				0.22 ± 0.065	0.22 ± 0.09
10^5 zoox.d^{-1}	10	0.39 ± 0.08 (58)	0.26 ± 0.06 (46)	0.20 ± 0.06 (64)	0.17 ± 0.08 (43)
J.d^{-1}		0.395 ± 0.08	0.264 ± 0.06	0.202 ± 0.06	0.17 ± 0.08

Table 6.2 Summary of 24h energy budget of ***S. pistillata*** and ***E. gemmacea*** at 1, 3, and 10m water depth during summer 1989 and winter 1990 at the study site in Sharm Ubhur.

		Zooxanthellae							Animal				
	Depth (m)	Photosynthesis	=	Respiration	+	Growth	+	Translocation	Respiration	+	Growth	+	Losses
S. pistillata													
Summer 89	1	193.10	=	33.93	+	1.62	+	157.55	99.75	+	13.1	+	44.70
		100%		17.57%		0.84%		81.59%	51.66%		6.78%		23.15%
	10	82.66	=	29.02	+	0.395	+	53.24	79.87	+	3.18	+	-29.81
		100%		35.11%		0.48%		64.41%	96.62%		3.85%		-36.06%
Winter 90	1	112.72	=	24.16	+	0.63	+	87.93	61.62	+	5.03	+	21.28
		100%		21.43%		0.56%		78.01%	54.67%		4.46%		18.88%
	10	82.81	=	18.66	+	0.26	+	63.89	50.97	+	2.16	+	10.76
		100%		22.53%		0.32%		77.15%	61.55%		2.61%		12.99%
E. gemmacea													
Summer 89	3	98.01	=	23.77	+	0.22	+	74.02	59.85	+	4.04	+	10.13
		100%		24.25%		0.22%		75.52%	61.07%		4.12%		10.33%
	10	69.17	=	20.16	+	0.20	+	48.81	57.97	+	3.74	+	-12.89
		100%		29.14%		0.29%		70.56%	83.80%		5.41%		-18.65%
Winter 90	3	99.13	=	13.17	+	0.22	+	85.74	60.05	+	4.06	+	21.63
		100%		13.29%		0.22%		86.49%	60.58%		4.10%		21.81%
	10	75.90	=	10.51	+	0.17	+	65.22	44.65	+	3.08	+	17.49
		100%		13.85%		0.22%		85.93%	58.83%		4.06%		23.04%

E. gemmacea exhibits a similar pattern. Respiration of the zooxanthellae amounts to 23.77J at 3m compared with 20.16J at 10m in summer, and 13.17J compared with 10.51J at 3 and 10m respectively in winter. Summer values are higher than winter, being 23.77J as against 13.17J at 3m and 20.16J as against 10.51J at 10m. The percentage of energy fixed range between 13.29% and 24.25% except in summer at 10m where it is 29.14%.

B) GROWTH

The tissue growth rates of both species (Tables 6.1) were estimated from the skeletal growth rates (Table 5.6) and the ratio of skeleton weight to tissue weight

(Table 5.1). Since the growth rates of tissue were approximately linear, it was assumed that growth of each nubbin was essentially apical. The growth rates of tissue were therefore not normalized to a 10g nubbin (see Davies, 1984). The values of the mean daily tissue growth rates were converted to energy units, using the energy values of tissue for each species in (Table 5.1)

The daily growth rates of zooxanthellae for the two species were calculated from the daily growth rates of tissue (Table 6.1), and the ratio of tissue weight to the number of zooxanthellae (Table 5.1). The values of growth, expressed as numbers of zooxanthellae per day were then converted to energy units (Table 6.2), by applying the energy values of zooxanthellae for each species (Table 5.1). Thereafter, the energy values of the animal tissue growth (Table 6.2), were obtained by subtracting the energy values of zooxanthellae growth from the energy values of the whole tissue growth.

In ***S. pistillata*** the energy allocated to growth in summer falls from 13.1J at 1m to 3.18J at 10m whilst in winter the change with depth is from 5.03 to 2.16J. On a seasonal basis, the energy for growth is lower in winter than in summer being 5.03J as against 13.1J at 1m depth, and 2.16J as against 3.18J at 10m depth. Animal tissue growth accounts for between 6.78% and 2.6% of the energy fixed over the two depths and two seasons.

In ***E. gemmacea***, there is a lower allocation of energy to growth with increasing depth but the differences are not as marked. In summer, the values are 4.04J at 3m and 3.74J at 10m, whilst in winter the corresponding values are 4.06J and 3.08J. There is very little difference in energy used in growth between summer

and winter. At 3m the values are the same, at 4.04J in summer and 4.06J in winter, whilst at 10m the values are 3.74J and 3.08J respectively. The energy used in growth as a percentage of energy fixed varies from 4.1% to 5.41%.

The pattern of energy allocation to growth and division of zooxanthellae at different depths and seasons follows that of the animal tissue. However, the percentage of the photosynthetic energy which this represents is considerably smaller. In *S. pistillata* between 0.32% and 0.84% is allocated to zooxanthellae growth and in *E. gemmacea* between 0.22% and 0.29%.

C) OTHER ENERGY COMPONENTS

Due to the difficulty in measuring other minor components, the energy expenditure on reproduction, zooxanthellae culling, nematocyst loss and skeletal and organic matrix growth was not included in the present study.

D) LOSSES

Losses from the colony were not measured directly, but were predicted by subtraction of the measured energy utilising processes from the energy fixed in photosynthesis.

A positive value for loss suggests that excess carbon compounds are lost as mucus lipid (Crossland *et al*, 1980 ; Crossland, 1987). A negative value indicates that photosynthetic input alone is not adequate to meet energy demands.

In *S. pistillata* it is predicted that there would be a surplus of 23.15% of photosynthetic input in summer at 1m depth whilst at 10m because of the very much reduced photosynthesis, there would be a deficit of 36.06%. In winter there would be a surplus of 18.88% at 1m, falling to a surplus of 12.99% at 10m.

In *E. gemmacea*, in summer the excess amounts to 10.33% at 3m, but falls into a deficit of 18.65% at 10m. As in *S. pistillata*, in winter a surplus is predicted at both depths investigated. At 3m the excess amounts to 21.81% and at 10m it is 23.04% of energy fixed in photosynthesis.

6.3 DISCUSSION

The energy budgets constructed for ***S. pistillata*** and ***E. gemmacea*** are similar to those of Davies (1984 and 1991a) and Edmunds and Davies (1986). However, the objectives of the present study are to compare the energy components for the two species with different polyp size, under different light intensities due to water depth (1, 3 and 10m) and at different seasons (summer and winter) which involved changes in both light and water temperatures.

At the study site, the P.A.R. decreases with depth and season. The daily integrated P.A.R. in winter (January 1990) at 10m depth was about 39% and 46% of that at 1m and 3m respectively, and in summer (July 1989) it was about 33% and 40%. In winter, daily integrated P.A.R. was 66%, 67% and 77% of that in summer at 1m, 3m and 10m respectively (Chapter III).

The sea water temperature varies with season and slightly with depth. In winter (January 1990) the average sea water temperature was 84% of that in summer at 3m with annual range of monthly mean temperature 25.5-31.0 °C. The temperature at 10m was 30 °C and 25 °C in July and January 1990 respectively. The annual variation in salinity was very narrow, about 1%. The study site during July 1989 and January 1990 received similar amounts of sedimentation at 3m.

In discussing the energy budgets of the two coral species, the general features of the budgets as demonstrated in the shallow water corals will be considered first. Then comparison between the two species will be made and finally the effects of depth and season on the energy budgets will be discussed.

A) General Features

For the purpose of the initial budget calculation, it will be assumed that the only input source is from photosynthesis of the zooxanthellae. In ***S. pistillata***, results of feeding experiments discussed in chapter II, suggest that heterotrophic input from zooplankton and by suspension feeding are of minimal importance. In ***E. gemmacea*** zooplankton feeding is again probably unimportant but suspension

feeding may make a significant contribution to the budget. This aspect will be considered further at the end of the discussion.

The model on which the energy budget calculation is based, assumes that the first call on the energy fixed in photosynthesis is for the respiration and growth of zooxanthellae. Any excess is then translocated to the host tissues. The energy used in respiration of the zooxanthellae is in the range of 13 to 24% of the energy fixed in photosynthesis during a 24h period. This compares with values of 21% for ***Porites porites*** at 10m (Edmunds and Davies, 1986) and 13.1% to 32.9% for ***Montipora verrucosa*** and ***Porites lobata*** (Davies, 1990). In ***Pocillopora eydouxi*** and ***P. damicornis*** the values are lower, 9.8% and 8.3 % respectively (Davies, 1984 ; 1991a). This may be because the former group comprising ***Porites spp.*** and ***Montipora*** have deep dewelling tissue containing zooxanthellae which may not be active in photosynthesis. In light-adapted ***S. pistillata*** Muscatine ***et al,*** (1984) calculated that the zooxanthellae respiration accounted for only 2.5% of energy fixation. However, different methods were used to determine this value and so the result is not directly comparable.

The energy expended by zooxanthellae in growth is very low, ranging from 0.2 to 0.8% of energy fixation, reflecting the low rate of growth of the algae when in symbiosis. The values obtained are similar to the range of values of 0.1% to 0.8%, obtained for ***Pocillopora eydouxi***, ***P. damicornis***, ***M. verrucosa*** and ***P. porites*** (Davies, 1984, 1991a ; Edmunds and Davies 1986), but lower than the values of 1.6 to 2.1% for ***P. lobata*** (Davies, 1991a) and 1.0% to 2.6% for light-and shade-adapted ***S. pistillata*** (Muscatine ***et al,*** 1984).

The quantity of carbon compounds translocated to the host tissues is determined by subtracting the sum of the zooxanthellae energy utilisation in respiration and growth from the total daily photosynthesis. It is generally assumed that zooxanthellae respiration and growth do not change in response to light level changes whilst the rate of photosynthesis will. As a result the percentage of energy translocated will also vary with light levels and translocation therefore can only be compared between species, under similar conditions of a cloudless "ideal" day. In the present study in shallow water, between 75% and 86% of fixed energy was translocated to the host over a 24h period. This is broadly similar to previously published values of 90% for ***P. eydouxi*** (Davies, 1984), 93% to 97% for shade and light adapted ***S. pistillata*** (Muscatine ***et al,*** 1984), 78% for ***P. porties*** (Edmunds

and Davies, 1986) and 66% to 91% for ***P. damicornis, M. verrucosa*** and ***P. lobata*** (Davies, 1991a).

The major consumption of energy over a 24h period is for the respiration of the animal tissues. The values recordered were in the range of 52-61% of energy fixation, which are broadly similar to values in previously published studies.

Animal growth is a minor sink for fixed energy, between 4% and 7% being utilised in this way. These values are again similar to the range of values in previous studies.

The energy budgets are balanced by assuming that energy which is not used in growth and respiration, is lost from the colony. This makes the assumption that the lipid stores are replete, since the model of energy flux developed by Davies (1991a) suggests that following a period of low daily light, some of the energy will be diverted to the lipid stores. The levels of loss, which are assumed to leave the colony as mucus and mucus-lipid (Crossland ***et al***, 1980a ; Crossland, 1987) vary from 10% to 23% of energy fixed. These values are similar to those of ***Pocillopora damicornis M. verrucosa*** and ***P. lobata*** which were in the range of 19- 32%. However, earlier studies have reported higher values e.g. 48% for ***P. eydouxi*** (Davies, 1991a) ; 45- 67% for ***P. porites*** (Edmunds and Davies, 1988), 54% for shade adapted ***S. pistillata*** (Muscatine ***et al***, 1984). The extent of the surplus energy is dependent upon the photosynthesis during the day and Davies (1991a) showed that on an overcast day ***P. damicornis*** and ***P. lobata*** in shallow water would not fix enough to meet the daily requirements, resulting in a deficit budget. During days of low light level, it was predicted that corals would draw upon their extensive lipid reserves (Stimson, 1987) to balance their energy budget.

B) Comparison of Energy Budgets of *S. pistillata* and *E. gemmacea*

It is not possible to make direct comparisons between 10g nubbins of the two species in terms of joules of energy fixed or expended, because of the differences in surface area, biomass of tissue etc. However, it is possible to compare the percentage utilisation of the energy fixed in a 24h period. In fact, the energy budgets of ***S. pistillata*** and ***E. gemmacea*** from shallow water are remarkably similar. There is no apparent difference in percentage of energy used in respiration

of zooxanthellae, animal tissue respiration, growth of animal tissues, nor energy loss as mucus-lipid. The only suggested difference is in the proportion of energy used in the growth of zooxanthellae, where values in ***S. pistillata*** are about 2-4 times of ***E. gemmacea.*** At the outset, it had been assumed from the model of Porter (1976) that the small polyp coral, ***S. pistillata***, would have a greater dependence upon autotrophic input than the large polyp ***E. gemmacea*** which was expected to have a greater dependence upon hetrotrophic zooplankton feeding. However, as noted in chapter II ***E. gemmacea*** is not a specialised carnivorous feeder and this is perhaps reflected in the similarity of the energy budgets of the two species.

C) Effect of Depth on the Energy Budgets

With increase in depth there is an attenuation of light (Chapter III). One response to this is for the zooxanthellae to undergo photoadaptation, manifest as an increase in α and decreases in I_k in the hyperbolic tangent equation relating photosynthesis to irradiance (Chapter IV). This results in an increase in efficiency of harvesting the available light for photosynthesis. Despite photoadaptation, it is clear that in both ***S. pistillata*** and ***E. gemmacea*** the daily photosynthetic production of corals at 10m is reduced in comparison to those from 1m or 3m. The rates of respiration of both zooxanthellae and animal tissues are reduced in corals from 10m, whilst the growth rates of ***S. pistillata***, but not ***E. gemmacea***, are also reduced. Despite these reductions, the actual surplus energy which would have to be excreted is lower at 10m than at 1 or 3m in both species and in both summer and winter.

The budgets of both ***S. pistillata*** and ***E. gemmacea*** from 10m during the summer time require special mention, since both of these budgets were in deficit. This was unexpected, and appears to be a direct result of the lowered rate of photosynthetic production.

The photosynthetic rate of ***S. pistillata*** is the same as the corresponding winter value and that of ***E. gemmacea*** is slightly lower than the winter value, despite the higher water temperature and the longer duration of higher levels of light during the summer. No hypothesis to explain this is yet available. However, similar results were obtained by McCloskey and Muscatine (1984) in comparing the

daily carbon budgets of ***S. pistillata*** from 3m and 35m (see Achituv and Dubinsky, 1990). Here the carbon fixed in photsynthesis in the deep corals was only 24% of the shallow corals. Although the deep corals had lower carbon utilization for respiration and growth of both zooxanthellae and animal tissue, the carbon budget of the deep coral had a significant deficit.

D) Effect of Season on the Energy Budget

In comparing the budgets of the two coral species in summer and winter, the effects of changes in both light and temperature have to be borne in mind. In winter, the daily light availability on a clear day in shallow water is 66% of that in summer and the water temperature is 26.6°C compared with 30.8.°C in summer (Chapter III). The lower light levels resulted in photoadaptation responses by the zooxanthellae as noted previously (Chapter V). The lower water temperature would be expected to cause a reduction in both the rates of photosynthesis and the rate of respiration (Coles and Jokiel, 1977). Because of the anomalous photosynthesis data of the 10m corals in summer, discussion will be confined to comparison of seasonal differences in the shallow water corals.

In ***S. pistillata*** the daily photosynthetic production in winter is only 58% of that in summer. Respiration rates and growth rates of both zooxanthellae and animal tissues are reduced by 50% or more. The overall result is that the surplus in the budget is approximately half of that in summer months. In ***E. gemmacea***, the photosynthetic production is not very different between winter and summer, suggesting that some temperature adaptation (thermal acclimation) process may be invoked. This may also explain the similarity in the energy expenditure in animal respiration between summer and winter and also in growth rate of both zooxanthellae and animal tissue. Only the respiration rate of the zooxanthellae appears to be reduced in winter. The outcome of this is that the energy surplus of ***E. gemmacea*** is higher in winter time.

E) Sources of Error in Energy Budget Determination

As noticed earlier, ***E. gemmacea*** may have a higher net daily energy input

as a result of feeding upon particulate matter (Chapter II). It is difficult to quantify the extent of this input. However, in the course of these experiments ***E. gemmacea*** was observed to trap and ingest a single large faecel pellet from a fish. This was retrieved and its energy content determined by bomb calorimetry. When the energy content is normalized to a 10g skeleton weight nubbin, it would result in an input of an additional 44.1J. This would be sufficient energy to bring the deficit budget of this coral at 10m in summer time into surplus.

The energy budget of both species may be in error as a result of difficulties in determining the rate of respiration of zooxanthellae in situ, and of the rate of respiration of both zooxanthellae and animal tissue during photosynthesis. It has been suggested that the respiration rates of freshly isolated zooxanthellae may be higher than those in situ (McCloskey and Muscatine, 1984 ; Muller-Parker, 1984). Furthermore, measurements of respiration rate of whole nubbins of ***P. porites*** which were made immediately after a period of photosynthesis, were elevated when compared to respiration measurements which were made following a dark phase (Edmunds and Davies, 1988). If respiration rate is elevated throughout a daylight period, the energy surpluses would be lower than in the budgets presented here. This will be investigated further in the next chapter.

CHAPTER VII

7. SURPLUS ENERGY AND ITS PATHWAY

7.1. GENERAL INTRODUCTION

Energy generated photosynthetically in corals is thought to be translocated to the host tissue as glycerol, fatty acids and lipid (Muscatine, 1967 ; Patton ***et al***, 1983 ; Patton and Burris, 1983). Previous studies have shown that on cloudless days in shallow water, this energy is sufficient to provide for the energy requirements for respiration and growth and there is an excess which is either stored or excreted (Davies, 1984, 1991a ; Muscatine ***et al***, 1984 ; Edmunds and Davies, 1986) see also Chapter VI). Conversely on cloudy days photosynthesis may not meet the total energy requirements and the corals may have to draw upon their lipid reserves. These reserves may be located in the basal tissue of the polyps (Stimson, 1987, 1990, see also chapter II), or in fat bodies in the coelenteron (Stimson, 1987). The ability of the coral to store sufficient lipid to withstand successive cloudy days is of ecological importance. For this reason it was considered important to investigate the levels of stored lipid in ***S. pistillata*** and ***E. gemmacea*** and determine whether there were any changes with season and with depth on the reef.

In addition, very recent studies have focused on the rhythmical variations of photosynthesis and respiration which might cause errors in calculating the energy budgets in corals(Edmunds and Davies, 1988 ; Shick, 1990), and in phytoplankton (Harding ***et al***, 1982). Since this phenomenon is a fundamental factor in the energy budget construction, it will also be considered.

7.2. RHYTHMICAL VARIATIONS IN PHOTOSYNTHESIS AND RESPIRATION

7.2.1. INTRODUCTION

Diel variation in photosynthesis has been recognized in plant-animal symbioses (Roffman, 1968 ; Chalker and Taylor, 1978 ; Dykens and Shick, 1984). These workers showed that the photosynthetic activities of the algae in coral decrease during the day time when exposed to constant light condition. Similar observations have been made in phytoplankton (Harris and Lott, 1973), and in marine algae (Downton ***et al***, 1976). Conversely, respiratory activities are higher during the day time than night time in both corals (Edmunds and Davies, 1988 ; Shick, 1990) and in

sea anemones (Muller-Parker, 1984). Dark respiration remains constant throughout the night (Muller-Parker, 1984) . In order to asses the possible effects of these variations on the energy budgets, experiments were carried out to measure the rates of respiration under constant darkness and after periods of illumination.

7.2.2. METHOD

The effect of time of day on dark respiration and net photosynthesis of ***S.pistillata*** and ***E. gemmacea*** was investigated by taking measurements at intervals between dawn and dark . An individually collected nubbin was placed in the running sea water tank overnight, after its tile had been carefully cleaned. The following day beginning at 8.00 hrs, the dark respiration of the nubbin was measured over a 10 min period at intervals of 3 hours at a temperature of 28 ^{0}C. Between measurements, the nubbin remained in darkness in the respirometer chamber . During this time pre-filtered aerated sea water was passed through the chamber. The final respiration measurement was at 20.00 hours. The respiration rate of 5 nubbins of each species was measured in this way . In a separate experiment, the net photosynthesis of a group of five nubbins from each species was obtained at a saturation irradiance 370 $\mu E.m^{-2}\ s^{-1}$ in the case of ***S. pistillata*** and 270 $\mu E.m^{-2}\ s^{-1}$ in ***E. gemmacea*** at 8.00 hours and then at intervals of 3 hours until 17.00 hours . Between measurements the nubbin was left in the chamber under a dark cycle and supplied with pre-filtered sea water. The dark respiration and the net photosynthesis were expressed as $\mu lO_2\ mg^{-1}$. d.t.wt. h^{-1}.

The effect of illumination on dark respiration was again measured at a temperature of 28 ^{0}C. Newly collected nubbins (n = 5 for each species) were maintained in the running sea water tank under darkness overnight. The nubbin was transferred in darkness to the respiration chamber and the initial rate of dark respiration measured. It was then exposed to saturation irradiance (370 $\mu E.m^{-2}\ s^{-1}$ for ***S. pistillata*** and 270 $\mu E.m^{-2}\ s^{-1}$ for ***E. gemmacea***) for a period of 10 mins. This was succeeded by a 20 min measurement of dark respiration, followed by a 20 min period of photosynthesis. When the percentage saturation of the water had reached 100%, aerated seawater was flushed through the chamber . This procedure of alternating photosynthesis and dark respiration measurements was repeated using photosynthesis exposure periods of 40 min and 80 min. In this way respiration measurements were made after cumulative light exposure periods of 10, 30, 70,

150 mins.

In another series of experiments, the effect of exposure to a light regime similar to that experienced by the corals at their shallow water site, on the rate of net photosynthesis was investigated . Dark respiration of a nubbin was measured at 6.00 hrs for 20 min. The coral was then exposed to gradually increasing light according to the previously measured daily light cycle at that depth (Chapter III) . When the oxygen level in the chamber had reached 100% saturation, aerated seawater was flushed through the chamber. At 8.00 hrs for ***S. pistillata*** the light level had reached photosynthetic saturation of 370 $\mu E.m^{-2}\ s^{-1}$. The inlet water was then stopped and the net photosynthesis was measured for 10 min, befor resuming the flow of water through the chamber . It was not possible to increase the light level further, but light was maintained at the saturation level until 16.00 hrs . Measurements of net photosynthesis were made at 10.00, 12.00, 14.00 and 16.00. After the reading at 16.00 the light levels were gradually reduced again, reaching 174 $\mu E.m^{-2}\ s^{-1}$ at 18.00 . At this point the light was switched off for 20 min in order to record dark respiration rate . The light was then switched on again and was gradually reduced to zero at 19.30. A final dark respiration rate was measured at 20.00 hrs . A sample of 5 nubbins of both species was measured on this way .

In ***E. gemmacea*** the procedure was similar, but its saturation light level of 270 $\mu E.m^{-2}\ s^{-1}$ was reached at 7.30 hrs, and measurements of net photosynthesis were made at 7.30, 9.30, 11.30, 13.30, and 15.30 hrs . Dark respiration was measured again at 17.30 hrs when the light level had fallen to 257 $\mu E.m^{-2}\ s^{-1}$ and at 19.30 hrs.

7.2.3.RESULTS

The daily respiration and photosynthetic rhythms of ***S. pistillata*** and ***E. gemmacea*** under constant darkness are presented in Tables 7.1 to 7.4.

The mean rate of dark respiration of ***S.pistillata*** and ***E.gemmacea*** during the dark cycle was 1.376 ± 0.03 and 1.078 ± 0.02 $\mu lO2.mg^{-1}$ $d.t.h^{-1}$. respectively. One way Anova tests showed no significant difference in the dark respiration during the day (Tables 7.1. and 7.2.). Similarly, the two species showed no changes in their

Table 7.1. Dark respiration rate ($\mu lO_2\ mg^{-1}.d.t.h^{-1}$) of ***S. pistillata*** (n = 5) recorded at 3h intervals under constant darkness. Respiration rate was not significantly different at different times of day, one-way ANOVA : F = 0.05 (4,20 d.f.) P > 0.05.

	Time of Day (hours)				
Time	8.00	11.00	14.00	17.00	20.00
Replicate					
1	1.458	1.350	1.242	1.363	1.460
2	1.900	1.950	1.880	1.968	1.933
3	1.550	1.366	1.405	1.496	1.444
4	1.111	1.235	1.235	1.235	1.247
5	0.854	0.804	0.916	1.015	0.990
Mean	1.375	1.341	1.336	1.415	1.415
S.D. ±	0.400	0.400	0.350	0.350	0.340

Table 7.2. Dark respiration rate ($\mu lO_2\ mg^{-1}.d.t.h^{-1}$) of ***E. gemmacea*** (n = 5) measured at 3h intervals under constant darkness. Respiration rate was not significantly different at different times of day, one-way ANOVA : F = 0.02 (4,20 d.f.) P > 0.05.

	Time of Day (hours)				
Time	8.00	11.00	14.00	17.00	20.00
Replicate					
1	0.786	0.786	0.725	0.891	0.838
2	1.128	1.085	1.137	1.050	1.207
3	1.525	1.654	1.676	1.397	1.525
4	0.881	1.023	1.039	1.156	1.006
5	0.901	0.901	0.918	0.876	0.834
Mean	1.044	1.090	1.099	1.074	1.082
S.D. ±	0.290	0.330	0.350	0.210	0.290

Table 7.3. Net photosynthesis ($\mu lO_2\ mg^{-1}.d.t.h^{-1}$) of ***S. pistillata*** (n = 5) recorded at 370 $\mu E.m^{-2}\ s^{-1}$ at 3hours intervals throughout the day. Net photosynthesis was not significantly different between times of measurement, one-way ANOVA : F = 0.47 (3,16 d.f.) P>0.05.

	Time of Day (hours)			
Time	8.00	11.00	14.00	17.00
Replicate				
1	3.529	4.165	4.122	4.320
2	5.076	4.756	4.809	4.796
3	4.264	4.690	4.873	4.629
4	3.019	3.549	3.814	4.124
5	4.803	5.015	4.972	4.803
Mean	4.138	4.435	4.518	4.534
S.D.±	0.860	0.580	0.510	0.300

Table 7.4. Net photosynthesis ($\mu lO_2\ mg^{-1}.d.t.h^{-1}$) of ***E. gemmacea*** (n = 5) recorded at 270 $\mu E.m^{-2}\ s^{-1}$ at 3hours intervals throughout the day. Net photosynthesis was not significantly different between times of measurement, one-way ANOVA : F = 0.48 (3,16 d.f.) P > 0.05.

	Time of Day (hours)			
Time	8.00	11.00	14.00	17.00
Replicate				
1	1.842	2.190	1.991	2.270
2	1.995	1.789	1.918	1.986
3	1.619	1.788	1.634	1.715
4	1.507	2.050	2.003	2.360
5	2.739	2.739	2.739	3.055
Mean	1.940	2.111	2.057	2.277
S.D.±	0.480	0.390	0.410	0.500

net photosynthesis rates at saturation light intensity during the day, with an average value of 4.406 ± 0.18 and 2.096 ± 0.14 $\mu lO_2.mg^{-1}$ d.t.h^{-1} for ***S. pistillata*** and ***E. gemmacea*** respectively (Table 7.3 and 7.4).

When the corals were exposed to saturating light for periods of 10, 20, 40, 80 mins, they were separated by darkness (thus giving cumulative light exposure of 10, 30, 70, and 150 min), a steady increase in post-illumination respiration was observed (Table 7.5 and 7.6 ; Figs. 7.1 and 7.2)

.

The mean respiration rates at time zero was about 69% and 62% of the maximum value at (150 min.) for ***S. pistillata*** and ***E.gemmacea*** respectively. The dark respiration in the two species was highly significantly different between exposure times (One-way Anova, $P < 0.01$). On the other hand, the net photosynthesis of ***S.pistillata*** under constant light was highly significantly different throughout the day (One-way Anova, $P < 0.01$), and the initial net photosynthesis 4.922 ± 0.73 $\mu lO_2.mg^{-1}$ d.t.h^{-1} at 8.00 hrs was approximately 72% of the last value 6.8 ± 0.98 $\mu lO_2.mg^{-1}$ d.t.h^{-1} at 16.00 hrs, whilst the mean dark respiration rate before and after the net photosynthetic measurements showed no significant difference (One-way Anova, $P > 0.05$) (Table 7.7).

Comparing the net photosynthesis of ***E. gemmacea*** revealed no significant difference (One-way Anova, $P > 0.05$), but the initial value 2.204 ± 0.51 $\mu lO_2.mg^{-1}$ d.t.h^{-1} at 7.30 hrs. was about 82% of the last value 2.688 $\mu lO_2.mg^{-1}$ d.t.h^{-1} at 15.30 hrs . There was a highly significant difference between the mean respiration rate before and after the net photosynthetic measurements (One-way Anova, $P < 0.01$), and the initial respiration rate 1.154 ± 0.36 $\mu lO_2.mg^{-1}$ d.t.h^{-1} at 6.00 hrs. was about 76% of the last two mean values 1.51 ± 0.3 $\mu lO_2.mg^{-1}$ d.t.h^{-1} at 17.30 and 19.30 hrs (Table 7.8).

7.2.4.DISCUSSION

The present results indicated that the dark respiration rate in the two species was constant throughout the day as it has been reported in the sea anemones ***Aiptasia pulchella*** (Muller-Parker, 1984) and in the corals ***Porites porites*** (Edmunds and Davies,1986). Furthermore, the net photosynthesis at saturation level

Table 7.5. Dark respiration rate ($\mu lO_2\ mg^{-1}.d.t.h^{-1}$) of ***S. pistillata*** (n = 5) after a cumulative exposure to 10, 20, 40, 80 min of light at 370 $\mu Em^{-2}\ s^{-1}$. Respiration rate was higly significantly different between exposures, one-way ANOVA : F = 14.91(4,16 d.f.) $P < 0.01$.

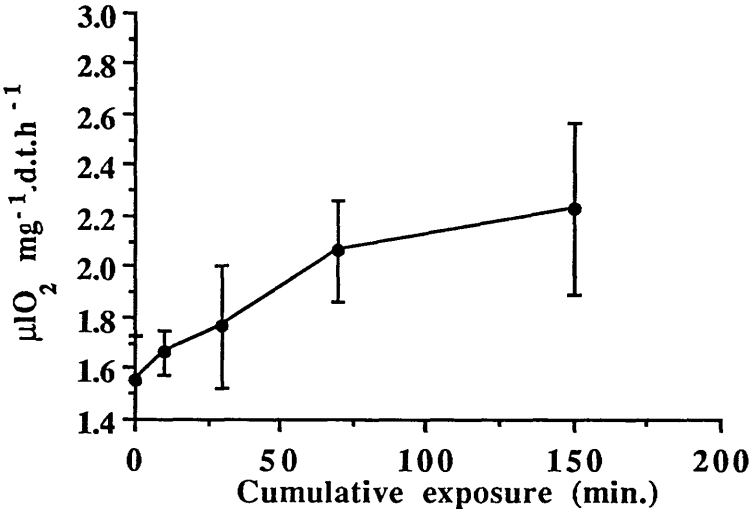
	cumulative duration of exposure (min.)				
Time	0	10	30	70	150
Replicate					
1	1.449	1.559	1.608	1.863	1.863
2	1.480	1.655	1.614	1.991	2.018
3	1.871	1.811	1.782	2.165	2.755
4	1.428	1.680	2.184	2.369	2.386
5	1.529	1.606	1.652	1.927	2.141
Mean	1.551	1.662	1.768	2.063	2.233
S.D. ±	0.180	0.090	0.240	0.200	0.340

Table 7.6. Dark respiration rate ($\mu lO_2\ mg^{-1}.d.t.h^{-1}$) of ***E. gemmacea*** (n = 5) after a cumulative exposure to 10, 20, 40, 80 min of light at 270 $\mu Em^{-2}\ s^{-1}$. Respiration rate was higly significantly different between exposures, one-way ANOVA : F = 9.74 (4,16 d.f.) $P < 0.01$.

	cumulative duration of exposure (min.)				
Time	0	10	30	70	150
Replicate					
1	0.570	0.732	0.773	0.716	0.887
2	0.527	0.545	0.627	0.920	0.881
3	0.694	1.038	1.090	1.000	0.978
4	0.408	0.544	0.544	0.653	0.725
5	0.467	0.527	0.557	0.626	0.795
Mean	0.533	0.677	0.718	0.783	0.853
S.D. ±	0.100	0.210	0.220	0.160	0.090

Fig. 7.1 Dark respiration rate of ***S. pistillata*** after different cumulative exposure times to saturating illumination (370 $\mu E.m^{-2}.s^{-1}$). Means ± s.d (n = 5)

Fig. 7.2 Dark respiration rate of of ***E. gemmacea*** after different cumulative exposure times to saturating illumination (270 $\mu E.m^{-2}.s^{-1}$). Means ± s.d (n = 5)


3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
µlO2 mg-1.d.t.h-1
0
50
100
150
200
Cumulative exposure (min.)

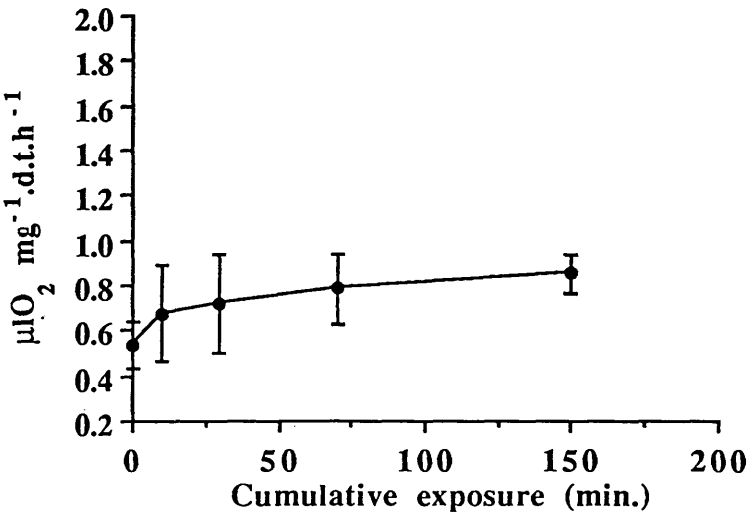

2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
µlO2 mg-1.d.t.h-1
0
50
100
150
200
Cumulative exposure (min.)

Table 7.7. Net photosynthesis rate ($\mu lO_2\ mg^{-1}.d.t.h^{-1}$) of ***S. pistillata*** (n = 5) measured at 370 $\mu Em^{-2}\ s^{-1}$ at 2 hours intervals from 8.00 hrs to 16.00 hrs . Following the dark respiration recorded at 6.00 hrs (R_1), the coral was exposed continuously to saturation light intensity (370 $\mu Em^{-2}\ s^{-1}$). Dark respiration was measured again at 18.00 hrs and 20.00 hrs (R_2 and R_3). Between measurements the chamber was flushed . Net photosynthesis was highly significant different through out the day, one-way ANOVA : F = 11.92 (4,16 d.f.) $P < 0.01$. Dark respiration rates showed no significant differences, one-way ANOVA : F = 1.96 (2,8 d.f.) $P > 0.05$

	cumulative duration of exposure (min.)							
	R_1						R_2	R_3
Time	6.00	8.00	10.00	12.00	14.00	16.00	18.00	20.00
Replicate								
1	2.310	4.820	4.902	5.156	5.588	5.461	1.803	1.981
2	2.207	4.060	4.568	4.645	6.718	6.718	2.399	2.361
3	2.006	4.591	5.683	5.772	6.240	6.351	2.206	2.028
4	2.788	5.084	6.068	5.630	6.614	7.953	2.350	2.296
5	3.197	6.055	6.565	7.551	8.096	7.517	2.653	2.721
Mean	2.500	4.922	5.557	5.751	6.651	6.800	2.282	2.277
S.D. ±	0.480	0.730	0.820	1.090	0.920	0.980	0.310	0.290

Table 7.8. Net photosynthesis rate ($\mu lO_2\ mg^{-1}.d.t.h^{-1}$) of ***E. gemmacea*** (n = 5) measured at 270 $\mu Em^{-2}\ s^{-1}$ at 2hours intervals from 7.30 hrs to 15.30 hrs . Following the dark respiration recorded at 6.00 hrs ((R_1)) the coral was exposed continuously to saturation light intervals (270 $\mu Em^{-2}\ s^{-1}$) . Dark respiration was measured again at 17.30 hrs and 19.30 hrs (R_2 and R_3) Between measurements the chamber was flushed . Net photosynthesis was not significantly different through out the day, one-way ANOVA : F = 2.32 (4,16 d.f.) P > 0.01. Dark respiration rates showed highly significant differences, one-way ANOVA : F = 17.87 (2,8 d.f.) P < 0.05

cumulative duration of exposure (min.)

	R_1						R_2	R_3
Time	6.00	7.30	9.30	11.30	13.30	15.30	17.30	19.30
Replicate								
1	0.653	1.422	1.565	1.701	1.260	1.701	1.006	0.945
2	1.260	2.008	2.189	2.205	2.299	2.473	1.654	1.732
3	1.150	2.432	2.211	2.137	1.990	2.255	1.518	1.445
4	1.042	2.375	2.416	2.375	3.416	3.583	1.583	1.666
5	1.667	2.783	2.312	3.035	3.223	3.428	1.824	1.730
Mean	1.154	2.204	2.139	2.291	2.438	2.688	1.517	1.504
S.D. ±	0.360	0.510	0.330	0.480	0.890	0.790	0.300	0.330

was also the same and showed no sign of variation during the day. Similar observations were made with ***Porites porites*** (Edmunds and Davies,1986). Since the respiratory and the net photosynthetic measurements of the two species were carried out under constant darkness, it seemes unlikely therefor that any error would be introduced in the measurement of respiration rate or photosynthesis made at different times of day, provided the coral had been kept in darkness before hand. However,the dark respiration rates of symbiotic cnidarians have been shown to increase after illumination (Black ***et al***, 1976; Downton ***et al***, 1976 ; Svoboda, 1978 ; Svoboda and Porrmann, 1980 ; Muller-Parker, 1984 ; Edmunds and Davies, 1988 ; Shick, 1990).

This may be due to photoinhibition or photorespiration (Black ***et al***, 1976; Downton ***et al***, 1976 and Crossland and Barnes, 1977), or due to stimulation of metabolic rates by the translocation of photosynthetic products (Svoboda and Porrmann, 1980 ; Muller-Parker, 1984). Edmunds and Davies (1988) suggested that the response could be in the form of a specific dynamic action (SDA) resulting from increased rates of tissue growth associated with increased uptake of nutrients in the light (Goreau, 1959 ; Szmant-Froelich and Pilson, 1977).

Shick (1990) suggested that in a number of anthozoa, the tissues were hypoxic in normal seawater, since the respiration rate could be stimulated by exposing them to hyperoxic seawater, thereby mimicking the effect of the zooxanthellae in sunlight. Edmunds and Davies (1986) showed that the respiration rate of ***Porites porites*** was increased by 58% after an exposure to saturation irradiance for 80 min. Their value was comparable to the present values of 44% and 60% in ***S. pistillata*** and ***E. gemmacea*** respectively. The foregoing results can introduce an inaccurate estimate in the energy budget calculation (Edmunds and Davies, 1988 ; Shick, 1990). On the other hand, under a constant saturation light intensity and continuous flushing after each measurement, net photosynthesis of the two species was increased by 38% and 22% in ***S. pistillata*** and ***E. gemmacea*** respectively. A constant net photosynthesis in cnidaria was observed by using a flushed bell jar system but not by a closed one (Svoboda, 1978). A peak value in net photosynthesis in freshly isolated zooxanthellae from ***Acropora cervicornis*** was reported in the morning and afternoon with a lower value during noontime (Chalker, 1977 ; Chalker and Taylor, 1978).

Moreover, an elevated net photosynthesis was found in ***Aiptasia pulchella*** from

the morning to noontime with a depression in the afternoon when changing the seawater in the respiration chamber after each measurement (Muller-Parker, 1984). These differences in the daily net photosynthesis may result from differences in the methods used for measuring the net photosynthesis. Some of these methods may produce hyperoxia in the animal tissue. This was avoided in the present study by continuously flushing the respirometer chamber between readings with normoxic seawater.

The initial respiration rate of ***S. pistillata*** at 6.00 hrs was not significantly different from the two final respiration rates, whilst in ***E. gemmacea***, the initial dark respiration was significantly lower from the last two dark respirations. One reason for this difference may be that the final respiration rates of ***E. gemmacea*** were measured when the intensity (257 $\mu E.m^{-2} s^{-1}$) was near its saturation light level (270 $\mu E.m^{-2} s^{-1}$), whilst in ***S. pistillata***, the light intensity (174 $\mu E.m^{-2} s^{-1}$) was close to its compensation point (110 $\mu E.m^{-2} s^{-1}$).

7.3. LIPID CONTENT

7.3.1.INTRODUCTION

Excess products of photosynthesis may be translocated from the zooxanthellae to the host either as glycerol (Muscatine and Cernichiari, 1969 ; Trench, 1971a) or as lipid (Crossland ***et al***, 1980b ; Patton ***et al***, 1983 ; Kellogg and Patton, 1983). Within the host tissues, these products are further metabolised and stored mainly as triacylglycerols and wax esters (Blanquet ***et al***, 1979 ; Harland ***et al***, 1991). Since the rate of photosynthetic production was found to vary with depth and season (chapter VI), experiments were undertaken to assess the influence of this on the levels of lipids stored in the coral tissues.

7.3.2. METHOD

A group of ten branch tips of about 2 cm. in length was collected from colonies of ***S. pistillata*** and ***E. gemmacea*** at 1, 3 and 10 m. water depth during January, 1990 and July, 1990. These samples were fixed in a solution of 10%

formalin and sea water for 24 hours. They were then washed in distilled water and dried at room temperature. Lipids from each branch were extracted with 15 ml. Chloroform : Methanol (2:1 v/v) for 24 hours using a separating funnel. The solvent and lipids were then filtered through a coarse paper filter into a pre-weighed beaker. The branch and the filter paper were washed with additional 10 ml. solvent. Thereafter, the beaker contents were evaporated at 50 ^{0}C in the oven overnight, whilst the nubbin was transferred into another container with a 10% solution of nitric acid to dissolve the coral skeleton. The decalcified tissue was washed with distilled water, dried at 60 ^{0}C and weighed. Finally, the percentage of lipid in coral tissue was calculated by the following equation:

$$\text{Lipid \%} = \frac{\text{Lipid wt.}}{\text{Lipid wt. + dry tissue wt.}} \times 100$$

7.3.3. RESULTS

Lipid as a percentage of dry tissue weight in ***S. pistillata*** and ***E. gemmacea*** in winter and summer 1990 at 3 depths is shown in Table 7.9 and 7.10 and Fig. 7.3

a) Species Variation

The mean lipid contents were higher in ***S.pistillata*** than ***E. gemmacea.*** They range from 28.58 ± 3.33 % in winter at 10 m. to 40.49 ± 5.47 % in summer at 1 m. whilst in ***E. gemmacea,*** they are between 21.42 ± 2.06 % and 27.48 ± 2.05 % during winter at 10 m. and summer at 3 m. respectively. There were significant differences between the two species (t-test $P<0.001$),except at 10 m. during summer the difference was not significant .

b) Seasonal Variation

S. pistillata

The average lipid content was higher 40.49 ± 5.47 (10)% during summer than winter 32.94 ± 0.62 at 1 m. The difference was significantly higher during summer at 1 m. (t-test $P<0.001$). There was a slight variation in the mean values of lipid

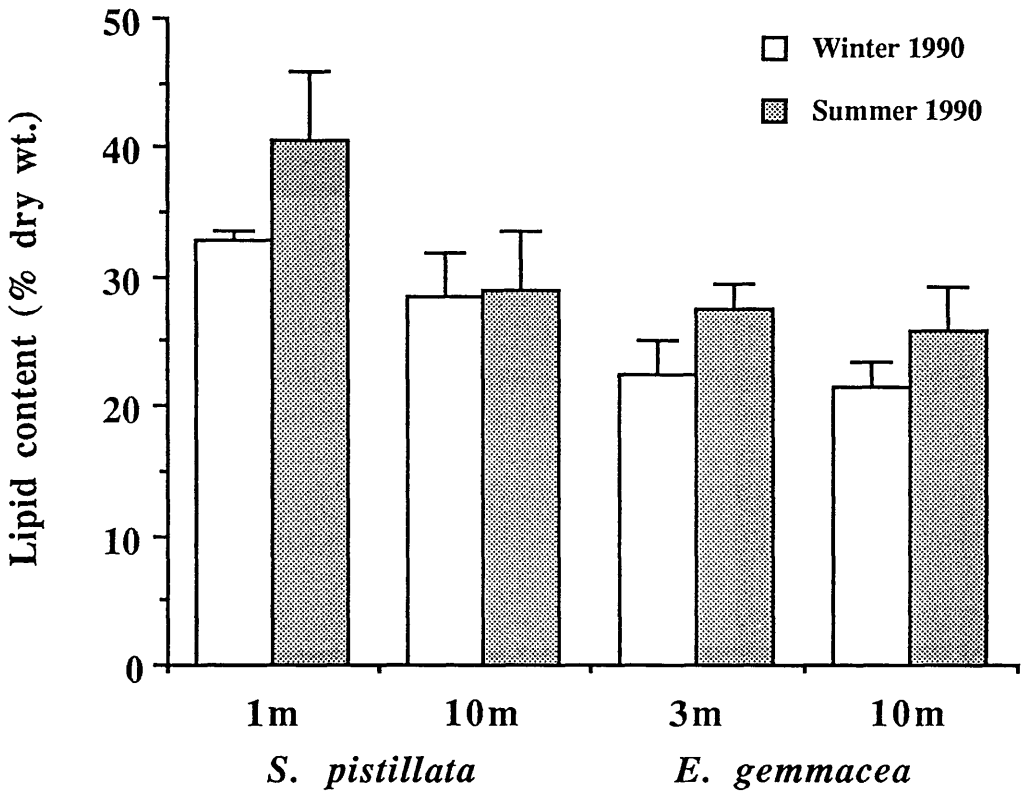
Table 7.9. Comparison of lipid levels (as % dry tissue weight) of ***S. pistillata*** and ***E. gemmacea*** with depth and season mean ± s.d. (n = 10).

	S. pistillata					*E. gemmacea*				
Depth (m)	Winter 90	Summer 90	t	d.f	Significance	Winter 90	Summer 90	t	d.f	Significance
1	32.94 ±0.62	40.49 ±5.47	4.34	18	P <0.0001					
3						22.55 ±2.55	27.48 ±2.05	4.75	18	P <0.001
10	28.58 ±3.33	28.91 ±4.59	0.18	18	N.S.	21.42 ±2.06	25.77 ±3.41	3.46	18	P<0.002

Table 7.10 Students t-test comparison of lipid levels (% of dry tissue weight) in ***S. pistillata*** and ***E. gemmacea*** . Comparisons.are made between species at different depths and between depths in each species

Comparison	Winter 90			Summer 90		
	t.	d.f	significance	t.	d.f	significance
BETWEEN SPECIES						
1m v 3m	12.5	18	P <0.001	7.04	18	P <0.001
10m v 10m	5.78	18	P <0.001	1.73	18	n.s.
BETWEEN DEPTHS						
S. pistillata						
1m v 10m	4.06	18	P <0.001	5.13	18	P <0.001
E. gemmacea						
3m v 10m	1.09	18	n.s	1.35	18	n.s

Fig. 7.3 Variation in lipid content, expressed as % dry tissue weight, with depth and season in ***S. pistillata and E. gemmacea.***


Lipid content (% dry wt.)
50
40
30
20
10
0
Winter 1990
Summer 1990
1m
10m
3m
10m
S. pistillata
E. gemmacea

between summer 28.91 ± 4.59 % and winter 28.58 ± 3.33 % at 10 m., but no significant difference.

E. gemmacea

The mean values of lipid were higher in summer 27.48 ± 2.05 % at 3 m and 25.77 ± 3.41 (10)% at 10 m. than winter, 22.55 ± 2.55 % and 21.42 ± 2.06 % at 3 and 10 m. respectively. There was a significant difference between seasons (t-test $P<0.001$).

c) Depth Variation

S. pistillata

The mean lipid concentration in the colony tissue decreased with increasing depth. The value was higher at 1 m. than at 10 m. during winter and summer, and it was significantly higher (t-test $P<0.001$).

E. gemmacea

During winter and summer 1990, the mean lipid percentage of dry tissue weight at 3 m was also higher than that at 10 m., but not significantly different.

7.3.4. DISCUSSION

The quantity of lipid in the tissue of ***E. gemmacea*** is about 33.43% to 47.34% of that in ***S. pistillata***, and this may be correlated with the lower net photosynthesis as compared to ***S. pistillata*** (Chapter V). Stimson (1987) showed variations in lipid concentrations between several coral species in Hawaii.

In the present study, the values of 32.94% to 40.49% lipid on dry tissue basis in ***S. pistillata*** at 1 m. during winter and summer respectively are similar to the values of 34% in ***Pocillopora capitata*** at 1 - 3 m.(Patton ***et al***, 1977), and 30 - 40% in Hawaian corals from shallow water (Stimson, 1987). All of these values however, are higher than 22.55 to 27.48% recorded for ***E. gemmacea*** at 3 m. during winter and summer time respectively. Once again, this may be due to deeper dwelling tissue containing zooxanthellae which are not active in photosynthesis, as has been reported for ***Porites porites*** at 10 m.(Edmunds, 1986). There are differences in lipid content between depths and seasons in the tissue of the two species. The mean lipid concentration in ***S. pistillata*** at 10 m is 86.8% and 71.4% of that at 1 m., whilst in ***E. gemmacea*** is 95% and 94% of that at 3 m during winter and summer respectively. This may be correlated with the lower photosynthetic

production of the two species at 10 m.

The lipid concentration is significantly higher during summer than in winter, except in ***S. pistillata*** from 10 m. The differences in lipid values between summer and winter may be related to a lower irradiance level and a lower sea water temperature, which reduce photosynthetic production (see chapter VI). In addition, planulation during winter in ***S.pistillata*** (Stimson, 1987) may reduce lipid reserves since the planula larva of ***S. pistillata*** contains a high lipid level (see Chapter V).

It will be recalled that there was little difference in the energy budgets of ***E. gemmacea*** between seasons (Chapter VI) and the slightly lower lipid level in winter at both depths may be related to the timing of reproduction. The lower level in January coincides with the end of reproduction which occurred during the end of November when the lipid may be at its lowest level and the animal may take a longer time to replace the lipid to its previous level. On the other hand, a slightly higher lipid level in July may coincide with the beginning of oogenesis when the lipid is at its highest level. Richmond (1987) reported that about 5% of the energy content of ***Pocillopora damicornis*** is lost monthly for planulation.

Since approximately 9% of coral dry tissue is structural lipid (Stimson, 1987) then the reserve lipid can be calculated in a 10 g. nubbin for both species and converted to joules, using the energy content of the wax ester cetyl palmitate of 42 $KJ.g^{-1}$ (Davies, 1991a) (Table 7.11).

If there was no other energy source available to these corals, to fulfil their daily energy requirements (Table 6.2), catabolism of the reserve lipid would last for between 8 and 13 days in ***S. pistillata*** and 10 - 13 days in ***E. gemmacea.***

Table 7.11. *S. pistillata* and *E. gemmacea*. Stored lipid content of the tissues of 10g skeleton weight nubbins, and the predicted number of days that could be met from the store, if there was no other nutritional source available.

Season 1990	Depth (m)	Dry tissue wt. (mg)	% Total lipid	Storage lipid	Energy value (J)	No.of days for daily demand
S. pistillata						
Summer	1	103.00	40.49	35.64	1496.88	10
Summer	10	103.00	28.91	22.54	946.68	8
Winter	1	103.00	32.94	27.10	1138.20	12
Winter	10	103.00	28.58	22.16	930.72	13
E. gemmacea						
Summer	3	128.60	27.48	26.12	1097.04	12
Summer	10	128.60	25.77	23.70	995.40	12
Winter	3	128.60	22.55	19.15	804.30	10
Winter	10	128.60	21.42	17.55	737.10	12

CHAPTER VIII

8. GENERAL DISCUSSION

Following the research of Yonge (1930), the widely held view of nutrition of corals was that they were specialised carnivores, feeding on zooplankton, whilst some species were also classified as suspension feeders. The zooxanthellae were thought to play a major role in excretion only, ridding the coral of phosphate and nitrogenous waste. However in 1958 Muscatine and Hand first showed translocation of organic carbon from symbiont to host in a symbiotic sea anemone. This was followed by work by Muscatine and Cernichiari (1969) and Trench (1971b) who showed unequivocally that a large proportion of the carbon fixed in photosynthesis was passed from the symbiont into the tissue of corals. Subsequently the quantitative importance of the translocation for the nutrition of corals was addressed. Davies (1984) constructed an energy budget for ***Pocillopora eydouxi*** whilst Muscatine ***et al,*** (1984) produced a carbon budget for ***Stylophora pistillata.*** Both of these studies showed that in shallow water on cloudless days, the respective corals would translocate more than 90% of the fixed carbon over a 24h. period. Furthermore, there was an excess of carbon produced which would have to be excreted back into the water, probably as mucus-lipid (Crossland ***et al***, 1980a). Subsequently, similar results were obtained with ***Porites porites*** from Jamaica (Edmunds and Davies, 1986).

These observation which suggested that some corals could achieve carbon autotrophy, but corals nevertheless have tentacles armed with nematocysts that could be used for capture of zooplankton. Porter (1976) proposed that growth form in corals had been selected for in the course of evolution and could be correlated with mode of nutrition. He showed an inverse correlation between relative surface area of corals and the size of the polyps, and suggested that these genera with small polyps and a large surface area were adapted for light-gathering and would have a more autotrophic mode of nutrition. Conversely, those with large polyps would be adapted for carnivory. Partial support for this hypothesis came from the observations of Johannes and Tepley (1974) and Edmunds and Davies (1986) who showed that small polyp ***Porites*** **spp**..displayed very low capabilities for zooplankton capture. By contrast, ***Montastrea cavernosa***, which has large polyps is avoracious carnivore, capturing a wide variety of organisms from the zooplankton.

At the commencement of the research described in this thesis, all published energy and carbon budgets (Muscatine ***et al***, 1984 ; Davies, 1984 ; Edmunds and Davies, 1986) had been determined with small polyp, branching corals. It was hypothesised that the differing nutritional modes of corals would result in basic differences in the form of their energy budgets. To investigate this, two species with differing growth form and polyp size were selected for comparison. These were ***Stylophora pistillata*** with small polyps and a branching morphology and ***Echinopora gemmacea*** with a more encrusting growth form and large polyps.

The nutritional strategies of the two species were investigated by comparing the feeding behaviour and histology of the feeding surfaces. It was found that, as expected, ***S. pistillata*** was unable to capture **Artemia** nauplii and showed little specialisation for suspension feeding. Confirmation of this came from histological observation of low numbers of mucus gland cells, and the virtual absence of venom-containing mastigophore nematocysts on the tentacles. ***E. gemmacea*** on the other hand, and despite the large polyp diameter, appeared to be adapted for suspension feeding. This was borne out by the histological study which demonstrated large numbers of mucus gland cells and spirocysts, and by behavioural studies.

Earlier compilation of energy budgets for corals (Davies, 1984 ; Edmunds and Davies, 1986 ; Davies, 1991a) have been confined to observations made at a single depth and at one time in the year. Because of the importance to the budget of the light-dependent input from photosynthesis, it was of interest to determine the effects of reduced light on corals living at 10m, in comparison with those living at 1-3m depth on the reef flat, and to examine differences between summer and winter.

At Sharm Ubhur, Jeddah, it was found that there was little difference in temperature between the shallow and deep site, but light attenuation with depth resulted in a shorter under-water day length and a reduction of between 65 and 56% in the maximum P.A.R, and between 67 and 60% in the integrated daily P.A.R.. On a seasonal basis, water temperature varied from a winter minimum average of 25.5°C to a maximum summer average of 31°C. The number of daylight hour was reduced by approximately 15% in winter and this was accompanied by a similar reduction in the maximum P.A.R., whilst the daily integrated P.A.R. fell by approximately 34%.

The reduction in light between 1 or 3m of the shallow reef and 10m produced differences in respiration rate, photosynthetic characteristics and the growth rate of the corals. In both species the dark respiration rates decreased with

depth, and a similar response was observed in the respiration rate of freshly-isolated zooxanthellae. This response has been recorded previously (Davies, 1977, 1980 ; Muscatine ***et al***, 1984) but the mechanism involved in the reduced rate has not been investigated. The deep-living corals exhibited differences in photosynthetic characteristics which could be explained by photoadaptation to reduced light by the zooxanthellae. Changes were observed in the shape of the P v I curves. Notably the deep corals had lower values of I_k, although values for α were similar. growth rate was reduced at depth, the reduction being more clear in ***S. pistillata*** than in ***E. gemmacea***.

Seasonal changes in photosynthesis, respiration rate and growth rate were also found in both species. Generally all three processes were lower in winter, correlated with lower water temperature and the lower irradiance levels, although the differences were very much less obvious in ***E. gemmacea*** than in ***S. pistillata.*** Both species displayed photoadaptation to the lower winter irradiances, the values of I_k being lower and the values of α larger than during the summer. Differences in the responses of the two species were observed in the reproductive cycle. In *S* ***pistillata*** testes are present in all months except the summer months of May to July, ovaries are present throughout the year and planula production was observed in the winter months only. This contrasts with observation in the same species from Eilat (Rinkevich and Loya, 1979b) where planulation lasted from December to July. In ***E. gemmacea,*** spawning probably occurred in the late autumn, and gonad development did not resume until early autumn of the next year. Both of these observation may suggest that the breeding cycle has adapted in order to avoid the production of planulae in the summer months when water temperatures reach 31°C. Temperature of the magnitude, although they do not induce 'bleaching' may nevertheless be sub optimal for corals in this region.

The twenty-four hour energy budget of both ***S. pistillata*** and ***E. gemmacea*** from shallow water, indicated a surplus of photosynthetic production over utilisation, so that excess mucus lipid would have to be excreted, during the winter months. However, in summer, the deeper water corals had energy budgets which were in deficit, indicating the requirement of other, heterotrophic sources of nutrition. A similar result was obtained for deep water ***S. pistillata*** in terms of its carbon budget by Muscatine ***et al*** (1984). The energy budgets which were determined in the course of the present work, were laboratory based and therefore

took no account of potential inputs over a 24 hour period from non-photosynthetic sources. Because of methodological difficulties, no information is yet available on the energy intake from suspension feeding. This could be adequate to create a balanced budget when the corals are living on the reef. Conversely if the energy input from this source proves to be a minor importance, it seems likely that in summer months both species in deeper water may have to draw upon lipid reserves (Davies, 1991a).

Seasonal differences in the energy budgets of the shallow-water forms were not detected. Budget excess were predicted at both seasons for both species. Finally, the comparison of the energy budgets of the two species revealed that , with the exception of the deeper forms in summer, on a cloudless day excess production resulted in similar energy surpluses. Intraspecific in comparison in absolute terms are difficult to make, because of differences in growth form. In this thesis budgets were normalised to a 10g. skeleton weight nubbins. The surface area of a nubbin of this size would be slightly higher in ***S. pistillata*** than in ***E. gemmacea*** (Table, 5.1). However ***S. pistillata*** has a significantly higher population of zooxanthellae for a given weight of skeleton or surface area. In summer this results in an almost 100% higher rate of daily photosynthetic production, and an almost four-fold higher rate of excretion of excess energy in equal weight nubbins. This may be a strong indication of selection for nutritional autotrophy in ***S. pistillata.*** However, in winter, because of seasonal changes in the characteristic of both respiration and photosynthesis, resulting from changes in both light availability and water temperature, the differences between the two species are less clear and both species excrete similar quantities of excess energy. Further research is needed to evaluate and explain some of these unresolved questions.

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	R $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	P $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	α $\mu lO_2.mg^{-1}$ $\mu E.m.^{-2}$ $s.^{-1}$	I_k $\mu E.m.^{-2}$ $s.^{-1}$	I_c $\mu E.m.^{-2}$ $s.^{-1}$	$I_{0.95}$ $\mu E.m.^{-2}$ $s.^{-1}$
1	-2.953	12.252	0.022	569	140	1042.408
2	-3.543	9.944	0.034	293	109	536.776
3	-2.532	7.706	0.024	322	110	589.904
4	-2.484	7.513	0.024	316	108	578.912
5	-2.851	8.088	0.023	357	131	654.024
6	-2.567	7.430	0.022	340	122	622.880
7	-2.319	12.400	0.017	744	141	1363.008
8	-2.940	9.524	0.022	430	137	787.760
9	-2.477	7.568	0.025	301	102	551.432
10	-2.565	7.911	0.022	368	124	674.176
11	-2.229	8.607	0.030	291	77	533.112
12	-2.299	10.455	0.039	269	60	492.808
13	-2.303	9.522	0.028	346	85	633.872
14	-2.373	10.713	0.031	350	79	641.200
15	-2.491	9.683	0.036	269	71	492.808
16	-2.289	9.001	0.023	396	103	725.472
17	-1.985	10.015	0.022	463	93	848.218
18	-2.772	11.782	0.035	341	82	624.712
19	-2.485	8.421	0.018	467	142	855.544
20	-3.138	5.021	0.022	230	168	421.360
21	-3.665	7.753	0.031	249	128	456.168
22	-2.982	8.092	0.028	293	113	536.776
23	-3.361	8.241	0.032	256	111	468.992
24	-3.205	8.809	0.027	332	127	608.224
25	-3.567	9.021	0.032	278	116	509.296
26	-2.898	6.142	0.027	230	118	421.360
27	-3.124	6.170	0.036	173	97	316.936
Mean	-2.755	8.807	0.0271	343.444	110.889	629.190
S.D.±	0.45	1.78	0.005	115.970	25.20	212.46
n	27	27	27	27	27	27

Appendix 1. Photosynthesis characteristics for 27 nubbins of ***S. pistillata*** from 1m water depth during summer 1989.

	R $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	P $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	α $\mu lO_2.mg^{-1}$ $\mu E.m.^{-2}$ $s.^{-1}$	I_k $\mu E.m.^{-2}$ $s.^{-1}$	I_c $\mu E.m.^{-2}$ $s.^{-1}$	$I_{0.95}$ $\mu E.m.^{-2}$ $s.^{-1}$
1	-2.123	5.899	0.031	190	72	348.080
2	-1.811	3.731	0.026	143	76	261.976
3	-2.472	5.188	0.035	148	77	271.136
4	-2.239	4.680	0.026	181	94	331.592
5	-2.262	3.709	0.024	152	107	278.464
6	-2.128	4.385	0.032	138	73	252.816
7	-2.067	4.022	0.026	155	88	283.960
8	-2.466	4.502	0.029	156	96	285.792
9	-2.511	4.106	0.021	197	140	360.904
10	-2.261	3.618	0.029	124	91	227.168
11	-2.075	4.292	0.028	151	80	276.632
12	-1.593	4.306	0.021	204	79	373.728
13	-2.773	6.286	0.028	227	108	415.864
14	-2.264	7.034	0.021	331	110	906.392
15	-3.190	8.225	0.035	236	97	432.352
16	-2.342	7.039	0.036	197	68	360.904
17	-1.904	6.116	0.026	235	76	430.520
18	-1.956	6.704	0.023	292	88	534.944
19	-2.168	5.969	0.026	229	87	419.528
20	-2.274	4.753	0.024	202	105	370.064
Mean	-2.244	5.228	0.274	194.40	90.60	371.141
S.D.±	0.34	1.330	0.004	53.22	17.36	148.020
n	20	20	20	20	20	20

Appendix 2 Photosynthesis characteristics for 20 nubbins of ***S. pistillata*** from 10m water depth during summer 1989.

	R $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	P $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	α $\mu lO_2.mg^{-1}$ $\mu E.m.^{-2} s.^{-1}$	I_k $\mu E.m.^{-2} s.^{-1}$	I_c $\mu E.m.^{-2} s.^{-1}$	$I_{0.95}$ $\mu E.m.^{-2} s.^{-1}$
1	-2.445	7.187	0.038	188	67	344.416
2	-2.678	7.466	0.044	170	64	311.440
3	-0.913	4.004	0.028	144	33	263.808
4	-1.125	4.602	0.034	137	34	250.984
5	-1.040	4.663	0.037	125	28	229.000
6	-2.042	5.200	0.028	189	78	246.248
7	-2.003	3.845	0.024	158	91	289.456
8	-1.870	5.045	0.029	172	67	315.104
9	-1.598	3.379	0.019	181	93	331.592
10	-2.248	5.292	0.018	290	132	531.280
11	-2.320	12.079	0.015	880	157	1612.160
12	-1.759	6.245	0.024	256	74	468.992
13	-2.031	8.172	0.016	502	127	919.664
14	-1.356	4.322	0.013	324	105	593.568
15	-1.479	4.161	0.025	166	62	304.112
16	-1.406	5.204	0.029	181	50	331.592
17	-1.157	3.487	0.012	284	98	520.288
18	-1.656	5.519	0.022	255	79	467.160
19	-1.009	3.099	0.019	163	55	298.616
20	-2.326	5.542	0.065	86	38	157.552
21	-2.405	8.606	0.056	153	44	280.296
22	-2.008	7.831	0.056	138	36	252.816
Mean	-1.767	5.680	0.0295	233.727	73.273	423.643
S.D.±	0.52	2.140	0.0100	169.590	34.910	312.67
n	22	22	22	22	22	22

Appendix 3 Photosynthesis characteristics for 22 nubbins of *S. **pistillata*** from 1m. water depth during winter 1990.

	R $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	P $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	α $\mu lO_2.mg^{-1}$ $\mu E.m.^{-2}$ $s.^{-1}$	I_k $\mu E.m.^{-2}$ $s.^{-1}$	I_c $\mu E.m.^{-2}$ $s.^{-1}$	$I_{0.95}$ $\mu E.m.^{-2}$ $s.^{-1}$
1	-1.233	4.614	0.028	163	43	298.616
2	-1.384	2.836	0.020	144	77	263.808
3	-1.184	4.053	0.027	150	45	274.800
4	-1.270	3.520	0.022	160	61	293.120
5	-1.733	4.630	0.029	159	62	291.288
6	-1.646	5.810	0.048	120	35	219.840
7	-1.579	5.634	0.050	113	32	207.016
8	-1.037	5.372	0.030	176	34	322.432
9	-1.651	4.679	0.033	144	53	263.808
10	-1.653	4.879	0.025	191	68	349.912
11	-1.589	5.874	0.036	164	45	300.448
12	-1.286	4.979	0.026	192	51	351.744
13	-1.408	4.404	0.025	174	57	318.768
Mean	-1.435	4.714	0.031	157.692	51.00	288.892
S.D.±	0.22	0.880	0.009	23.83	13.74	43.65
n	13	13	13	13	13	13

Appendix 4 Photosynthesis characteristics for 13 nubbins of ***S. pistillata*** from 10m water depth during winter 1990.

	R $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	P $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	α $\mu lO_2.mg^{-1}$ $\mu E.m.^{-2}$ $s.^{-1}$	I_k $\mu E.m.^{-2}$ $s.^{-1}$	I_c $\mu E.m.^{-2}$ $s.^{-1}$	$I_{0.95}$ $\mu E.m.^{-2}$ $s.^{-1}$
1	-1.535	4.416	0.021	211	76	386.552
2	-1.404	3.977	0.022	178	66	326.096
3	-1.245	2.934	0.017	174	79	318.768
4	-1.404	3.668	0.024	154	62	282.128
5	-1.607	4.174	0.026	159	65	291.288
6	-1.721	4.889	0.027	184	68	337.088
7	-1.054	2.567	0.018	142	62	260.144
8	-1.112	2.990	0.025	120	47	219.840
9	-1.372	2.758	0.017	160	87	293.120
10	-1.420	3.959	0.022	181	68	331.592
11	-1.580	5.539	0.024	229	67	419.528
12	-1.300	3.551	0.014	247	95	452.504
13	-1.252	3.816	0.022	172	59	315.104
14	-1.422	4.053	0.021	189	69	346.248
15	-1.397	4.171	0.021	198	69	362.736
16	-1.546	3.532	0.019	187	88	342.584
17	-1.397	3.765	0.023	161	63	294.952
18	-1.329	3.949	0.021	185	65	338.920
19	-1.397	3.832	0.019	199	76	364.568
20	-1.130	4.036	0.017	240	69	439.680
Mean	-1.381	3.829	0.021	183.50	70.00	336.172
S.D.±	0.16	0.690	0.003	31.69	11.01	58.06
n	20	20	20	20	20	20

Appendix 5 Photosynthesis characteristics for 20 nubbins of ***E. gemmacea*** from 3m water depth during summer1989.

	R $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	P $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	α $\mu lO_2.mg^{-1}$ $\mu E.m.^{-2} s.^{-1}$	I_k $\mu E.m.^{-2} s.^{-1}$	I_c $\mu E.m.^{-2} s.^{-1}$	$I_{0.95}$ $\mu E.m.^{-2} s.^{-1}$
1	-1.179	2.888	0.018	158	69	289.456
2	-1.440	5.308	0.026	208	58	381.056
3	-1.542	4.603	0.027	171	60	313.272
4	-1.232	2.999	0.016	193	84	353.576
5	-1.187	2.499	0.015	172	89	315.104
6	-1.213	2.945	0.018	164	72	300.448
7	-1.312	3.478	0.018	190	75	348.080
8	-1.577	4.142	0.018	232	93	425.024
9	-1.173	3.319	0.022	150	56	274.800
10	-1.002	3.300	0.018	179	56	327.928
11	-1.593	3.808	0.017	223	100	408.536
12	-1.111	2.059	0.015	139	84	254.648
13	-1.365	3.112	0.020	154	73	282.128
14	-1.244	3.281	0.013	252	100	461.664
15	-1.207	3.288	0.018	174	67	318.768
16	-1.083	3.382	0.016	211	70	386.552
17	-1.242	3.222	0.018	183	74	335.256
18	-1.735	4.193	0.024	177	63	324.264
19	-1.164	2.996	0.016	188	77	344.416
20	-1.236	3.049	0.017	182	78	333.424
Mean	-1.292	3.394	0.0185	185.00	74.90	338.92
S.D.±	0.19	0.720	0.0030	28.57	13.50	52.35
n	20	20	20	20	20	20

Appendix 6 Photosynthesis characteristics for 20 nubbins of ***E. gemmacea*** from 10m water depth during summer 1989.

	R $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	P $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	α $\mu lO_2.mg^{-1}$ $\mu E.m.^{-2}$ $s.^{-1}$	I_k $\mu E.m.^{-2}$ $s.^{-1}$	I_c $\mu E.m.^{-2}$ $s.^{-1}$	$I_{0.95}$ $\mu E.m.^{-2}$ $s.^{-1}$
1	-0.730	2.477	0.017	142	43	260.144
2	-0.883	3.993	0.023	176	40	322.432
3	-0.840	3.397	0.022	154	39	282.128
4	-0.810	2.521	0.017	148	49	271.136
5	-0.668	2.566	0.018	141	37	258.312
6	-0.823	3.243	0.016	205	53	375.560
7	-1.629	7.011	0.046	154	36	282.128
8	-1.011	5.161	0.023	221	44	404.872
9	-0.775	2.259	0.016	138	49	252.816
10	-2.197	6.415	0.046	140	50	256.480
11	-0.896	3.257	0.021	154	43	282.128
12	-1.037	3.831	0.025	154	43	282.128
13	-2.056	7.295	0.036	205	59	375.560
14	-0.864	3.060	0.020	156	45	285.792
15	-1.038	3.971	0.025	158	42	289.456
16	-1.773	6.346	0.041	156	45	285.792
17	-1.251	4.911	0.026	186	48	340.752
18	-0.915	4.176	0.024	175	39	320.600
19	-2.208	11.251	0.044	258	51	472.656
20	-1.968	8.779	0.035	250	57	458.000
21	-1.118	4.128	0.031	132	37	241.824
Mean	-1.214	4.764	0.0272	171.571	45.19	314.319
S.D.±	0.52	2.330	0.0100	36.39	6.45	66.68
n	21	21	21	21	21	21

Appendix 7 Photosynthesis characteristics for 21 nubbins of ***E. gemmacea*** from 3m water depth during winter 1990.

	R $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	P $\mu lO_2.mg^{-1}$ d t wt.h^{-1}	α $\mu lO_2.mg^{-1}$ $\mu E.m.^{-2} s.^{-1}$	I_k $\mu E.m.^{-2} s.^{-1}$	I_c $\mu E.m.^{-2} s.^{-1}$	$I_{0.95}$ $\mu E.m.^{-2} s.^{-1}$
1	-1.377	4.327	0.045	96	32	175.872
2	-1.082	4.457	0.038	117	28	214.344
3	-0.719	2.379	0.020	121	38	221.672
4	-0.683	3.011	0.031	98	23	179.536
5	-1.090	4.508	0.027	165	41	302.280
6	-0.664	2.544	0.020	124	33	227.168
7	-1.369	5.194	0.048	109	29	199.688
8	-1.323	5.451	0.031	176	44	322.432
9	-1.027	3.247	0.026	126	41	230.832
10	-1.115	4.224	0.031	136	37	249.152
11	-0.757	2.880	0.021	137	37	250.984
12	-0.395	2.284	0.017	137	24	250.984
13	-1.216	4.113	0.033	125	38	229.000
14	-1.032	3.200	0.033	97	33	177.704
15	-0.785	3.221	0.030	106	26	194.192
16	-1.392	4.356	0.042	104	34	190.528
17	-0.556	1.993	0.016	125	36	229.000
18	-0.593	2.415	0.022	111	28	203.352
19	-0.471	2.341	0.018	132	27	241.824
20	-0.554	3.125	0.016	201	36	368.232
Mean	-0.910	3.464	0.0283	127.15	33.25	232.939
S.D.±	0.32	1.030	0.0090	27.17	5.99	49.78
n	20	20	20	20	20	20

Appendix 8 Photosynthesis characteristics for 20 nubbins of ***E. gemmacea*** from 10m water depth during winter 1990

DATE From To Specimen	1 - 8 - 89 12 - 8 - 89	12 - 8- 89 19 - 8- 89	19 - 8 - 89 24 - 8 - 89	Mean
1	85.673	97.943	78.000	87.205
2	75.436	74.529	79.460	76.475
3	79.427	81.371	64.200	74.999
4	60.091	65.357	64.500	63.316
5	57.790	65.414	57.600	60.268
6	55.127	64.114	46.440	55.227
7	52.882	59.414	62.400	58.232
8	44.482	52.643	53.440	50.188
9	52.364	52.657	58.480	54.500
10	42.527	45.900	27.060	38.496
11	33.164	36.200	56.720	42.028
12	47.391	54.157	42.080	47.876
13	48.236	63.886	*	56.061
14	41.391	40.471	*	40.931
15	35.782	41.643	*	38.713
16	56.227	64.957	*	60.592
17	71.073	79.371	*	75.222
18	36.727	35.614	*	36.171
19	40.464	43.071	*	41.768
20	*	32.400	*	32.400
Mean	53.487	57.556	57.532	54.533
S.D ±	15.200	17.390	14.530	15.32
n	19	20	12	20

Appendix 9 Daily growth rate of skeleton ($mg.d^{-1}$) of ***S. pistillata*** at the study site, measured at 1m in summer 1989.

Symbol (*) indicates that the data are not available

DATE From To Specimen	28 - 7 - 89 7 - 8 - 89	7 - 8 - 89 12 - 8 - 89	12 - 8 - 89 19 - 8 - 89	19 - 8 - 89 24 - 8 - 89	Mean
1	8.680	28.280	15.714	17.900	17.644
2	14.980	12.800	21.771	13.220	15.693
3	17.650	11.720	14.157	13.060	14.147
4	16.390	11.640	17.129	8.180	13.335
5	12.060	8.440	18.729	14.020	13.312
6	15.670	13.040	14.629	14.440	14.445
7	10.070	8.660	10.471	12.820	10.505
8	13.770	17.280	8.729	11.600	12.845
9	7.190	12.360	14.886	15.040	12.369
10	13.110	14.460	13.614	*	13.728
11	19.940	16.960	12.000	*	16.300
12	17.240	15.940	14.314	*	15.831
13	17.670	14.980	12.557	*	15.069
14	11.600	10.340	11.186	*	11.042
15	9.850	11.800	9.343	*	10.331
16	11.360	11.160	7.843	*	10.121
17	12.940	*	*	*	12.940
Mean	13.539	13.741	13.567	13.364	13.509
S.D ±	3.570	4.680	3.720	2.630	2.250
n	17	16	16	9	17

Appendix 10 Daily growth rate of skeleton ($mg.d^{-1}$) of *S. **pistillata*** at the study site, measured at 10m in summer 1989.

Symbol (*) indicates that the data are not available

DATE From To Specimen	10 - 1 - 90 21 - 1 - 90	21 - 1 - 90 25 - 1 - 90	25 - 1 - 90 3 - 2 - 90	Mean
1	27.855	19.300	22.389	23.181
2	20.109	15.350	26.444	20.634
3	33.355	35.950	22.222	30.509
4	15.809	14.775	25.156	18.580
5	21.527	17.475	23.567	20.856
6	14.482	22.025	11.267	15.925
7	15.164	10.700	30.478	18.781
8	29.282	17.300	15.589	20.724
9	28.482	37.650	24.122	30.085
10	13.055	18.800	19.833	17.229
11	25.373	20.350	27.611	24.445
12	14.745	19.675	26.989	20.470
13	17.864	17.200	22.422	19.162
14	23.500	24.150	15.800	21.150
15	21.482	43.175	14.967	26.541
16	34.564	11.300	*	22.932
17	16.845	12.875	*	14.860
18	22.955	*	*	22.955
19	15.909	*	*	15.909
Mean	21.703	21.062	21.924	21.312
S.D ±	6.610	9.320	5.430	4.37
n	19	17	15	19

Appendix 11 Daily growth rate of skeleton ($mg.d^{-1}$) of ***S. pistillata*** at the study site, measured at 1m in winter1990.

Symbol (*) indicates that the data are not available

DATE From To Specimen	3 - 1 - 90 11 - 1 - 90	11 - 1 - 90 19 - 1 - 90	19 - 1 - 90 29 - 2 - 90	Mean
1	8.125	8.438	11.220	9.261
2	7.188	8.238	7.620	7.682
3	8.213	14.675	12.350	11.746
4	6.300	9.750	11.040	9.030
5	10.725	5.988	6.740	7.818
6	6.425	6.225	6.040	6.230
7	8.713	12.013	8.680	9.802
8	12.613	10.063	8.800	10.492
9	11.375	8.913	10.000	10.096
10	11.238	5.763	6.760	7.920
11	8.163	8.588	6.360	7.704
12	7.075	13.575	8.410	9.687
13	9.363	5.425	10.610	8.466
14	12.413	11.888	9.400	11.234
15	9.375	7.150	*	8.263
16	13.613	*	*	13.613
17	14.088	*	*	14.088
Mean	9.706	9.113	8.859	9.596
S.D ±	2.500	2.880	2.000	2.130
n	17	15	14	17

Appendix 12 Daily growth rate of skeleton ($mg.d^{-1}$) of ***S. pistillata*** at the study site, measured at 10m in winter 1990.

Symbol (*) indicates that the data are not available

DATE From To Specimen	30 - 7 - 89 9 - 8 - 89	9 -8 - 89 19 - 8 - 89	19 - 8 - 89 25 - 8 - 89	Mean
1	8.300	12.400	13.120	11.273
2	12.420	16.090	15.660	14.723
3	10.150	5.760	13.540	9.817
4	15.490	20.460	9.600	15.183
5	18.920	12.770	15.420	15.703
6	10.980	11.220	16.140	12.780
7	12.060	8.920	8.360	9.780
8	11.600	17.420	7.260	12.093
9	11.420	16.070	19.020	15.503
10	8.990	7.810	19.260	12.020
11	18.400	16.120	17.160	17.227
12	14.330	*	9.100	11.715
13	18.330	*	14.300	16.315
14	8.140	*	*	8.140
15	15.290	*	*	15.290
16	20.120	*	*	20.120
Mean	13.434	13.185	13.688	13.605
S.D. ±	3.94	4.50	4.00	3.17
n	16	11	13	16

Appendix 13 Daily growth rate of skeleton ($mg.d^{-1}$) of ***E. gemmacea*** at the study site, measured at 3m in summer 1989.

Symbol (*) indicates that the data are not available

DATE From / Specimen	26 - 7 - 89 / 5 - 8 - 89	5 -8 - 89 / 14 - 8 -89	14 - 8 - 89 / 20 - 8 - 89	26 - 9 - 89 / 26 - 9 - 89	Mean
1	14.02	9.622	13.583	8.280	11.376
2	12.18	13.344	5.400	9.200	10.031
3	9.29	14.478	15.117	15.760	13.661
4	15.35	23.788	15.550	11.320	16.502
5	12.92	11.411	24.983	11.520	15.209
6	13.66	13.178	11.650	11.020	12.377
7	16.92	9.289	13.667	10.560	12.609
8	12.95	10.033	9.567	10.620	10.793
9	12.01	15.078	11.733	12.160	12.745
10	13.43	6.778	10.400	6.760	9.342
11	17.06	10.644	8.250	13.480	12.359
12	7.91	21.833	17.117	8.000	13.715
13	10.90	7.778	6.967	9.9400	8.896
14	6.32	14.189	9.983	10.160	10.163
15	14.52	*	24.467	13.540	17.509
16	16.99	*	8.417	17.080	14.162
17	*	*	10.033	*	10.033
18	*	*	13.167	*	13.167
Mean	12.902	12.960	12.781	11.213	12.480
S.D. ±	3.13	4.88	5.31	2.74	2.41
n	16	14	18	16	18

Appendix 14 Daily growth rate of skeleton ($mg.d^{-1}$) of ***E. gemmacea*** at the study site, measured at 10m in summer 1989.

Symbol (*) indicates that the data are not available

DATE From To Specimen	7 - 1 - 90 17 - 1 - 90	17 - 1 - 90 24 - 1 - 90	24 - 1 - 90 6 - 2 - 90	Mean
1	6.990	9.143	8.331	8.155
2	16.790	12.514	13.823	14.376
3	11.120	14.586	16.169	13.958
4	19.510	22.771	11.823	18.035
5	16.330	10.843	15.123	14.099
6	15.320	4.357	15.300	11.659
7	8.220	8.200	17.285	11.235
8	13.100	21.271	7.392	13.921
9	5.180	14.600	16.292	12.024
10	19.260	6.486	28.292	18.013
11	9.820	8.543	10.577	9.647
12	12.140	5.929	10.577	9.549
13	*	16.600	*	16.600
14	*	24.429	*	24.429
15	*	10.100	*	10.100
16	*	18.029	*	18.029
17	*	22.400	*	22.400
Mean	12.815	13.577	14.249	14.485
S.D ±	4.73	6.41	5.48	4.58
n	12	17	12	17

Appendix 15 Daily growth rate of skeleton ($mg.d^{-1}$) of ***E. gemmacea*** at the study site, measured at 3m in winter1990.

Symbol (*) indicates that the data are not available

DATE From To Specimen	6 - 1 - 90 18 - 1 - 90	18 - 1 - 90 27 - 1 - 90	27 - 1 - 90 9 - 2 - 90	Mean
1	9.500	10.844	19.538	13.294
2	11.917	15.089	6.146	11.051
3	10.625	11.889	20.923	14.479
4	11.383	10.122	12.623	11.376
5	14.375	12.678	18.962	15.338
6	6.783	17.533	21.308	15.208
7	5.442	10.633	6.015	7.363
8	6.342	8.256	16.654	10.417
9	6.633	5.489	10.331	7.484
10	7.242	4.744	3.377	5.121
11	6.333	3.900	2.654	4.296
12	*	19.178	2.777	10.978
13	*	9.989	6.654	8.322
14	*	*	8.331	8.331
15	*	*	6.208	6.208
17	*	*	7.223	7.223
16	*	*	7.762	7.762
18	*	*	14.331	14.331
19	*	*	11.238	11.238
Mean	8.780	10.800	10.687	9.991
S.D ±	2.93	4.64	6.24	3.44
n	11	13	19	19

Appendix 16 Daily growth rate of skeleton (mg.d^{-1}) of ***E. gemmacea*** at the study site, measured at 10m in winter1990.

Symbol (*) indicates that the data are not available