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Distribution and Abundance of Benthic Diatoms in a Tropical Mangrove Forest and Effects of Grazing on them by *Telescopium telescopium* (Linnaeus, 1758)

Thesis submited by
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for the degree of Doctor of Philosophy in
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I. B. Hendrarto
30 October 1992

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I dedicate this work to

my wife Srie and my children

Tito, Yesika and Ino.

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CHAPTER 1

INTRODUCTION

1. General Introduction.

The term of mangrove is given to a group of angiosperm plants which grow on the sea shore between mean sea-level and the high water mark of the highest tide. These plants are widely distributed in tropical oceans and are comnon in areas sheltered from strong wave action. They often grow on coral reef lagoons that provide suitable habitats. They also penetrate deep into the estuaries of rivers. Their distribution is always related to the penetration of salt water. They can tolerate saline conditions but other tropical angiosperm plants species do not (De Haan, 1931; Richards, 1964; MacNae, 1968; Chapman, 1975).

Occupying as it does the region between land and sea, the ecosystem of mangroves may have sharp environmental gradients. The tidal factor causes high fluctuations in some environmental factors, such as temperature and salinity. Hence, only a few animals and plants have a sufficiently wide tolerance of these extreme conditions to survive and settle in mangrove areas. Because of this the heterogeneity of living organisms is restricted, but the population abundance may be high. The number of trees and shrubs constitutting in the mangrove forest is limited and conversely the mangrove plants are generally restricted to this habitat and are not found inland. It appears that each mangrove species has its own niche, in accordance with its own requirements as to habitat and life cycle (Steenis, 1958). Hence, mangrove forests differ in composition from place to place, and even contain a limited amount of zonation.

The existence of mangrove forests in an area provides a big contribution to marine life in the adjacent sea. Heald and Odum (1970) showed that leaf detritus from mangroves contributes a major energy input into coastal fisheries. The detritus is produced by the activity of fungi, bacteria and protozoa, which use the plant remains as an energy source which is decomposed and accumulates as organic detritus. Studies of these microorganisms associated with mangroves have been appearing in recent years. Kohlmeyer and Kohlmeyer (1979) for example published a summary of mangrove fungi whereas Hendrarto (1984), who carried out an intensive study of mycoflora living in mangrove sediment in Java, Indonesia, found that soil fungal assemblages within seaward and landward habitats were different.

Another group of microorganisms living in mangrove sediments is benthic diatoms. Compared to the other microorganisms, studies on benthic diatoms which live predominantly in and on mangrove sediments are few. The majority of recent ecological investigations on sediment-associated diatoms have been in non-mangrove, intertidal areas (Foged, 1975; John, 1983). Diatoms in soft-bottom and sublittoral habitats have been investigated extensively (Taasen & Hoiaseter, 1989). In tropical mangrove habitats, however, ecological studies on benthic diatoms are few (Cooksey, 1984). Studies on diatoms in natural mangrove areas have been limited to investigations of species composition of diatoms associated with mangrove roots that exist in sediments adjacent to mangrove areas (Foged, 1978; Navarro, 1982; Maples, 1983; Cooksey, 1984) and on various substrata (Foged, 1978; Wah and Wee, 1988). However these studies did not emphasise investigations of benthic diatoms living on mangrove sediments. Therefore studies of benthic diatoms living on mangrove sediments are needed.

Benthic diatoms are recognised to be important as a food component of many animals living on the surface of mangrove sediments. Some of these animals include mudskippers (Milward, 1974), juvenile prawns (Hartono, 1982, pers. com.) and molluscs (Houbrick, 1991). However, further investigations on the ecological and trphic roles of benthic diatoms are needed.

The estuarine snail *Telescopium* Montfort (Potamididae H & A. Adam, 1854) is one of the most common gastropod molluscs found in tropical mangrove forests. In the Indo-Pacific region two species have been recognised *i.e. T. telescopium* Linnê, 1758 and *T. mauritsi* Butot, 1954 (MacNae, 1968). In Panaitan Island, Sunda Strait, Indonesia, one species only is now recognised, because *T. mauritsi* has been shown to be the adult form of *T. telescopium* (Brandt, 1974; Houbrick, 1991). According to Houbrick (1991) fossils of this gastropod have been found from Cenozoic deposits in East Africa, Indonesia and the Philippines.

T. telescopium is considered to be the largest gastropod inhabiting Indo-Pacific mangrove forests and is considered somewhat characteristic of such forests (see MacNae, 1968; Budiman, 1988 and Houbrick, 1991). The size of the shell may differ in different mangrove forests. Short and Potter (1987) reported an average shell size (length) of 6.5 cm (in North Queensland). Budiman (1988) noted that shell length ranged between 20 to 100 mm and fresh body weight (*i.e.* with shell) was between 1.70 to 100 g (in Maluku, Indonesia). Houbrick (1991) reported shell lengths of *T. telescopium* of 130 mm length and 50 mm width (at Magnetic Island, North Queensland). The shell is a thick, solid, conical trochoid type consisting of 12 to 16 flat-sided whorls with an apical angle of 30 - 36 degrees. Shell colour is uniformly dark reddish-brown to black, with a whitish to light brown columellar callus.

This gastropod is found frequently on soft mud in the *Rhizophora* forest, on the surface of the mud in shallow pools and on the shady muddy banks and flats of the middle and landward zones of the mangrove intertidal (MacNae, 1968; Perkins, 1974; Sasekumar, 1974; Budiman, 1988). Movement of this snail is very much influenced by tide. *T. telescopium* become inactive when covered with water (Lasiak and Dye, 1986).

According to Houbrick (1991) the species is distributed widely from the western Pacific through Taiwan, the Philippines, New Guinea, tropical coasts of Australia, the Indonesian archipelago, coasts of Southeast Asia, the Mergui archipelago, the Andaman, along the coasts of India and Ceylon west to Karachi and may be found also in Reunion and Madagascar (see Figure 1.1). The occurrence in mangrove forests of Australia has been recorded by MacNae (1966), Hutchings and Recher (1981), Lasiak and Dye (1986), Short and Potter (1987) and Houbrick (1991). Several authors *viz.* Budiman *et.al.* (1977) and Budiman (1984; 1988) noted this species in Indonesian coastal areas. In mangrove areas of Thailand, Singapore, Malaysia and Pakistan the snail has been recorded also by Nateewathana and Tantichodok (1984), Chou *et.al.* (1980), Sasekumar (1974) and Tirmizi (1987), respectively.

In some parts of the Indo-Pacific region, the populations of *T. telescopium* have been reduced dramatically. Degradation of mangrove ecosystems by human activities affect the populations of this gastropod both directly and indirectly. A decrease in abundance of *T. telescopium* in some Asian and western Pacific countries is due to intensive collection for human consumption. Pollution and habitat disturbances (*e.g.* felling of mangroves) have indirect effects on the distribution and abundance of this snail.

In Indonesia considerable numbers of this species are collected by coastal inhabitants for food (Soegiarto and Soemodihardjo, 1987). Kasinathan and Shanmugam (1988) reported that in a period of six months, about 22 bags each weighing 70 - 80 kg were collected every week of unknown area of mangrove forests of Pitchavaram for the lime industry. Traditional fisheries in Matang, Malaysia, also target *T. telescopium*, as well as *Cerethidea obtusa*. About 7 to 10 kg per day are harvested from the unkown area of Matang (Chan and Nor, 1987).

Effects of pollution in mangrove areas of the Indo-Pacific have increased in the last decade. This maybe responsible for population decreases of certain mangrove fauna including *T. telescopium* in some parts of the region. In Singapore *T. telescopium* (and another gastropod, *Melanoides*), originally were harvested as food. Due to increased levels of pollution these species are now imported (Chou *et.al.*, 1980). Pollution effects on mangrove ecosystems have been recognised also in New South Wales, Australia and India (Allaway, 1987 and Untawale, 1987 respectively).

In many parts of the world, especially in the Indo-Pacific region, mangrove habitats have been modified by coastal inhabitants. Mangrove areas are converted into aquaculture ponds, provide infrastructure (for marinas, roads *etc.*), are used in agriculture and provide areas for industrial zones, housing and garbage dumps (Dixon, 1989; Hundloe and Boto, 1990). In the densely populated coastal areas of northern Central Java, for example, approximately 25,600 Ha of mangrove area are believed to have been converted into aquaculture ponds (Hendrarto, 1980). Exploitation and destruction of mangrove ecosystems has been recorded also in Australia (Allaway, 1985), India (Untawale, 1985), Malaysia (Chan and Nor, 1987) and SriLanka (Amarasinghe, 1988). Jara (1987) mentioned "if the rate of mangrove depletion continues, in 35 years there will be no more mangrove in the Philippines". IUCN/UNEP in 1991 say about 80 % of Philippine mangroves are now gone (Rush, 1994; *personal communication*). Soepadmo (1987) recorded that by the first half of the 1980s, about 42.5 % of the original 5.2 million ha. of mangroves in Southeast Asia has been extirpated by man. Table 1.1 presents data of the length of coastlines, total area of mangroves and total mangrove area which has been converted into fish ponds or otherwise destroyed in Southeast Asian countries. Destruction of mangrove habitats obviously may affect abundance of *T. telescopium* as well as that of other mangrove fauna.

These problems have not yet been solved by efforts to conserve and manage the exploitation of populations of this gastropod. This is not surprising because the basic biological and ecological knowledge necessary to manage the species effectively is still scant. Research on this species is, therefore, needed urgently.

Ecological studies of *T. telescopium*, including determination of their natural population densities and their effects of grazing on benthic microflora, have been few. MacNae (1968), Nateewathana and Tantichodok (1984) and Perkins (1974) for example, determined distributional patterns of this gastropod, however they did not provide detailed quantitative information on population density.

Table 1.1. Length of coastline, total area of mangroves and total mangrove area which has been converted into fish ponds or otherwise destroyed by man in Southeast Asian countries.

Country	Coastline (km)	Mangrove area (ha)	Mangrove area has been converted (ha)	% Lost
Indonesia	54,716[a]	4,251,039[b]	1,522,000[c]	33 %
Malaysia	4,675[a]	628,805[b]	300,000[c]	50 %
Philippines	22,540[a]	400,340[d]	306,000[c&d]	75 %
Singapore	193[a]	500[b]	1,250[c]	n.a.
Thailand	3,219[a]	287,302[b]	130,189[c]	46 %
Brunei Darussalam	161[e]	184[e]	n.a.	-

Source : (a) Kent and Valencia (1985) in Hundloe and Boto (1990); (b) Fortes (1988); (c) Soepadmo (1987); (d) Jara (1987); (e) Zamora (1987) in Hundloe and Boto (1990)

Considerable research on the effects of grazing by gastropods in littoral habitats has been carried out *e.g.* Castenholz (1961), Fenchel (1972), Nicotri (1977), Pace *et al.* (1979), Connor *et al.* (1982). A review by Steneck and Watling (1982) of 251 references relating to 106 species of herbivorous molluscs contained no information on *T. telescopium*. The diet of this snail has not yet been clearly elucidated. Some authors consider this snail is a detritivore (Alexander *et.al.*, 1979; Budiman, 1988; Houbrick, 1991) or that it feeds on algae and diatoms (Das *et.al.*, 1982; Short and Potter, 1987).

If this species consumes benthic microalgae the grazing activities of *T. telescopium* may be very important trophodynamically in mangrove ecosystems. However the specific role that this gastropod plays in the trophic structure of mangrove ecosystems has not been evaluated. During foraging movements, this gastropod may change the physical characteristics of the sediment surface and simultaneously affect abundance and community structure of benthic microalgae in and on the sediment.

The relationship between *T. telescopium* and benthic diatoms living in mangrove sediments may be significant. The benthic microalgae in mangrove sediments are dominated numerically by benthic diatoms (Cooksey, 1984). Considering the size of both individuals and populations of *T. telescopium*, the potential of this species to affect the abundance and community structure of benthic diatoms in mangrove forests appears to be substantial. This may in turn affect primary productivity on mangrove sediments directly. Another smaller mangrove gastropod, *Bembicium auratum*, is known to affect microalgae in mangrove muds (Branch and Branch, 1980). Similar impacts by many other gastropods have been recorded in muddy habitats (Fenchel and Kofoed, 1976; Pace *et.al.*, 1979; Connor *et.al*, 1982) and in littoral habitats (Castenholz, 1961; Nicotri, 1977; Underwood, 1978a and 1978b). The link between the distribution, abundance and grazing activities of *T. telescopium* and benthic microalgae may be significant. It is thus important to conduct a study which includes investigation of the ecology of both *T. telescopium* and benthic diatoms in natural mangrove forests.

This study includes investigation of benthic diatom assemblages on soft substrata within different mangrove zones and the effects of *T. telescopium* grazing on benthic diatoms. The specific aims of the present study were to determine within a natural (*i.e.* undisturbed) mangrove area

(1) the distribution and abundance of benthic diatom assemblages on and in mangrove sediments
(2) the distribution and abundance of *T. telescopium*,
(3) aspects of the feeding habits and growth of this species,
(4) the relation between levels of density of *T. telescopium* and the composition and primary production of benthic diatom assemblages in sediments.

These objectives were met by determining the composition and abundance of benthic diatom assemblages across different mangrove zones and then investigating the effects of grazing of the snail on diatoms in a field experiment.

Results of this study may be of general significance to trophodynamic models of mangrove ecosystems and thus provide data needed for managing the tropical conservation and exploitation of national mangrove ecosystems.

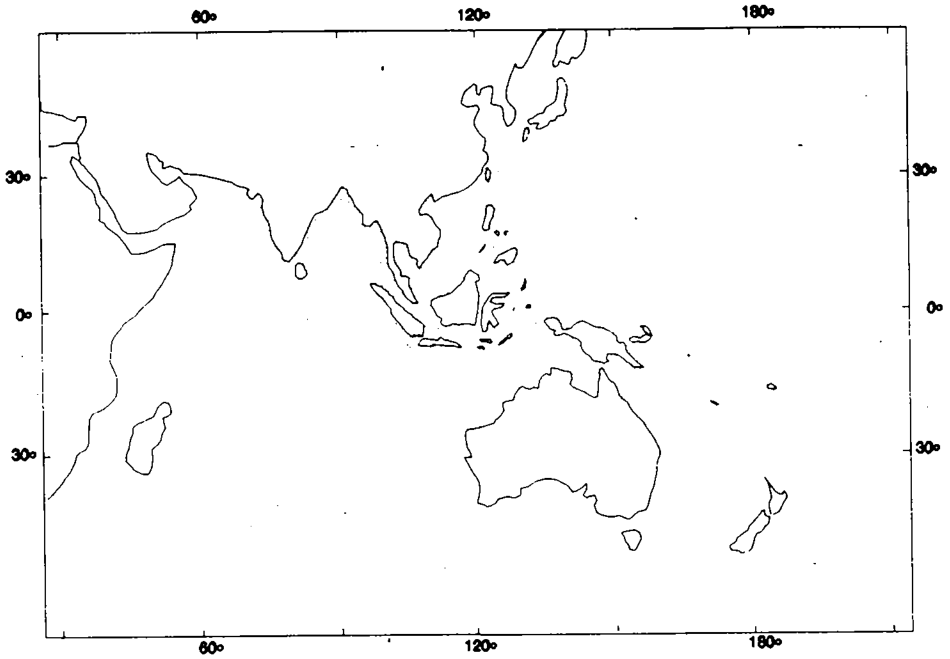


Figure 1.1. A map showing the geopraphical distribution of *T. telescopium* (after Houbrick, 1991)

CHAPTER 2

LOCATION OF STUDY

2. Location of Study.

The study was carried out in two natural mangrove areas adjacent to Chunda Bay, near the Australian Institute of Marine Science (AIMS), North Queensland, between 19°30' - 19°45' South and 147°15' - 147°25' East (Royal Australian Survey Corps, 1973) (Figure 2.1). The intertidal areas were shallow and gently sloping, dominated by a sandy-mud substratum. Landward or higher areas were inundated only when seawater levels were above mean high water (M.H.W.) level or higher than 2.79 m chart datum (Lasiak and Dye, 1986; Queensland Department of Transport, 1989).

The habitat included some shallow natural waterways which drained into three creeks. These waterways drained the mangrove areas during ebbing tides. During wet seasons, these waterways discharged a large amount of freshwater into the mangrove areas.

The climate at these study sites in Chunda Bay can be classified as hot tropical (see Robertson and Duke, 1987). Average daily temperatures were estimated to be between 22.7 - 31.3 °C and 13.4 - 27.4 °C during summer and winter respectively. The highest mean levels of rainfall were in December (116 mm), January (297 mm), February (300 mm) and March (212 mm) (Commonwealth Bureau of Meteorology, 1988).

Mangrove trees were distributed mainly along the river banks. Zonation of mangrove communities was distinct. Outer zones (*i.e.* adjacent to the sea and rivers) were dominated by dense stands of *Rhizophora stylosa*. Landward areas were dominated by a zone of dense *Ceriops tagal* trees. The canopy of these trees was dense, preventing sunlight from reaching the substratum. The substratum was composed mainly of muddy soils. Directly behind the mangrove areas there was a zone of *Eucalyptus* forest.

In some areas there were open sandy-mud flats. These were located between the *Rhizophora stylosa* and *Ceriops tagal* zones. Inner parts of the flats were covered by *Ceriops tagal* trees in low density. These flats were surrounded by saltmarsh vegetation (*e.g. Sacorconia*) in the middle parts. The outer parts, however, consisted of open sandy-mud soils and this was usually bordered by shallow waterways. Mangrove saplings *i.e.* 1 - 2 m high *Avicennia marina, Rhizophora stylosa* and *Ceriops tagal*, were found commonly in these waterways. Canopies of these saplings were sparse, thus allowing sunlight to reach the substratum. Evaporative water loss of the shaded areas was almost 3 to 4 times lower compared with that in open areas (Lasiak and Dye, 1986).

The most common forms of benthic fauna of mangrove ecosystems in the Indo-Pacific regions were dominant also in the sites studied here. These were species of Littorinidae, Cerithiidae, Potamididae (the latter three families in the phylum Mollusca, Class Gastropoda), and Sesarminae and Paguridae (Phylum Arthropoda, Class Crustacea) (MacNae, 1968; Sasekumar, 1974; Wells, 1980; Wells, 1984; Little and Stirling, 1984). Adult Potamididae viz. *T. telescopium*, *Terebralia* and *Cerethidea* were abundant in the shallow pools and waterways covered by mangrove saplings. *T. telescopium* appeared to prefer more open areas than did *Terebralia*. *T. telescopium* was not common under the very dense canopy in the *Ceriops tagal* and *Rhizophora stylosa* forests. Large numbers of *Terebralia* could, however, be found inside mangrove forests under *Rhizophora stylosa* trees even in the outer zones. *Littorina* were predominantly found on *Avicennia marina* trees on the seaward fringe, with few *Littorina* inhabiting the landward zones.

Crabs, especially *Sesarma, Uca* and *Scylla* were abundant. It was likely that *Sesarma* was the most widespread crab in this ecosystem (Warren, 1989 personal communication). *Uca*, however was more locally distributed, *i.e.* in wet, muddy, open areas between mangrove saplings and saltmarsh vegetation. During high tides, considerable numbers of *Scylla* were seen in the mangrove forests.

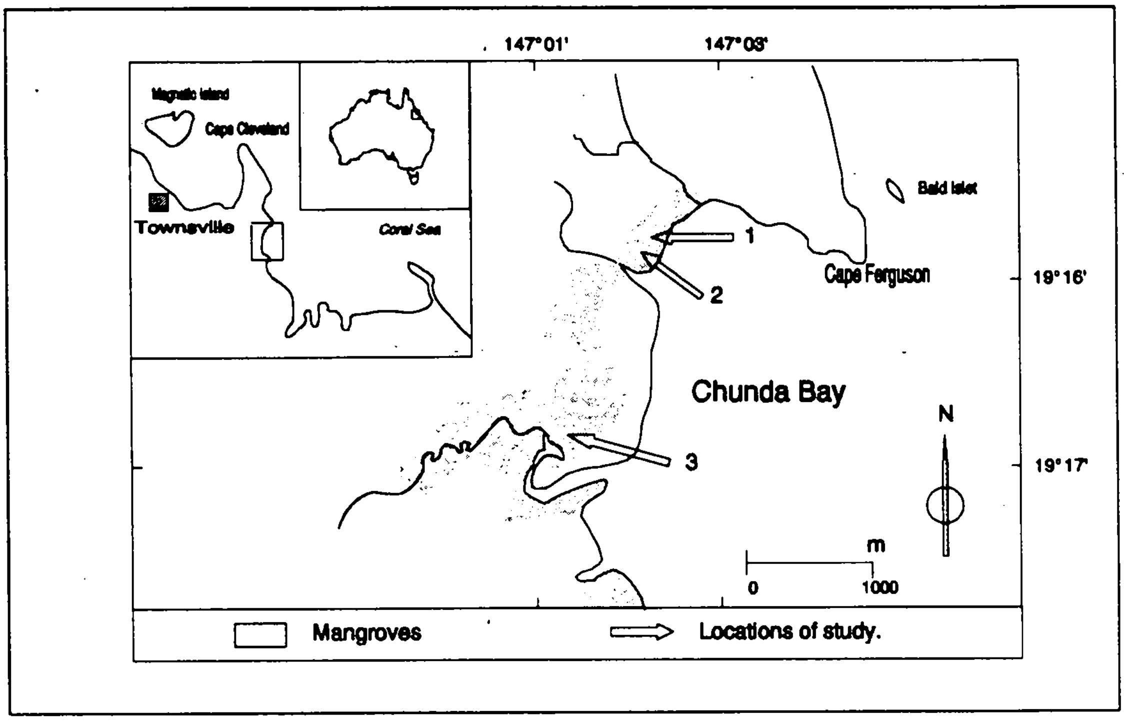


Figure 2.1. Locations of study at mangrove areas adjacent to Chunda Bay.

The study of the benthic diatom community were undertaken at location 2. Study of distribution and abundance of *T. telescopium* was carried out at Locations 1, 2 and 3. The field based experiment, studies of feeding habits, growth of *T. telescopium* were carried out at location 2.

CHAPTER 3

COMMUNITIES OF BENTHIC DIATOM IN MANGROVE AREAS.

CHAPTER 3

COMMUNITIES OF BENTHIC DIATOM IN MANGROVE AREAS.

3.1. Introduction.

Benthic diatoms can be divided into two groups: the diatoms that live attached to the substratum (rocks or plants) and those living free on and in sediments. The assemblage of benthic diatoms growing on the surface of intertidal sediments is often called the "epipelon" (see Round, 1971 and Round *et al.,* 1990). Epipelic diatoms have been recognised to play an important role in maintaining primary production in periodically inundated shallow-water habitats (Shaffer and Onuuf, 1983; Colijn and de Jonge, 1984).

Information available on the ecology of benthic diatoms in mangrove areas is more scarce an that for planktonic diatoms (Admiral *et.al.*, 1982 and Round, *et al.*, 1990). The majority of recent ecological studies on sediment-associated diatoms have been in non-mangrove ecosystems. Research has been reported from freshwater environments (Round, 1961; Stockner and Shortreed, 1978 ; Stevenson *et.al*, 1991), rivers and estuaries (John, 1983; Hudon and Bourget, 1983; de Jonge, 1985) and intertidal mud flats and shores (Round, 1960; Drum and Weber, 1966; Admiral *et.al.*, 1982; Oppenheim, 1991).

Few studies are available on diatoms in natural mangrove areas (Cooksey, 1984). These studies were carried out mainly in subtropical mangrove ecosystems and included studies of species composition in Eastern Australian mangroves (Foged, 1978) and studies of diatoms associated with mangrove roots in USA (Navaro, 1982; Maples, 1983). Benthic diatoms in tropical, mangrove sediments have not been investigated extensively. A review by Wah and Wee (1988) demonstrated that publications on benthic diatoms in Indo-Malaysian mangroves were few. In Indonesia, one of the largest areas of coastal-belt mangrove in the world, some limited studies of the sediment fungal community exist (Hendrarto, 1983) but studies of benthic diatoms are not yet available.

In tropical coastal areas of Australia, several authors have recognised the potential significance of the relationship between benthic diatoms and certain types of estuarine fauna. Benthic diatoms have been found as a food component of Queensland mudskippers (Milward, 1974) and juvenile banana prawns (Hartono, 1992, pers. com.). However, ecological studies on assemblages of benthic diatoms in mangrove areas are still few. A recent study on mangrove benthic diatoms was limited to the determination of the effects of the felling of mangrove trees on the composition of the benthic diatom community (Hendrarto, 1989).

Different sites within vegetation zones of mangrove areas contain different types of soil. One of the most important factors affecting distribution and community structure of benthic diatoms is the type of soil (Round *et.al*, 1990). Therefore it can be hypothesised that community structure of benthic diatom species could be different at different locations in tropical mangrove areas depending upon factors such as soil type, tidal inundation, or vegetation type. To test such hypotheses, the approach of this study was based on the assumption that benthic diatom assemblages could be sampled effectively using knowledge of the strong diurnal vertical migration rhythm of diatoms (Round *et.al*, 1990). These diatoms can be trapped or removed from the sediment surface using either coverglasses or tissue traps. These sampling methods can remove 75.5 % or 87.5 % of diatoms cells from sediments, respectively (Eaton and Moss, 1966).

The present study provides a general description of the benthic diatom community in a tropical mangrove ecosystem. The study aimed specifically at determining (1) the composition of species of benthic diatoms, and (2) the similarity and dissimilarity of benthic diatoms assemblages in different sites of tidal inundation and vegetation type in a tropical mangrove area.

3.2. Materials and methods.

3.2.1. Study sites.

This study was carried out in mangrove areas adjacent to Chunda Bay in North Queensland (see Figure 3.1) during March and September 1990. Samples were taken from six sites (approximately 100 m^2) located in semi-open areas in two different areas within intertidal habitats *i.e.* landward and seaward areas. The upper, landward area was inundated during spring high tides (approximately ≥ 2.8 m) only (Lasiak and Dye, 1986; Queensland Department of Transport, 1989). Three sites *viz.* HS1, HS2 and HS3 were located in the landward area (height about datum was approximately 1.5 m). The other sites *i.e.* LS1, LS2 and LS3, represented the seaward area (height about datum was approximately 0.5 m). Mangrove vegetation within the sites was approximately 1 to 4 m high. The sites were dominated by different mangrove vegetation as follows:

HS1 - *Ceriops tagal, Avicennia marina.*
HS2 - *Ceriops tagal, Avicennia marina* and young *Rhizophora stylosa.*
HS3 - *Rhizophora stylosa, Avicennia marina.*
LS1 - *Avicennia marina.*
LS2 - *Avicennia marina, Rhizophora stylosa.*
LS3 - *Rhizophora stylosa, Avicennia marina.*

Sites HS3, LS1 and LS2 were located in a small waterway approximately 2 m wide. This waterway was always filled with running water during ebbing tide. The other sites contained small pools during ebbing tides, but the pools were often completely dry during hot sunny days. Generally the landward (higher intertidal) sites dominated by *Ceriops* with Avicennia present, the seaward (lower intertidal) sites by *Avicennia* with *Rhizophora* present.

3.2.2. Collecting benthic diatoms.

Collecting of benthic diatoms was carried out during March 1990 and September 1990. The method of collecting benthic diatoms living on the mangrove sediments involved removing the sediment from habitats and trapping the benthic diatoms. Sampling points (n = 15) at each 100 m^2 site were selected randomly using a grid system (Andrew and Mapstone, 1987). At each selected point a block of sediment 4 cm x 4 cm and 2 cm deep was removed using a small trowel (18.5 cm total length with a metal part 8 cm long and 2.5 cm wide). The samples were retained whole in sealed polyethylene bags and transported to the laboratory.

The samples were stored in the dark for 6 to 8 hours after which the supernatant water is removed (*see* Eaton and Moss, 1966 and Round *et al.*, 1990). The whole sample was poured into a 100 ml container, wetted with sterile, clean seawater and shaken to mix the sample. The sample was shaken to distribute the algae uniformly then a suitable portion was poured into a 90 mm diameter petridish. Four 2 cm x 2 cm lens tissues (Kimwipes, fine grade from Kimberly-Clark Australia) were placed onto the wet sample surface. Diatoms adhered to the lens tissue and each lens tissue represented the sample unit for benthic diatoms. There were 15 blocks of sediment per site and four lens tissue subsamples per block, giving a total of 360 subsamples from the six sites.

The subsample was placed in sunlight. The subsample was never exposed to artificial light, even at night and experienced the natural cycle of light and darkness for one full 24 hour cycle. The lens tissues were harvested the next morning between 08:00 and 11:00 (Eaton and Moss, 1966). Each lens tissue was placed in a vial and preserved with 3 ml of 5 % formaldehyde solution and 1.5 % sodium hypochlorite (1 : 1 by volume).

The algae were released by macerating the lens tissue in the preservative in a concave dish using a pair of mounted needles. Two drops of this suspension were transfered to a counting chamber (an improved Neubauer counting chamber made by Assistent, Germany; see Figure 6.4). Diatoms in five selected fields (1 mm x 1 mm) were identified under a light microscope with phase contrast equipment (Taasen and Hoisæter, 1989). This microscopic procedure was replicated three times for each vial. The dominance of benthic diatom species was calculated based upon values of frequency of occurrence. The absolute and relative frequencies of each species were determined using the following formulae (Greigh-Smith, 1983):

$$\boxed{FA = \frac{F}{n} \times 100\ \%}$$

and

$$\boxed{FR = \frac{FA}{N} \times 100\ \%}$$

where

FA is absolute frequency (in %); F is absolute frequency of one species; n is total number of samples (*i.e.* n = 360 for the whole sample with n = 60 per site), FR is relative frequency or abundance of one diatom species relative to other diatom species (in %), N is total frequency of all species.

3.2.3. Textural analyses of mangrove soil

Three soil samples of each site (*i.e.* two from the edge and one from the middle of the site) was collected at 10 cm depth and placed into polyethylene bags. Sampling was carried out in September 1990. After transportation to the laboratory samples were spread thinly for air-drying at room temperature around 27 °C. Samples were passed through a 2 mm mesh sieve (Ball, 1976). Large lumps were crushed using a pestle and a porcelain mortar. 10 g of soil was poured into a 1000 ml beaker glass and stirred. Separation of the sand fraction was done after the suspension was transfered into a one litre measuring cylinder through a 63 µm sieve. This sieve was then placed on a watch glass in an oven at 60 °C, dried overnight and the mass of sand was determined by weighing the dry residue.

Silt and clay fractions were determined by a pipette method. The volume in the measuring cylinder was made up to 1 litre. This suspension was stirred and allowed to come to thermal equilibrium. 20 ml of sample was then immediately taken with a pipette from 15 - 20 cm depth. The pipette was then drained into a tared evaporating basin to which was added two 5 ml rinses of water from the pipette.

The clay fraction was determined by making up to 1 litre again and stirring for 30 sec. The sampling was similar to that of the clay + silt fraction but the pipette was lowered carefully to 10 cm depth (below the surface) at the requisite time. The settling time at 10 cm depth for the clay fraction depended on the temperature of the suspension (Avery and Bascomb, 1974). The proportion of sand, silt and clay were calculated in percentage terms.

3.2.4. Vegetation coverage.

Coverage of vegetation in the areas used for sampling benthic diatoms was determined using 5 m x 5 m quadrats. Aerial coverage of every tree within these quadrats was determined by measuring the projection of the outermost canopy onto the ground (see Greigh-Smith, 1983). The area on ground covered by tree canopy was defined as the coverage of the tree.

3.2.5. Data analysis.

Similarity between benthic algal communities at different sampling sites was analysed using a multivariate method: normal (q-type) cluster analysis (Field *et al.*, 1982). Only dominant taxa were included in the analysis (Taasen and Hoisæter, 1989). The data (*i.e.* diatom abundance values) were standarized using general relativisation (McCune, 1987):

$$b_{ij} = \frac{x_{ij}}{(\Sigma x_j^{p})^{\frac{1}{p}}}$$

where b_{ij} = score of abundance of the *i*th species in the *j*th sample; x_{ij} = abundance of the *i*th species in the *j*th sample; p = parameter of relativisation.

Similarity between benthic diatom communities then was measured using the index of Sorensen (Bray and Curtis, 1957):

$$C = \frac{2p_{jk}}{(p_j + p_k)}$$

where p_j and p_k represent the sums of diatom species values (*i.e.* number of diatom cells per unit area) for samples *j* and *k*. P_{jk} is the sum of the lesser species values for those species common to both samples.

The relationship between benthic diatom communities at different sampling sites was then determined using (1) a classification or cluster analysis based on a group-average sorting (Field *et al.* 1982) and (2) ordination (Bray and Curtis, 1957). The chi square test (Zar, 1984) was used to analyse patterns of distribution of species richness at different sampling sites. To analyse differences in average number of species per site, one-way analyses of variance were used (Underwood, 1981; Zar, 1984).

3.3. Results.

3.3.1. Species composition.

The total number of species of benthic diatoms found in this study was 223 belonging to 18 families and 48 genera. This number did not include the small, unidentified species (*i.e.* smaller than 10 µm). A list of species of benthic diatoms is provided in Table 3.1. The highest number of species recorded belonged to the Naviculaceae with 14 genera and 123 species. This represented 55.15 % of the species of diatoms identified in this study. Total numbers of species and absolute frequency of occurence of diatoms are shown in Table 3.2.

A total of 34 species could be classified as "dominant" species (*i.e.* which had a value of frequency of occurence higher than 30 % of all samples). Table 3.3 shows the values of relative frequency of occurrence of these dominant species in the samples. The most frequent species of benthic diatoms found in the samples were *Amphora coffeaeformis* (= Rank 1), *Amphora ovalis* (=Rank 4), *Navicula tripunctata* (= Rank 3) and *Nitzschia punctata* (= Rank 2). These species were found in almost every sample (*i.e.* more than 80 % of samples).

3.3.2. The benthic diatom community.

The total number of species found within sites varied (see Table 3.2). The lowest number of species of benthic diatoms was found at site LS3 of seaward area (117 species). The highest number of species occurred at site HS3 in the landward area (216 species). Table 3.4 shows the results of statistical tests comparing the number of benthic diatom species between areas and sites (within the areas). The number of species differed significantly among sites ($P < 0.01$). In the landward area, the number of species among sites differed significantly also ($P < 0.05$). In the seaward area, however, the number of species did not differ between sites ($P > 0.05$).

In the seaward area, benthic diatoms at site LS1 had relative frequency values consistently under 5 % . At site LS2 only *Navicula tripunctata* had a value greater than 5 % . The pattern of species dominance at site LS3, however, was more similar to that found at sites HS1 and HS2 in the landward area. At this seaward area diatoms *Amphora coffeaeformis*, *Amphora ovalis* and *Nitzschia punctata* were commonly found.

Environmental conditions did not appear to have a strong effect on the total numbers of species of benthic diatom. The results of analyses of variance on number of species under different environmental conditions are shown in Table 3.5. The number of species in wetter areas (*i.e.* HS3, LS1 and LS2) did not differ significantly from those in dry areas ($\underline{P} > 0.05$). Intertidal location did not influence the numbers of species of benthic diatoms. The total numbers of species in the landward and seaward areas were 170.7 ± 99.1 and 136 ± 42.1 (95 % confidence interval) species respectively. The difference between these numbers was not significant ($\underline{P} > 0.05$). Grouping the data based upon the availability of water showed that the total numbers of species in dry and wet areas were 137.7 ± 47.77 (95 % C.I.) and 169.7 ± 99.8 (95 % C.I.) respectively. These levels of species richness were not significantly different ($\underline{P} > 0.05$).

The result of the multivariate analysis based upon data for the 34 dominant species is shown in Figure 3.2. This result is clarified by constructing an ordination diagram (Figure 3.3). The dendogram and ordination suggested that based on the dominant benthic diatom assemblages, the site were assembled into two distinct groups. The first group consisted of sites HS1, LS3 and HS2 (= Dry sites), and the second group consisted of sites HS3, LS1 and LS2 (= Wet sites).

The environmental factors may be plotted on the axes of the ordination diagram (Figure 3.3) by examining the physical factors at each site (see Figure 3.1). The first group of sites were located in a drier habitat dominated by the mangroves *C. tagal* or a mixture of *C. tagal* and *A. marina*. The second group represented sites from wetter areas. These sites were located along a waterway where the vegetation was mainly *A. marina* and *R. stylosa* bushes. By including these physical factors, both the dendogram and the ordination suggest strongly that the availability of water affected community structure of benthic diatoms substantially.

Some diatom species showed similar patterns of dominance with respect to availability of water. These patterns are shown in Figure 3.4. In Figure 3.4A *Amphora coffeaeformis*, *Nitzschia punctata*, *Gyrosigma scalproides*, *Nitzschia cocconeiformis* and *Surirela ovalis* were relatively more dominant in dry than in wet sites (see Table 3.3). In Figure 3.4B other species of benthic diatom *viz*. *Navicula cincta*, *Achnanthes brevipes*, *Cocconeis heteroidea*, *Nitzschia hungarica* and *Navicula salinarum* had greater dominance at wet sites (see Table 3.3).

3.3.3. Soil texture and vegetation coverage.

Soil texture and vegetation coverage within the sampling areas are shown in Table 3.6. Soils from the landward areas contained more sand particles than soils from seaward areas. However soils from seaward areas had more clay. Almost all sampling sites had a high vegetation coverage. The lowest vegetation coverage was found at Site 2 in the landward area *viz*. only 51.14 % of ground was covered by mangrove canopy.

3.4. Discussion.

Benthic diatoms found in this study consisted of 223 taxa belonging to 48 genera . This number of species of diatom was somewhat higher than that found previously studies at other Indo-Malaysian tropical mangrove ecosystems. In a mangrove environment in Singapore, Wah and Wee (1988) recorded a total of 72 taxa belonging to 25 genera of diatoms collected from various habitats (*i.e.* wood, leaves, roots of *Avicennia*, mud, muddy water and stones). Of this total, only 36 of the taxa were found in mud habitats. The difference may be influenced by factors such as sampling methodology and levels of disturbance to mangrove habitats.

In the present study, sampling and collection of benthic diatoms was carried out on a smaller spatial scale. However, the lens tissue method used was specific for collection of benthic diatoms and was probably able to remove at least 70 % of the diatoms from the substratum (Eaton and Moss, 1966). The present study therefore could be classified as an intensive examination of the benthic diatom communities. In their study, Wah and Wee (1988) collected benthic diatoms simply by picking them off the substrata and specialised methodologies to collect benthic diatoms were not employed.

The location of the present study in Chunda Bay was in an area of undisturbed mangrove. Singaporean mangrove ecosystems apparently are in a highly degraded state (Wah and Wee, 1988). Disturbance frequency may have contributed to the lower number of taxa recorded compared to that in the present study.

The total number of species of benthic diatom recorded in this north Queensland mangrove was higher also than in some other areas. Some workers have recorded lower numbers of species of benthic diatom in certain estuarine and marine sediments (Kenett and Hargraves, 1984; Stidolph, 1985, respectively) and on mangrove pneumatophores (Maples, 1983). Navaro (1982), however, found a higher number of species epiphytic on mangrove roots in Florida than of epipelic diatoms recorded in the present study.

The most frequently recorded families of benthic diatoms in the present study were the Naviculaceae and Nitzschiaceae. These two families may perhaps be amongst the most important trophodynamically in mangrove areas. These diatoms were recognised to have highly motile cells (Hudon and Bourget, 1983) and not only occur as epipelic forms in mangrove ecosystems, but may dominate other types of substratum also. The dominance of these families has been recorded also by Foged (1978) in mangroves on the East Coast of Australia, Navaro (1982) in the Indian River, Florida, U.S.A., Maples (1983) in Lousiana, U.S.A. and Wah and Wee (1988) in Singaporean mangrove areas. In other marine and estuarine habitats, the dominance of these families was marked. Kenett and Hargraves (1984) included the family Surirellaceae, in addition to Naviculaceae and Nitzschiaceae, as the most important families of benthic diatom in a subtidal area. Wood (1963) suggested that only the Nitzschiaceae was common on the east Australian coast. In the Philippines, Mann (1925) recorded that the Naviculaceae was the dominant taxon. Taasen and Hoisæter (1989), working in sublittoral localities in Western Norway, showed that the families Naviculaceae and Nitzschiaceae were the dominant taxa also.

Most of the 34 dominant species of diatom in this study have been recorded in previous studies of Australian mangroves and estuaries. Approximately 55.88 % of the taxa had been recorded in eastern Australian mangroves (mainly subtropical). However, a total of 88.24 % of the dominant taxa had been found previously in eastern Australia (*i.e.* New South Wales, Victoria and Queensland) (see Foged, 1978). About 64.71 % of the taxa were recorded in the Swan River, Western Australia (John, 1983). Compared to other subtropical mangrove ecosystems in northern latitudes, only around

55.88 % and 41.18 % of the dominant taxa occurred in mangrove areas of Florida and Lousiana, U. S. A., respectively (see Navaro, 1982 and Maples, 1983). However, 52.94 % of the taxa have been recorded in China (Jin *et.al.*, 1985) and only 23.53 % of the dominant taxa were recorded in a tropical Indo-Malaysian mangrove ecosystem (see Wah and Wee, 1988).

The community of benthic diatoms.

Site LS3 (= site 3 in the lower intertidal habitat) had the lowest number of species. The most important factor determining this was perhaps availability of sunlight. Mangrove trees at site LS3, were relatively higher and the coverage of the canopies was much denser than that at the other sites (85.45 % of mean of the other 5 sites = 71 %). This canopy may have reduced availability of direct sunlight to the sediment surface. Reduction of light intensity has been recognised as an important factor affecting benthic diatom physiology *viz*. the rate of movement (Hopkins, 1963), taxic movements (Hudon and Bourget, 1983) and metabolism (Round, 1971; Kristensen *et.al.*, 1988; Zimba *et.al.*, 1990).

Toxic substances in the sediments may reduce the number of species of benthic diatoms also. In some areas adjacent to the site LS3, *i.e.* inside the *R. stylosa* forest, a number of mangrove trees had been cut down (Hendrarto, 1989). The decomposition process of mangrove roots and trees in the area may have released toxic substances, such as sulphide. The concentration of sulphide was not measured during this study, but sediments at this site possessed a strong odour of hydrogen sulphide. This toxic substance may have accumulated and been distributed to adjacent sediments. The existence of sulphide in sediments has been known to affect epipelic diatoms (see Taasen and Hoisæter, 1981 and Round *et al.*, 1990). In the case of site LS3 perhaps only certain species were able to survive in these toxic conditions.

The multivariate and ordination analysis indicated that sites along the waterway were grouped closely in terms of benthic diatom assemblages. This suggested that the effect of water availability in sediments was more important than tidal height per se. Benthic diatoms in the sites adjacent to the waterway were not generally subjected to desiccation at low tide. Away from this waterway benthic diatoms may have suffered from the effects of desiccation and high salinity. These factors have been shown to be important physical factors that may control assemblages of epibenthic diatom in estuarine areas (Kaufman, 1982). To study the effect of water availability more directly, it may be better to design a sampling scheme to collect benthic diatoms in transects running at 90° to the direction of the waterway. This may better elucidate the relationship between diatom assemblages and water availability.

The results reported here differ somewhat with those of other studies in salt marshes and intertidal mud habitats (*i.e.* Round, 1960; Drum and Weber, 1966; Baillie, 1987). These authors suggested that the soil texture was a more important factor determining numbers of diatom taxa in the sediment than availability of soil water. Soil texture has been known to determine dominance of soil fungal species in both mangrove and salt marsh sediments (Hendrarto, 1983 and Hendrarto and Dickinson, 1984, respectively). In this study the effects of soil texture on number of species was not significant. This was likely due to the effects of water availablity (that closely related to soil temperature) was greater than the effects of soil texture on the diatom assemblages.

Sediments in the drier sites were dominated by *Amphora coffeaeformis*, *Nitzschia punctata*, *Gyrosigma scalproides*, *Nitzschia cocconeiformis* and *Surirela ovalis*. These sites may have had less influence from freshwater during the wet season. Salinity may also have been higher at these sites since seawater would have been evaporated during low tide. Only diatoms with a wide range of salinity tolerance may have been expected to dominate these sites. The five dominant taxa at these sites, however, have been recognised as marine species (Jin *et.al.*, 1985). These species appear to be able to survive better in drier sites than other benthic diatom species.

Sediments at the wet or waterway sites were probably more influenced by freshwater, especially during ebbing tides in the wet summer season. This may have accounted for *Navicula cincta*, *Achnanthes brevipes*, *Cocconeis heteroidea*, *Nitzschia hungarica* and *Navicula salinarum* being more dominant at these sites. Perhaps these species were better able to grow in habitats influenced by freshwater. Hustedt (1938) recorded that these diatoms were dominant in freshwater environments of Java, Sumatra and Bali. Foged (1978) mentioned that *Achnanthes brevipes*, *Cocconeis heteroidea*, *Nitzschia hungarica* and *Navicula salinarum* were cosmopolitan in Australia .

Ordination analysis suggested that the diatom assemblages could be grouped on the basis of dominance of the mangrove taxa also. The mangroves themselves may be determined by water availability. Diatoms such as *Amphora coffeaeformis, Gyrosigma scalproides, Nitzschia closterium, Nitszhia cocconeiformis, Nitzschia punctata* and *Surirela ovalis* in general were more dominant in the *C. tagal* - *A. marina* zone. Other diatoms, *viz. Achnanthes brevipes, Cocconeis heteroidea, Navicula cincta, Navicula salinarum* and *Nitzschia hungarica* appeared to be associated with other mangrove zones dominated by a combination of *A. marina* - *R. stylosa*. This suggests that horizontal zonation of benthic diatoms in this mangrove area may have been associated with the zonation of the mangrove vegetation. Some authors have recorded that different dominance patterns of diatoms occur on roots of different mangrove species (Navaro, 1982 and Maples, 1983). The pattern of diatom zonation may be related to the pattern of zonation of soil mycoflora. Studies within mangroves in Java and salt marshes of Alnmouth, England (Hendrarto, 1983 and Hendrarto and Dickinson, 1984, respectively) recorded that the zonation of soil fungi was associated clearly with zonation of higher plants.

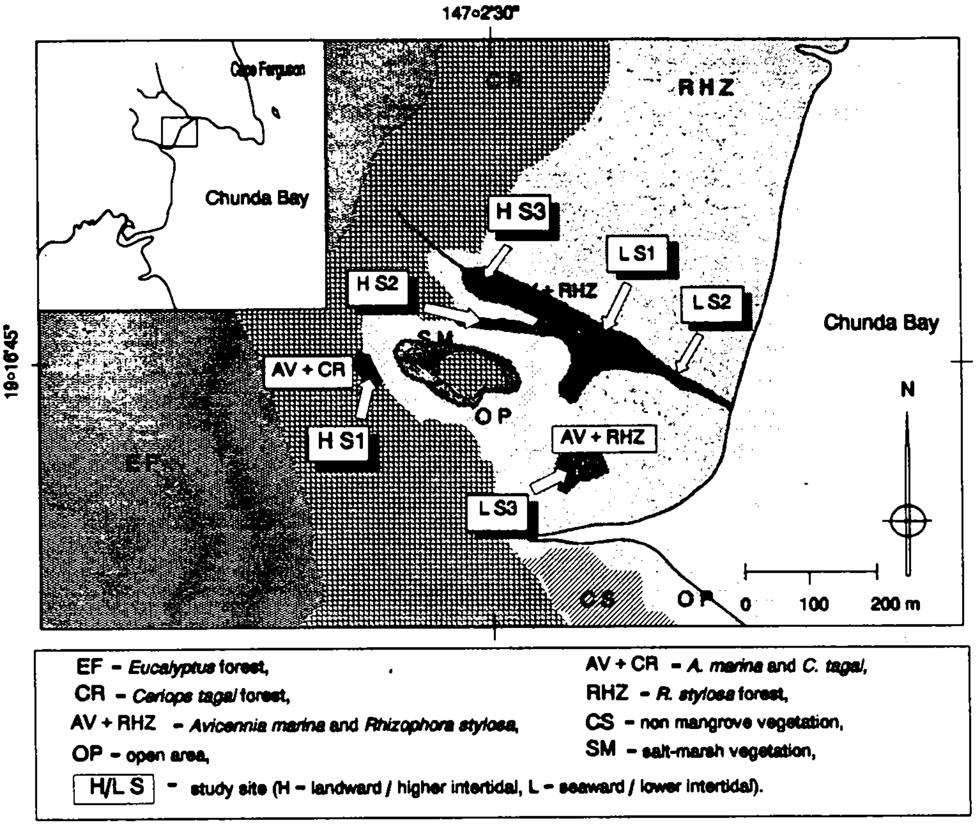


Figure 3.1. A map showing the location of sampling sites for benthic diatoms in a mangrove forest adjacent to Chunda Bay, North Queensland. Zonation of the mangroves is indicated by the different patterns of shading.

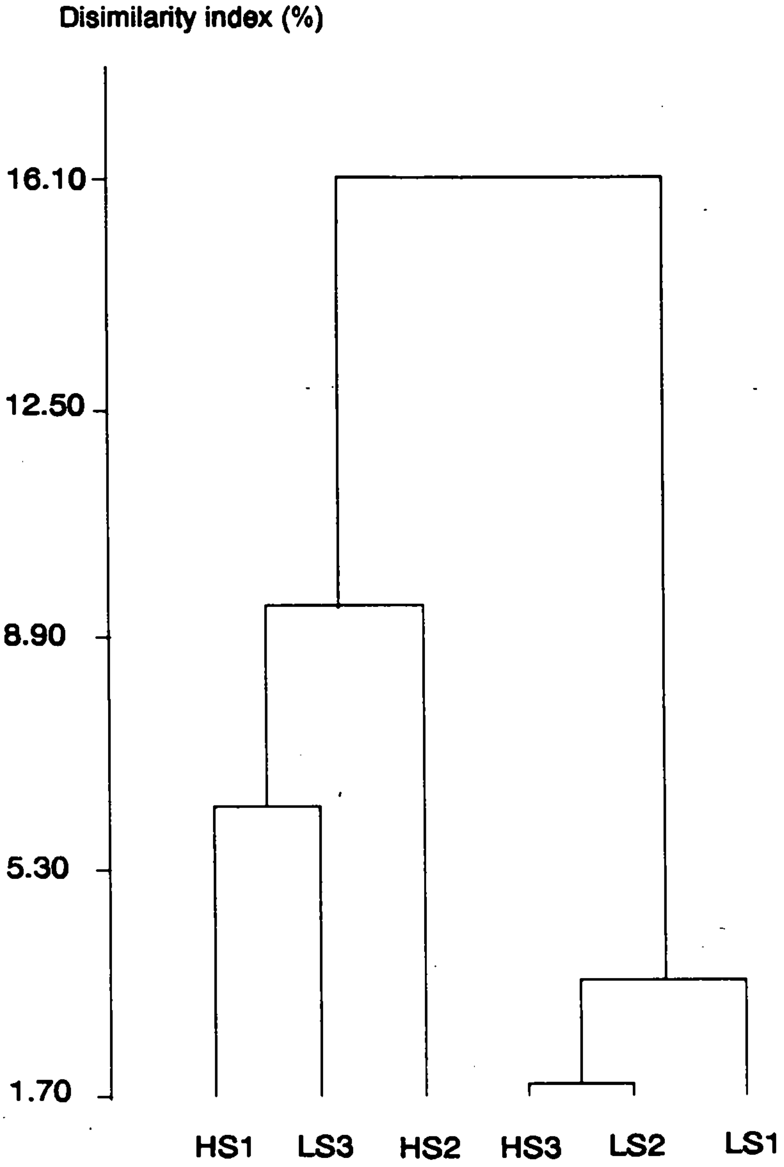


Figure 3.2. Dendrogram comparing six sites in two different location of the mangrove adjacent to Chunda Bay.

This dendrogram was based upon total relative frequency data

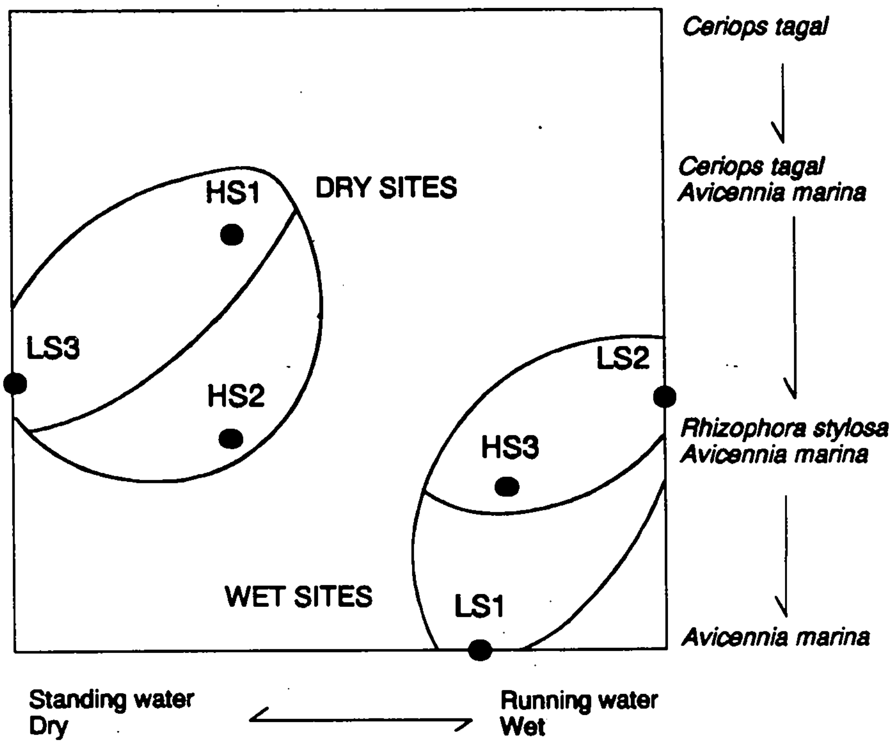


Figure 3.3. Ordination of six sites in the mangrove area adjacent to Chunda Bay based upon relative frequency of common benthic diatom species.

H and L are landward and seaward locations respectively. Sn is the site number. The X and Y axes indicate the relation of the sites to particular environmental factors.

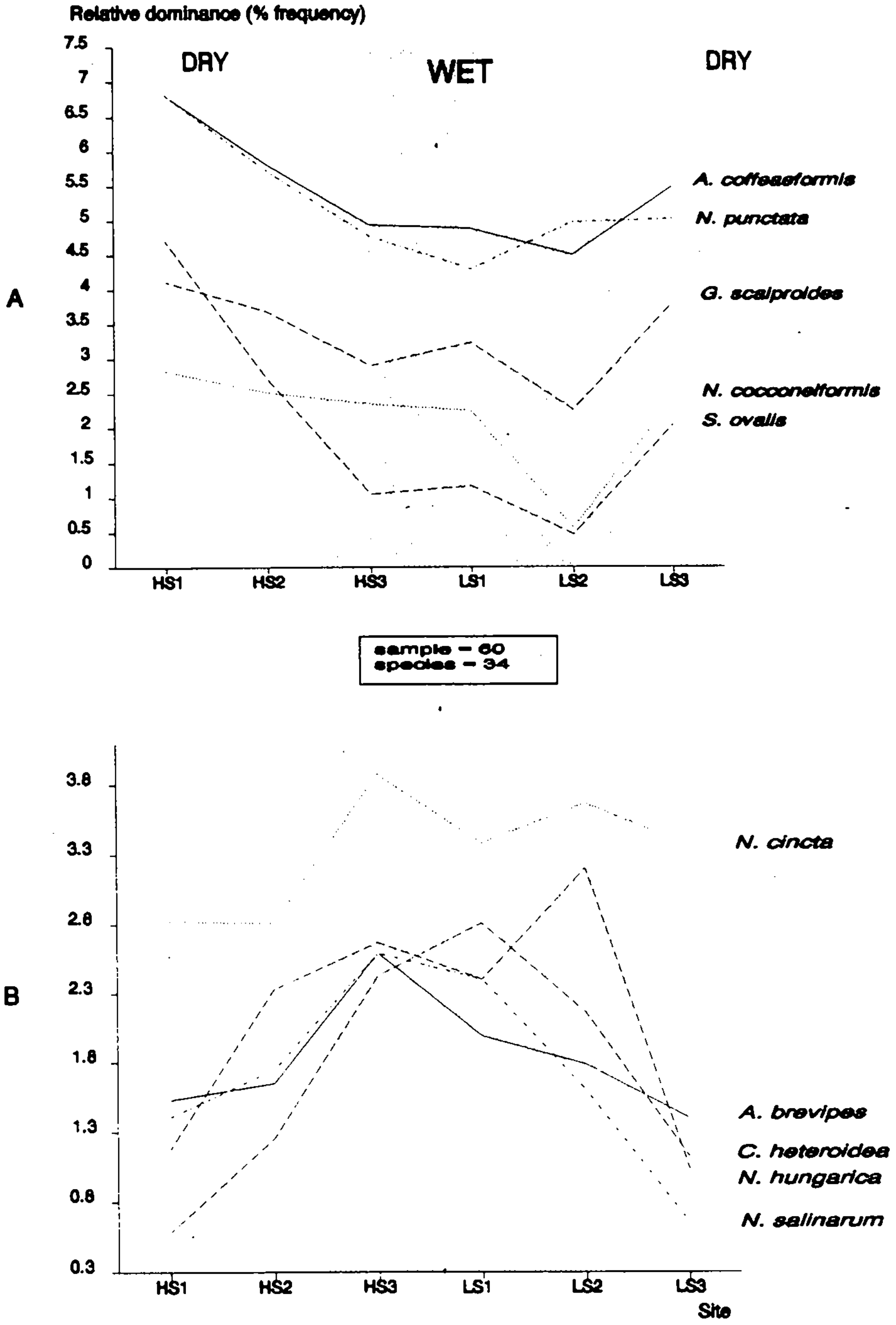


Figure 3.5. Dominance of some benthic diatom species at six different sites.
The condition of sediments during ebbing tide can be classified into dry and wet (darker shading).

Table 3.1. Species of benthic diatoms found in mangrove sediments in an area adjacent to Chunda Bay, North Queensland, Australia.

Family/Genus	Species
Achnanthaceae	
Achnanthes Bory	*Achnanthes brevipes* Ag.
	Achnanthes delicatula (Kütz.) Grun.
	Achnanthes hauckiana Grun.
	Achnanthes javanica Grun.
	Achnanthes lanceolata (Bréb.) Grun.
	Achnanthes longipes Ag.
	Achnanthes oblongella Ostrup.
Cocconeis Ehr.	*Cocconeis costata* Greg.
	Cocconeis dirupta Greg.
	Cocconeis diruptoides Hust.
	Cocconeis heteroidea Hantzsch
	Cocconeis peltoides Hust.
	Cocconeis scutellum Ehr.
Anaulaceae	
Eunotogramma Weiss	*Eunotogramma marinum* (W. Smith) Perag.
Biddulphiaceae	
Biddulphia Gray	*Biddulphia mobiliensis* (Bail.) Grun.
	Biddulphia pulchela Gray
Terpsinoe Ehr.	*Terpsinoe americana* (Bail) Rafs.
Coscinodiscaceae	
Coscinodiscus Ehr.	*Coscinodiscus asteromphalus* Ehr.
	Coscinodiscus crenulatus Grun.
	Coscinodiscus devius A. Schmidt
	Coscinodiscus exentricus Ehr.
	Coscinodiscus janischii A. Schmidt
	Coscinodiscus lacustris Grun.
	Coscinodiscus minor Ehr.
Cymbellaceae	
Amphora Ehr.	*Amphora acustiuscula* Kütz.
	Amphora angusta Greg.
	Amphora arenaria Donk.
	Amphora australiensis John
	Amphora coffeaeformis (Ag.) Kütz.
	Amphora costata W. Smith
	Amphora crassa Greg.
	Amphora eunotia Cleve
	Amphora fontinalis Hust.
	Amphora holsatica Hust.

	Amphora hyalina Kütz.
	Amphora ostreaia Bréb.
	Amphora ovalis Kütz.
	Amphora proteus Greg.
	Amphora richardiana Chonolky.
	Amphora robusta Greg.
	Amphora subturgida Hust.
	Amphora turgida Greg.
	Amphora veneta Kütz.
	Amphora ventricosa Greg
Cymbella Ag.	*Cymbella aspera* (Ehr.) Cleve
	Cymbella gracilis (Rabh.) Cleve
	Cymbella japonica Reichelt
	Cymbella naviculiformis Auerswald
	Cymbella pussila Grun.
	Cymbella sumatrensis Hust.
	Cymbella turgida (Greg.) Cleve
	Cymbella ventricosa Kütz.
Entomoneidaceae	
Entomoneis Ehr.	*Entomoneis sp.*
Epithemiaceae	
Epithemia Bréb.	*Epithemia reichelti* Fricke
	Epithemia sorex Kütz.
Rhopalodia O. Müller	*Rhopalodia gibba* (Ehr.) Grun.
	Rhopalodia gibberula (Ehr.) Grun.
	Rhopalodia musculus (Kütz.) O. Müller
Eunotiaceae	
Eunotia Ehr.	*Eunotia formica* Ehr.
Fragilariaceae	
Asterionella Hassall	*Asterionella japonica* Cleve
Gramatophora Ehr.	*Gramatophora marina* (Lyngbye) Kütz.
	Gramatophora oceanica (Ehr.) Grun.
	Grammatophora hamulifera Kutz.
Licmophora Ag.	*Licmophora ehrenbergii* (Kütz.) Grun.
	Licmophora gracilis (Ehr.) Grun.
	Licmophora lyngbyei (Kütz.) Grun.
	Licmophora paradoxa (Lyngbye) Ag.
Meridion Agardh	*Meridion circulare* (Grev.) Ag.
Plagioramma Grev.	*Plagioramma rhombicum* Hust.
Rhaponeis Ehr.	*Rhaphoneis superba* Grun.
Striatella Ag.	*Striatella unipunctata* (Lyngbye) Ag.
Synedra Ehr.	*Synedra acus* Kütz.
	Synedra fasciculata (Ag.) Kütz.

	Synedra parasitica (W. Smith) Hust.
	Synedra pulchella (Ralfs) Kütz.
	Synedra tabulata (Ag.) Kütz.
	Synedra ulna (Nitzsch) Ehr.
Gomphonemaceae	
Gomphonema Ag.	*Gomphonema gracile* Ehr.
Heliopeltaceae	
Actinoptychus Ehr.	*Actinoptychus splendens* (Shadb.) Ralfs.
Hemidiscaceae	
Actinocyclus Ehr.	*Actinocyclus ehrenbergi* Ralfs.
	Actinocyclus ovatus Wood.
Melosiraceae	
Hyalodiscus Ehr.	*Hyalodiscus laevis* Ehr.
Melosira Agardh	*Melosira granulata* (Ehr.) Ralfs.
	Melosira moniliformis (Muller) Ag.
	Melosira nummuloides Ag.
	Melosira sulcata (Ehr.) Kütz.
	Melosira varians Ag.
Naviculaceae	
Amphiprora Ehr.	*Amphiprora alata* Kütz.
	Amphiprora paludosa W. Smith
Anomoeoneis Pfitz.	*Anomoeoneis sphaerophora* (Kütz.) Pfitz.
Caloneis Cl.	*Caloneis bacilum* (Grun.) Mereschk
	Caloneis gjeddeana Foged
Diploneis Ehr.	*Diploneis chersonensis* (Grun.) Cleve
	Diploneis crabo E.
	Diploneis gravelleana Hagelstein
	Diploneis notabilis (Grev.) Cleve
	Diploneis ovalis (Hilse) Cleve
	Diploneis smithi (Bréb.) Cleve
	Diploneis vacillans (A. Schmidt) Cleve
	Diploneis weissflogi (A. Schmidt) Cleve
Frustularia Rabh.	*Frustularia rhomboides* (Ehr.) de Toni
	Frustularia vulgaris (Thwaites) de Toni
Gyrosigma Hassal	*Gyrosigma acuminatum* (Kütz.) Rabh.
	Gyrosigma attenuatum (Kütz.) Rabh.
	Gyrosigma balticum (Ehr.) Cleve
	Gyrosigma fonticulum Hust.
	Gyrosigma scalproides (Rabh.) Cleve
	Gyrosigma spencerii (W. Smith) Cleve
Mastogloia Thwaites	*Mastogloia acustiuscula* Grun.
	Mastogloia angulata Lewis
	Mastogloia apiculata W. Smith

	Mastogloia baldjikiana Grun.
	Mastogloia braunii Grun.
	Mastogloia elliptica (Ag.) Cleve
	Mastogloia exigua Lewis
	Mastogloia liatungensis Voigt
	Mastogloia mauritiana Grun.
	Mastogloia pumila (Grun.) Cl.
	Mastogloia smithi Thwaites
Navicula Bory	*Navicula cincta* (Ehr.) Kütz.
	Navicula confervaea (Kütz.) Grun.
	Navicula cryptocephala Kütz.
	Navicula cuspidata Kütz.
	Navicula densa Hust.
	Navicula directa (W. Smith) Ralfs.
	Navicula dissipata Hust.
	Navicula elegans W. Smith
	Navicula eta Cleve
	Navicula gothlandica Grun.
	Navicula gregaria Donk.
	Navicula halophila (Grun.) Cleve
	Navicula humerosa Bréb.
	Navicula ilopangoensis Hust.
	Navicula impressa Grunow
	Navicula inseriata Hust.
	Navicula longa (Greg.) Ralfs.
	Navicula monilifera Cleve
	Navicula mutica Kütz.
	Navicula nivaloides Bock.
	Navicula nyella Hust.
	Navicula pseudoforcipata Hust.
	Navicula pusilla W. Smith
	Navicula radiosa Kütz.
	Navicula ramosissima (Ag.) Cleve
	Navicula raphoneis Ehr.
	Navicula salinarum Grun.
	Navicula schroeteri Meister
	Navicula subrynchocephala Hust.
	Navicula terminata Hust.
	Navicula tripunctata (O.F. Müller) Bory
	Navicula yarrensis Grun.
Neidium Pfitzer	*Neidium productum* (W. Smith) Cl.
Pinnularia Ehr.	*Pinularia borealis* Ehr.
	Pinnularia gibba Ehr.
	Pinnularia rectangulata Grég.
	Pinnularia splendida Hust.
	Pinnularia subcapitata Greg.
	Pinnularia viridis (Nitzsch) Ehr.
Pleurosigma W. Smith	*Pleurosigma aestuarii*(Bréb. ex Kütz.)W. Smith

	Pleurosigma angulatum W. Smith
	Pleurosigma elongatum W. Smith
	Pleurosigma longum Per.
	Pleurosigma naviculaceum Bréb.
	Pleurosigma normanii Ralfs.
	Pleurosigma salinarum Grun.
Stauroneis Ehr.	*Stauroneis acuta* W. Smith
	Stauroneis anceps Ehr.
	Stauroneis dubitalis Hust.
	Stauroneis spicula Hickie
Trachyneis Cleve	*Trachyneis aspera*
Tropidoneis Cleve	*Tropidoneis lepidoptera* (Greg.) Cleve
	Tropidoneis longa Cleve
	Tropidoneis pussila (Greg.) Cleve
Nitzschiaceae	
Bacillaria Gmelin	*Bacillaria paradoxa* Gmelin
Cylindrotheca Rab.	*Cylindrotheca gracilis* (Bréb.) Grun.
Hantzschia Grun.	*Hantzschia amphioxys* (Ehr.) Grun.
	Hantzschia virgata (Roper) Grun.
Nitzschia Hassall	*Nitzschia acuminata* (W. Smith) Grun.
	Nitzschia acuta Hantzsch.
	Nitzschia amphibia Grun.
	Nitzschia apiculata (Greg.) Grun.
	Nitzschia circumsuta (Bail.) Grun.
	Nitzschia closterium (Ehr.) W. Smith.
	Nitzschia cocconeiformis Grun.
	Nitzschia distans Greg.
	Nitzschia fasciculata Grun.
	Nitzschia granulata Grun.
	Nitzschia hungarica Grun.
	Nitzschia hybrida Grun.
	Nitzschia incurva Grun.
	Nitzschia levidensis (W. Smith) Grun.
	Nitzschia linearis W. Smith
	Nitzschia longirostris Hust.
	Nitzschia longissima (Bréb.) Ralfs
	Nitzschia lorenziana Grun.
	Nitzschia obtusa W. Smith
	Nitzschia palea Kütz.
	Nitzschia panduriformis Greg.
	Nitzschia perversa Grun.
	Nitzschia punctata (W. Smith) Grun.
	Nitzschia sigma (Kütz.) W. Smith
	Nitzschia sigmoidea (Ehr.) W. Smith
	Nitzschia sinuata (W. Smith) Grun.
	Nitzschia tropica Hust.
	Nitzschia tryblionella Hantzsch.

	Nitzschia vermicularis (Kütz.)Hantzsch.
	Nitzschia vidovichii (Grun.) Grun.
	Nitzschia frustulum (Kütz.) Grun.
Surirellaceae	
Campylodiscus Ehr.	*Campylodiscus decorus* Bréb.
Surirella Turpin	*Surirella gemma* (Ehr.) Kütz.
	Surirella kurzii Grun.
	Surirella linearis W. Smith
	Surirella ovalis Bréb.
	Surirella tenera Greg.
Thalassiosiraceae	
Cyclotella Kütz.	*Cyclotella meneghiniana* Kütz.
	Cyclotella striata (Kütz.) Grun.
	Cyclotella stylorum Brightw.
Thalassiosira Cleve	*Thalassiosira weissflogii* (Grun.) Fry.and Has.

Table 3.2. **Total numbers of species and total absolute frequency of occurence of benthic diatom within different habitats and sites.**

H = Higher or landward habitat, L = Lower or seaward habitat, S = sites.

Species and occurence	Landward or higher intertidal area			Seaward or lower intertidal area		
	HS1 (Dry)	HS2 (Dry)	HS3 (Wet)	LS1 (Wet)	LS2 (Wet)	LS3 (Dry)
Species	141	155	216	144	149	117
Frequency of occurence	1339	1685	2379	1826	1609	1524

Table 3.3. **Values of relative frequency (in percentage) of dominant species at six sites (n = 60), total of absolute frequency of each species of benthic diatom (n = 360) and P values of ANOVA Dry vs. Wet sites (data transformation using *arcsine* $\sqrt{n}$).**

The dominant species are those that occurred in ≥ 30% of all 360 samples.

Species	Landward or Higher intertidal area			Seaward or Lower intertidal area			Total Absolute Frequency of Occurence (%)	Rank	P of ANOVA Dry Vs. Wet
	HS1 (Dry)	HS2 (Dry)	HS3 (Wet)	LS1 (Wet)	LS2 (Wet)	LS3 (Dry)			
Achnanthes brevipes	1.53	1.65	2.59	1.99	1.79	1.40	33.33	30	0.0441*
Achnanthes delicatula	1.76	3.69	3.64	3.56	4.42	3.45	62.50	8	0.2579
Amphiprora alata	1.18	2.04	2.10	1.82	1.50	1.49	30.83	33	0.4649
Amphora angusta	0.94	0.97	1.54	2.90	2.54	2.70	35.56	27	0.2985
A. coffeaeformis	6.82	5.82	4.94	4.88	4.51	5.50	95.83	1	0.0394*
Amphora ovalis	4.24	5.04	4.53	4.47	4.89	5.22	85.00	4	0.5844
Amphora proteus	3.29	2.62	2.83	2.24	1.69	2.42	44.72	20	0.2771
Amphora subturgida	3.29	1.94	2.75	3.06	3.48	3.36	53.33	16	0.6442
Amphora turgida	1.53	1.84	1.78	1.41	3.48	2.14	36.39	26	0.6355
Amphora veneta	3.06	3.59	3.56	3.39	4.04	4.19	65.56	7	0.8834
Amphora ventricosa	2.59	2.72	2.83	3.15	3.10	4.01	55.28	14	0.9143
Bacillaria paradoxa	2.82	1.65	2.75	2.48	2.63	2.14	43.33	21	0.2886
Cocconeis heteroidea	0.59	1.26	2.43	2.81	2.16	1.12	32.50	31	0.0092**
Gyrosigma scalproides	4.12	3.69	2.91	3.23	2.26	3.82	59.17	12	0.0027**
Mastogloia exigua	3.29	3.69	2.75	3.15	3.95	3.82	61.39	10	0.4435
Navicula cincta	2.82	2.81	3.88	3.39	3.67	3.36	60.28	11	0.0482*
N. cryptocephala	2.71	2.33	2.10	2.15	2.44	1.30	38.61	24	0.7449
Navicula cuspidata	3.76	3.39	2.59	3.56	2.44	3.63	57.50	13	0.1179
N. gothlandica	0.59	2.42	2.18	2.65	2.63	0.75	34.72	28	0.1126
Navicula halophila	4.94	4.17	3.88	3.73	4.32	4.29	75.00	5	0.1709
Navicula salinarum	1.41	1.75	2.59	2.40	1.60	0.65	31.94	32	0.0120*
Navicula tripunctata	5.18	4.56	4.94	3.97	5.36	4.66	85.28	3	0.9069
Nitzschia amphibia	1.88	2.72	2.99	2.24	3.10	2.52	46.67	18	0.3465
Nitzschia closterium	2.94	2.81	2.91	2.40	2.63	1.86	46.39	19	0.7524
N. cocconeiformis	2.82	2.82	2.35	2.24	0.56	2.42	38.33	25	0.0216*
Nitzschia granulata	3.18	4.66	3.72	4.22	4.51	4.38	74.17	5	0.8628
Nitzschia hungarica	1.18	2.33	2.67	2.40	3.20	1.03	39.17	23	0.0422*
Nitzschia lorenziana	2.59	1.94	2.18	2.48	2.35	2.05	40.56	22	0.5279
Nitzschia obtusa	1.29	1.26	1.62	3.15	2.26	3.08	38.6	24	0.5205
Nitzschia punctata	6.82	5.72	4.77	4.30	4.98	5.03	93.06	2	0.0475*
Nitzschia sigma	4.24	3.69	4.05	3.15	2.54	3.17	61.94	9	0.4341
Rhopalodia gibberula	2.71	2.81	2.18	2.98	1.88	4.29	50.28	17	0.1892
Rhopalodia musculus	3.18	3.20	3.40	2.90	2.63	2.70	53.89	15	0.8564
Surirella ovalis	4.71	2.72	1.05	1.16	0.47	2.05	33.89	29	0.0311*
Total	100	100	100	100	100	100			

* = Significantly different at level 95 % , ** = Significantly different at level 99 %

Table 3.4. **Comparisons of numbers of benthic diatom species at different sites.**

(H) and (L) are landward (higher) and seaward (lower) within a mangrove intertidal area respectively.
(Sn) is the site number.
(*) and (**) indicate that the differences are significant at the 95 % and 99 % levels respectively.

Spatial Comparison	Df	Overall Chi square	P value
HS1-HS2-HS3-LS1-LS2-LS3 (whole area)	5	17.30	0.0040 **
HS1-HS2-HS3 (landward/higher intertidal area)	2	8.874	0.0118 *
LS1-LS2-LS3 (seaward/lower intertidal area)	2	2.244	0.3257

Table 3.5. Analyses of variance of the total number of species of benthic diatoms in different environmental conditions.

Source	Df of F	F value	P value
Dry vs. wet areas (HS1,HS2,LS3 vs. HS3,LS1,LS2)	1,4	1.55	0.2815
Landward vs. seaward areas (HS1,HS2,HS3 vs. LS1,LS2,LS3)	1,4	1.84	0.2467

Table 3.6. Soil texture and vegetation coverage in different sampling sites *i.e.* landward (HS) and seaward (LS) within a mangrove area .

No	Site	Soil	Percentage (%) ± SE (n = 3)	Vegetation coverage (% / 25 m^2) ± SE (n = 4)	The most dominant mangrove trees	Hydrological condition during high and low tide
HIGH Land-ward	HS1	Sand	82.42 ± 1.50	76.56 ± 6.58	*C. tagal and A. marina*	Standing water and dry
		Silt	9.41 ± 2.15			
		Clay	8.17 ± 2.90			
	HS2	Sand	85.56 ± 3.78	51.14 ± 5.37	*A. marina*	Standing water and dry
		Silt	8.26 ± 1.68			
		Clay	6.18 ± 1.42			
	HS3	Sand	86.12 ± 2.75	80.15 ± 5.25	*R. stylosa and A. marina*	Running water and wet
		Silt	7.75 ± 1.25			
		Clay	6.13 ± 2.10			
LOW Sea-ward	LS1	Sand	50.45 ± 2.45	77.25 ± 4.47	*A. marina*	Running water and wet
		Silt	22.85 ± 3.95			
		Clay	26.17 ± 2.61			
	LS2	Sand	53.41 ± 5.60	72.26 ± 5.54	*A. marina and R. stylosa*	Running water and wet
		Silt	24.14 ± 3.05			
		Clay	22.45 ± 2.55			
	LS3	Sand	60.36 ± 6.01	85.45 ± 6.25	*R. stylosa and A. marina*	Standing water and dry
		Silt	20.55 ± 2.13			
		Clay	19.09 ± 2.16			

Chapter 4

Distribution, Abundance and Morphometrics of *Telescopium telescopium*

4.1. Introduction.

In mangrove forests *T. telescopium* is found commonly in more exposed parts of the forest, in small pools, water ways and on river banks. The distribution of *T. telescopium* is restricted to the middle and landward zones of the mangrove intertidal zone (MacNae, 1968). It is often associated with another mangrove snail *Terebralia* (see ; Roberts, 1980; Budiman, 1988 and Houbrick, 1991). *T. telescopium* can be remain submerged for about three or four hours during one tidal cycle (Alexander *et al.*, 1979).

Recent studies of *T. telescopium* have emphasised mainly non-ecological aspects of their biology. These studies included investigations of physiology (Alexander and Rae, 1974; Alexander *et al.* 1979; Kasinathan and Natarajan, 1980-1981; Dash *et al.*, 1982), effects of pollution (Chou, 1980; Siddiqui *et al.*, 1988) and a detailed systematic review (Houbrick, 1991).

Aspects of the ecology of *T. telescopium* which have been studied include distribution and density (Perkins, 1974; Budiman, 1988; Jahan *et al.*, 1990), behavioural adaptations (Lasiak and Dye, 1986) and reproduction (Ramamoorthi and Natarajan, 1973; Budiman, 1988). Several studies of distribution and abundance have been carried out outside Australia. Budiman (1988) and Jahan *et al.* (1990) for example conducted their studies in mangrove areas of Bangladesh and Indonesia, respectively. Some general accounts of distribution of *T. telescopium* in Australia, have been provided by MacNae (1968); Roberts (1980); Hutchings and Recher (1981); Lasiak and Dye (1986); Short and Potter (1984); Houbrick (1991). With the exception of Roberts (1980) these other studies did not make quantitative comparisons of density and size structure of this gastropod in different zones within intertidal areas.

Sites at different vertical heights within the intertidal zone of mangrove ecosystems have different local environments created by exposure times, temperature, tidal inundation levels and mangrove canopy factors (*see* MacNae, 1968) and Lasiak and Dye, 1986). These factors were believed to be important in controlling patterns of movement (Lasiak and Dye, 1986), distribution and abundance (Roberts, 1980) and indirectly affecting size of *T. telescopium* . Two mangrove zones in tropical North Queensland mangrove forests are the *R. stylosa - A.. marina* and *C. tagal - A. marina* zones.

The aim of this part of the study was to determine distribution, abundance and morphometric characteristics of *T. telescopium* in relation to different zones of mangrove vegetation. The predictive hypothesis for this study was that both abundance and size structure of *T. telescopium* would differ in different landward and seaward zones of the mangrove forest.

4.2. Materials and Methods.

4.2.1. Location of the study.

This study was carried out from 5 March to 20 June 1989. The location of the field work was in undisturbed mangrove areas at 147°01' - 147°02' East and 19°15' - 19°17' South latitude (Royal Australian Survey Corps Map, sheet 8359 - III, ed. 1, series R 733, 1973). The area was approximately 55 km Southeast of Townsville, North Queensland, near the Australian Institute of Marine Science (AIMS), and adjacent to Chunda Bay (Figure 4.1).

The zonation of mangroves in this area was defined clearly into five different areas. (1) The lower zone (tidal height range approximately 0 m - 1.50 m) or outermost of mangrove areas were dominated by dense stands of *R. stylosa*. This species was predominant also on the river banks. The adjoining canopy resulted in reduction of light intensity on the ground. The substratum was mainly sandy soil. (2) In some parts, immediately behind the zone described above (tidal height range approximately 0 m to 0.75 m), there was a mixture of mangrove bushes composed of *R. stylosa* and *A. marina*. The ground received more sunlight because the canopy mainly was not continuous and stands of trees were less dense than in the previous (seaward) zone. The substratum was composed mainly of sandy-clay soil. (3) The mixed zone of *C. tagal* and *A. marina* normally occurred behind the previous zone of mixed mangrove bushes (tidal height range approximately 0 m to 0.50 m). The distribution of trees was sparse with a disconnected canopy and the substratum was mainly sandy-clay soil. (4) In some parts, adjacent to the zone no. (3) , salt marsh areas occurred also (tidal height range approximately 0 m - 0.75 m). These open areas were dominated by *Sacorconia* vegetation. (5) The landward intertidal (tidal height range approximately 0 m to 0.30 m) areas were found a zone of the thick *C. tagal*. The canopies of these trees often overlapped and thus impeded the penetration of sunlight to the ground. The substratum consisted of muddy soil.

Sampling was conducted in three locations (Figure 4.1). Each location contained two different areas ; *i.e.* landward zone (mostly in zones 4 and 5 with tidal height range 0 m to 0.75 m) described above) and seaward zone (mostly in zones 1, 2 and 3 described above with tidal height range 0 m to 1.50 m). The landward areas were inundated only when seawater levels were above mean high water (M.H.W.) level or higher than 2.79 m chart datum (Lasiak and Dye, 1986; Queensland Department of Transport, 1989). The distance between location 1 (*i.e.* the most northerly location) and location 2 (*i.e.* the middle location) was approximately 350 m. The distance between locations 2 and 3 (*i.e.* the latter being the most southerly location) was around 2 km. The environmental conditions of location 3 differed from those in the two northern locations. This mangrove area was found to be more exposed, and its landward zone contained a large shallow pool.

4.2.2. Determination of transect size.

The size of the transect used to study the pattern of distribution and abundance of *T. telescopium* in mangrove areas was determined by applying precision and accuracy tests (Southwood, 1966; Downing and Anderson, 1985; Andrew and Mapstone, 1987) on three different sizes of transect: 1 m x 2 m, 1 m x 4 m, and 1 m x 6 m. The decision for using these sizes was based on the assumption that transects smaller than 1 m x 2 m would contain only a few of the animals (Warren, 1988 personal communication). These sizes of transect were applied in two mangrove zones: *R. stylosa - A. marina* and *C. tagal - A. marina*. The populations of snails within these two zones were previously found to be different in the term of density (Robertson, 1989 personal communication).

Three randomly selected sites were sampled in each of the two zones. At each site four replicate transects of each size were sampled independently. A total of 24 samples per size of transect were thus collected with the number of samples of each size of transect at each site within one mangrove zone being 12. The sampling design is shown in Figure 4.2a.

The precision of density estimates made by each size of transect was calculated using the formula

$$p = \frac{SE}{\bar{x}} \quad , \quad p = \frac{SD \,/\, \sqrt{n}}{\bar{x}}$$

where (1) p is precision, (2) SE is standard error, (3) SD is standard deviation, (4) n is number of replicates and (5) x is the mean (Andrew and Mapstone, 1987).

The precision was calculated as if 24 m² had been sampled for each transect size. For example for the 1 x 4 m transect, n = 6 since six transects are required to sample a total of 24 m². The most appropriate size of transect was decided after comparing the mean precision using two-way analysis of variance (Scheffe, 1959; Underwood, 1981). The decision to use n = 6 was based on the assumption that the distribution of the animal was clumped mostly due to association with small salt water pools (*see* Roberts, 1980; Lasiak and Dye, 1986 and Warren, 1988 personal communication)

4.2.3. Determination of number of replicate transects.

The number of replicate transects required in studying the pattern of distribution and abundance of *T. telescopium* also was determined using the precision tests described above. This involved several stages of field work conducted in the same areas where the determination of transect size was carried out.

Three sample sizes *i.e.* four, five and six replicate transects, were examined using the transect which had been chosen previously in the determination of transect size (Figure 4.2b). The sites for sampling were selected by random numbers (Zar, 1984) and positioned by placed a grid over a map. The number of animals which were found in each sample was determined and precision of these values calculated using the formula:

$$p = \frac{SE}{\bar{x}}$$

where (a) p is precision, (b) SE is standard error and (c) x is the mean.

Precision was calculated as if 60 replicate transects (or 240 m² area) had been sampled for each sample size. For example for the five replicates, n = 12 since 12 replicate samplings are required to sample a total of 60 replicate transects (or 240 m²). The most appropriate sample size in this study was decided upon after comparing the means of precision of each number of replicates. These comparisons were conducted using the analysis of variance (Scheffe, 1959; Underwood, 1981; Zar, 1984). The sample size which gave the smallest precision (actually imprecision) (Snedecor and Cochran, 1956) was selected for use in this pilot study.

4.2.4. Distribution and abundance of *T. telescopium*.

This study involved sampling the three different locations described previously. The sampling was conducted at sites in two different zones (inner parts or landward and outer parts or seaward intertidal zones within mangrove areas) within each location. These sites were randomly selected by using random numbers (Zar, 1984) and positioned by placed a grid over a map. The sampling units used were those which had been selected in the determinations of transect size and sample size. The number of living *T. telescopium* was counted in each transect, and the density was expressed in number of animals per m^2. The sampling design is shown in Figure 4.3.

The data on density of *T. telescopium* was analysed using three-factor analysis of variance (Underwood, 1981; Zar, 1984) where the factor, location was a fixed factor: the factor, zone, was a fixed factor: the factor, site, was random and nested within combinations of location and zone. Before the analysis, Cochrans test (Underwood, 1981) was used to test the assumption of homogeneity of variance, and the logarithmic transformation was applied when the data were heterogenous. A multiple comparison procedure; *i.e.* Student-Newman-Keuls (SNK) tests, were employed if the ANOVA indicated significant effects (Underwood, 1981; Zar, 1984).

4.2.5. The frequency distribution of size and weight.

This study was conducted in location-two at both mangrove zones *i.e.* landward and seaward within intertidal areas. The transect size selected above was employed. The data was collected from 20 sampling points which were determined using random numbers (Zar, 1984). In each transect the size (*i.e.* shell-length) was measured using callipers with 0.1 mm accuracy. These measurements followed the terminology introduced by Russel-Hunter (1961) and Calow (1975). The live weight was measured using a mechanical balance (*i.e.* triple beam balance) to 0.1 g accuracy. Each snail was dried with tissue paper before being weighed. The frequency distribution of size and weight of *T. telescopium* between zones was compared using the Chi-Square test (Zar, 1984). This test used 100 data points for each parameter. The data used here was selected from the total data set by using random numbers.

4.2.6. Size - weight relationship.

The animals which were used in this study were *T. telescopium* living in the landward and seaward zones of mid intertidal mangrove areas at Location 2. All sizes of snails were measured and animals weighed. The methods and criteria for measurement of size and weight of *T. telescopium* were as described previously.

To find an equation describing the relationship between size and weight, simple linear and multiple regressions (method of least squares) were applied. In the analysis of simple linear regression, the data tended to be a power curve which had an equation (Calow, 1975):

$$\boxed{y = a\,x^{b}}$$

where y is weight, x is shell-length, a is the intercept, and b is the regression coefficient. This power curve was converted to a straight line by transforming both x and y to logarithms; therefore:

$$\boxed{\log y = \log(ax^{b}) = \log a + b \log x, \quad y = a + bx}$$

4.3. Results

4.3.1. Transect size.

In this study, three different sizes of transect (*i.e.* 1 m x 2 m, 1 m x 4 m, 1 m x 6 m) were examined. The results of the determination of density of *T. telescopium* using these transects are given in Figure 4.4. The average density obtained for each transect size was similar. A one-way analysis of variance indicated that the difference in density estimates between transects was not significant ($F_{2,15}$ = 0.4728, $P > 0.50$) (Table 4.1). The density of the snail in 6 m^2 transects was the closest to the mean density of the population. However, the 4 m^2 transect possessed the smallest standard error and the estimate of density from this transect size was closer to the mean density of the population than that of the 2 m^2 transect.

Figure 4.5 shows the precision for each transect size. Although the analysis of variance found that the difference in precision between transect sizes was not significant ($F_{2,15}$ = 1.8027, $P > 0.10$) (Table 1), the precision (actually imprecision) in the 4 m^2 transect was the lowest.

Based upon the advantages indicated in Figures 4.4 and 4.5, the transect of 4 m^2 was chosen to determine the number of replicates and to carry out further studies of the distribution and abundance of the species.

4.3.2. Number of replicate transects.

The results of the determination of density of *T. telescopium* using three sample sizes (*i.e.* 4, 5 and 6 replicate transects) are shown in Figure 4.6. These sample sizes did not produce significant differences in the estimates of density of the snail ($F_{2,9}$ = 0.036, $P > 0.50$) (Table 4.1). A sample size of 5 replicates produced the smallest standard error and an estimate of mean density closer to the population mean density than that in a sample size of 4 replicates (Figure 4.6).

The estimated precision from each sample size is presented in Figure 4.7. The values of precision per sample size did not differ significantly ($F_{2,9}$ = 0.8951, $P > 0.25$) (Table 4.1). Thus, each sample size may be suitable for further studies.

Among the three sample sizes, however, the sample size with 5 replications tended to be preferable since the level of precision was relatively better than that in samples of 6 replicates. The standard error of the mean precision of this size of sample also was the smallest (Figure 4.7). This sample size was thus selected to be used in determining the distribution and abundance of the snail within mangrove zones in this study.

4.3.3. Distribution and abundance of *T. telescopium* in three locations.

Density of *T. telescopium* for habitat zones and locations are presented in Figures 4.8 and 4.9 respectively. Density estimates in the landward and seaward areas did not differ significantly. Density of the snail in location 3 was almost four times higher than that at locations 1 and 2.

Location had a strong effect on the density of the snail ($F_{2,12}$ = 29.4788, $P < 0.0005$) (Table 4.2). The difference in density of snails between location 3 (the southern location) and other locations was significant (SNK analysis, q = 0.1429, $P < 0.05$) (Table 4.3)

The habitat zones, however, did not have a significant effect on the density of *T. telescopium* ($F_{1,12}$ = 0.9606, $P > 0.25$) thus, the density of *T. telescopium* in seaward areas (habitat 1), which were occupied by *R. stylosa* trees, did not differ with that in landward areas (i.e. habitat 2), dominated by *C. tagal* trees.

4.3.4. Size of *T. telescopium.*

The size frequency distributions of the snail within two intertidal mangrove areas are presented in Figures 4.10, 4.11 , which show the frequency distributions of shell length and total fresh weight respectively. The difference in the proportion of these variates between the two habitats i.e. (H1) landward and (H2) seaward of mangrove areas, was tested using the Chi-square test (Table 4.4).

4.3.4.1. Shell length.

The frequency distribution of shell length in the two intertidal habitats differed. Smaller *T. telescopium* appeared more often in the higher intertidal (H1). Snails of length 10 to 30 mm did not occur in the seaward habitat (H2) (Figure 4.10). In both habitats, on the other hand, the snails of length 80 to 90 mm were most common. Larger snails, *i.e.* more than 90 mm in length, were more frequent in H2 than in H1. The frequency distribution of shell length between habitats was significantly different (Chi-square analysis, $P < 0.001$) (Table 4.4).

Habitat had a strong effect on the mean shell length. The mean length in H2 was almost 24 % greater than the mean length in H1 (Table 4.5). This difference was significant (ANOVA, $P < 0.001$) (Table 4.6). Habitat thus had strong effects on shell length.

4.3.4.2. Total fresh weight.

The frequency distribution of total fresh weight in each habitat is shown in Figure 4.11. In higher intertidal mangrove areas (*i.e.* H1) most of the snails were in the lower weight classes. In the seaward zone most snails were in the larger weight classes. This difference was significant (Chi-square test, $P< 0.001$) (Table 4.4).

The mean weight of this mangrove whelk was 37.29 g and 67.54 g in H1 and H2 respectively (Table 4.5). Thus the mean weight in H2 was almost twice than that in H1, a significant difference (ANOVA, $P< 0.001$) (Table 4.6). Habitats thus had a strong effect on total fresh weights.

4.3.5. The length-weight relationship.

The length-weight relationship was determined using linear regression of logarithmic-transformed data (Figures 4.12 and 4.13). Table 4.7 shows the values of slope and intercept coefficients of these regression lines. The equation for the regression line between weight and length in the landward habitat (H1) was

$$\text{Log } W = -2.796 + 2.337 \text{ Log } L.$$

whereas that in the seaward habitat (H2) was

$$\text{Log } W = -2.385 + 2.166 \text{ Log } L.$$

These regression lines were both significant ($P< 0.001$). Table 4.8 shows the results of the analyses of variance and the correlation coefficients. Strong positive correlations occurred between length and weight of the snail in each habitat. The correlation coefficients were always more than 0.91 (Table 4.8). These regressions could be used to predict values of weight from the values of length within the two habitats.

The type of growth of this snail, based upon the length-weight relationships in both habitats, was not isometric (*i.e.* b values were significantly different from 3, Table 4.7).

4.4. Discussion

The 4 m^2 transect was chosen and used in this study. Mean estimates of abundance produced by this size of transect had a greater precision than those of other transect sizes. The size of this transect was probably slightly larger than the scale of clumping of *T. telescopium*, hence the data collected using it may not be highly variable. Using transects which are smaller or equal to the scale of clumping of organisms, result in estimates of abundance more variable than those obtained using transects which are larger than the scale of clumping (Wiebe, 1971; Green, 1979).

Results of analysis of variance indicated that the differences in precision of different sizes of transect were not significant ($P > 0.1$, N.B. significance level was $P = 0.05$). However, 2 m^2 and 6 m^2 transects resulted in relatively smaller values of precision than 4 m^2 transects. Thus the use of transects of 2 or 6 m^2 for estimating density of the snail was considered inferior to use of the 4 m^2 transect.

The distribution of *T. telescopium* may be aggregated (Lasiak and Dye, 1986) like that of other intertidal snails e.g. *Thais emarginata* and *Thais lamellosa* (Spight (1982) and other tropical gastropods, particularly the cerithids (Moulton, 1962; Rhode and Sandland, 1975; Hazlet, 1984). In such an aggregated population, smaller transects may miss aggregations or contain too many organisms. Transects of larger size may include part of at least one aggregation and so very small or zero counts occur rarely (Southwood, 1966; Elliot, 1977; Andrew and Mapstone, 1987). To avoid such problems the middle size of transect *i.e.* 4 m^2 was probably the most appropriate to be used in this study. Weibe and Holland (1968) and Wiebe (1971) also stated that the most efficient sample unit was not always the largest.

This pilot study used analysis of variance to determine the desired precision. Using this statistical analysis with the replicate measures of precision as data provides a potentially informative design to determine the desired precision (Scheffe, 1959; Andrew and Mapstone, 1987). The case of a non-significant difference between means of precision (as found in this study), may occur often. Several workers (Downing and Anderson, 1985; McCormick and Choat, 1987), have indicated that sometimes no particular transect size tends to have significantly higher precision estimates than others.

A sample size with five replicates (using a 4 m^2 transect) was used in this pilot study. This choice was based upon the small values of the standard error of precision, and estimates of mean density of the organism by this sample size. When an analysis indicates that the difference between means is not significant, a level of precision can be chosen as a suitably small value for the standard error (Underwood, 1981).

Costs of the units of sampling were not determined in this study. Such costs are normally included in determining the efficiency of sampling units (Downing, 1979; Pringle, 1984; Downing and Anderson, 1985; Downing and Cyr, 1985; Morin, 1985; McCormick and Choat, 1987). The calculation of the desired sample size may be considered as determination of costs among sample sizes. Andrew and Mapstone (1987) indicated that when differences in the costs among units are negligible, the cost of sampling is proportional only to sample size.

In theory, for any size of sampling unit, precision will increase with sample size because the standard error and confidence intervals decrease with increasing replication (Green, 1979). Increased precision, however is compensated for by the increase in cost (factors such as flexibility of movement and fatigue of the observer in this study). The rate of increase in precision with increasing sample size is initially great but declines as sample size becomes large (Cochran, 1963; Green, 1979; Andrew and Mapstone, 1987). In consideration of these problems a sample size of four replication, could have been chosen. The precision of this sample size had a larger standard error, however it was considered better to use five replicates. Despite this, precision of both of these sample sizes did not differ significantly ($P > 0.1$, significance level was $P = 0.05$). Phil and Rosenberg (1982) also decided to use more replicates than required in their study on fish and crustacean abundance.

The effect of location (over several kilometres) on density of *T. telescopium* was significant ($P < 0.005$). This difference probably can be related to environmental factors, such as the extent of tidal inundation, high temperature of the habitats and availability of food. Lasiak and Dye (1986) reported that the movement of *T. telescopium* is initiated by tidal inundation. The inactive snails could be encouraged to move only in the presence of standing water. This species did not move on either damp or dry mud. Feeding activities of this species may increase also during tidal wetting. Some sedentary marine species (*e.g.* barnacles) tend to increase feeding activities after tidal wetting (Southward and Crisp, 1965; Taylor, 1971; Price, 1984).

Problems of heat stress and water loss are also important to mobile gastropods in tropical areas. Some workers maintain that mobile gastropods move to areas which provide shelter under the strong tropical heat (Levinten and Kohn, 1980; Bertness *et al.*, 1981; Leving and Garrity, 1983; Lasiak and Dye, 1986).

The difference in the estimate of population density between locations may be a result also of the availability of food. Areas which have a better food supply are able to support larger populations. According to Spight (1982), size of populations of *Thais emarginata* and *Thais lamellosa* changed dramatically in every littoral habitat each year. These population changes corresponded roughly to changes in the food supply.

To understand the most important environmental factors which influence the density of *T. telescopium* in locations, it is necessary to conduct further studies which should include the factors in the observed areas. If possible, observations should be carried out regularly because the size of populations probably fluctuates throughout the year.

The result of a non-significant habitat effect on density is a little surprising. It was likely that environmental factors, especially the availability of food in the two habitats, was only slightly different. Both habitats may have sufficient food to support the population, so that the difference in density was not significant. The lack of a detectable difference in density may have occurred also because of insufficient replication. Using more replicates and sampling monthly, a difference may have been detected. However, the lack of a significant difference in density appears to be a real effect (Figure 4.8).

The results suggest a strong correlation between shell-length and weight of *T. telescopium*. Budiman (1988) in Maluku, Indonesia recorded *T. telescopium* from 20 to 100 mm total length. He mentioned also that the length was highly correlated with the body-weight (with shell).

The size and weight of *T. telescopium* were significantly different ($P < 0.001$) between habitats . In landward mangrove areas, size and weight were smaller than that in the seaward habitat. Some environmental factors which have been discussed above were probably responsible for these differences *e.g.* desiccation, temperature, food availability, period of inundation.

Physical stress such as heat and availability of standing water may have strong direct and indirect effects on the growth of this snail. The upper levels of the mangrove system are subject to long periods of dry and heat. On sunny days the temperature on the bare substratum rises to 50 °C (Lasiak and Dye, 1986). Snails occupying this habitat would have problems at such high temperature. Water conservation and water loss problems would occur more often than in snails living in the seaward areas. The effects of heat may be even more substantial, since these snails have been shown to suffer mortality after three days of exposure to direct solar radiation (Lasiak and Dye, 1986). Under such stress, energy is directed more toward maintenance of metabolic stability than to growth. Thus, growth of this animal in the landward (upper) intertidal area may be hampered. The size as well as the weight may thus be limited. Several workers such as Paine (1969) and Underwood (1984a) also have suggested that the growth of intertidal gastropods was slower at higher intertidal levels than that at lower levels on rocky shores.

Because of the longer periods of aerial exposure, the availability of standing water at the landward intertidal habitat was relatively less than that at the seaward habitat. The activity of *T. telescopium*, which may correspond to its feeding activity, appeared to be initiated by wet conditions. This snail probably feeds only in wet conditions and withdraws into its shell when covered with water or during longer periods of aerial exposure (Alexander *et al.*, 1979; Lasiak and Dye, 1986). Thus when occupying the landward habitat, individuals may have less time for feeding compared with snails which live in the seaward habitat. This situation may influence the growth of *T. telescopium* within these two habitats.

The availability of food may be important in determining the size of *T. telescopium* in the two habitats. Even though the main diet of this snail has not yet been determined (Alexander *et al.*, 1979), it is believed that the animal may graze on benthic microalgae like other common intertidal gastropods (Paine, 1969; Underwood, 1984a; Black *et al.*, 1988; Peckol and Guarnagia, 1989). The availability of benthic microalgae in landward areas of the mangrove system was probably lower than that in the lower, seaward areas. This situation has been examined in other intertidal areas, where the benthic intertidal microalgae (mostly diatoms) did not extend to high levels in areas with more exposure to insolation during low tide (Castenholz, 1961; 1963; Underwood, 1984b). The limitation of food availability in fact has been recognised to be the main factor restricting the growth of some intertidal gastropods (Underwood, 1984a).

The values of the regression slope, b, of the linear regressions in this study were not significantly different, but the elevations were significantly different. Any values of shell length in the outer zone, were thus associated with higher values of total fresh weight in the landward area. Thus, in individuals of similar shell length, fresh weight would be greater in the lower than the higher intertidal habitat. This may be a result of the difference of shell weight (*i.e.* as a result of shell thickness), rather than a difference in weight of soft body tissue. The shell of *T. telescopium* in the lower habitat is thicker than that in the landward habitat. Calow (1975) showed that the shell ash values of some freshwater snails were considerably greater than the ash values found in the soft body tissue and were approximately 95 % of the total shell dry-weight. He suggested that the dry weight of snails was influenced mainly by the shell weight.

It was likely that the difference in fresh weight was controlled also by the availability of minerals within the two habitats. Minerals such as Calcium are very important in constructing the shell of snails (Russell-Hunter *et al.*, 1967). Because the landward intertidal mangrove area was closer to the land, this area may tend to have more terrestrial characteristics such as the availability of freshwater. The seaward habitat may be more marine. Seawater has a richer mineral composition and physical stress (*e.g.* wave action) may also be higher. These conditions may influence the possibly different shell thicknesses. Marine molluscs generally have heavier shells than freshwater or terrestrial species (Calow, 1975).

The difference of size of this snail in these two habitats appeared to be affected by age. A large number of *T. telescopium* living around pools in higher areas was mainly in juvenile stage with smaller and thinner shells. However, at seaward areas the snail was older, therefore the shells were larger and heavier. Roberts (1980), by investigating its behaviour, found that adult *T. telescopium* were capable of migrating to adjacent areas. A large number of adults even penetrated into exposed channels within different stands of mangrove.

Based on the results of this study, to overcome logistical problems, a study of the distribution and abundance of *T. telescopium* was carried out by determining the correct size of transects and the correct number of replicates.

This study demonstrated that *T. telescopium* differed significantly between locations (separated by distances of 0.5 to 1.8 km) but not between intertidal habitats. Furthermore the size of this gastropod was significantly greater in the seaward than the inner, landward intertidal mangrove habitat. This information can now be used to help address questions about the feeding and growth of this gastropod.

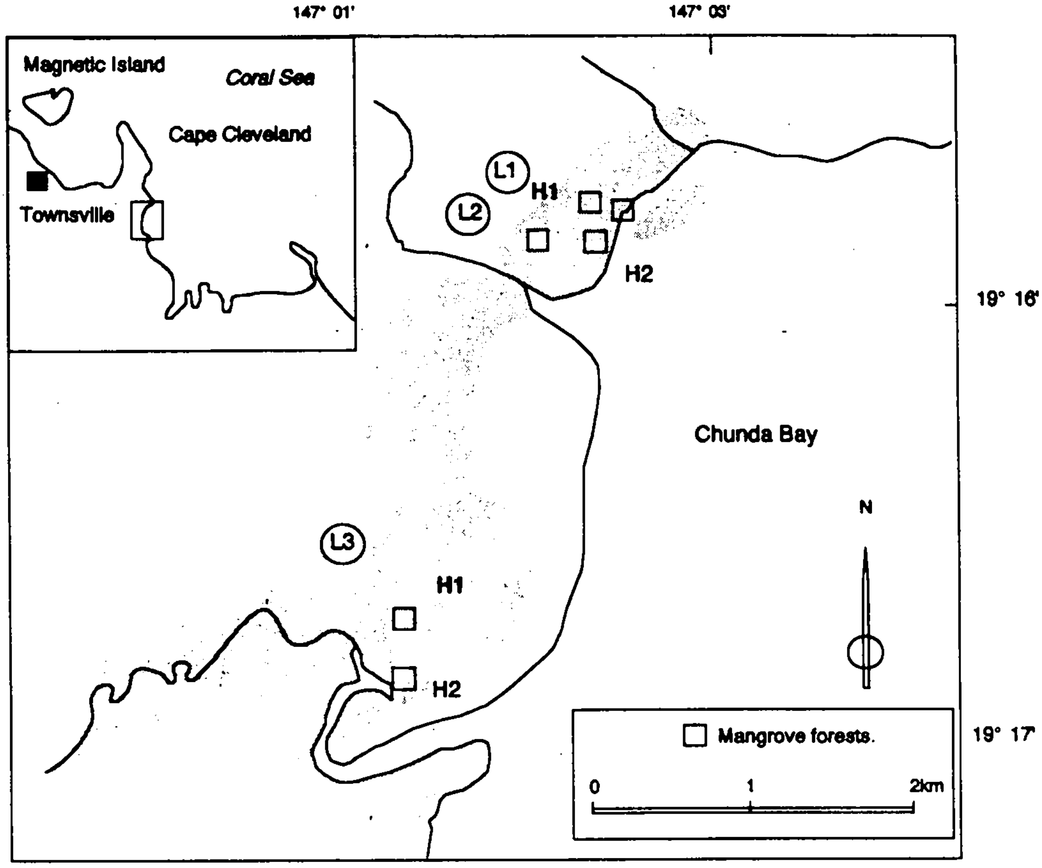


Figure 4.1. A map of Chunda Bay showing study area.

L = location, H1 = higher intertidal (= Landward) habitat and H2 = lower intertidal (= Seaward) habitat.

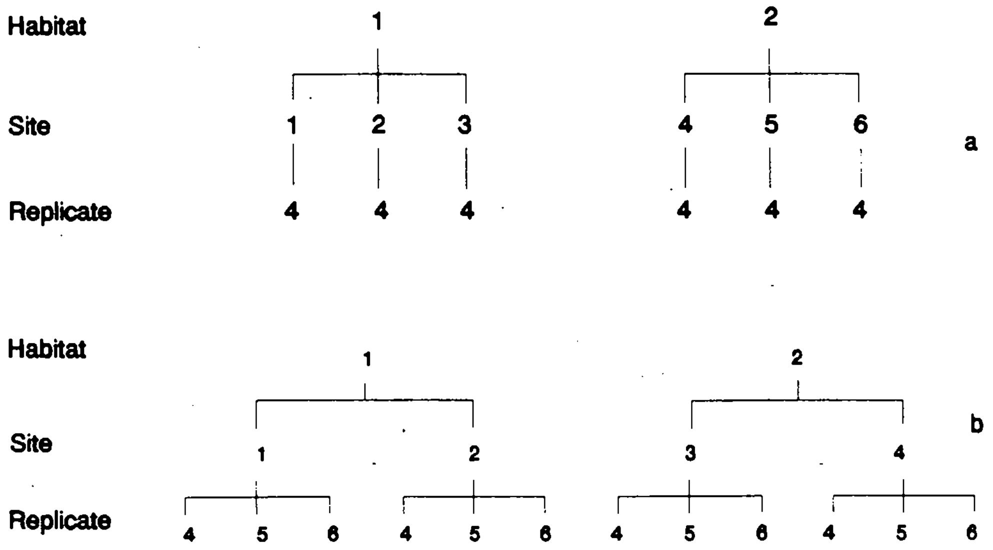


Figure 4.2. Design of the study to determine (a) transect size and (b) sample size.

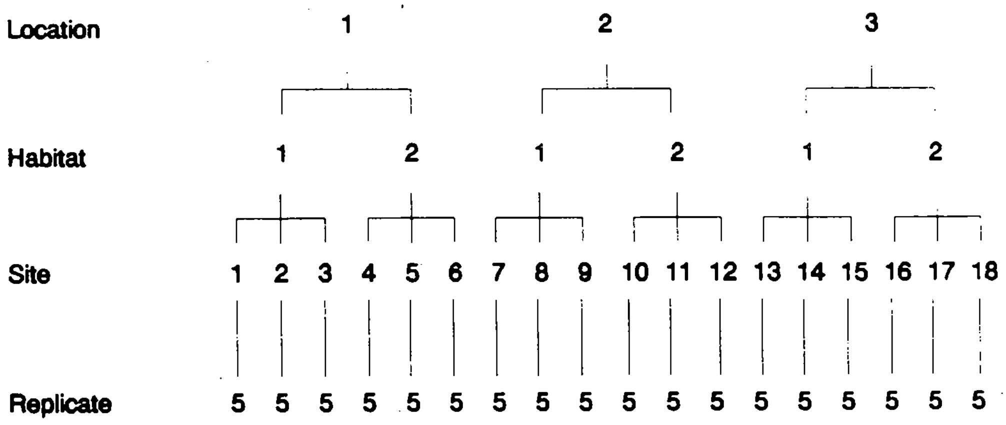


Figure 4.3. Design of the sampling scheme to determine density and abundance of *Telescopium telescopium*.

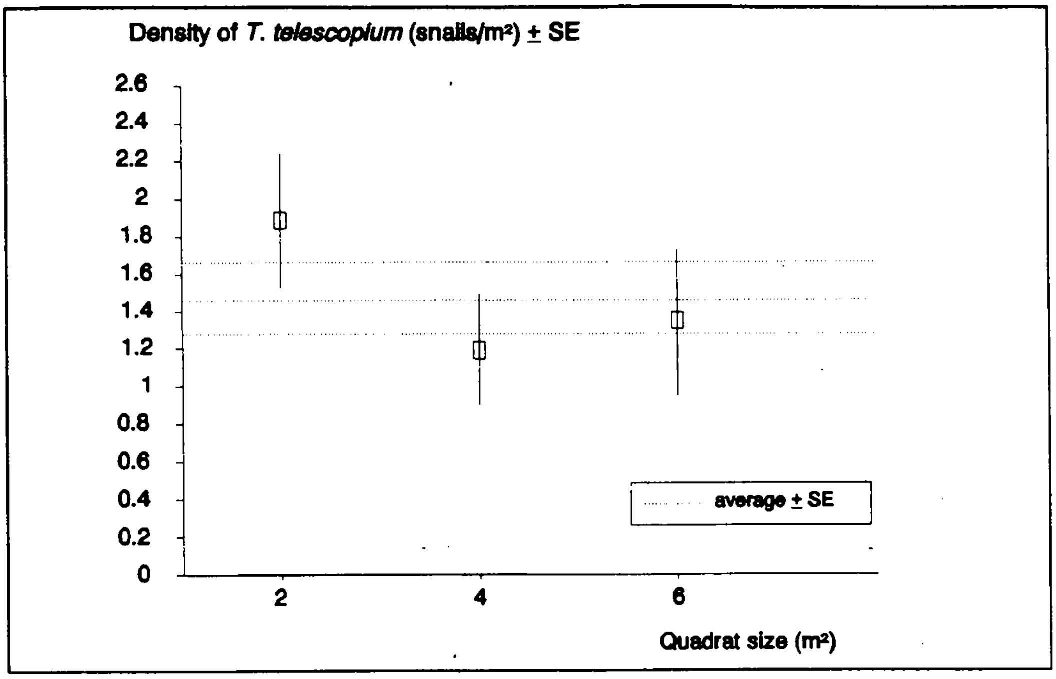


Figure 4.4. Mean density of *T. telescopium* using different transect sizes.

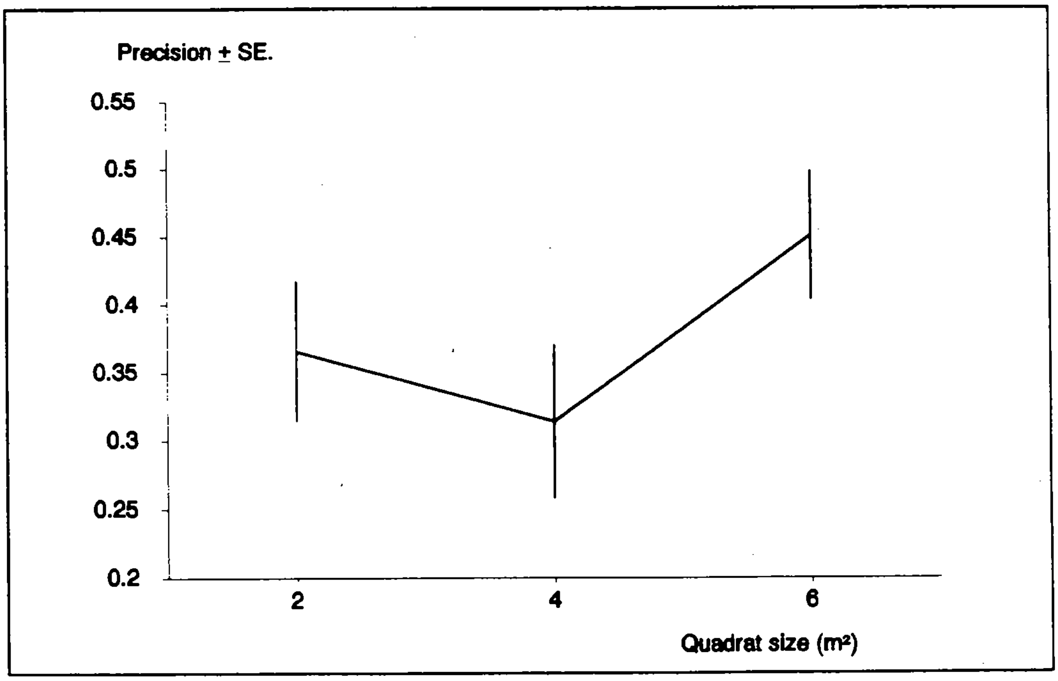


Figure 4.5. Precision of different transect sizes.

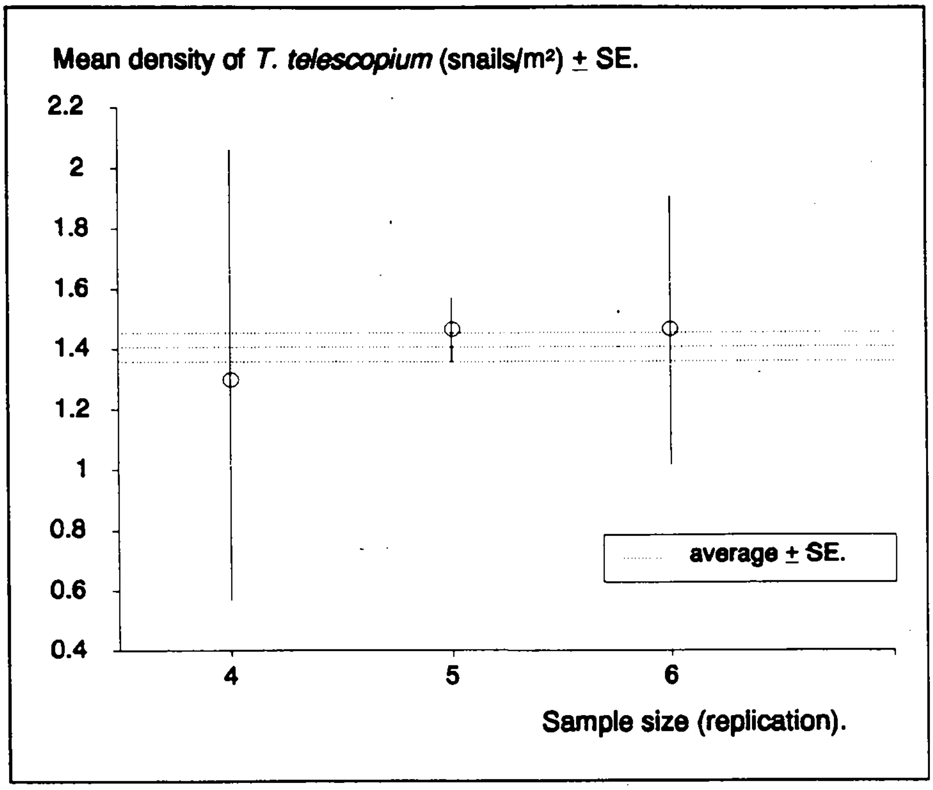


Figure 4.6. Mean density of *T. telescopium* calculated using threesample sizes.

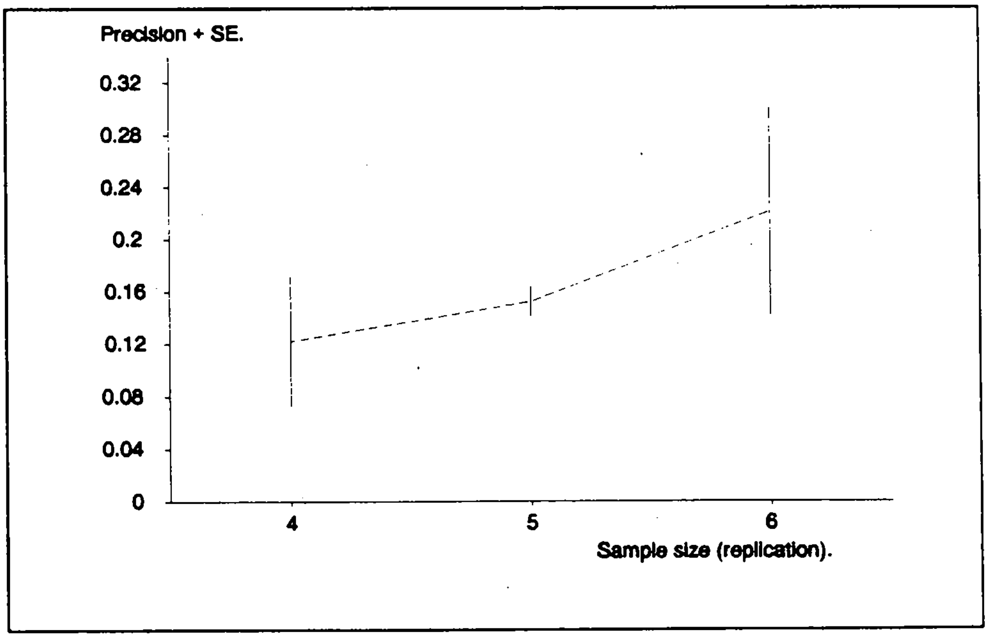


Figure 4.7. Precision of different sample sizes.

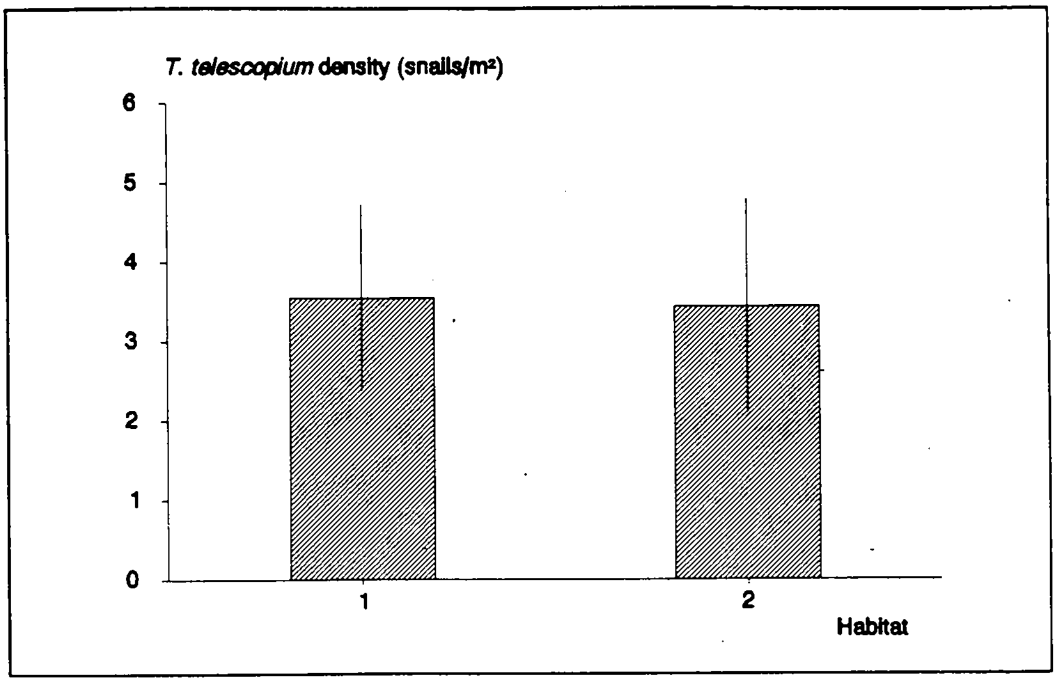


Figure 4.8. Average density per m^2 ± 95 % C.L. of *T. telesopium* in landward (Habitat 1) and seaward (Habitat 2) zones.

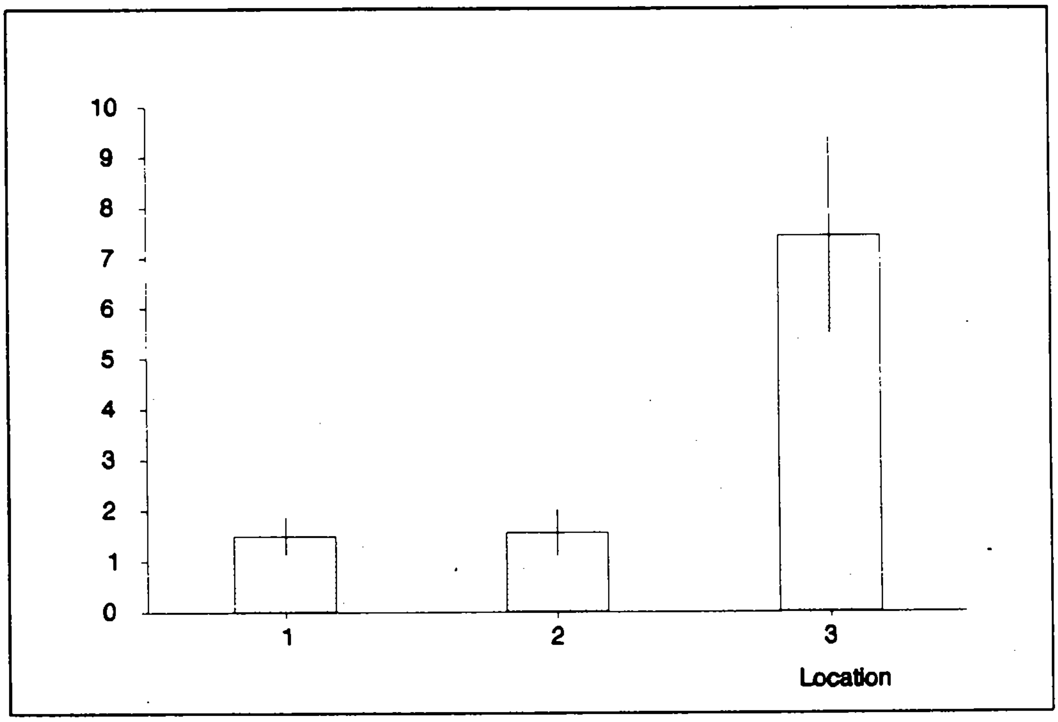


Figure 4.9. Average density per m^2 ± 95 % C.L. of *T. telescopium* in different locations

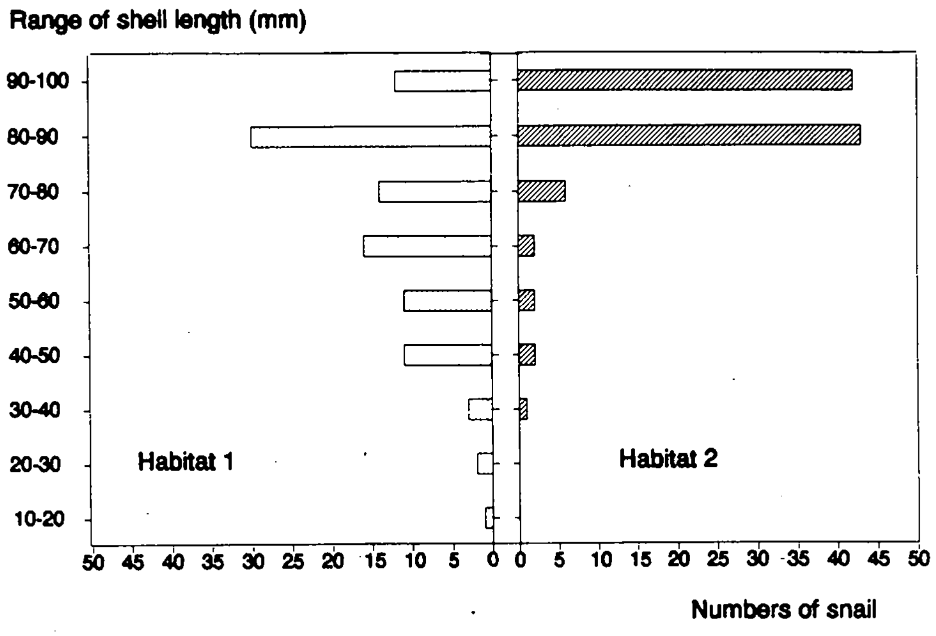


Figure 4.10. Frequency distribution of shell length data of *T. telescopium* in two habitats. Habitat 1 = landward zone; Habitat 2 = seaward zone.

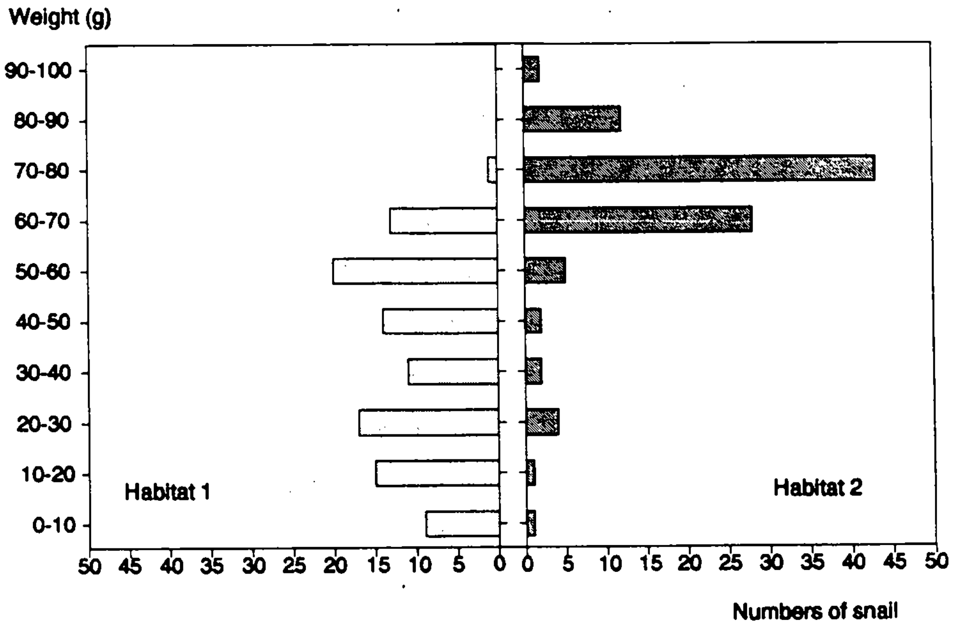


Figure 4.11. Frequency distribution of weight of *T. telescopium* in two habitats. Habitat 1 = Landward habitat; Habitat 2 = Seaward habitat.

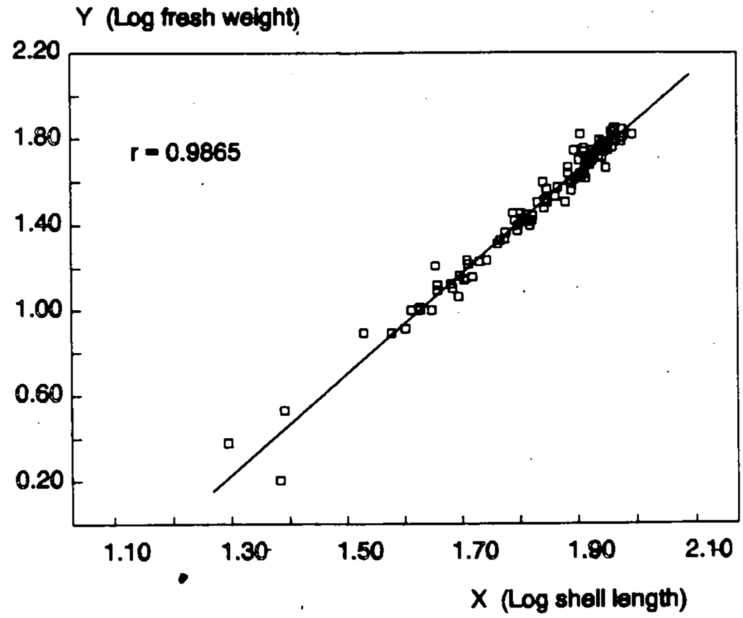


Figure 4.12. Regression of fresh weight and shell length of *T. telescopium* in the landward zone (habitat 1).

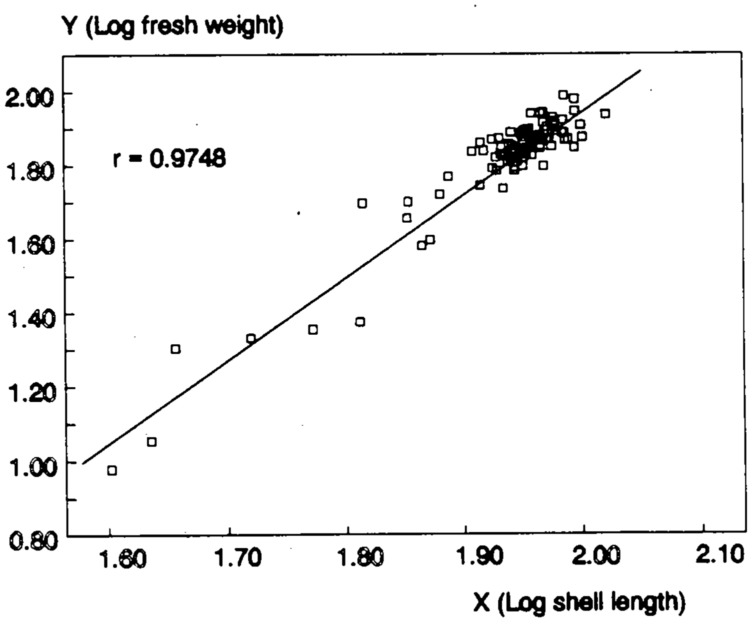


Figure 4.13. Regression of fresh weight and shell length of *T. telescopium* in the seaward zone (habitat 2).

Table 4.1. Analysis of variance of *T. telescopium* density and precision using different transect and sample sizes.

Source of variation		F ratio	D.f. of F ratio	P
Transects	Density	0.4728	2 , 15	> 0.50
	Precision	1.8027	2 , 15	> 0.10
Sample sizes	Density	0.0366	2 , 9	> 0.50
	Precision	0.8951	2 , 9	> 0.25

Table 4.2. Three factor analysis of variance of density of *T. telescopium*.

***) significantly different at level $P < 0.001$.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F ratio	DF. of F ratio	P
Location (A)	2	3.8912	1.9456	29.4788	2 , 12	< 0.001 ***
Habitat (B)	1	0.0634	0.0634	0.9606	1 , 12	> 0.25
Interaction (AxB)	2	0.2421	0.1210	1.8333	2 , 12	> 0.10
Site ($C_{(AxB)}$)	12	0.7924	0.0660	0.9219	12 , 72	> 0.25
Residual (e)	72	5.1549	0.0716			
Total	89	10.1440				

Table 4.3. Student-Newman-Keuls test of the mean density of *T. telescopium* in three locations.

L is location
*) significantly different at level 0.05.

Comparison	Difference	S:E.	q	p	$q_{0.05,12,p}$	Conclusion
L3 vs L1	0.4444	0.0469	9.4755	3	3.773*	Reject Ho
L3 vs L2	0.4377	0.0469	9.3326	2	3.082*	Reject Ho
L2 vs L1	0.0067	0.0469	0.1429	2	3.082	Accept Ho

Table 4.4. Homogeneity tests for comparing the frequency distribution of sizes of *T. telescopium* from two habitats.

l is length, w is fresh weight of the snail and H is habitat.
***) significantly different at level 0.001.

Frequency distribution	X^2	Degrees of freedom	<u>P</u>
lH1 vs lH2	49.0859	5	< 0.001***
wH1 vs wH2	97.2950	8	< 0.001***

Table 4.5. Summary statistics of sizes of *T. telescopium* in habitat 1 (higher area) and habitat 2 (lower area).

H1 = habitat 1, H2 = habitat 2, l = shell length, w = snail fresh weight.

Size observed	Mean	Standard errors	Maximum	Minimum
lH1 (mm)	70.644	1.846	98.800	19.700
wH1 (g)	37.299	1.939	70.500	1.600
lH2 (mm)	87.072	1.138	105.000	40.000
wH2 (g)	67.542	1.651	97.200	9.500
l pooled	78.858	1.542		
w pooled	52.420	1.796		

Table 4.6. Analysis of variance of *Telescopium telescopium* sizes between habitat 1 (high intertidal) and habitat 2 (low intertidal).

w = log weight, l = log shell length.
***) = significantly different at level 0.001.

Treatment	Df. for F ratio	F ratio	P
lH1 vs lH2	1 , 198	57.380	< 0.001 ***
wH1 vs wH2	1 , 198	141.016	< 0.001 ***

Table 4.7. Slope and intercept coefficients of linear regression lines and the value of *t* for testing b = 3.

w = fresh weight, l = shell length, H = habitat, ***) = significantly different at level 0.001.

Regression (y)	 (x)	Slope ± SE (b)	Intercept ± SE. (a)	*t*	P
w H1	l H1	2.337 ± 0.04	- 2.796 ± 0.072	16.575	< 0.001***
w H2	l H2	2.166 ± 0.01	- 2.385 ± 0.192	8.34	< 0.001***

Table 4.8. Analyses of variance of linear regressions of weight-shell length and weight-shell diameter for habitat 1 and habitat 2.

w = fresh weight, l = shell length, H = habitat, ***) = significantly different at level 0.001.

Linear regression	Degree of freedom	F ratio	P	r
wH1 - lH1	1 , 98	3567.888	< 0.001***	0.9865
wH2 - lH2	1 , 98	1869.570	< 0.001***	0.9107

Chapter 5

Feeding and Growth of *Telescopium telescopium.*

5.1. Introduction.

The mangrove whelk *T. telescopium* is distributed mainly on muddy substrata, along waterways or close to small pools, in semi-open tropical mangrove forests. This snail lives upon the surface of organically rich mangrove sediments (MacNae, 1968). Various authors suggests that *T. telescopium* was a detritivore, an algal-detritivore or a deposit feeder (Houbrick, 1991 and Budiman, 1988). These arguments were based mainly on the type and enzyme content of the crystalline style (Alexander *et al.*, 1979), field observations (Budiman, 1988) and the structure of the taenioglossate radula of the species (Houbrick, 1991). The morphology of the radula suggests that *T. telescopium* might consume large amounts of benthic microalgae similar to other taenioglossan gastropods *e.g.* the genus *Cerithidea* (Steneck and Watling, 1982). *Cerithidea* lives commonly on the surface of mangrove sediments also (MacNae, 1968; Whitlatch and Obrebski, 1980). Another study in the Townsville region by Roberts (1980) assumed that *T. telescopium* feed on detritus because it has a specialised digestive organ for processing detritus and its radulae possessed scoop-shaped teeth for feeding on fluid layers of the substratum. Therefore, while it does consume detritus, *T. telescopium* can graze either microalgae or other small plants. The microalgae on sediment surfaces of mangrove soils is dominated by diatoms (Cocksey, 1984 and Chapter 4 of this thesis).

The morphology of the radulae alone is unlikely to predict the feeding habits of intertidal molluscs. Some molluscs may be more dependent on the availability of algae than the morphology of the radular (Raffaelli, 1979, 1985). The examination of gut contents has proven to be a reliable index of the feeding habits of molluscs (Luckens, 1974; Raffaelli, 1985). The availability of food on mangrove sediments may influence selectivity of feeding of *T. telescopium.*

Stomach content analysis has been carried out on other marine and intertidal molluscs (*e.g.* Foster, 1964; Alexander, 1979; Whitlach and Obrebski, 1980, 1985). However, information on the diet of *T. telescopium* based upon analysis of stomach contents is lacking. This information is required to show the composition of the diet quantitatively and for use as a basis for assessing the impact of feeding by this species.

Within mangrove forests, *T. telescopium* can be found at different levels of the intertidal zone *i.e.* at both landward and seaward (see Chapter 4). The environmental factors of each zone are likely to differ (*e.g.* availability of seawater, type of substratum). These differences may affect growth of *T. telescopium* living in each habitat. Some intertidal molluscs grow at different rates in different habitats (*e.g.* see McLachlan and Lombard, 1981). Information on the growth rate of *T. telescopium* in general and in particular, its growth rate in different habitats are not yet available. However, studies on other mangrove gastropods, mainly on *Cerithidea,* have been carried out (Vohra, 1970; Cockcroft and Forbes, 1981; McLachlan and Lombard, 1981; Sreenivasan and Natarajan, 1986). Growth rates of other marine molluscs have been reported also by many authors (*e.g.* Poore, 1972; Borkowski, 1974; Balaparameswara Rao, 1976; Wright, 1976 and Bretos, 1978).

The aims of this study were twofold: Firstly to determine the diet of *T. telescopium* in natural mangroHx areas; secondly, to determine the growth rate of *T. telescopium* in the field.

Predictive hypotheses of this study were:

1. *T. telescopium* consumed benthic diatoms as an important part of its diet.
2. The growth rate of *T. telescopium* was differed in different habitats.

5.2. Materials and methods.

5.2.1. Study sites.

The studies were carried out on undisturbed mangrove areas adjacent to Chunda Bay, North Queensland, Australia (see Figure 5.1). Sampling was carried out within two habitats in the mangrove area *i.e.* landward (L) and seaward (H) zones of the shore. The duration of the study was six months, from June to December 1990.

The landward (H; see Figure 5.1) was inundated during spring high tides (approximately ≥ 2.8 m above mean datum) only (Lasiak and Dye, 1986; Queensland Department of Transport, 1989). This habitat was a semi-open area, dominated by 1 - 2 m high *Ceriops tagal* and *Avicennia marina* (1 - 3 m high) trees. The substratum was a sandy soil.

Vegetation in the seaward habitat (L; see figure 5.1) was dominated by *A. marina* (2 - 3 m high) and young *Rhizophora stylosa* (1 - 2 m high) trees. This area was submerged by sea water more frequently than the landward area (height about datum was approximately 1.5 m). The area had a small shallow waterway that always contained water even during low tide. The substratum was also softer, and the soil was more muddy than in the landward zones.

5.2.2. Feeding of *T. telescopium.*

5.2.2.1. Stomach contents.

This study used *T. telescopium* living in habitat H and habitat L. Thirty adult snails (between 80 and 90 mm total shell length; see Figure

5.2) were collected from each habitat by hand during ebbing tides. Only moving snails were collected. The stomach of each snail was removed after breaking the shell carefully (using a hammer). The stomach was then dissected out and all stomach contents were placed into a 30 ml vial which contained a preservative solution *i.e.* 3 ml of 3 % formaldehyde (see Prescot, 1970 and Raffaelli, 1985). The contents were mixed thoroughly by shaking the vial for about two minutes.

Stomach contents were examined using a modification of the method introduced by Jones (1968). One drop or 0.05 ml of the mixture was placed on a glass slide which had a 2 mm x 2 mm grid and the drop was covered with a coverglass. Five random areas on each slide were examined under a compound, phase-contrast microscope at 100x to 400x magnification. Materials in the stomach were grouped into five categories: (1) detritus (organic material of unidentifiable origin), (2) microalgal non-diatoms (green algae, dinoflagellates, blue green algae) and (3) benthic diatom cells. This procedure was repeated five times for each vial (*i.e.* n = 5 replicate drops per vial). The abundance of the different constituents from each habitat was estimated based on the frequency of occurrence in each stomach. The relative frequency of occurrence was determined as a percentage of the total frequency of occurrence for the whole sample in each habitat.

Benthic diatoms were identified to species level whenever possible using the following literature: Kutzing (1844); Peragallo (1897 - 1908); Mann (1925); Hustedt (1930, 1938); Hendey (1951); Wood (1963); Foged (1975, 1978); Hustedt (1976); Navaro (1982); John (1983); Crosby and Wood (1985); Jin *et al.* (1985); Hustedt and Jensen (1985); Krammer and Lange-Bertalot (1986); Krammer and Lange- Bertalot (1988); Wah and Wee (1988). The abundance of species of diatoms per sample, was calculated using the formula:

$$N = \frac{A}{a} \times n \times \frac{1}{R} \times \frac{V_d}{V_m}$$

where:

N is the abundance of diatom cells per vial (= cells/ml)

A is the total number of areas in a grid (= 36).

a is the number of areas which are studied (= 5).

R is the number of replicates per vial (= 5).

V_d is the dilution factor per vial (= 3)

v_m is the volume of mixture on a glass slide (= 0.05 ml).

The value of the relative frequency of occurrence of each diatom species was estimated as a percentage of the total occurrence in the whole sample. Diversity of benthic diatoms in each sample was determined using the diversity index of Shannon-Weaver (1963).

5.2.2.2. Abundance of benthic diatoms inside and outside foraging tracks made by *T. telescopium*.

This study involved examination of the community structure of benthic diatoms in two types of tracks *i.e.* natural foraging tracks and artificial tracks. The natural track was created by the foraging movement of *T. telescopium* across the surface of the substratum. The artificial track was a simulation of a natural track, made by "bulldozing" the surface of the sediment with the shell of a living snail. In this case the animal was pulled across the substratum using a flexible string attached to the shell. This field work was carried out during an ebbing tide.

In each habitat, twenty replicates of each type of track (natural and artificial) were selected haphazardly. Samples of sediment from inside and outside of both natural and artificial tracks were collected using a small trowel *i.e.* 18.5 cm total length, with the size of the metal blade 8 cm long by 2.5 cm wide. The size of the sediment sample was approximately 2 cm wide x 8 cm long x 2 cm deep. This size was selected in anticipation of the depth and width of soil removed the grazing activity of individual *T. telescopium* (see Houbrick, 1991). Sediments inside each natural and artificial track were sampled haphazardly, directly behind the animal. Four sub-replicate samples per track were taken. Four sub-replicate samples were collected haphazardly from each natural and artificial track, two on the left side and two on the right side of the track.

The samples were then stored in the dark for 6 to 8 hours (see Eaton and Moss, 1966 and Round 1990). The whole sample was poured into a 100 ml container, wetted by sterile, clean seawater and homogenised by shaking (by hand). The sample was then poured into a 90 mm diameter petridish. Two 2 cm x 2 cm lens tissues (Kimwipes, fine grade; Kimberly-Clark Australia) were placed onto the surface of the sample. Diatoms adhered to the lens tissue and this was the sample unit used to sample benthic diatoms.

The sample was placed under sunlight (no artificial light) for one natural cycle of light and darkness. The lens tissues were harvested the next morning between 08:00 and 11:00. Each lens tissue was placed in a vial and preserved with 3 ml of 5 % formaldehyde solution and 1.5 % sodium hypochlorite (1 : 1 by volume).

The algae were released by macerating the tissue in the preservative in a concave dish using a pair of mounted needles. Two drops of this suspension were placed onto a counting chamber (an improved Neubauer counting chamber made by Assistent, Germany; see Figure 3.4). Diatoms in 80 selected fields (under 400x magnification) were counted and identified under a light microscope with phase contrast equipment (Taasen and

Hoisæter, 1989). This microscopic work was replicated three times for each vial.

The number of benthic diatom cells per unit area of original habitat was determined using a modification of the formula of Baker and Silverton (1985) as shown below.

$$N = \frac{n}{f} \times D \times \frac{A}{a} \times \frac{1}{b} \times 10^4$$

where

N = Total number of diatom cells in the original habitat (cells/ cm^2).

f = Numbers of microscope fields of 1 mm x 1 mm examined in a chamber.

n = Numbers of cells counted in f.

D = Dilution factor or volume of suspension in the vial (ml).

A = Area of the incubation container (cm^2).

a = Area of the lens paper (cm^2).

b = Area of the original sample (cm^2).

Benthic diatoms were identified to species level whenever possible using the literature cited in section 5.2.2.1.

Similarity between communities of benthic diatoms was determined using the Sorensen coefficient of similarity (Bray and Curtis, 1957):

$$C = \frac{2p_{jk}}{(p_j + p_k)} \times 100\%$$

where C is a similarity index (in percentage),

p_j and p_k are the sums of species values for samples *j* and *k* ;

p_{jk} is the lesser species values for those species common to both samples.

The dissimilarity index then was calculated as:

$$\boxed{D = 100\ \% - C}$$

where D is a dissimilarity value (in percentage) between the communities.

5.2.3. Growth of *T. telescopium.*

Growth rates of snails were studied using a mark/recapture method (Morgan, 1987). A total of 300 healthy snails (*i.e.* with unbroken shells) between 30 and 75 mm total shell length were collected from habitat H. The total length of each shell was measured using a calliper to the nearest to 0.1 mm accuracy (see Figure 5.2). After washing off mud and debris each snail was paper dried then tagged by sticking a plastic embossing tape label (Dymo tape: 9 mm wide) onto the shell using 'Araldite 5 minute, twin syringe' glue (Burrows and Hughes, 1989). 150 tagged snails then were distributed in each habitat (*i.e.* high and seaward areas). After six month periods these tagged snails were recaptured and the length of the shells were measured. This tagging method was modified from a method outlined by Spight (1982) and Peckol *et al.* (1989). Growth of *T. telescopium* was then estimated using growth increment data and a Gulland and Holt plot (Gulland and Holt, 1959) combined with Munro's method (Munro, 1982).

5.3. Results.

5.3.1. Feeding of *T. telescopium.*

5.3.1.1. Stomach contents.

The stomach contents of *T. telescopium* consisted of three main dietary types *viz.* benthic diatoms, other microalgae and detritus (other organic materials). The proportion of these three dietary types varied between samples. The three occurred individually or in combinations of (1) diatom-other microalgae-detritus, (2) diatom-other microalgae, (3) diatom-detritus and (4) diatom only. The frequency of items in stomach contents based on occurrence by habitat is shown in Figure 5.3. One hundred percent of samples of *T. telescopium* gut contents contained benthic diatoms. Approximately 10 to 30 % (mean = 20 %) of samples contained diatom cells only. None of the samples contained either microalgae or detritus only. Microalgae and detritus were always found mixed with diatom cells. In landward and seaward areas, the numbers of stomachs containing a mixture of diatom-other microalgae-detritus were slightly higher than those containing other types of food.

Chi-square statistical tests on the distribution of samples by food types are shown in Table 5.1. The proportion of dietary types was not significantly different from 1 : 1 : 1 : 1 ratio in the landward (Table 5.1). However, samples containing a mixture of diatom-other microalgae-detritus occurred significantly more frequently than other dietary groups in the seaward habitat. Pooling the data over habitats resulted in the number of samples in each dietary type not differing significantly ($P > 0.05$; Table 5.1).

The absolute values of frequency of occurrence and abundance of diatom species consumed by *T. telescopium* are shown in Table 5.2. Figures 5.4 to 5.6 show the relative values of frequency of occurrence and abundance of these diatom taxa. Thirty species of diatom were found in the pooled samples of *T. telescopium* stomach gut contents.

Almost all samples contained five particular species of diatom *i.e. N. punctata, M. exigua, A. coffeaeformis, A. proteus* and *N. halophila*. The values of average number of cells/ml and absolute frequency of occurrence of these species combined per stomach exceeded the values of all other diatom species combined. Patterns of dominance of these species differed in the landward and seaward , however. In the higher parts of the mangrove area, *N. punctata, M. exigua* and *A. coffeaeformis* were abundant. However, *N. halophila* and *A. proteus* occurred in smaller numbers in stomach contents from this landward habitat. In the seaward habitat, only *N. punctata* occurred in considerable abundance. *N. halophila* and *M. exigua* were dominant also in stomach contents in the seaward habitat. The other species occurred in limited numbers per stomach (see Figure 5.4 and 5.5).

Frequency of occurrence and abundance of each diatom species in the diatom assemblages from data pooled from both habitats is shown in Figure 5.6. This figure shows that the most dominant species in the diet of *T. telescopium* was *N. punctata*. The number of cells of this species exceeded that of all the other species. However, the frequency of *N. punctata* in pooled samples was slightly lower than *M. exigua* and *A. coffeaeformis* (see Figure 5.6).

Table 5.3. shows the results of Kruskal-Wallis tests on the numbers of cells, species richness and diversity indices (Shannon-Weaver index) of diatom communities consumed by *T. telescopium*. This table shows that the number of diatom cells found within the stomach contents from the landward and seaward habitats did not different significantly ($P > 0.05$). Total number of species of benthic diatoms in stomach content samples did not differ significantly between habitats ($P > 0.05$). Values of the diversity index of benthic diatom assemblages in stomach content samples were in the range

of 0.6000 to 0.8000. This index did not differ significantly between landward and seaward habitats ($P > 0.05$) (see Table 5.3).

5.3.1.2. Abundance of benthic diatoms inside and outside foraging tracks made by *T. telescopium*.

Table 5.4 shows the absolute abundance of benthic diatom species inside and outside natural foraging tracks of *T. telescopium* in two different habitats. Table 5.5 shows the relative abundance of dominant diatom species inside and outside foraging tracks made by *T. telescopium*. The values of relative dominance of some diatom species including *A. coffeaeformis, N. halophila* and *N. punctata* were slightly higher than those of other species. Some species for example *A. subturgida*, *N. cryptocephala*, *N. amphibia*, *N. closterium*, *N. levidensis* and *N. longissima* were more dominant in landward intertidal samples. However, *A. ovalis*, *A. ventricosa*, *C. heteroidea*, *M. exigua*, *N. cincta* and *N. halophila* were more dominant in seaward intertidal samples.

The effects of creation of artificial and natural foraging tracks of *T. telescopium* on diatoms living on the surface of mangrove sediment are shown in Figure 5.7A. The creation of artificial tracks in the landward and seaward habitats reduced the population density of benthic diatoms slightly inside the tracks. This bulldozing effect, however did not reduce diatom abundance significantly. Analysis of variance did not detect any significant differences in total number of diatom cells inside and outside artificial tracks in each habitat ($P > 0.05$; see Table 5.6).

The natural foraging movement of *T. telescopium*, however, reduced the abundance of benthic diatoms. Total numbers of diatom cells inside the natural tracks were significantly lower than found outside the tracks. In the landward habitat, benthic diatom populations inside natural tracks were approximately 25 % lower than benthic diatom population outside natural tracks ($P < 0.05$, see Figure 5.7A). In the seaward , the mangrove sediments outside natural tracks had 75 % more diatoms than the sediments inside natural tracks ($P < 0.001$) (see Table 5.6 and 5.7A).

Figure 5.7B shows the average number of species of benthic diatom found inside and outside natural and artificial foraging tracks in the landward and seaward habitats. The number of species in the seaward habitat was slightly higher than that in the landward habitat. Results of analyses of variance of number of species by track type and habitat are shown in Table 5.7. The artificial track treatment did not have a significant effect on the species richness ($P > 0.05$). The effect of the natural feeding movement of *T. telescopium* on species richness of diatoms in this habitat was not significant also. However, the feeding movement of this snail in the seaward habitat reduced the number of diatom species significantly ($P < 0.001$; see Table 5.7).

Table 5.8 shows the comparison of benthic diatom communities inside and outside tracks of *T. telescopium*. In the landward habitat, the foraging movement of this snail did not affect the benthic diatom community composition substantially. The similarity value between the communities inside and outside natural tracks was 76 % . The effect of this activity in the seaward habitat, however, was more marked. The value of similarity inside and outside natural tracks was below 69 % . This was 13 % lower than the similarity value inside and outside artificial tracks in the same habitat.

5.3.2. Growth of *T. telescopium*.

One hundred and fifty tagged *T. telescopium* were released in to each habitat. However, not all of them were recaptured after six months at large. In the landward habitat the total number of snails recaptured was 94.

In the seaward habitat 80 snails were recaptured.

Growth increment data of *T. telescopium* in the landward and seaward habitats were analysed using the Gulland and Holt (1959) method (Figure 5.8 and 5.9, respectively). Figure 5.8 shows that the estimation of growth parameters for the landward habitat produces an asymptotic length (L*oo*) = 66.91 mm and growth constant (K) = 1.35 per year). This analysis used 38 out of 94 data points. The biggest shell length recorded in this habitat was approximately 100 mm (see Table 3.5 in Chapter 3). When the value of L*oo* = 100 mm was used as a 'seed' value, the 'slope' or K value was reduced to 0.28 ± 0.036 (S.E.) per year. This regression line ('forced' Gulland and Holt plot) was more realistic because larger *T. telescopium* (*i.e.*range of shell length between 90 to 100 mm, see Figure 3.10 in Chapter 3) were common.

In the seaward habitat, from 80 increment data points, only 30 % of these were included in the Gulland and Holt plot analysis. The values of the asymptotic length (L*oo* = 70.42 mm) and growth constant (K = 1.582 per year) of *T. telescopium* shells in the preliminary estimation were slightly higher than those in the landward (Figure 5.9). Large *T. telescopium* (shell length 90 to 100 mm) were found in the seaward habitat in considerable numbers (see Figure 3.10 in Chapter 3). Using L*oo* = 100 mm, the 'forced' Gulland and Holt plot resulted in a regression line with slope K = 0.36 ± 0.052 (SE). This value of K was slightly higher than the value obtained for the landward habitat. The growth rate of *T. telescopium* in the seaward habitat, may have been slightly higher than that in the landward habitat.

5.4. Discussion.

Amongst the dietary groups consumed by *T. telescopium*, a mixture of diatoms-microalgae-detritus was the most common. It is possible that diatoms may not be fed upon selectively by *T. telescopium*. Diatoms may have been ingested when the snail engulfed mud particles and detritus. Benthic diatoms thus may be less important as a dietary item than detritus and other microalgae. Without examining the stomach contents some workers suggested that this snail is a deposit feeder or detritivore which engulfs fine mud and detritus (Alexander *et.al.*, 1979, Budiman, 1988).

The results of the present study suggest that benthic diatoms may be a very important food or perhaps the main dietary item of *T. telescopium*. The two other basic dietary components *i.e.* other microalgae and detritus, may represent supplementary components of the diet only. Several points support this contention. Firstly, all samples contained diatom cells. Approximately 20 % of the total stomach content contained diatom cells only. Detritus and microalgae were less abundant among the samples. Their occurrence inside the stomach was always in combination with diatom cells (Figure 5.3). *T. telescopium* in this case may prefer diatoms more than the other dietary types. Secondly, the abundance of benthic diatoms inside natural foraging tracks created by living *T. telescopium* was significantly lower than that outside such tracks. This difference may not simply be a result of a bulldozing effect because the abundance of diatoms inside and outside artificial tracks was the same (Figure 5.7a and Table 5.7). Significant numbers of diatoms appear to be consumed by *T. telescopium* during natural foraging movements. This result agrees with that of Houbrick (1991) that the snail is an algal-detritivore.

Further field and laboratory studies are required to confirm that diatoms play an important role in the metabolism of the snails. These studies should include estimates of faecal content and output, rates of ingestion (Black *et.al.*, 1979 and 1988), analysis of specific pathways of dietary carbon (Haines and Montague, 1979) and study of the growth rate of snails kept on different diets (Brenchley, 1987). Steneck and Watling (1982) suggested that to recognise the main diets of molluscs careful field observations, experimental preference experiments and analysis of gut and fecal contents was required.

In this chapter the analysis which explicitly compared community structure of gut contents with samples from sediments was not carried out. However, by comparing Table 5.2, 5.4, 5.5, 5.8 and data on community structure from natural sediments in Chapter 5, the abundance of benthic diatoms species inside stomach contents of *T. telescopium* was found to be similar in that on mangrove sediments. Diversity indices, numbers of species and the pattern of species dominance of the diatom community in the stomach contents were similar to those on sediments also. This suggests that the snail may not selectively remove particular diatom species from the sediment surface. Diets of the snail may be correlated with the availability of diatoms. The non selectivity of *T. telescopium* in removing diatom species from sediments may be consistent with other mud snails with taenioglossate radulae (Whitlatch and Obrebski, 1980 and Houbrick, 1991). Steneck and Watling (1982) concluded that marine molluscs with taenioglossan "rakes" fed predominantly on microalgae (diatoms and blue green algae) and filamentous algae (*e.g. Cladophora, Ectocarpus, Acrochaetium*). Raffaelli (1985) found that the diet of marine molluscs depended also on the availability of algae.

The results show that the growth parameter K predicted using the maximum size attainable in the seaward habitat was only slightly higher than that in the landward habitat. Environmental conditions between the two habitats may not have been substantially different, thus a large difference in snail growth was not detected. McLachlan and Lombard (1981) found that the growth rate of the gastropod *Turbo sarmaticus* on two remote habitats (*i.e.* having different environmental conditions) was different.

A large proportion of data on *T. telescopium* shell length increments was rejected in estimating the growth parameters. If one assumes that the uncaptured or missing snails had a similar pattern of growth to those recaptured, it suggests that perhaps only 40 % and 30 % of the snail populations in the landward and seaward habitat respectively were able to produce detectable growth increments in the growth study. The "dormancy" of many of the snails could be attributed to at least two factors: the growth of *T. telescopium* in the population was impeded experimentally and the shells were damaged or they simply grew very slowly. Cockcroft and Forbes (1981) believed that their data was affected by such factors.

An estimate of the total number of deaths of snails over the study period was not available. No estimates of emigration were available either. Thus it was difficult to determine the rate of mortality in the population of *T. telescopium*. Based on the data on "dormant" snails, a very preliminary estimate of mortality rate perhaps may be made. A large number, between 60 and 70 percent, of the dormant snails were juveniles (see Figure 5.8 and 5.9). The juvenile *T. telescopium* were more likely to be attacked by predators such as mangrove crabs, birds and mammals (Houbrick, 1991). The rate of mortality of *T. telescopium* may be very low, as found for other estuarine gastsropod. *Cerithidea decollata* was estimated to have an annual mortality of approximately 38 % (Cockcroft and Forbes, 1981). Further studies of mortality rates of *T. telescopium* in natural mangrove ecosystems are required.

The mortality of adult *T. telescopium* may not be related strngly to a predatory effect. Adult snails have a large, thick shell. Thus only large and powerful natural predators (*e.g.* the mud crab *Scylla serrata* (Forskål)) may be able to attack and eat this snail (Houbrick, 1991). Extreme temperatures may have caused high mortality. In North Queensland mangrove forests, Lasiak and Dye (1986) recorded significant mortality of adult *T. telescopium* (10 - 12 cm total length) after three days exposure to direct solar radiation. However, during dry, inactive periods, individuals clustered together in shady places beneath the mangrove trees (Lasiak and Dye, 1986; Houbrick, 1991). Some other tropical gastropods, especially cerithids, showed clustering behaviour to escape from dry conditions and high temperatures also (Moulton, 1962; Rohde and Sandland, 1975; Hazlett, 1984).

The growth rate (based on shell length measurements) of large snails *i.e.* larger than 70 mm total length, was shown to be slow. However, the snails may be adding whorls and increasing body size by expanding and consolidating the shell lips (Cockcroft and Forbes, 1981 and Sreenivasan and Natarayan, 1986). Futhermore, differences in growth rates between juvenile and adult gastropods have been recognised by some authors (Vohra, 1970; Poore, 1972 and Borkowski, 1974).

The results of the growth rate study of *T. telescopium* may have been improved if the snails were kept in their "own" habitat. In the present study, to determine the growth rate of *T. telescopium* in the seaward intertidal habitat, the snails were transplanted from the landward intertidal habitat. This methodology was used because of difficulties in collecting small *T. telescopium* (shell length between 30 to 70 mm) from the seaward intertidal habitat (see Figure 3.10 in Chapter 3). The growth rate of the seaward intertidal animals could thus have been affected by the transplant procedure. This, however, may suggest that large numbers of *T. Telescopium* were in the juvenile stage in the landward habitat but then moved to lower areas of the shore when adult. A similar result was found in a study of Roberts (1980) in the Townsville area where small sizes of *T. telescopium* were difficult to find in the outermost parts of the shore. Studies on growth rates of intertidal gastropods usually use animals from the same sampling sites (*i.e.* McLachland & Lombard (1981) and Sreenivasan

& Natarajan (1986) on *Turbo sarmaticus* and *Cerithidea obtusa*, respectively).

The growth of *T. telescopium* (as well as other gastropods) may consist of several components including growth in length, width, weight of shell and weight of flesh. Several authors used width instead of shell length (McLachlan and Lombard, 1981; Sreenivasan and Natarayan, 1986; Checa, 1991); some combined these with dry flesh weight (Cockcroft and Forbes, 1981). Further experimental work can be done *e.g.* to examine the pattern of growth of this species under different degrees of environmental stress (*i.e.* desiccation and high temperatures in both exploited and unexploited areas).

This chapter has demonstrated that *T. telescopium* feeds extensively on diatoms and that its foraging activities can reduce the abundance of diatoms on a very local scale (at the scale of foraging tracks). The chapter investigated the impact of grazing by *T. telescopium* on diatoms at larger spatial scales. It further demonstrated that the growth rate of this species appeared not to differ significantly in habitats at High and Low levels with respect to tidal datum.

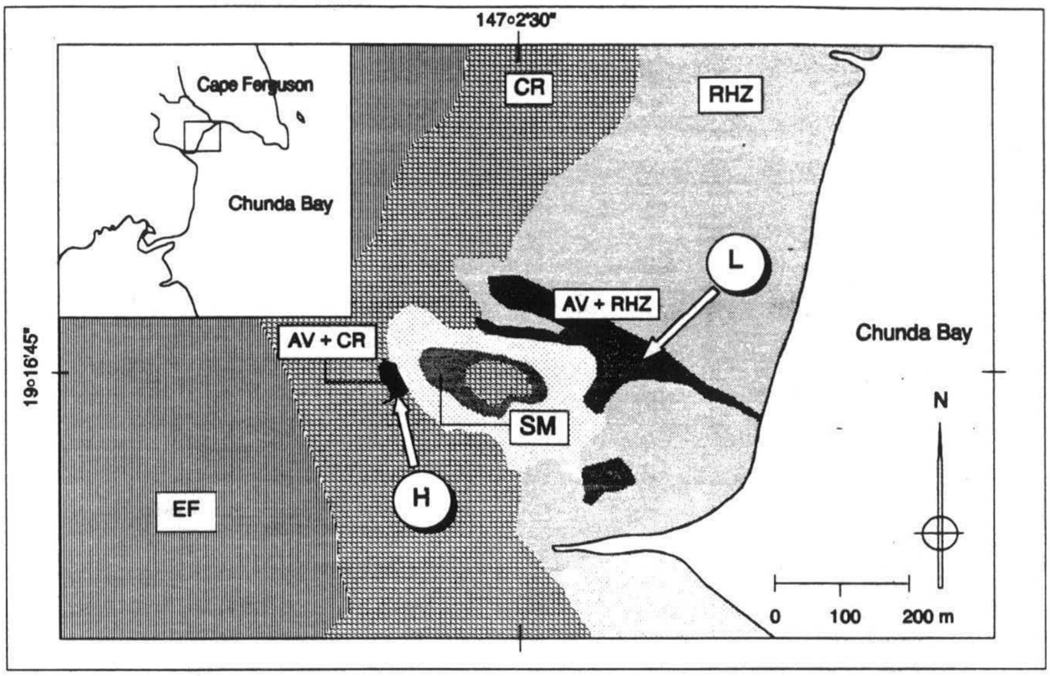


Figure 5.1. A Map showing the sites of studies on feeding and growth of *T. telescopium*.

The zonation of the vegetation, including mangrove trees are shown. *R. stylosa* (RHZ), *C. tagal* (CR), *A. marina* (AV); salt marsh plants (SM) and *Eucalyptus* forests (EF).
The studies were carried out in both landward (H) and seaward (L) areas.

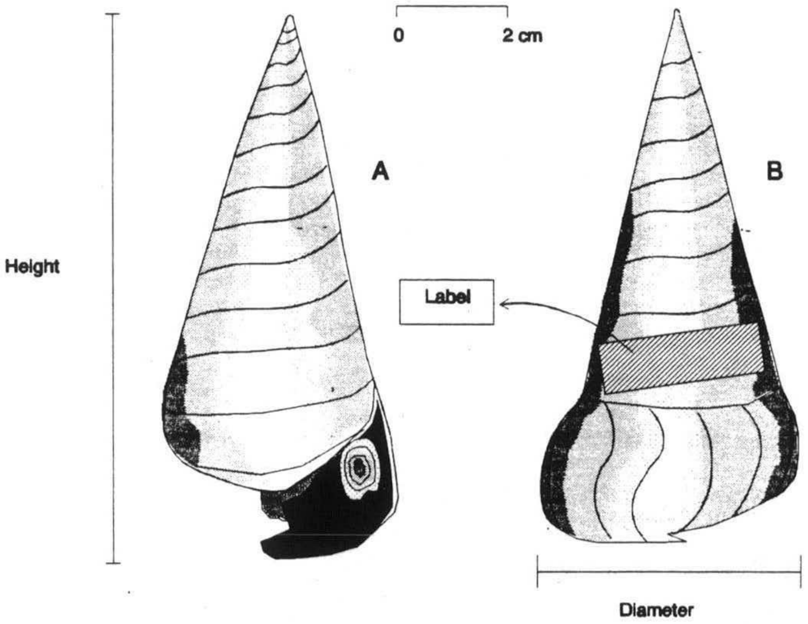


Figure 5.2. Diagram of adult *T. telescopium* shells showing the methods of measuring length and labelling the shells.

Shells are in apertural (A) and dorsal (B) views.

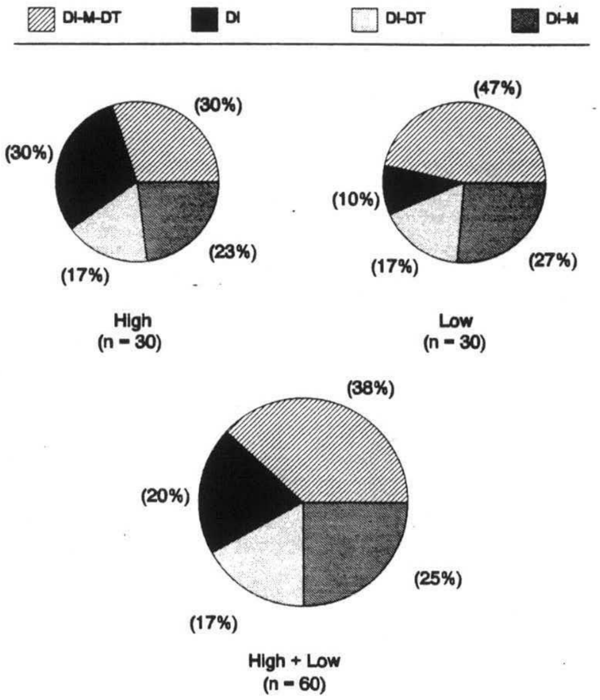


Figure 5.3. Frequency (in percentage) of dietary types in diet of *T. telescopium* collected from different areas.

'High' is landward and 'Low' is seaward area. 'High+Low' represents analysis using data pooled over areas. Food items are diatom - other microalgae - detritus (DI-M-DT), diatom - other microalgae (DI-M), diatom - detritus (DI-DT) and diatom only (DI).

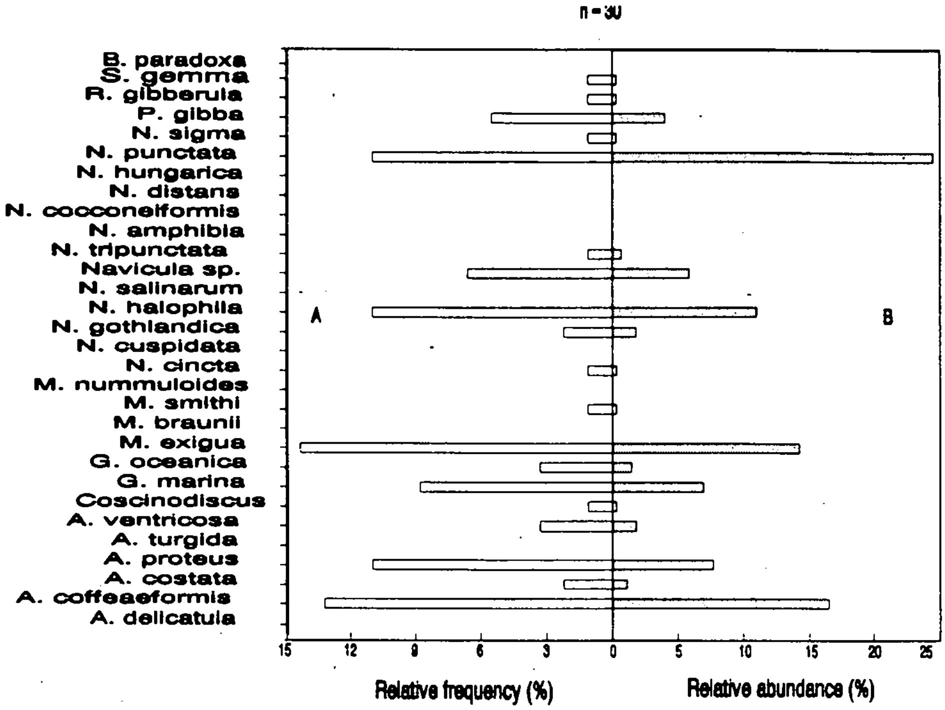


Figure 5.4. Relative frequency (A) and relative abundance (B) (in percentage) of diatom species found in stomach contents of *T. telescopium* in the landward area.

The relative frequency is based on the percentage of occurrence in samples. The relative abundance is expressed as percentage in terms of cells/ml.

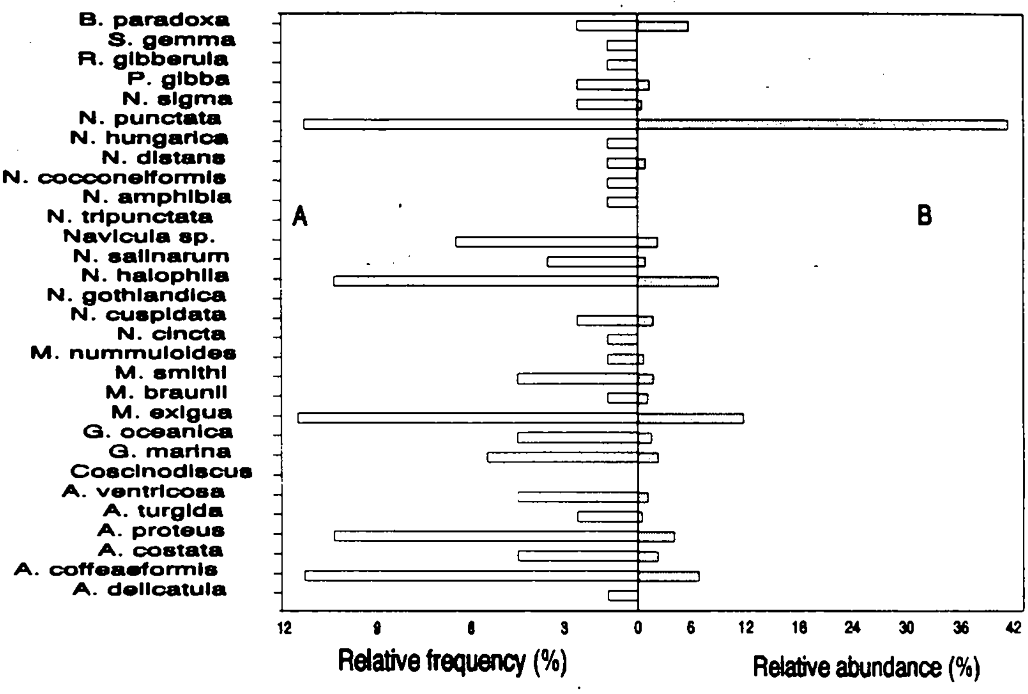


Figure 5.5. Relative frequency (A) and relative abundance (B) (in percentage) of diatom species found in stomach contents of *T. telescopium* in the seaward areas.

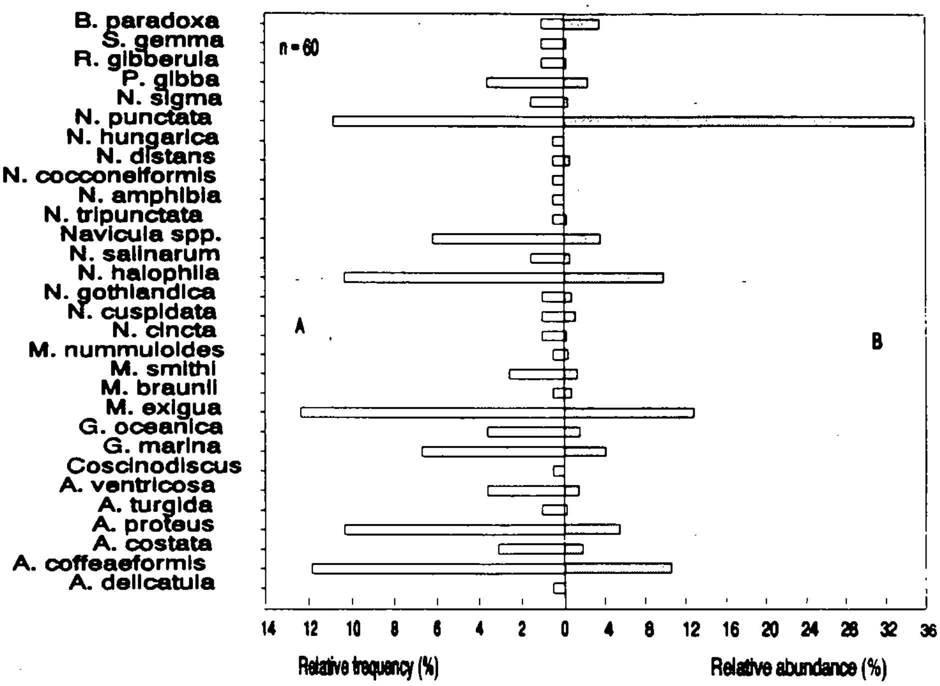
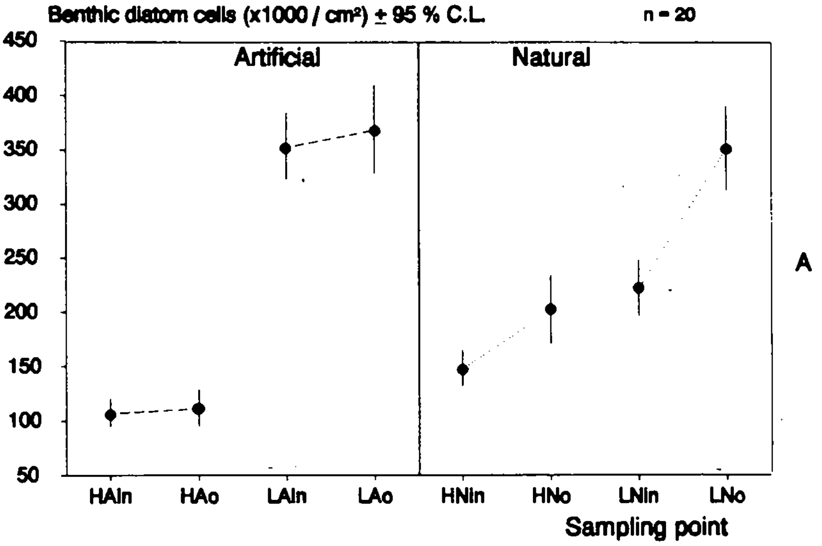


Figure 5.6. Relative frequency (A) and relative abundance (B) (in percentage) of diatom species in stomach contents of *T. telescopium* in pooled samples.



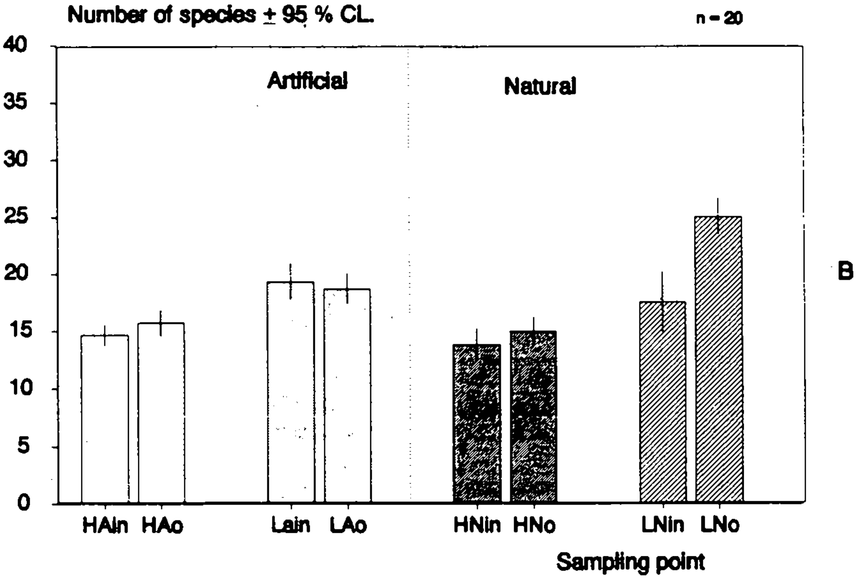


Figure 5.7. Abundance (A) and number of species (B) of benthic diatoms inside and outside artificial and natural foraging tracks of *T. telescopium* in two different areas.

(H) and (L) = landward and seaward areas respectively; (A) and (N) = artificial and natural tracks respectively; (in) and (o) represent inside and outside the tracks respectively; n = 20 tracks.

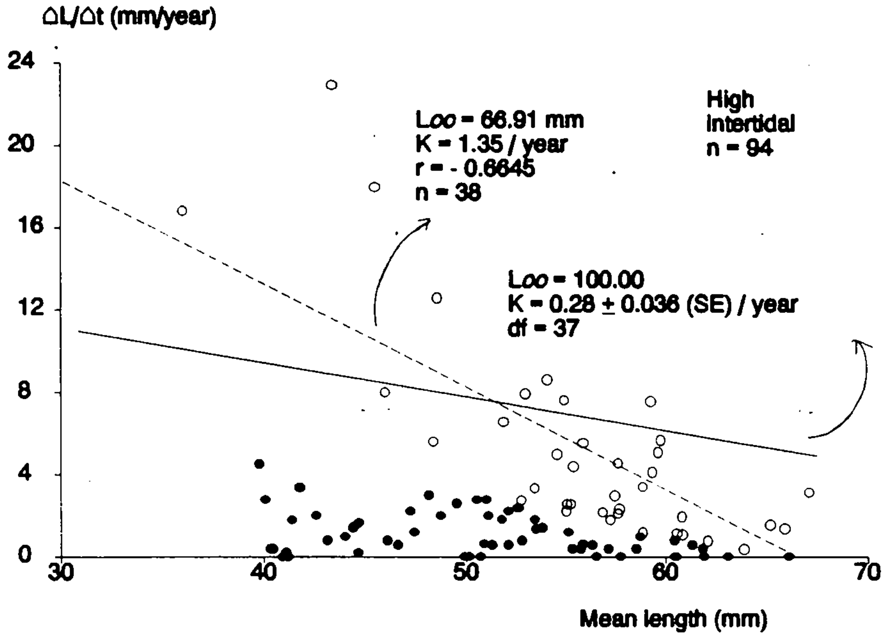


Figure 5.8. Gulland and Holt plot (dotted line) and forced Gulland and Holt plot (using Munro's method; solid line) of *T. Telescopium* shell length increment data in the high intertidal (= landward) habitat.

Some growth increment data (solid points) were not selected in the analysis. The L∞ in the forced plot was maximum length for the low intertidal habitat (= 100 mm, see Figure 4.10 and Table 4.5 in Chapter 4)

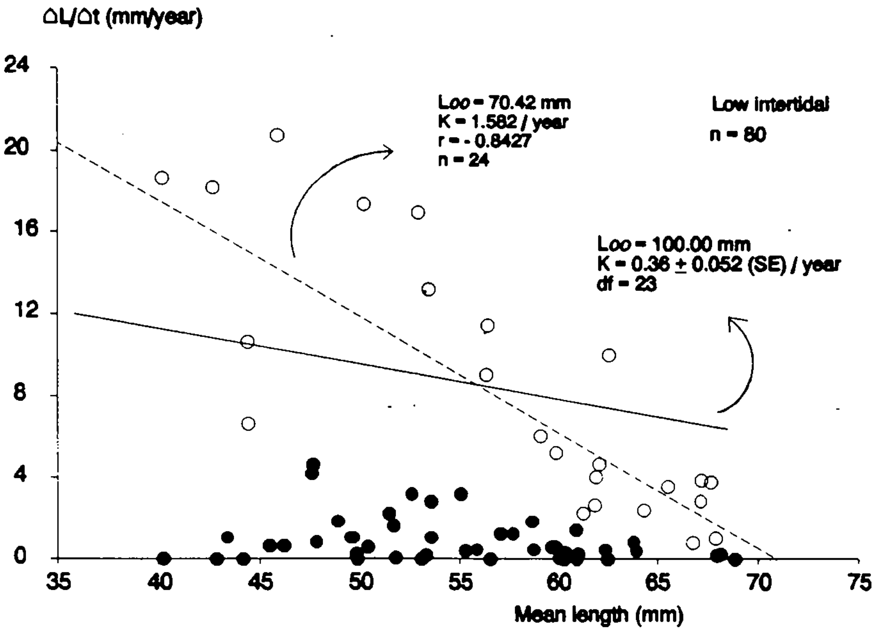


Figure 5.9. Gulland and Holt plot (dotted line) and forced Gulland and Holt plot (using Munro's method; solid line) of *T. Telescopium* shell length increment data in the low intertidal (= seaward) habitat.

Some growth increment data (solid points) were not selected in the analysis. The L∞ in the forced plot was maximum length for this area (= 100 mm, see Figure 4.10 and Table 4.5 in Chapter 4)

Table 5.1. Chi-square test for absolute frequency of food items found in the stomach contents of *Telescopium telescopium* in each area and in areas pooled.

Food items are (1) Diatoms-Other microalgae-Detritus, (2) Diatoms-Other microalgae, (3) Diatoms-Detritus and (4) Diatoms only.

*) = the Ho is that the population sampled has a 1:1:1:1 ratio of food items 1 to 4 is rejected at level 5 % .

Area	Food item				n	Chi-square	Df.
	1	2	3	4			
Landward	9	7	5	9	30	1.47	3
Seaward	14	8	5	3	30	9.20 *	3
Data pooled in area	23	15	10	12	60	6.53	3

Table 5.2. Absolute frequency and average abundance of benthic diatom species in the stomachs of *T. telescopium* by sampling area and for samples pooled over samling areas.

No	Species	Seaward (n = 30)		Landward (n = 30)		Pooled samples (n = 60)	
		Freq.	Av. Abund. (cells/ml)	Freq.	Av. Abund. (cells/ml)	Freq.	Av. Abund. (cells/ml)
1	*Achnanthes delicatula*	2	33.23	0	0.00	2	16.62
2	*Amphora coffeaeaformis*	25	996.92	29	1500.65	54	1248.78
3	*Amphora costata*	9	332.31	4	99.69	13	216.00
4	*Amphora proteus*	23	598.15	23	697.85	46	648.00
5	*Amphora turgida*	5	66.46	0	0.00	5	33.23
6	*Amphora ventricosa*	9	166.15	7	166.15	16	166.15
7	*Coscinodiscus sp*	0	0.00	1	33.23	1	16.62
8	*Grammathophora*	12	332.31	18	631.38	30	481.85
9	*Grammathophora*	9	232.62	7	132.92	16	182.77
10	*Mastogloia exigua*	25	1728.00	30	1296.00	55	1512.00
11	*Mastogloia braunii*	2	166.15	0	0.00	2	83.08
12	*Mastogolia smithi*	9	265.85	2	33.23	11	149.54
13	*Melosira nummuloides*	1	99.69	0	0.00	1	49.85
14	*Navicula cincta*	3	33.23	2	33.23	5	33.23
15	*Navicula cuspidata*	5	265.85	0	0.00	5	132.92
16	*Navicula gothlandica*	0	0.00	6	166.15	6	83.08
17	*Navicula halophila*	23	1329.23	23	996.92	46	1163.08
18	*Navicula salinarum*	7	132.92	0	0.00	7	66.46
19	*Navicula sp.*	14	332.31	14	531.69	28	432.00
20	*Navicula tripunctata*	0	0.00	2	66.46	2	33.23
21	*Nitzschia amphibia*	2	33.23	0	0.00	2	16.62
22	*Nitzschia*	2	33.23	0	0.00	2	16.62
23	*Nitzschia distans*	2	132.92	0	0.00	2	66.46
24	*Nitzschia hungarica*	2	33.23	0	0.00	2	16.62
25	*Nitzschia punctata*	24	6014.77	24	2229.00	48	4121.88
26	*Nitzschia sigma*	4	66.46	1	33.23	5	49.85
27	*Pinnularia gibba*	6	199.38	13	365.54	19	282.46
28	*Rhopalodia gibberulla*	2	33.23	2	33.23	4	33.23
29	*Surirella gemma*	2	33.23	2	33.23	4	33.23
30	*Bacillaria paradoxa*	5	847.11	0	0.00	5	423.55
	Total		14538.18		9079.80		11808.99

Table 5.3. Kruskal-Wallis tests on numbers of cells, species and diversity indices of benthic diatom communities found in the stomach contents of *T. telescopium*.

Variate	Area	Value ± 95 % CI	Kruskal-Wallis statistic (H)	DF	<u>P</u> value (using X^2 approximation)
Numbers of cells (Cells/ml)	Landward	9080 ± 4790	0.7104	1	0.3993
	Seaward	14540 ± 4896			
Numbers of species	Landward	7.00 ± 0.80	0.8281	1	0.3628
	Seaward	7.97 ± 1.34			
Diversity index	Landward	0.7245 ± 0.0534	0.7800	1	0.3796
	Seaward	0.6747 ± 0.0672			

Table 5.4. Abundance of benthic diatom species (in x 1000 cells/cm²) inside and outside natural tracks of *T. telescopium* in two different areas.

Species	Landward - Artificial		Landward - Natural		Seaward - Artificial		Seaward - Natural	
	In	Out	In	Out	In	Out	In	Out
Achnanthes brevipes	2.384		4.739	2.417				
Achnanthes delicatula	4.768				9.214	2.72	9.150	19.566
Achnanthes oblongella			7.108	7.251				
Amphiphora alata					3.949	2.72	3.431	3.261
Amphiphora paludosa				2.417				
Amphora angusta	4.768				7.898	2.72	2.287	2.174
Amphora australiensis	2.384	2.717			3.949	2.72		
Amphora coffeaeformis	9.535	21.73	10.89	9.184	13.427	19.0	25.924	47.827
Amphora ovalis	3.576	4.076	2.369	2.417	38.701	33.8	7.625	10.145
Amphora proteus			2.369	4.834	7.898	9.54		4.348
Amphora robusta						w727		2.174
Amphora subturgida	7.151	2.717	4.739	4.834	3.949	2.72	2.287	2.174
Amphora turgida							4.575	2.174
Amphora veneta	2.384		3.554		3.949	2.72		2.174
Amphora ventricosa					12.834	10.9	6.100	4.348
Asteroinella japonica	2.384	2.717		2.417				
Bacillaria paradoxa			7.108				2.287	4.348
Cocconeis heteroidea			7.108	2.417	3.949	5.45	2.287	6.522
Cocconeis dirupta		5.434		7.251			9.150	4.348
Cocconeis peltoides			4.739	2.417				
Cylindrotheca striata							2.287	2.174
Entomoneis sp.		2.717						
Frustularia vulgaris			2.369	2.417				
Gomphonema			2.369		3.949			
Gomphonema gracile						5.45		
Gyrosigma balticum					3.949	2.72	4.575	
Gyrosygma scalproides	2.384		2.369	3.625	15.796	7.63	13.724	4.348
Melosira nummuloides								2.174
Mastogloia exigua					13.822	12.2	2.287	
Nacivula aucklandica			2.369					
Navicula cincta	2.384					10.9	5.718	11.957
N. cryptocephala	7.946	5.434	8.530	9.668	9.873	16.3		8.696
Navicula cuspidata	2.384	2.717	2.369	9.668	6.582	8.18	16.012	7.247
Navicula gothlandica			2.369		3.949		2.287	2.174

Species	Landward - Artificial		Landward - Natural		Seaward - Artificial		Seaward - Natural	
	In	Out	In	Out	In	Out	In	Out
Navicula halophila	3.973	2.717	5.923	9.668	41.860	39.8	19.824	60.146
Navicula mutica				2.417		6.81	3.431	2.174
Navicula ramosissima				4.834				
Navicula salinarum				2.417		2.72	2.287	4.348
Navicula tripunctata	2.384	6.793	2.369	4.834	5.924	4.09	11.437	20.290
Nitzschia amphibia	2.384	5.434	2.369	7.251		4.09		2.174
Nitzschia closterium	2.384	5.434	4.739	6.042				
Nit. cocconeiformis						5.45	3.431	2.174
Nitzschia granulata	2.384		3.554	2.417	3.949			9.783
Nitzschia hungarica	2.384			2.417	3.949			
Nitzschia hybrida					3.949			
Nitzschia incurva					8.885	4.54	2.287	2.174
Nitzschia levidensis	4.768	5.434	5.923	7.251				
Nitzschia longissima	7.151	5.434	9.478	11.60		2.72	3.431	10.870
Nitzschia lorenziana				3.625	3.949	5.45		6.522
Nitzschia obtusa	2.384	2.717	4.739	4.834		2.72		4.348
Nitzschia palea			2.369	2.417				
Nitzschia punctata	12.713	14.94	5.923	11.48	58.446	53.4	24.017	24.638
Nitzschia sigma		2.717	2.369	2.417	8.885	10.9	9.150	5.797
Nit. tryblionella				4.834	3.949		2.287	
Nitzschia vidovichii		2.717						
Pinnularia gibba						2.72		2.174
Pleurosigma angulatum					7.898	19.0		
Rhopalodia gibberula						2.72	2.287	
Rhopalodia musculus			2.369	2.417	5.924	2.72	2.287	
Surrirela ovalis					7.898	8.86	2.287	
Surrirela gemma	3.576		2.369	2.417	3.949			2.174
Synedra fasciculata			2.369	9.668	3.949	2.72		2.174
Synedra tabulata			2.369	4.834				
Synedra ulna				4.834				
Trachineis aspera								2.174
Trepsinoe americana			2.369					
Navicula sp.	5.959	6.793	8.885	14.50	10.860	20.7	11.437	32.609
TOTAL	106.87	111.4	147.9	202.6	351.86	363.	221.87	351.094
Total species	25	20	34	37	34	39	32	39

Table 5.5. Relative abundance (in precentage) of common species of benthic diatoms inside and outside artificial and natural foraging tracks of *T. telescopium* in two different areas.

	Species	Landward - Artificial Track		Landward - Natural Track		Seaward - Artificial Track		Seaward - Natural Track	
		In	Out	In	Out	In	Out	In	Out
1	*Achnanthes brevipes*	2.54	0.00	4.55	1.59	0.00	0.00	0.00	0.00
2	*Achnanthes*	5.08	0.00	0.00	0.00	3.10	0.86	4.97	6.25
3	*Amphora angusta*	5.08	0.00	0.00	0.00	2.65	0.86	1.24	0.69
4	*Amphora*	10.17	21.62	10.47	6.05	4.51	6.02	14.08	15.28
5	*Amphora ovalis*	3.81	4.05	2.28	1.59	13.01	10.67	4.14	3.24
6	*Amphora proteus*	0.00	0.00	2.28	3.18	2.65	3.01	0.00	1.39
7	*Amphora subturgida*	7.63	2.70	4.55	3.18	1.33	0.86	1.24	0.69
8	*Amphora ventricosa*	0.00	0.00	0.00	0.00	4.31	3.44	3.31	1.39
9	*Cocconeis*	0.00	0.00	6.83	1.59	1.33	1.72	1.24	2.08
10	*Cocconeis dirupta*	0.00	5.41	0.00	4.77	0.00	0.00	4.97	1.39
11	*Gyrosygma*	2.54	0.00	2.28	2.39	5.31	2.41	7.45	1.39
12	*Mastogloia exigua*	0.00	0.00	0.00	0.00	4.64	3.87	1.24	0.00
13	*Navicula cincta*	2.54	0.00	0.00	0.00	0.00	3.44	3.11	3.82
14	*Navicula*	8.47	5.41	8.19	6.36	3.32	5.16	0.00	2.78
15	*Navicula cuspidata*	2.54	2.70	2.28	6.36	2.21	2.58	8.70	2.31
16	*Navicula halophila*	4.24	2.70	5.69	6.36	14.07	12.56	10.77	19.21
17	*Navicula tripunctata*	2.54	6.76	2.28	3.18	1.99	1.29	6.21	6.48
18	*Nitzschia amphibia*	2.54	5.41	2.28	4.77	0.00	1.29	0.00	0.69
19	*Nitzschia closterium*	2.54	5.41	4.55	3.98	0.00	0.00	0.00	0.00
20	*Nitzschia granulata*	2.54	0.00	3.41	1.59	1.33	0.00	0.00	3.13
21	*Nitzschia levidensis*	5.08	5.41	5.69	4.77	0.00	0.00	0.00	0.00
22	*Nitzschia longissima*	7.63	5.41	9.10	7.64	0.00	0.86	1.86	3.47
23	*Nitzschia lorenziana*	0.00	0.00	0.00	2.39	1.33	1.72	0.00	2.08
24	*Nitzschia obtusa*	2.54	2.70	4.55	3.18	0.00	0.86	0.00	1.39
25	*Nitzschia punctata*	13.56	14.86	5.69	7.56	19.64	16.86	13.04	7.87
26	*Nitzschia sigma*	0.00	2.70	2.28	1.59	2.99	3.44	4.97	1.85
27	*Pleurosigma*	0.00	0.00	0.00	0.00	2.65	6.02	0.00	0.00
28	*Surrirela ovalis*	0.00	0.00	0.00	0.00	2.65	2.80	1.24	0.00
29	*Synedra fasciculata*	0.00	0.00	2.28	6.36	1.33	0.86	0.00	0.69
30	*Navicula spp.*	6.36	6.76	8.53	9.55	3.65	6.54	6.21	10.42
	TOTAL	100.0	100.0	100.0	100.0	100.0	100.00	100.00	100.00

Table 5.6. Analysis of variance of abundance of benthic diatom cells inside and outside artificial and natural foraging tracks of *T. telescopium* in two different areas.

*) = significantly different at level 0.05
**) = Significantly different at level 0.01
***) = significantly different at level 0.001.

Source	D. f.	Df for F	F value	P value
Inside and outside artificial tracks in landward area.	1	1,38	0.43	0.5143
Inside and outside artificial tracks in seaward area	1	1,38	0.44	0.5130
Inside and outside natural tracks in landward area.	1	1,38	7.24	0.0106 *
Inside and outside natural tracks in seaward area	1	1,38	34.32	0.0000 ***

Table 5.7. Analysis of variance of species richness of benthic diatom inside and outside natural and artificial tracks of *T. telescopium* in different areas.

*) = significantly different at level 0.05
**) = Significantly different at level 0.01
***) = significantly different at level 0.001.

Source	Df	Df for F	F value	P value
Artificial tracks.				
Inside and outside, landward area	1	1,38	2.11	0.1547
Inside and outside seaward area	1	1,38	0.40	0.5285
Natural tracks.				
Inside and outside, landward area	1	1,38	1.64	0.2078
Inside and outside, seaward area	1	1.38	24.10	< 0.0001 ***

Table 5.8. Comparison of benthic diatom communities inside and outside artificial and natural tracks of *T. telescopium* in two different areas.

The analysis using Sorenson's index was based on data in Table 5.4. (A) and (N) are artificial and natural tracks respectively; (in) = inside and (o) = outside the tracks.

Area	Comparison	Similarity (%)	Dissimilarity (%)
Landward	A-in and A-o	68	32
	N-in and N-o	76	24
Seaward	A-in and A-o	82	18
	N-in and N-o	69	31

Chapter 6.

Effects of Grazing by *T. telescopium* on Benthic Diatoms and Primary Productivity.

6.1. Introduction.

A considerable number of studies have investigated the effects of grazing of gastropods on benthic algae in marine intertidal habitats. A large number of these studies examined effects of marine gastropods on rocky shore macroalgae (*e.g.* Dayton, 1975; Nicotri, 1977; Hawkins and Hartnoll, 1983; Lubchenco, 1978; Sousa, 1979; Underwood, 1980; Geller, 1991) and microalgae (Castenholz, 1961; Nicotri, 1977; Underwood, 1978a and 1978b). Studies on grazing effects of gastropods on benthic microflora of soft or muddy substrata include those conducted in mudflat and saltmarsh areas (*e.g.* Fenchel and Kofoed, 1976; Pace *et.al.*, 1979; Connors *et.al.*, 1982) and on mangrove sediments (Branch and Branch, 1980). All were located in subtropical and temperate areas.

Studies of the effects of grazing by gastropods living on tropical, soft-muddy substrata, especially in mangrove intertidal areas, however are rare. Mangrove sediments often support many types of gastropods (MacNae, 1968; Sasekumar, 1974) and many of these may consume large numbers of benthic microalgae (Branch and Branch, 1980; Rodelli *et.al.*, 1984). Their existence in this environment may contribute significantly to energy flow in this ecosystem (Kuipers *et.al.*, 1981).

It has been reported that in general, grazing of herbivores affects benthic microalgae in several ways,

(1) Directly influencing community structure or succession of benthic microalgae (Castenholz, 1961);

(2) selective feeding by gastropods on certain benthic diatoms, reducing species richness of benthic microflora (Nicotri, 1977);

(3) size structure of diatom cells shifts towards dominance by smaller cells after heavy grazing by gastropods (Fenchel and Kofoed, 1976);

(4) significant correlation between microalgal standing stock or biomass and the density of herbivores (Branch and Branch, 1980; Montagna *et.al.*, 1983; Decho and Castenholz, 1986; Bianchi and Rice, 1988; Decho and Fleeger, 1988);

(5) primary production may be stimulated by low to moderate grazing pressures (Pace, *et.al.*, 1979; Connors *et.al.*, 1982; Fenchel and Kofoed, 1976);

(6) removal of these epibenthic grazers may result in significant increases of algal biomass and productivity (Pace *et.al.*, 1979; Darley *et.al.*, 1981);

(7) an optimum curve relating biomass of herbivores and primary productivity of benthic microalgae may exist. Both lower and higher biomass of herbivores have been reported to decrease primary production of benthic microalgae (Hargrave,1970; Cooper,1973).

T. telescopium is an important component of the gastropod fauna on muddy substrata in tropical Indo-west Pacific mangrove ecosystems. Large numbers of benthic diatom cells have been found in the gut contents of *T. telescopium* (Chapter 5 of this thesis). The grazing of this gastropod, therefore could have significant effects on the abundance and community structure of benthic diatoms and upon benthic algal primary productivity.

Measurement of primary production of microphytobenthos using the O_2 production method has been used widely. The production values measured by this method have been reported to correlate well with ^{14}C methods (Hunding and Hargrave, 1973; Revsbech *et.al.*, 1981). The O_2 production method offers great advantages for 24 hour budget estimations in microphytobenthic communities (Lindeboom and de Bree, 1982). In tropical mangrove ecosystems, measurements of primary production of microphytobenthos are still relatively rare (see Kristensen *et.al.*, 1988).

Both the grazing animal and benthic diatoms would be affected by environmental factors occured seasonally (eg. temperature, humidity, light intensity). Therefore the existence of grazers may give different effects to benthic algae in different seasons.

This study aims at determining the changes in (1) abundance and community structure of benthic diatoms and (2), the productivity of benthic algae under different magnitudes of grazing intensity by *T. telescopium* in different seasons. Productivity will be measured by the oxygen production method. The results may be beneficial in determining relationships between this important mangrove gastropod and the primary producers in the ecosystem leading to better management of biotic resources in tropical mangrove ecosystems.

Hypotheses of this study were

1. Community structure of benthic diatom may be determine by different densities of *T. telescopium* .
2. Different densities of *T. telescopium* would affect productivity of benthic algae of mangrove sediments.

6.2. Materials and methods.

6.2.1. Study sites.

This experiment was carried out from June 1990 to June 1991 in a sandy-mud flat within an undisturbed mangrove area near Chunda bay (Figure 6.1). The area had a shallow slope and a semi-exposed flat and was located in the marine national park 'A' zone (Great Barrier Marine Park Authority, 1987). Landward areas were inundated only during spring high tides (*i.e.* ≥ approximately 2.8 m). Seaward areas, however remained submerged when seawater levels were approximately 0.4 m above Mean Sea Level (see Lasiak and Dye, 1986 and Queensland Department of Transport, 1989).

Landward and seaward areas (tidal heights approximately 1.5 m and 0.5 m, respectively) were dominated by different types of mangrove. The landward area(= habitat H) was dominated by 1 - 2 m high *Ceriops tagal*. *Avicennia marina* trees (1 - 3 m high) existed between the two habitats. Mangroves occurred in greater density in the seaward area (= habitat L) than in habitat H. Trees were 1 - 2 m high, on average, and were dominated by *Avicennia marina*. There were also a large number of young *Rhizophora stylosa* trees.

6.2.2. Mechanical analyses of mangrove soils.

Samples of soils were collected haphazardly from the sites within habitats H and L (landward and seaward areas respectively) (see Figure 6.1). Five samples of soil (15 cm x 15 cm x 10 cm deep) were collected per site (3 per tidal height) using a spade. After transportation to the laboratory samples were spread thinly for air-drying. Large lumps of sample were crushed using a pestle and porcelain mortar and were passed through a 2 mm mesh sieve. The samples were then dried overnight in the oven at 60 °C (Ball, 1976; Day, 1965). Fractions of sand, silt and clay for each sample were determined by the method given in section 3.2.3.

6.2.3 Effects of grazing by *T. telescopium* .

6.2.3.1. Design of experiment and setting up enclosures.

This study was a field based experiment and involved three factors: density of *T. telescopium* , habitat and sites. There were no laboratory based survivorship experiments laboratory because of difficulties in manipulating environmental factors affecting benthic diatom communities under natural conditions such as tide, light, natural nutrient levels and sedimentation rate. The design of the experiment is shown in Figure 6.2. Density and habitat were treated as fixed factors, sites were nested within habitat and treated as a random factor (Underwood, 1981). Variates investigated were (1) abundance of benthic diatoms, (2) diversity of species of benthic diatoms and (3) benthic algal productivity. The experiment was conducted over a one year period (*i.e.* June 1990 to June 1991) to determine seasonal effects.

Four different densities of snail were used in the experiment. These were zero density, low density (*i.e.* one half of natural density), natural density and high density (*i.e.* twice natural density). Natural density of *T. telescopium* was determined from a previous study to be 4 snails/m^2 (Chapter 3). Low density and high density treatments, thus consisted of 2 and 8 snails/m^2 respectively.

Two habitats were selected for the experiment. These were the landward (tidal height approximately 1.5 m) and seaward (tidal height approximately 0.5 m) areas or habitat H and habitat L, respectively as described above. Three sites in each habitat were selected haphazardly. In this case only sites which contained *T. telescopium* were selected. Each site was mapped and a 2 mm square grid superimposed on the map. Using this map the location of 12 enclosures were selected randomly. Random numbers were generated from an electronic, scientific calculator (Casio Fx-3200). Each density in every site had three replicates, hence a total of 72 enclosures (*i.e.* 36 in each habitat) were built.

Each enclosure was made from 1.5 cm mesh size "gutter guard". The size of each enclosure was 1 m x 1 m and 10 cm high. Based on a pilot study, this size was sufficient to prevent or reduce (1) physical changes of the substratum inside the enclosure and (2) either loss or entry of snails into the enclosures. Poles (length 30 cm and diameter 1.5 cm) were used to fix the enclosures into position on the substratum. These were placed at each corner of the enclosures. Another two poles were added between each of the corners also (see Figure 6.3). These poles were hammered into the mud. Strong electric wire was then used to hold each enclosure to the poles. The bottom of each enclosure was submerged approximately 2 cm into the mud.

A diagram of the type of enclosure used is shown in Figure 6.3. Every enclosure was labelled using 3 x 9 cm^2 thin formica plate. All the information needed was printed on 9 mm wide Dymo tape, attached to the formica plate on each enclosure using PVC wire. Most enclosures did not suffer any serious damage over the one year period of the experiment.

The origin of the *T. telescopium* used in the enclosures in each habitat was different. Snails enclosed in habitats H and L, were collected from landward and seaward areas, respectively. Healthy (shell not damaged) adult snails of 80 - 90 cm total length were used. A total of 252 (*i.e.* 42 at each site) *T. telescopium* were used in the experiment.

Densities of snails and the condition of enclosures were checked every three weeks.

6.2.3.2. Sampling of benthic diatoms.

Sampling of benthic diatoms was carried out at three monthly intervals, in June 1990 (initial sampling), September 1990, December 1990, March 1991 and June 1991. Initial sampling was conducted immediately after the enclosures had been set up. This was to determine the initial condition of benthic diatoms before being subjected to different densities of *T. telescopium* .

Benthic diatoms were collected by removing small amounts of mud from each enclosure and trapping the diatoms. Three blocks of mud of 4 cm x 4 cm and 20 mm deep were collected haphazardly from each enclosure. This size of sample was based upon an estimation of occuring benthic diatoms and the depth of which *T. telescopium* grazed (Aleem, 1950a; Hopkins, 1963, 1964; Palmer and Round, 1965; Eaton and Moss, 1966; Round, 1982, Round *et al.* 1990, Houbrick, 1991). These blocks of mud were removed carefully from the substratum using a 4 cm wide mini spade, stored in self-sealed polyethylene pouches and transfered to the laboratory.

Trapping of benthic diatoms was based upon the principle of the positive phototaxis characteristic of the diatoms (Hopkins, 1969 *in* Harper, 1977). In the laboratory, the samples were stored in the dark for 6 to 8 hours (see Eaton and Moss, 1966 and Round *et al.* 1990). The whole sample was poured into a 100 ml container, wetted by sterile, clean seawater and mixed by shaking. The samples were then poured into 90 mm diameter petridishes. Two 2 cm x 2 cm lens tissues were placed onto the surface of the samples. Diatoms adhered to the lens tissue and this was the sample unit used for benthic diatoms (see also Chapter 3).

The sample was placed under sunlight where there was no artificial light, even at night. The sample experienced the natural cycle of light and darkness for one full cycle. The lens tissues were harvested the next morning between 0800 and 1100. This time of harvesting often provides the highest population density of diatoms on the surface of the sample (Hopkins, 1969 *in* Harper, 1977). Each lens tissue was placed in a vial and preserved with 3 ml of 5 % formaldehyde solution and 1.5 % sodium hypochlorite (1 : 1 by volume).

The identification of species and the counting of the number of cells of diatoms required an optical light microscope. The algae were released by macerating the tissue in the preservative in a concave dish using a pair of mounted needles. Two drops of this suspension were transfered to a counting chamber (*i.e.* improved Neubauer counting chamber made by Assistent, Germany) (see Figure 6.4). Diatoms in selected fields were counted and identified under a light microscope with phase contrast equipment (Taasen and Hoisæter, 1989). This microscopic work was replicated three times for each vial.

The number of cells of benthic diatoms per unit area of original habitat was determined using a modification of the formula of Baker and Silverton (1985) as shown below.

$$\boxed{N = \frac{n}{f} \times D \times \frac{A}{a} \times \frac{1}{b} \times 10^4}$$

where

N = Total number of diatom cells in the original habitat (cells/ cm^2).

f = Number of microscope fields of 1 mm x 1 mm examined in a chamber.

n = Numbers of cells counted in f.

D = Dilution factor or volume of suspension in the vial (= 3 ml).

A = Area of the incubation container (= 63.58 cm^2).

a = Area of the lens paper (= 4 cm^2).

b = Area of the original sample (= 16 cm^2).

Benthic diatoms were identified to species level whenever possible using the following literature: Kutzing (1844); Peragallo (1897 - 1908); Mann (1925); Hustedt (1930, 1938); Hendey (1951); Wood (1963); Foged (1975, 1978); Hustedt (1976); Navaro (1982); John (1983); Crosby and Wood (1985); Jin *et al.* (1985); Hustedt and Jensen (1985); Krammer and Lange-Bertalot (1986); Krammer and Lange- Bertalot (1988); Wah and Wee (1988).

6.2.3.3. Measuring productivity of benthic algae.

The productivity of benthic algae was measured on a sediment surface basis. The method of measurement of productivity is shown in Figure 6.5. Factors involved in the analyses of productivity data were density of *T. telescopium* (4), habitats (2), and sites (3) nested in habitats and replicates (3).

Production of benthic algae was estimated by an oxygen production method. The method was based on measurement of the changes in dissolved oxygen concentration over undisturbed sediments (with associated benthic microflora) per unit of time, in both light and dark conditions (Pomeroy, 1959; Pamatmat and Fenton, 1968; Hargrave, 1969; Hunding and Hargrave, 1973; Asmus, 1982; Lindeboom and De Bree, 1982; van Es, 1982; Hargrave *et al.*, 1983).

Oxygen production by benthic microalgae was measured in situ using a modification of the technique of Pomeroy (1959) and van Es (1982) (*i.e.* bell-jars); Hargrave (1969) and Hunding and Hargrave (1973) (*i.e.* clear glass cylinders) and Lindeboom and De Bree (1982) (*i.e.* cylindrical plexiglass enclosures or domes).

To measure the amount of oxygen released by the benthic algal community, bell-shaped jars were used. The jars were made by cutting the top portion of a short necked, two litres, clear plastic bottle. Each jar was 11 cm in diameter and 15 cm in height and equipped with a removable original plastic screw top lid (see Figure 6.5). Dark jars were made by covering the jars with a black "Scotch Tape" and aluminium foil (Strickland, 1960).

Measurements were carried out between 9.00 am and 12.00 md., during high tide or when the areas were inundated by seawater to a depth of about 20 cm. In each enclosure, the jars without the lid (*i.e.* 2 light and 2 dark per enclosure) were pressed down gently 2.5 to 3.0 cm into the sediment. The jars were rotated slightly as they were pressed into the substratum to prevent distortion of the surface sediment. Sea water was allowed to over flow into the jars, then each jar was sealed with a screw top lid and the dark jars were covered by aluminium foil. After a period of one hour exposure (Pomeroy, 1959) oxygen content was measured using an oxygen meter (Lindeboom and De Bree, 1982). The oxygen meter was a portable dissolved oxygen meter (Hanna instrument: HI 8543) with a four digit LCD display, a resolution of 0.1 mg/l and an accuracy ± 0.2 mg/l.

Estimation of gross photosynthesis or production of oxygen was determined by subtracting the oxygen content in the light jars from that inthe dark jars (Strickland, 1960). Values of oxygen production were converted into carbon units using the formula of Strickland, 1960 and Parson *et al.*, 1984:

$$C = \frac{O}{PQ} \times \frac{12}{32}$$

where :

C = Carbon assimilated by photosynthesis (mg/unit area/unit time).

O = Oxygen produced (mg/unit area/unit time)

PQ = Photosynthetic Quotient.

In this study, PQ = 1.2 (Ryther, 1956; Strickland, 1960; Asmus, 1982).

6.2.4. Data analyses.

Data from this experiment were analysed using three factor Analysis of Variance (ANOVA). The model involved two orthogonal factors: density and habitat and one nested factor *i.e* site. The linear model for the sources of variation was a follows:

$$X_{ijkl} = \mu + D_i + H_j + DH_{ij} + S(H)_{k(j)} + DS(H)_{ik(j)} + e_{l(ijk)}$$

where

D_i (i = 1 ...a; a = 4) represented the effect of the ith Density; H_j (j = 1 ...b; b = 2) represented the effect of the jth habitat; DH_{ij} represented the interaction between the ith Density and the jth Habitat; $S(H)_{k(j)}$ represented the effect of the kth Site nested in Habitat j, $DS(H)_{ik(j)}$ represented the interaction between the ith Density and the kth Site nested in Habitat j and $e_{l(ijk)}$ represented the error associated with the lth enclosure (l = 1 ...n; n = 3) in the kth Site at Density i in Habitat j. The variates of cell numbers or species diversity of benthic diatoms within each density, habitat, site and replicate combination is represented by X_{ijkl}.

A Cochran's test (Winer, 1971) was employed to test the assumption of homogeneity of variances (Underwood, 1981). Some data were transformed (*i.e.* logarithmic transformation) to remove heterogeneity of variances which were detected by Cochran's test.

Mean square estimates and F-ratios for this experiment were estimated by constructing an auxiliary table (Underwood, 1981). In some cases, to test the factors a *post hoc* pooling procedure (Underwood, 1981) was used. If the analysis of variance rejected any of the null hypotheses, the Student-Newman- Keuls (SNK) test (Underwood, 1981 and Zar, 1984) was applied to compare pairs of means.

The Kruskal-Wallis analysis of variance by ranks (Kruskal-Wallis, 1952 *in* Zar, 1984) was used to analyse the effects of season on abundance of benthic diatoms and productivity of benthic algae. If the Kruskal-Wallis test rejected any of the null hypotheses, the nonparametric Student-Newman-Keuls multiple comparison (Zar, 1984) was used to determine differences between means.

Three types of diversity indices were used to describe the benthic diatom communities (Heip and Engels, 1974). Community diversity was determined using the Shannon-Weaver index (1963) and evenness was determined according to Pielou (1969). Species richness was determined using the index of Margalef (1968). The formulae of these indices are given in Table 6.1.

The similarity between benthic algal communities in different densities of *T. telescopium* was analysed using a multivariate method: normal (q-type) cluster analysis (Field *et al.*, 1982). Only dominant taxa were included in the analysis (Taasen and Hoisæter, 1989). The data (*i.e.* diatom abundance values) were standarized using general relativisation (McCune, 1987):

$$b = \frac{x_{ij}}{(\Sigma x_j^p)^{1/p}}$$

where

b = score of abundance of the ith species in the jth sample; x_{ij} = score for the ith species in the kth sample; p = parameter of relativisation.

Table 6.1. Diversity and evenness indices of benthic diatoms.

Index	Formula
Community diversity:	
Shannon-Weaver (H)	$H = - \Sigma(n_i/N \log n_i/N)$
Species diversity:	
Margalef (Ma)	$Ma = (S - 1)/\ln N$
Evenness:	
Pielou (E)	$E = H/H_{max} = H/\log S$

N = total number of individuals.
n_i = number of individuals of the ith species.
S = number of species.

Similarity between benthic diatom communities was measured using the index of Sorensen (Bray and Curtis, 1957):

$$C = \frac{2p_{jk}}{(p_j+p_k)}$$

where

p_j and p_k represent the sums of diatom species values (*i.e.* numbers of diatom cells per unit area) for sample j and k. P_{jk} is the sum of the lesser species values for those species common to both samples.

The relationships between benthic diatom communities in different densities of *T. telescopium* were determined using a classification or cluster analysis. The analysis was based on a group-average sorting strategy (Field *et al.* 1982).

6.3. Results

6.3.1. Environmental characteristics.

6.3.1.1. Maximum/minimum air temperature and rainfall

Monthly fluctuations in maximum and minimum air temperatures as well as rainfall totals from May 1990 to July 1991 in the Townsville and adjacent areas, are shown in Figure 6.6. Maximum and minimum air temperatures and rainfall totals within the area of the specific field experiment at Chunda bay were unavailable. To estimate these environmental factors, data from Townsville and surrounding areas was used. Although these data may not give a detailed description of the specific environmental conditions at the experimental sites, they may used to indicate the general climatic pattern in these mangrove areas.

In the winter period during the first month of the experiment (June 1990), the maximum air temperature in Townsville and surrounding areas was 24.2 °C. This rose gradually to between 30 and 32°C in the hot periods of the year (November 1990 to March 1991) and decreased slowly as the next winter (1991) was approached. The minimum air temperatures, however, were recorded in August 1990 and July 1991 *i.e.* 12.5 and 12.4 °C respectively. The patterns of fluctuation of minimum and maximum air temperatures were closely linked.

The ranges of maximum and minimum air temperatures in each month (June 1990 to June 1991) were not always consistent. Differences between maximum and minimum temperatures in summer were lower than those in winter *viz.* 7.30 °C and 10.45 °C respectively.

The effect of the cyclonic season on rainfall totals in Townsville and surrounding areas was significant. In the beginning of the experiment

(June 1990) rainfall for the month was 96.6 mm. Monthly totals decreased gradually until November 1990 *i.e.* down to below 13.0 mm. The most significant impact was imposed by cyclone 'Joy' in January 1991. The rainfall total increased sharply from 0.2 mm to 377.8 mm in November and December 1990 respectively, peaked at 865.4 mm in February 1991 and dropped to 15.8 mm in March 1991. During the cooler periods of 1991 (April to June 1991), rainfall totals were below 18.00 mm.

6.3.1.2. Soil textural classes.

Results of analyses of soil texture are shown in Figure 6.7. The texture of the soils in landward and seaward areas differed. In the landward area the soil was more sandy and the substratum was thus firmer. The sand content of this soil was approximately 82 %, whereas silt and clay constituted less than 18 % . This type of soil could be categorised as a sandy type.

The soil of the seaward areas, however, was softer than that in landward habitats. Sand aggregates totalled approximately 41 % of soil particles, half that of the landward habitats. Silt and clay contents were almost six and two times higher, respectively, than in soils at habitat H (landward area). Soil in the seaward area thus could be classified as a loam type.

Statistical analyses using two way nested ANOVA showed that the sand content in soil from the landward and seaward areas differed significantly ($\underline{F} = 240.90$; $\underline{P} < 0.0001$). Differences between silt and clay content between habitats were significant also ($\underline{F} = 598.74$; $\underline{P} < 0.0001$ and $\underline{F} = 18.46$; $\underline{P} = 0.0002$, respectively).

6.3.1.3. Tidal inundation.

The frequency of tidal inundation in the experimental areas each month during the experiment was estimated from tide tables (Queensland Department of Transport, 1989 and 1990; see Figure 6.8). From December 1990 to April 1991, the presence of standing water in the mangrove intertidal areas was more frequent than usual (i.e. between 15 to 23 times per month). From June to November 1990 and from June to September 1991, however, these areas were inundated less frequently by tides *viz*. < 15 times per month.

The frequency of tidal inundation may be used to indicate the likely degree of activity of *T. telescopium* . Activity of this snail was associated with tidal inundation. The activity of the animal increased immediately before the substratum was exposed during ebbing tides. During this period the snail displayed increased activity, moving over the substratum and probably increasing or beginning its feeding activity. These activities were terminated during high tide and also when the substratum was completely dry. By recording the frequency of tidal inundation, the intensity of activity of the animal in the mangrove intertidal areas could be estimated.

6.3.2. Effects of grazing on benthic diatoms.

6.3.2.1. Abundance of benthic diatoms.

The effects of grazing by *T. telescopium* and the effects of habitat on the abundance of benthic diatoms in each period of sampling are shown in Figures 6.9 - 13. Results of statistical analyses are shown in Table 6.2. These analyses indicated that densities of *T. telescopium* and habitat had generally insignificant impacts on abundance of benthic diatoms.

Initial sampling (June 1990) showed that abundance of benthic diatoms on sediments within experimental enclosures were not significantly different (Figure 6.9). Number of diatoms per unit area in the seaward area appeared to be slightly higher than that in the landward intertidal habitat. However, this difference was not significant. The effect of site, on the other hand, was significant (Table 6.2). Several sites had greater abundance of benthic diatoms than other sites. Multiple comparison tests (Student-Newman-Keuls test with S.E = $(0.0316/12)^{1/2}$ and 66 degrees of freedom) showed that benthic diatoms in site HS3 (i.e. the landward area), sites LS1 and LS2 (i.e. the seaward area) were more abundant than at sites HS1, HS2 and LS3. Abundances of benthic diatoms at sites HS3, LS1 and LS2, did not differ significantly (Table 6.2).

Three months after the beginning of the experiment (*i.e.* September 1990), density of *T. telescopium* did not affect abundance of benthic diatoms significantly. Total number of diatom cells in natural density treatments of *T. telescopium* were slightly higher than that in other density treatments (Figure 6.10), but this difference was not significant (Table 6.2). Effects of habitat, however were significant. Abundance of diatom cells in the seaward area was almost twice that in the landward area(Figure 6.10) and this difference was statistically significant (Table 6.2).

During summer (i.e. the December 1990 and March 1991 periods) effects of grazing by *T. telescopium* on benthic diatoms was not significant also. Abundance of benthic diatoms within different density treatments of *T. telescopium* were almost the same (Figure 6.11 and 6.12). Analyses of variance showed no significant differences in the numbers of benthic diatoms between the two habitats also (Table 6.2).

After one year of the experiment, density of *T. telescopium* began to affect abundance of benthic diatoms significantly (Table 6.2). By winter (i.e. June 1991) total numbers of diatom cells within different density treatments of *T. telescopium* were significantly different (Table 6.2). Diatoms were more abundant in zero and natural densities of *T. telescopium* compared with abundances in the half and twice natural density treatments (Figure 6.13). A Student-Newman-Keuls test using S.E = $(5254.517/18)^{1/2}$ and 68 degrees of freedom indicated the differences were significant (see Table 6.2).

The effect of habitat on diatom abundance in June 1991 was not distinct. Although the number of cells of benthic diatoms was slightly higher in the seaward area(Figure 6.13), this difference was not significant (Table 6.2). The effect, however was more marked at individual sites. Using S.E. = $(4963.6/12)^{1/2}$ and 66 degrees of freedom, the Student-Newman-Keuls multiple comparison test showed that the numbers of benthic diatom cells at site HS3 (site 3 in the landward area) was the highest. Site 1 in the landward area(= HS1) contained the lowest number of diatom cells (Table 6.2).

6.3.2.2. Diversity indices of benthic diatom communities.

The effects of density of *T. telescopium* and habitat on diversity indices of communities of benthic diatoms including the Margalef diversity index, the Shannon-Weaver index and the Evenness index are shown for every period of sampling in Figures 6.14, 6.15 and 6.16, respectively. Results of analyses of variance are given in Tables 6.3, 6.4, and 6.5, respectively.

In every period of sampling, numbers of species of benthic diatoms did not differ significantly between different density treatments of *T. telescopium* . Table 6.3 shows that differences between the species richness index in different density treatments of *T. telescopium* were not significant (ANOVA, $\underline{P} > 0.05$), nor were the numbers of species between habitats (Figure 6.14). Margalef species diversity in the seaward and landward mangrove habitats did not differ significantly (ANOVA, $\underline{P} > 0,05$; see Table 6.3).

Patterns of species dominance of benthic diatom communities were not influenced significantly by densities of *T. telescopium* . In every period of sampling, the Shannon-Weaver indices were not significantly different between different density treatments of *T. telescopium* (Table 6.4). But in June 1991 Shannon-Weaver index was much higher at the highest grazer density ($0.05 < P < 0.01$). The Shannon-Weaver index in the seaward areawas slightly higher than that in the landward habitat throughout the experiment (see Figure 6.15). Tests showed, however, that the index in the two habitats was not significantly different at any period (Table 6.4). The effects of habitat on Shannon-Weaver diversity of the diatom community were, therefore, not significant.

The patterns of the evenness index at different densities of *T. telescopium* showed some consistencies. In September 1990 and December 1990 the index was low at natural densities (Figure 6.16). Statistical analyses, however showed that differences between the mean index at different densities were not significant at these times (Table 6.5). In the last period of the experiment (June 1991), the effects of density were significant. The highest density (i.e. twice natural density) had the highest value of the evenness index (Figure 6.16 and Table 6.5). This suggested that the high density of the snail affected species evenness of the benthic diatom community. The distribution of individuals in each species was more even, therefore the community was more diverse (see Figure 6.16). The effects of habitat on the evenness index were not significant. Figure 6.16. shows the inconsistent pattern of the index in the two habitats over time. Tests showed that the index in seaward and landward mangrove habitats did not differ significantly (Table 6.5).

6.3.2.3. Community structure of benthic diatoms.

Only dominant taxa (*i.e.* abundance > 1 % of all taxa) were used in the multivariate analyses. Lists of the taxa recorded in each of the periods of sampling are given in Tables 6.6 to 6.10. Fewer dominant taxa were recorded in the initial sampling period (June 1990) and in June 1991. The highest number of taxa was found in September 1990. Most taxa were recorded in every period of sampling. Only a few of these were recorded as non-dominant species, and this occurred mainly in June 1990 and in June 1991. Dendrograms (Figures 6.17A to 6.17E) show the affinities of the diatom communities at different densities of *T. telescopium* and in different habitats, based on the abundance scores of the taxa in Tables 6.6 to 6.10.

Initial sampling (Figure 6.17A) suggested that diatom communities did not display any tendency for strong differentiation by habitat or density treatments. In September 1990, a habitat effect on diatom community structure was apparent. Using an arbitrary line drawn at 75 % similarity, most of the communities in the landward area(densities zero, natural and a half) clustered together. Zero and natural density *T. telescopium* in the landward area, thus appeared to affect benthic diatom community structure in a similar manner. In the seaward areacommunities at zero, half and twice the natural snail density clustered together. The community of diatoms in the treatment twice natural density in the landward habitat was distinctive from all other communities (see Figure 6.17B and Table 6.7).

There was a strong suggestion of a habitat effect on the community composition of diatoms in December 1990 also (Figure 6.17C). As in the previous sampling period, density of *T. telescopium* did not appear to affect diatom community composition. Diatom communities in the seaward area subjected to *T. telescopium* densities of zero, natural and twice natural clustered together, along with the D2H treatment (Figure 6.17C). Two density treatments (zero and half natural) in the landward area formed a distinctive cluster (Figure 6.17C)

In March 1991, there was no clear effect of either habitat or density treatment on the community composition of benthic diatoms (Figure 6.17D). Communities in the natural density treatment in landward and seaward areas , showed a high level of similarity. There is a suggestion of a density effect simply because all the 0 and 1/2 densities cluster together.

Non-grazed communities in the two habitats had a high level of similarity in community composition in the winter period (June 1991) (Figure 6.17E). Apart from this, the analysis indicated no consistent effects of either habitat or *T. telescopium* density on the composition of the benthic community.

Figure 6.18 provides a graphical summary of the dendograms in Figure 6.17. This figure displays the relationships of benthic diatom communities within and between the two habitats. This summary helps to clarify the effects of grazing on community structure of benthic diatoms.

In the landward area, zero and half natural density of *T. telescopium* had similar effects on diatom community composition. These densities frequently clustered closely. At the low density of *T. telescopium* (*i.e.* low grazing activities = 0.5 density), the community was similar to that in the non grazed treatment. Zero density treatments in some periods clustered closely with natural density treatments (landward area) or with zero density treatments (Seaward area). These occasions were, however, less frequent. The effects of natural density on diatom community composition were not clear but in certain periods the effect was similar to that of zero density of *T. telescopium* . In this landward area , the effect of grazing at natural density, however, was never similar to that when the density was doubled or halved. If density of *T. telescopium* was doubled, the effect of grazing was always different from that of other density treatments.

In the seaward area , however, the effects of zero density on diatom community structure was related closely with effects of double and half natural density. Heavy grazing at double the natural density of *T. telescopium* changed the community mostly to one similar with that of the non grazed community. In certain periods zero densities produced similar communities with those in half density treatments and vice versa. However, the benthic diatom communities with these densities were never similar to those grazed by natural densities of *T. telescopium* .

Some relationships existed between grazing effects in the two habitats. At certain times, the diatom community in zero density treatments in the two habitats were similar. This applied also to natural density treatments. By reducing the numbers of snails to half natural density, the community in the seaward area could be similar with that in the natural density treatment of the landward area. By doubling the density, on the other hand, the community in the landward area changed to be similar with that in the natural density treatments of the seaward area . Generally, there was a much stronger tendency of diatom community affinities within habitats than between habitats, somewhat independent of density treatments.

6.3.3. Effects on non-diatom algae.

The occurence of non-diatom algae (*i.e.* Blue-Green, filamentous algae) was recorded during the studies of abundance of benthic diatoms in samples. Frequency of occurrence of non-diatom algae in samples (*i.e.* % of times this category was recorded in samples) as a function of densities of *T. telescopium* and of habitats in each period of sampling are shown in Figure 6.19. Results of statistical analyses using chi square goodness of fit tests are provided in Table 6.11.

Some patterns in the frequency of non-diatom algae occurred. Comparing densities, twice natural and natural density of *T. telescopium* from September 1990 to June 1991, for example, the frequency of algae in the twice natural density treatment was consistently lower than that at natural density (see Figure 6.19). Statistical analyses indicated that the frequency of occurrence of non-diatom algae did not differ significantly between different treatments ($\underline{P} > 0.05$) with the exception of September 1990 ($\underline{P} < 0.0001$). In September 1990 the high density of *T. telescopium* decreased abundance of non-diatom algae significantly (see Table 6.11). Consistent patterns of habitat effects were found. The frequency of non-diatom algae in the seaward area was always slightly higher than that in the landward area(see Figure 6.19). Statistical analyses, however showed that this difference was not significant (Table 6.11). Habitat thus did not affect abundance of non-diatom algae significantly.

6.3.4. Effects on productivity of benthic algae.

The effects of grazing by *T. telescopium* and of habitats on the productivity of benthic algae are shown in Figure 6.20. Results of statistical analyses are shown in Table 6.12. Productivity of benthic algae was affected significantly by both grazing of *T. telescopium* and habitat.

During December 1990, density of *T. telescopium* influenced production of benthic algae ($\underline{P}. < 0.0005$; see Table 6.12). The Student-Newman-Keuls multiple comparison statistic (i.e. with standard error = $\sqrt{}(90.04916/18$ and 18 degrees of freedom) showed that productivities at zero and natural densities were greater than those at the two other densities ($\underline{P}. < 0.05$; see Table 6.12). Algal productivity in the natural density treatment was the highest (*i.e.* 82.24 mg C/m²/hr; Figure 6.20). The effect of habitat on productivity was significant also. Mean total carbon assimilated in the landward area(= 47.32 mg C/m²/hr) was nearly two times lower than that in the seaward area (Figure 6.20). This difference was statistically significant (P. < 0.0005; see Table 6.12). In this period, the interaction between snail density and habitat was significant also (P. > 0.0005). In the seaward (= L) area , increasing density resulted in a high algal productivity in enclosures with a natural density of snails. In landward (= H) area, algal productivity decreased slightly as snail density increased (Figure 6.20).

Strong density and habitat effects on production of benthic algae occurred in March 1991. Total carbon assimilated differed significantly between density treatments of *T. telescopium* (P < 0.0005) as shown in Table 6.12. The highest density of *T. telescopium* had a productivity (= 36.35 mg C/m²/hr) significantly less than the other three density treatments. In zero, half and natural density treatments, algal carbon production did not differ significantly (P. < 0.05; Student-Newman-Keuls test with standard error = $(309.9916/18)^{1/2}$ and 18 degrees of freedom). The effect of habitat on algal productivity was significant also. The pattern of algal productivity between habitats in March 1991 was different from that observed in December 1990. In March 1991 the productivity in the seaward mangrove area (= 51.59 mg C/m²/hr) was almost 20 % lower than that in the landward area (Figure 6.20). This difference was significant (P. < 0.005; see Table 6.12). There was a strong interaction between snail density and habitat. In the landward mangrove habitat, when snail density was increased from zero to natural density, productivity of benthic algae increased. Increasing density in the seaward mangrove habitat, however, decreased algal productivity (see Table 6.12 and Figure 6.20).

During winter (i.e. June 1991), the effects of snail density and habitat were strong also. Average productivity of benthic algae differed significantly between density treatments (P. < 0.0005; see Figure 6.20). At zero and natural density, productivity was greater than in the other two density treatments (Student-Newman-Keuls test with standard error = $(309.9916/18)^{1/2}$ and 18 degrees of freedom); P. 0.05; see Table 6.12). Productivity in the seaward area(= 191.6 mg C/m^2/hr) was almost one and a half times higher than that in the landward area(= 134.9 mg/m^2/hr; Figure 6.20). This difference was highly significant (P. < 0.001); Table 6.12). During this month, the interaction between density of *T. telescopium* and habitat was not significant (P. > 0.05).

In September 1991, there was a marked influence of density of *T. telescopium* on benthic algal productivity. Analyses of variance showed a significant effect of density on benthic algae (P. < 0.0005). A Student-Newman-Keuls test with $\sqrt{(13488.01/18)}$ standard error and 18 degrees of freedom indicated that treatments of half and twice natural densities had significantly lower algal productivity than zero and natural density treatments (P. < 0.05; see Figure 6.20 and Table 6.12). In this period a strong effect of habitat on carbon production existed also. Productivity in the seaward area(= 395.0 mg C/m^2/hr) was more than one and a half times higher than that in the landward area(= 249.3 mg C/m^2/hr). The interaction between habitat and snail density was significant also. In the landward (= H) area , production of benthic algae was greater in the zero density treatment than the natural density treatment. In the seaward (= L) area , however production of the algae in the zero density treatment was slightly lower than that in the natural density treatment (see Figure 6.20 and Table 6.12).

By comparing density effects in every period of sampling, some consistent patterns of benthic algal productivity emerged. For example, during December 1990, June 1991 and September 1991, production of carbon in mangrove sediments on non-grazed surfaces and on surfaces grazed by natural densities of *T. telescopium* were consistently higher than those on the sediments grazed by densities of *T. telescopium* lower and higher than natural (*i.e.* 0.5 and 2.0 times natural). In March 1991, algal productivity on sediment grazed by *T. telescopium* in treatments of twice natural density was consistently lower than that of productivity on sediment grazed by this snail at natural density or zero density.

Some consistent patterns were obtained for algal productivity between the two intertidal mangrove habitats also. In early summer (December 1990) and winter (June, September 1991) production of carbon by benthic algal communities in the seaward area was consistently higher than that in the landward area . In late summer (March 1991) this pattern, however was reversed (see Figure 6.20).

6.3.5. Effects of season.

6.3.5.1. Abundance of benthic diatoms.

The effects of season on abundance of benthic diatoms are shown in Figure 6.21. Results of non-parametric tests on abundance using mean ranks are shown in Table 6.13. These figures and table show that the effect of season on abundance of benthic diatoms was significant. Fluctuations in diatom abundance in each density treatment of *T. telescopium* was related to season. During the summer period all density treatments (Figure 6.21A) had low numbers of diatom cells. During winter (June), however diatom abundance increased sharply. In this season the most distinct increases in abundance occurred in the zero and half density treatments. Thus there was a suggestion of a season by *T. telescopium* density interaction, with the greatest seasonal increase in diatom abundance occurring within *T. telescopium* densities which were zero or low.

By pooling data of density and habitat treatments for each period of sampling (n = 72), abundance of diatoms at the experimental sites was influenced by season significantly. During winter (June 1990) total numbers of diatom cells were significantly higher than at other times. In late winter this number decreased sharply until late summer of 1991. By winter (June 1991), benthic diatom abundance had increased again. The abundance of diatom cells in this period and the previous winter (June 1990) were very similar (see Figure 6.21 and Table 6.13).

6.3.5.2. Diversity in benthic diatom communities.

The effects of season on diversity of benthic diatom communities are shown in Figure 6.22. Results of non-parametric statistical tests are given in Tables 6.14 to 6.16.

Figure 6.22A shows that numbers of species of diatoms in density treatments of *T. telescopium* displayed similar patterns with season. Species richness in all density treatments was significantly higher in winter (June 1990 and June 1991). This index was low in late winter (September 1990) and summer (December 1990, March 1991) (see Table 6.14). The average number of species of benthic diatoms, therefore, was highest in winter. Species richness between periods of sampling in summer were not significantly different ($P > 0.05$). The correlation between species richness and abundance of benthic diatoms (Figures 6.22A.2 and 6.21) was strong. The Spearman rank correlation test showed that the positive correlation between number of species and abundance of benthic diatoms was significant ($n = 20$, Spearman statistic $rs = 0.8093$; $P < 0.001$).

The effects of season on diversity of the benthic diatom communities was significant only in the highest density treatment of *T. telescopium* . The Shannon-Weaver diversity index was significantly higher in the winter

(June 1990 and June 1991) (see Figure 6.22B.1 and Table 6.15). Averaged over all density treatments, however, the effects of season were significant (Figure 6.22B.2). The diversity index in June 1991 was significantly higher than at all other other times. Differences in this index among other periods of sampling were not significant.

The evenness index of the benthic diatom communities was influenced by season also. Differences between each evenness index in the density treatments of *T. telescopium* between periods of sampling were highly significant. Each density had low evenness values in winter. Averaged over all density treatments, the evenness index was low in winter also. The values of species richness, diversity and abundance of benthic diatoms were high at this time. The peaks in evenness in summer indicate that the numbers of individual diatom cells were distributed more evenly amongst species in summer (see Figure 6.22C.1&2 and Table 6.16).

6.3.5.3. Structure of the community of benthic diatoms.

The effects of season on the affinities of the diatom communities at different densities of *T. telescopium* and in different habitats are shown in Figure 6.23. This dendrogram was based upon relative abundances of dominant benthic diatom species. Dominant species were those with abundance > 1 % of total diatom abundance. Table 6.17 provides abundance data for the dominant taxa recorded in each of density treatment of *T. telescopium* at different periods of sampling.

There was a strong suggestion of a seasonal effect on the community composition of benthic diatoms. In the summer (December 1990 and March 1991), the communities of benthic diatoms in almost all density treatments of *T. telescopium* clustered together. In the winter/spring (June 1991 and September 1990), however, the communities of benthic diatoms consisted of two distintive clusters.

6.3.5.4. Productivity of benthic algae.

Seasonal fluctuations in the productivity of benthic algae are shown in Figure 6.24. The results of non-parametric statistical analyses are given in Table 6.18.

Productivity of benthic algae, (mg carbon assimilated per m^2 per hour) in different density treatments of *T. telescopium* varied with season. Each density treatment had the lowest productivity in summer (December, March). Productivity increased significantly in winter/spring (June, September). During summer, differences between values of productivity within individual densities of zero, half and natural density were similar. In the two times natural density treatment, however, mean productivity within all periods of sampling differed significantly (Table 6.18). It is of interest that the largest increase in productivity between March 1991 and June 1991 and between June 1991 and September 1991 occurred in the zero density treatment. This implies that grazing by *T. telescopium* (at a half, natural and twice natural densities) may reduce productivity.

Averaged over all density treatments, production of carbon during summer (December, March) was consistently low. During the winter period (June) carbon assimilated was significantly higher (Figure 6.24 and Table 6.18) than in summer. The correlation between productivity of benthic algae and abundance of benthic diatoms was significant for certain sampling periods. During December 1990 and June 1991, for example the quantity of carbon assimilated by benthic algae was positively correlated with total number of cells of benthic diatoms. In March 1991, however this correlation was not significant (see Table 6.19).

The overall mean productivity of benthic microalgae (± S.E.) in zero, 0.5, natural and twice natural density treatments of *T. telescopium* were 203.86 ± 19.37, 115.05 ± 11.07, 180.88 ± 17.74 and 111.89 ± 10.34 mg C/m^2/hr, respectively. The overall mean of productivity in the landward area (124.13 ± 13.72 (SE) mg C/m^2/hr) was lower than that in the seaward area(181.74 ± 17.14 (SE) mg C/m^2/hr).

6. 4. Discussion

6.4.1. Abundance and community structure of benthic diatoms.

The results showed that after three to nine months of the experiment, density treatments of *T. telescopium* had no significant effect on the abundance of benthic diatoms. Effects were detected, however, after one year of the experiment. This suggests that a three to nine month period may be too short to detect any effects of grazing by the snail. A similar result was reported by Bianchi and Levinton (1981). They found that after 106 days of a laboratory experiment on effects of grazing by gastropods, the density of mud snails *Hydrobia* and *Ilyanassa* did not affect relative abundance of benthic diatoms significantly. In this case there was no obvious effect of snail density on abundance of benthic diatoms.

Some studies on muddy substrata have found that effects of grazing could be detected in shorter experiments. Levinton and Bianchi (1981), for example, found significant effects of grazing by mud snails (Hydrobiidae) on benthic diatoms after a period of 72 days. In this case, total density of diatoms reached a maximum at the lower density of the snails. Connors *et.al.* (1982) carried out a laboratory experiment of 7 days duration only and demonstrated that a density treatment of 6 snails (*Ilyanassa obsoleta* Say) decreased the number of migratory diatom cells more compared with a density treatment of 12 snails (the treatments using 0, 6 and 12 snails, were equivalent to 0, 80 and 160 snails/m^2 respectively)

A possible mechanism to explain the results reported here is that the recovery rate (from grazing effects) of the benthic diatom community may be extremely fast. Studies on recovery of benthic intertidal diatoms have been carried out mainly on rocky substrata. For example, MacLulich (1983, cited in Underwood, 1984) studied microflora (*i.e.* blue-green algae, diatoms) on rocky shores in New South Wales, Australia. He found that diatoms and other taxa of the microflora on clean scraped rocks were able to recover their abundance and diversity within four weeks of being cleared. Underwood (1984) found that microalgae on intertidal rock substrata needed approximately 6 weeks to recover natural abundances.

Recovery rate of densities and diversity of benthic diatoms on soft substrata in mangrove areas may be higher than that on other types of substratum. Mangrove areas are influenced by tidal currents, but substrata are subjected to relatively less physical stress including force of tidal and wave action (MacNae, 1968). Tropical mangrove soils, especially in the low mid-intertidal regions, contain a high abundance of mud particles and are rich in organic matter (MacNae, 1968; Hendrarto, 1983; Alongi, 1987). In this type of soil, motile, epipelic species are dominant. The large epipelic diatoms are highly motile and migrate easily in muddy sediments (Baillie, 1987; Round *et al.*, 1990). The combination of calm hydrodynamic conditions and the mobility of benthic diatoms may help to explain the rapid rate of recovery of benthic diatoms following disturbance.

A laboratory study was carried out by Connors *et.al.* (1982) on muddy substrata on which the microbenthic algae was dominated by pennate diatoms. He found that after being grazed by low densities of the mud snail *Ilyanassa obsoleta*, the population density of benthic diatoms recovered within approximately one week. Gould and Gallagher (1990) suggested that benthic diatom populations on muddy, intertidal sediments, have specific growth rates perhaps a tenth of those recorded for pelagic diatoms in the open ocean. In addition, they found that the growth rate of epipelic diatoms from muddy substrata varied between 0.06 cells/day and 0.21 cells/day. Admiraal *et.al.* (1982) showed that exponential growth of benthic diatoms occurred in low-density natural populations, in cultures of mixed diatoms on their natural sediment and in unialgal cultures.

In the zero density treatment in the experiment reported here, growth rate of benthic diatoms may have been limited. This limitation may have been created by products of diatom cells. The surface of an epipelic diatom community is bound by a layer of mucus excreted by the cells. Excretion of the mucus increases as diatom biomass increases (Gould and Gallagher, 1990). This biofilm helps to stabilise the sediment, but may limit exchange of nutrients and gasses to and from the diatom community (Grant *et.al.*, 1986). As diatom biomass increases, diffusion processes may be limited and growth rate may decline. The combination of a slow growth rate in the zero density treatment and the potentially fast recovery in grazed plots, may have resulted in a non significant effect of grazing of *T. telescopium* on benthic diatoms over three to nine month periods.

The results show that in each period of sampling, the density of *T. telescopium* did not affect species richness, community diversity or evenness of communities of benthic diatoms. Both the number of species and species composition were similar in each density treatment of the snail. The multivariate analysis indicated that the effects of habitat or density treatments of *T. telescopium* on the composition of the benthic diatom community were not consistent also. There was, however, a stronger tendency of diatom community affinities within than between habitats. Oppenheim (1991), using multivariate analyses, demonstrated that various environmental variables influenced the structure of diatom assemblages seasonally.

The results of the present study suggested that *T. telescopium* may not graze the benthic diatoms selectively. Based upon the small size of the radula, jaws and buccal mass, this gastropod ingests fine particulate food only (Houbrick, 1991). Similar feeding patterns have been reported by Pace *et.al* (1979) for *Nasarius obsoletus*. They suggested that (1) the gastropod *Nasarius obsoletus* is not discriminating between the microbes ingested, (2) selective ingestion was less likely in muddy habitats because organisms were not being scraped from a hard surface. A different result was reported by Connors *et.al* (1982). They found that grazing by mud snails altered the community of benthic diatoms. In this example grazing caused a shift in diatom species composition from larger migratory epipelic forms to smaller, non-migratory species. Fenchel and Kofoed (1976) found that grazing by the snails also changed the composition of diatoms towards smaller cells on grazed sediment after 8 days. On hard substrata, Nicotri (1977) found that intertidal gastropods removed microalgal species selectively. But the change in species composition was not always related to grazing. Some diatom species may disappear from substrata in the absence of grazing (Castenholz, 1961).

Benthic diatoms collected in mangrove sediments in this study consisted mainly of migratory forms. It is possible that the method used to collect the benthic diatoms may discriminate against the non migratory forms (Eaton and Moss, 1966). Small non-migratory diatom cells were not collected adequately during the experiment. These non-migratory forms have generally been considered to be unimportant due to the continual deposition of sediment over them by tides (Sulivan, 1975; Pace *et.al.*, 1979 and Connors *et.al.*, 1982). Due to the large numbers and similar composition of migratory diatom cells in density treatments of *T. telescopium* , significant alteration of the migratory diatom composition by grazing was possibly unlikely. This type of benthic diatom may continuously redistribute themselves on each tide. Such effects could lead to continuous immigration of diatoms therefore swamping any effect of grazer removal in the experiment. Abundance of migratory diatoms in mangrove sediments may be very much higher than non-migratory forms anyway as has been found for other estuarine mudflat sediments (Admiral *et.al.*, 1982, 1984; de Jonge, 1985 and Baillie, 1987).

Meiofaunal grazers may affect the abundance of benthic diatoms also. This effect also may not have been significant since it is likely that only a small fraction of benthic diatom biomass is grazed by these animals (Admiral *et al.*, 1983). Davis and Lee (1983) found that only 6 % of the biomass of benthic diatoms was used by grazers daily. Using measurement of ^{14}C in diatoms and investigating major meiofaunal grazers Montagna (1984) concluded that a growth rate of 0.107 cells/day may be sufficient to maintain the diatom community in a steady state. A study in tropical Australian mangroves found that meiofauna appear to have little impact on microbial standing stock (Alongi, 1987). Further studies on recovery rate of benthic diatoms following disturbances in tropical mangrove ecosystems are required.

6.4.2. Productivity of benthic algae.

In some periods of sampling, mangrove sediments grazed by natural densities of *T. telescopium* had levels of primary production of benthic algae consistently higher than those on sediments with 0.5 and 2.0 times natural density. These results differed with those of Pace *et al.* (1979). They found that *Nassarius obsoletus* at natural density reduced benthic microalgal productivity. Other studies, however, have found that the producers (*i.e.* benthic microalgae) were able to compensate for the effect of grazing by low levels of grazer biomass by increasing productivity. At certain levels of grazer biomass, productivity decreased (see Hargrave, 1970; Cooper, 1973; Flint and Goldman, 1975; Connors *et al.*, 1982). The natural density of *T. telescopium* of 4.0 snails/m^2 may thus have been a threshold density. Above this level, productivity decreased. This suggests that the natural density may be able to stimulate productivity. If this is the case, *T. telescopium* at natural density may be important in mangrove ecosystems, by enhancing benthic productivity.

The consistently low productivity in the 0.5 times natural density treatment, may have been caused by the high grazing activity of *T.*

telescopium . Underwood (1984) hypothesised that fewer grazers at a high level intertidal habitat led to more active and efficient grazing by grazers. Thus reduced density of *T. telescopium* in the present experiment may have enhanced grazing activity and efficiency. Some studies on herbivorous gastropods have demonstrated that primary production was low with higher but also with lower herbivore biomass (Hargrave, 1970 and Cooper, 1973)

The non-grazed treatment consistently had a high level of productivity. This suggests that by removing *T. telescopium* from the substratum, productivity of benthic algae is increased. This result was similar to those found by Brock (1967), Brenner *et al.* (1976) and Pace *et al.* (1979). On hard substrata, Nicotri (1977) also found that grazed areas had significantly less chlorophyll-a compared to ungrazed areas.

Some other mechanisms may have influenced the results. These mechanisms could be termed secondary effects of grazing by *T. telescopium* . Firstly, during feeding activities *T. telescopium* may not remove all benthic algal cells (*i.e.* benthic diatoms and non-diatoms) from the mud substratum. The snail may remove the older, senescent, benthic algae from the substratum thus maintaining the community in a highly productive form. At higher grazing intensities, however, the primary producers (*i.e.* benthic algae) may be unable to compensate for the increase in rate of removal (Flint and Goldman, 1975; Cooper, 1973). This argument may explain why the natural density treatment had higher productivity compared to that in the 2.0 times natural snail density treatment.

The second factor could be disruption of the sediment surface by *T. telescopium* . At the time of feeding *i.e.* the ebbing tide, this grazer may disturb the surface sediment. This process may reduce sediment stability and increase resuspension of benthic algal cells into the water column (de

Jonge and Van den Bergs, 1987; Baillie and Welsh, 1991; Delgado *et.al.*, 1991). This process would reduce the availability of the microalgae on the sediment surface. Heavy grazing may increase the rate of the resuspension process, therefore abundance of benthic algae may decline and productivity may be reduced.

Thirdly, grazing by *T. telescopium* may affect nutrient regeneration also. Important nutrients for microalgal growth may be supplemented by excretion from the gastropod. Connor (1980 *cited in* Connor *et.al.*, 1982) based upon laboratory work, found that approximately 5.7 µg N/cm^2 was produced daily from snail excretion. He concluded that the amount of nitrogen excreted by snails grazing at low densities was sufficient to account for increased production found in his experiment. This scenario, however, has not been demonstrated in the field, where environmental factors are likely to be more complex and not likely to be predicted easily.

There was strong evidence that productivity in the seaward area was higher than that in the landward area. Similar results have been found by Pomeroy (1959) in salt marshes of Georgia. He recorded that productivity of benthic algae in a seaward area was almost twice that in the landward area. Cadée and Hegeman (1974) found that productivity on surface sediments of an intertidal habitat was higher than that in a subtidal habitat. Similar studies comparing productivity at different intertidal levels on hard substrata are rare. Many workers, however, have described a greater concentration of chlorophyll (Nicotri, 1977; Black *et al.*, 1979; Underwood, 1984; MacLulich, 1987) or number of diatoms (Aleem, 1950b; Round, 1971) at lower tidal levels of intertidal gradients.

The characteristics of the habitats in this study differed and these may have been responsible for the observed differences in benthic algal productivity. On average, the clay content of the soil in the landward area was lower than that in the seaward area (Figure 6.7). The soil in the seaward area was more muddy. These two types of soil generally have different abundances of water and total organic matter. Sandy soils have less water and organic matter than muddy soils (Hendrarto, 1983; Alongi, 1987). The water content of the soil may have differed seasonally also. In summer the water content of the soil may be higher than that in winter (Alongi, 1987; Oppenheim, 1991). Water content of the soil is important to benthic microalgae, especially during prolonged periods of desiccation and at increased temperatures during low tide. This is especially true at higher levels of the shore (Round, 1971). Castenholz (1961 and 1963), working on hard substrata, found that the vertical distribution of intertidal microalgae (*i.e.* diatoms) was largely determined by physical factors at low tide. The probability of survival of benthic algae during dry conditions may thus be higher in the seaward area than the landward area. Such situations may obviously influence productivity.

The size of sediment particles may have influenced the levels of production of the benthic microflora also. De Jonge (1985) showed that the role of mud particles as a substratum for microalgae differed from that of sand particles. Mud often exists in the form of aggregations consisting of clay minerals, detritus particles including bacteria and organic substances that act as adhesives. The organic compounds are adsorbed by mineral particles (Niehof and Loeb, 1972). These organic compounds can stimulate diatom growth and possibly growth of other benthic microalgae (Admiral and Peletier, 1979). Diatoms appear to prefer mud rather than sand as a substratum (de Jonge, 1985). Diatoms are important components of the benthic microalgae in mangrove sediments (Cooksey, 1984). A positive correlation between their abundance and the productivity of benthic algae in this present study was significant. The muddy habitat (*i.e.* the seaward area) thus had greater productivity than the sandy habitat (*i.e.* the landward area).

The average primary production of benthic algae in this mangrove ecosystem was between 58.29 ± 5.15 (95% C.L.) to 322.1 ± 35.8 (95% C.L.) mg C/m²/hour. In general, the level of productivity in the present study is higher than that found by other workers in subtropical mudflat areas. This is possibly due to the fact that many of the other studies used the ^{14}C technique to determine primary production. Production values determined by the ^{14}C method are often much lower than those recorded by the oxygen production method (Lindeboom and de Bree, 1982). The ^{14}C uptake technique may determine the levels of net production only (Williams *et al.*, 1979) and the levels may be somewhat between net and gross production (Eppley and Sloan, 1965; Nalewajko, 1966; Bittaker and Iverson, 1976). Oxygen measurements, however, determine gross production (Lindeboom and de Bree, 1982). The ^{14}C method may thus underestimate the primary production (Harris and Piccinin, 1977; Giekes *et.al.*, 1979; Lancelot, 1979; Marra et. al., 1981). Kristensen *et.al* (1988), for example, used ^{14}C in tropical mangrove sediments at Ao Nam Bor, Thailand found the primary production of benthic algae was 0.75 - 1.28 *mg C/mg chl a/hr* .

The high primary production in the mangrove sediments at Chunda Bay may result from the inability of the technique to discriminate between the various types of flora living in the sediment. All fauna and flora in the sediment were included in the measurement of oxygen production. The oxygen method thus may not only provide accurate values of microphytobenthos production, but may represent the total community production also (Lindeboom and de Bree, 1982).

The concentration of nutrients may also support high levels of primary production in mangrove sediments. Compared with other mudflats, the concentration of important nutrients is perhaps higher in mangrove sediments. The combination of sufficient light intensity, nutrient availability and warm climate may cause primary production in tropical mangrove sediments to be higher than those in sediments from temperate or subtropical areas.

6.4.3. Seasonal effects.

6.4.3.1. Benthic diatoms.

There was a suggestion of an interaction between season and density of *T. telescopium* affecting abundance of benthic diatoms. The seasonal increase in abundance was greater at zero and low density treatments of *T. telescopium* (see Figure 6.21). This situation may be explained by considering other environmental factors *viz*. temperature, rainfall and frequency of inundation. During dry-winter periods, the maximum air temperature was low, approximately between 24 to 28 °C. This level of temperature may have been sufficient to support maximum grazing activity of *T. telescopium* . The gastropod may have grazed benthic diatoms in open areas without suffering from heat stress. *T. telescopium* is more active when the soil temperature is between 29 and 30 °C (Budiman, 1988). Dry conditions and high temperature, however may cause this snail to become inactive and to cluster together in shaded areas. This clustering behaviour may be an adaptation of *T. telescopium* to these extreme conditions (Lasiak and Dye, 1986; Budiman, 1988; Houbrick, 1991). During the period of maximum activity of *T. telescopium* (*i.e.* winter), high densities of this snail may have had greater effects on benthic diatom abundance.

In general, abundance of benthic diatoms was lower in summer than in winter. A similar result was reported by Hendrarto (!989), working in the same area as the present study, but further within the *Rhizophora stylosa* forests. He found that total numbers of benthic diatom cells were also low in summer. Other studies in tropical Australian mangrove sediments reported low levels of chlorophyll-a content during summer also (Alongi, 1987, 1988). Abundance of microalgae (*i.e.* possibly diatoms) on New South Wales rocky intertidal substrata showed similar trends (Underwood, 1984). Reports from higher latitudes, however, have revealed that populations of benthic microalgae or diatoms were low in abundance in winter, but had maximum abundance in summer (Shaffer and Onuf, 1983; Gould and Gallagher, 1984).

A combination of high temperature and prolonged monsoonal rain during summer perhaps minimised the population growth of benthic diatoms. The average maximum air temperature during summer was between 30 and 32 °C (see Figure 6.6). Lasiak and Dye (1986) reported that the temperature of mangrove sediments in areas adjacent to that of this study reached between 34.8 and 35.1 °C in shaded areas and 45.7 - 50.8 °C in open areas during summer. The influence of freshwater as a result of maximum rainfall may increase also during the Austral wet-summer season (see Figure 6.6 and Alongi, 1987, 1988). In this study the levels of salinity at the sediment surface were not measured, but it could be suggested that during heavy rain, the salinity of surface sediments may decrease substantially. During hot sunny days the salinity may increase to high levels. The growth of benthic diatoms in summer may be affected by such fluctuations in salinity . It has been reported that marine benthic diatoms from a saltmarsh grew well at salinity levels of 10 to 30 °/oo (Williams, 1964). McIntyre and Cullen(1988, *cited in* Montagna and Won, 1991) found that the biomass of microalgae living in sediments (*i.e.* possibly epipelic diatoms) was lower in the freshwater zone than that in the brackishwater zone.

Increase of surface salinity may also inhibit the activity of *T. telescopium* . This gastropod is able to tolerate a wide range of salinities from 15 ppt. to 35 ppt. (Alexander and Rae, 1974). *T. telescopium* , may, however be detrimentally affected by low salinity, as are other tropical marine fauna (Goodbody, 1961; Ganapati and Rao, 1962; Krishnamurthy *et.al*, 1984; Alongi, 1987).

Another factor that may affect abundance of benthic diatoms during summer is light intensity. Both quality and quantity of light may relate closely to tidal inundation. Light intensities on the sediment surface are limited by daily tidal submergence (Admiral, 1988, *cited in* Oppenheim, 1991). Mangrove areas in this study were more frequently inundated by seawater during summer (Figure 6.8) and thus the availability of light for photosynthesis may have been limited. The growth of benthic diatoms therefore could have been impeded, especially on cloudy days. High levels of light intensity, however can also limit the growth of benthic diatoms. Although marine benthic diatoms are capable of photosynthesizing at extremely low light intensities, high intensities of light often inhibit photosynthesis significantly (Round, 1971). Light intensity was not recorded in this study, but the levels are likely to be within the range recorded in other mangrove areas (see Alongi 1988). Light intensity was thus likely to be high in summer and low in winter. High light intensity on mangrove sediment surfaces could disturb both community structure and abundance of benthic diatoms. Hendrarto (1989) recorded that increase of light intensity and desiccation on sediments, as a result of mangrove felling, reduced the number of diatom cells by approximately 30 % .

The grazing effects of other fauna may also have resulted in low abundance of benthic diatoms in summer. During this period the population of juvenile fish and crustacea (especially prawns) is high at the study sites and in an adjacent area (Alligator Creek) (Robertson and Duke, 1987). Besides detrital material, these fauna consume benthic diatoms (Odum and Heald, 1975). Some fish feed on diatoms (Round, 1971). Crosby and Wood (1959), for example found almost pure masses of the diatom *Melosira moniliformis* in the guts of mullet and leather jackets. Mugilidae, *Liza parsia* (see Chattopadhyay, *et.al.*, 1987) and *Liza grandisquamis* (see

King, 1986), living in mangrove waters feed on benthic diatoms also. A study on feeding by juvenile banana prawns (*Penaeus merguiensis*) in Ross River creek (near Townsville) recorded benthic diatoms in large proportions in stomach contents (Hartono, 1992, personal communication). Sasekumar and Chong (1987) found that many of the commercially important prawns consumed benthic diatoms also. During summer high abundances of these fauna are found in this area and they were likely to consume benthic diatoms during high tide.

Milward (1974) found small numbers of diatoms in gut contents of mudskippers in mangroves. These fishes mainly feed on copepods (Harpacticoidae), other meiofauna and molluscs. During the present study these fishes *i.e. Periopthalmus vulgaris, Periopthalmus gracilis and Periopthalmus expeditionium* were present in the area, but were never found inside enclosures. The absence of this fish decreased grazing and perhaps contributed to increases in the population of their prey inside enclosures. It has been shown that the effect of grazing of meiofauna on benthic diatoms and microalgae is substantial (Montagna and Won, 1991; Admiral, *et al.*, 1983; Montagna *et.al.*, 1983; Decho and Castenholz, 1986; Bianchi and Rice, 1988; Decho and Fleeger, 1988; Pinckney and Sanduli, 1990). All meiofauna, except molluscs and polychaetes, ingest microalgae to a greater extent than they ingest bacteria (Montagna and Won, 1991). Meiofauna often can control benthic microalgal production (Davies and Lee, 1983). In tropical mangrove ecosystems, abundance of the meiofauna is higher in summer than in winter (Alongi, 1987). The low abundance of benthic diatoms in the wet-summer season, may have been partially a result of high meiofaunal density.

The occurrence of deposit-feeding crabs may influence measurements of abundance of benthic diatoms also. There is some evidence that the deposit-feeding crabs *Uca puguax* and *Sesarma reticulatum* consume great numbers of benthic diatom cells (Haines and

Montague, 1979). Crab burrows were always found in enclosures and it was difficult to control or remove crabs from these enclosures. The effect of crabs and crab burrows on oxygen production measurements on mudflats has been reported by Pomeroy (1959).

Cluster analysis indicated that the species composition and relative abundance of species in communities of benthic diatoms changed seasonally (see Figure 6.23). Summer communities could be distinguished from winter communities. This was essentially due to changes in the relative dominance of some benthic diatom taxa (see Table 6.17). For example *Bacillaria paradoxa, Navicula cuspidata, Nitzschia punctata, Nitzschia sigma* and small, unidentified-naviculoid diatoms were relatively more dominant in summer. The relative dominance of other taxa *e.g. Amphora coffeaeformis, Amphora ventricosa, Mastogloia exigua and Gyrosigma scalproides*, decreased slightly in summer. Seasonal changes of community structure of benthic diatoms has been reported also on intertidal shores (*i.e.* salt marshes, sand flats and mudflats) (Oppenheim, 1991) and mudflats (Admiral *et.al.*, 1984; Colijn and Dijkema, 1981). Several studies of sediment-associated diatoms (Amspoker and McIntyre, 1978; Cook and Whipple, 1982; Whitting and McIntyre, 1985; Taasen and Hoisæter, 1989) however reported that no clear seasonal variation of species composition occurred.

The cluster analysis indicated also (1) two separate groups of winter diatoms and (2) affinities of high and low density *T. telescopium* treatments in winter with the summer assemblage. These patterns may reflect low levels of replication in the experiment. The study was conducted over one year only. The results may have differed if the duration of the study was longer than a year and if the sampling interval had been reduced to monthly rather than three monthly. Expansion of this study would have required more logistic support. Several reports on seasonal alterations of benthic diatom assemblages in subtropical areas have been based on data collected at monthly intervals over more than one year of study (for example Taasen and Hoisæter, 1989 and Oppenheim, 1991).

6.4.3.2. Productivity of benthic algae.

There was strong evidence that the effect of grazing by *T. telescopium* on primary production of benthic algae in mangrove sediments was affected by season. The greatest increase in productivity occurred at zero density of *T. telescopium* especially between March 1991 and September 1991 *i.e.* the winter period. A similar result was reported by Pace *et.al.* (1979),working on grazing by gastropods on mudflats. Other studies, however have found that grazers stimulated population growth (Connors, *et.al.*, 1982) and led to increases in productivity of microalgae (Fenchel and Kofoed, 1976).

The effects of the interaction between *T. telescopium* density and habitat on productivity differed in two periods of summer *i.e.* December 1991 differed with that in March 1991 (Figure 6.20 and 6.24). This may have been influenced by the activity patterns of the snail which related to tidal inundation (see Figure 6.8). In December 1990, both population growth of benthic algae and activity of the snails in the landward area may have been limited by heat stress. This may have decreased primary production and the effect of grazing of *T. telescopium* on benthic algal productivity was not significant. Because of a shadowing effect by mangrove trees, the sediment in the seaward area , however, may still have had high levels of water content during hot sunny days. Abundance of benthic algae in this type of sediment thus was probably greater than that in dry sediments (Round, *et.al.*, 1990). Although tidal inundation may have affected activity of *T. telescopium* , the snail was probably more active in the seaward area than in the landward area. The effect of *T. telescopium* density, was thus more apparent in this habitat than in the landward area.

In late summer (March 1991), the frequency of tidal inundation was high, but the average temperature was slightly lower (Figures 6.6 and 6.8). Salinity at the sediment surface may have decreased due to the influence of freshwater in the landward area. Decreases of salinity may have affected *T. telescopium* as well as other gastropods adapted to more typically marine salinities (Brenchley, 1987). *T. telescopium* thus may have been more active in the seaward area . Thus the effect of grazing on benthic algal productivity would be more significant in this area than that in the landward area.

In general, seasonal fluctuations in primary production levels of benthic algae reflect those of benthic diatom abundances in having the highest values in winter and the lowest values in summer. A similar seasonal fluctuation was found also by Pomeroy (1959) on sediments flooded by high tides. Other reports (Hargrave, 1969; Cadèe and Hegeman, 1974; Lindeboom and de Bree, 1982; Shaffer and Onuf, 1983; Colijn and de Jonge, 1984) however, found that primary productivity in temperate region was highest in summer and lowest in winter. Many complex factors may contribute to the difference between results of this study and those of other studies. These factors include chlorophyll-a concentration, levels of solar radiation, temperature, sediment type and respiration (see Shaffer and Onuf, 1983). Temperature perhaps is more important in inhibiting metabolism of benthic microalgae than light intensities. Some studies have reported no inhibition at high light intensities in benthic microalgae (Pamatmat, 1968; Gargas, 1970; Hunding, 1971).

The magnitude of these many factors in tropical Australian mangrove ecosystems may differ from those in temperate intertidal sediments. These factors in tropical mangrove areas are dependent upon a prolonged dry winter season and monsoonal rains during the summer (Alongi, 1988). Further studies on important abiotic and biotic factors and levels of primary production of benthic algae in tropical mangrove ecosystems are needed.

6.4.4. The technique for measuring primary productivity.

Techniques and equipment for measuring oxygen production in this study were simpler than those used by other workers (Pomeroy, 1959; Hargrave, 1964; Hunding and Hargrave, 1973; Lindeboom and de Bree, 1982 and van Es, 1982). The equipment was easily transported into mangrove areas, which are often difficult to sample. The novelty of the present study was that oxygen containers were made from light, clear plastic bottles rather than thick, fragile glass bottles or cylinders. A large number of the jars could be transported into mangrove areas at one time. This increased the number of replicate readings possible at one time.

The size of the jars used in this study was smaller than those of bell jars used by other workers (for example Pomeroy, 1959; Lindeboom and de Bree, 1982; Lindeboom and Sandee, 1989). These smaller jars were more appropriate for study of mangrove sediments which have abundant stands of pneumatophore roots. The jars were small enough to be placed among the pneumatophores without including these mangrove roots in oxygen measurements. The diameter of the jar *viz.* 9.50 cm, allowed the container to cover a sufficient area of sediment surface. This surface area for measurement was larger than that used by Hargrave (1969) and Hunding and Hargrave (1973).

As in other studies, measurement of oxygen production was carried out during high tide or when the substratum was inundated by seawater. The measurements, however, could be carried out also during low tide by utilising a technique developed by Pomeroy (1959). This involves collecting estuarine water from adjacent areas and siphoning it slowly into the bell jars. The measurements thus may be conducted at all times and do not depend upon seawater inundation.

The period of incubation for oxygen production measurements in this study was one hour, similar to that used by Pomeroy (1959). This period was used so as to prevent bubble formation due to oxygen supersaturation. Formation of bubbles on the walls of bell jars can occur even in short periods of exposure (Hunding and Hargrave, 1973). Shaffer (1982, in Shaffer and Onuf, 1983) showed that bubbles occurred in his chamber during measurements in water containing oxygen concentrations of only 22 % .

This chapter has demonstrated that the grazing of *T. telescopium* does not affect abundance and community structure of benthic diatoms significantly. Some evidence suggested a small effect of density after 12 months. Density treatments had little effect on benthic algal productivity until after 12 months of the experiment. There was evidence that a greater abundance, diversity and productivity of benthic diatoms occurred in the lower than in the upper intertidal habitat. The study demonstrated a clear seasonal pattern, with diatom abundance, diversity and productivity significantly greater in winter than summer.

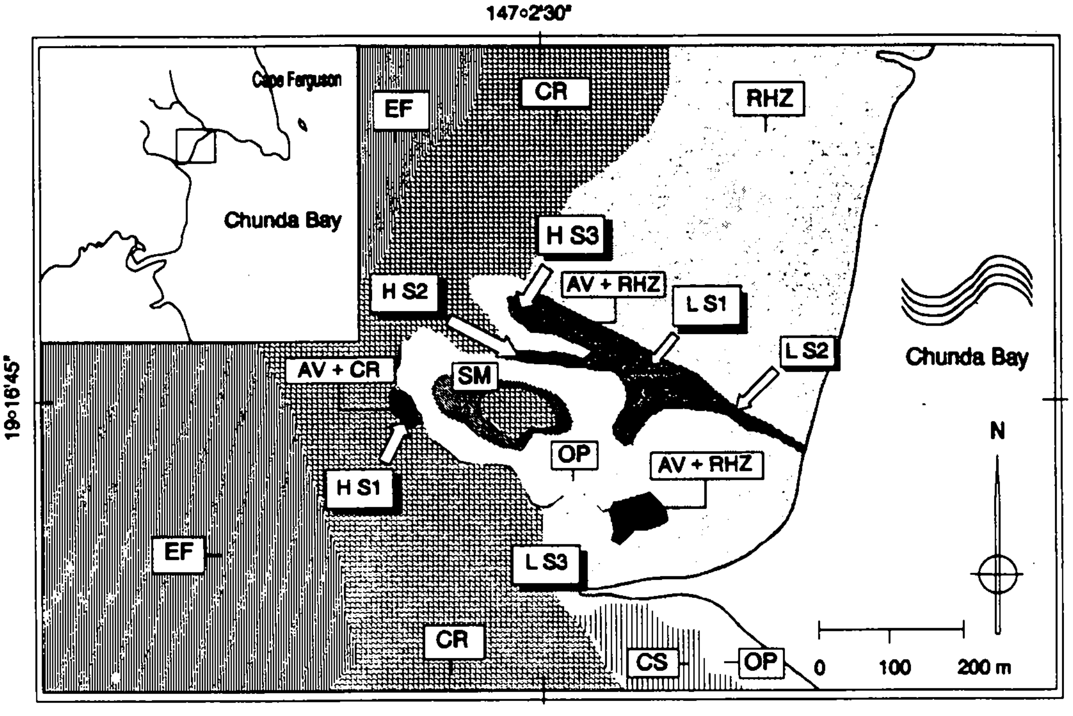


Figure 6.1. A map showing the location of the field based experimental sites in two different intertidal habitats of the mangrove area adjacent to Chunda Bay, North Queensland. Zonation of the mangroves is shown.

EF = *Eucalyptus* forest
CR = *C. tagal* forest
AV + RHZ = *A. marina* and *R. stylosa*
OP = open area

AV + CR = *A. marina* and *C. tagal*
RHZ = *R. stylosa* forest
CS = non mangrove vegetation
SM = Salt marsh vegetation

H/L S = Study site.
H = Landward habitat (Higher intertidal habitat)
L = Seaward habitat (Lower intertidal habitat)
S = Site

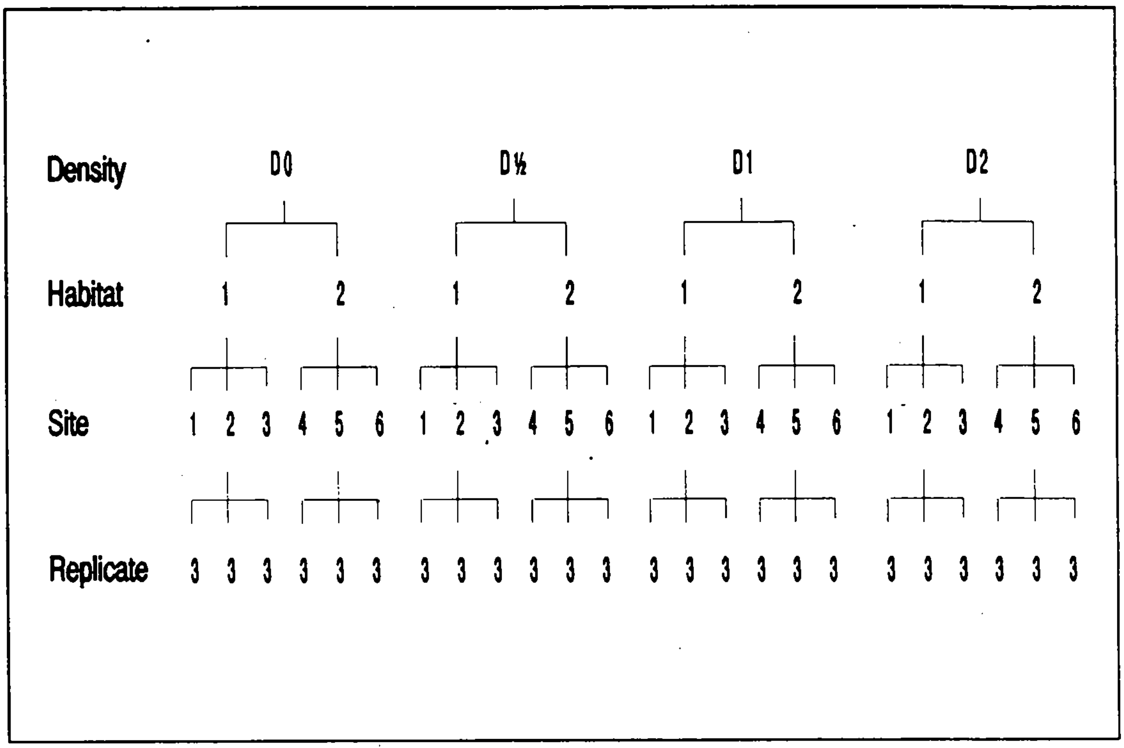


Figure 6.2. Design of the experiment to determine the effects of grazing by *T. telescopium* on benthic diatoms. Densities are snails/m^2 (mean natural density = 4 / m^2.

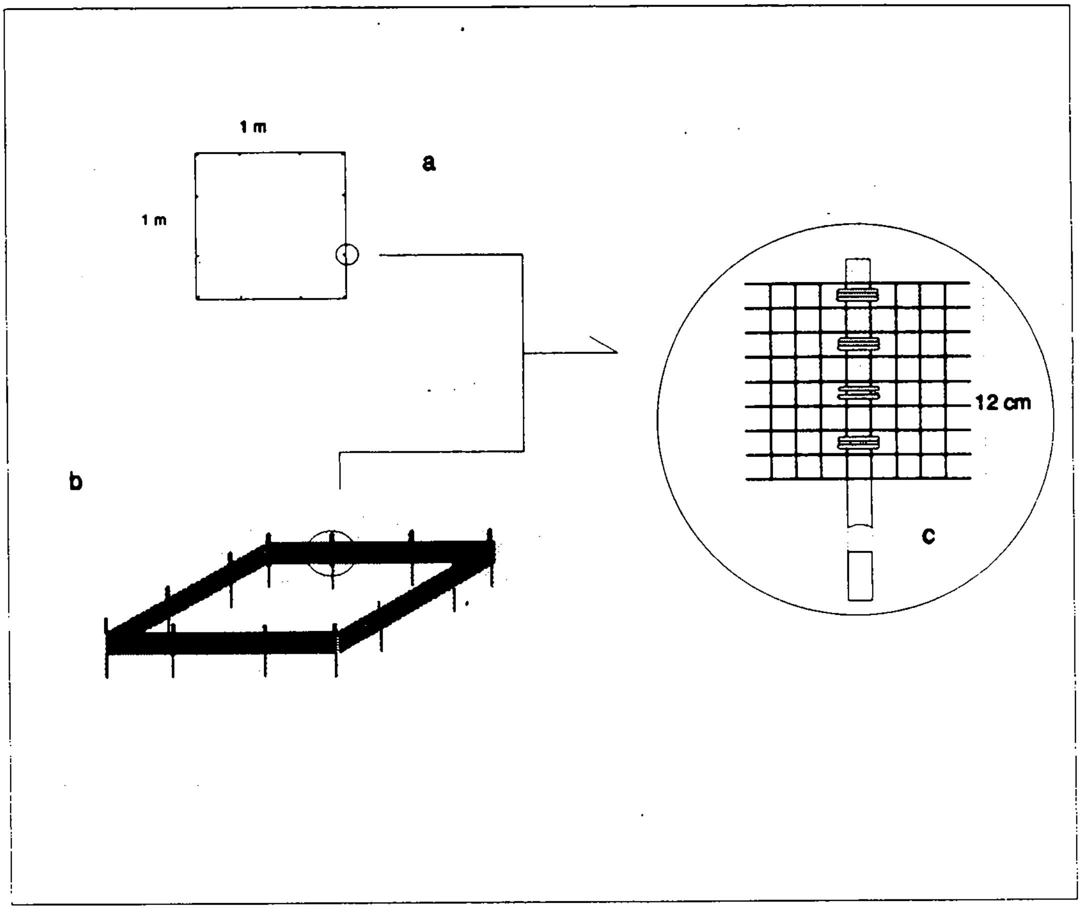


Figure 6.3. Diagram of enclosure used in the experiment.

(a) showing the shape of the enclosure with the position of poles.
(b) showing the position of the enclosure on the substratum
(c) detail of poles attached on the side of an enclosure.

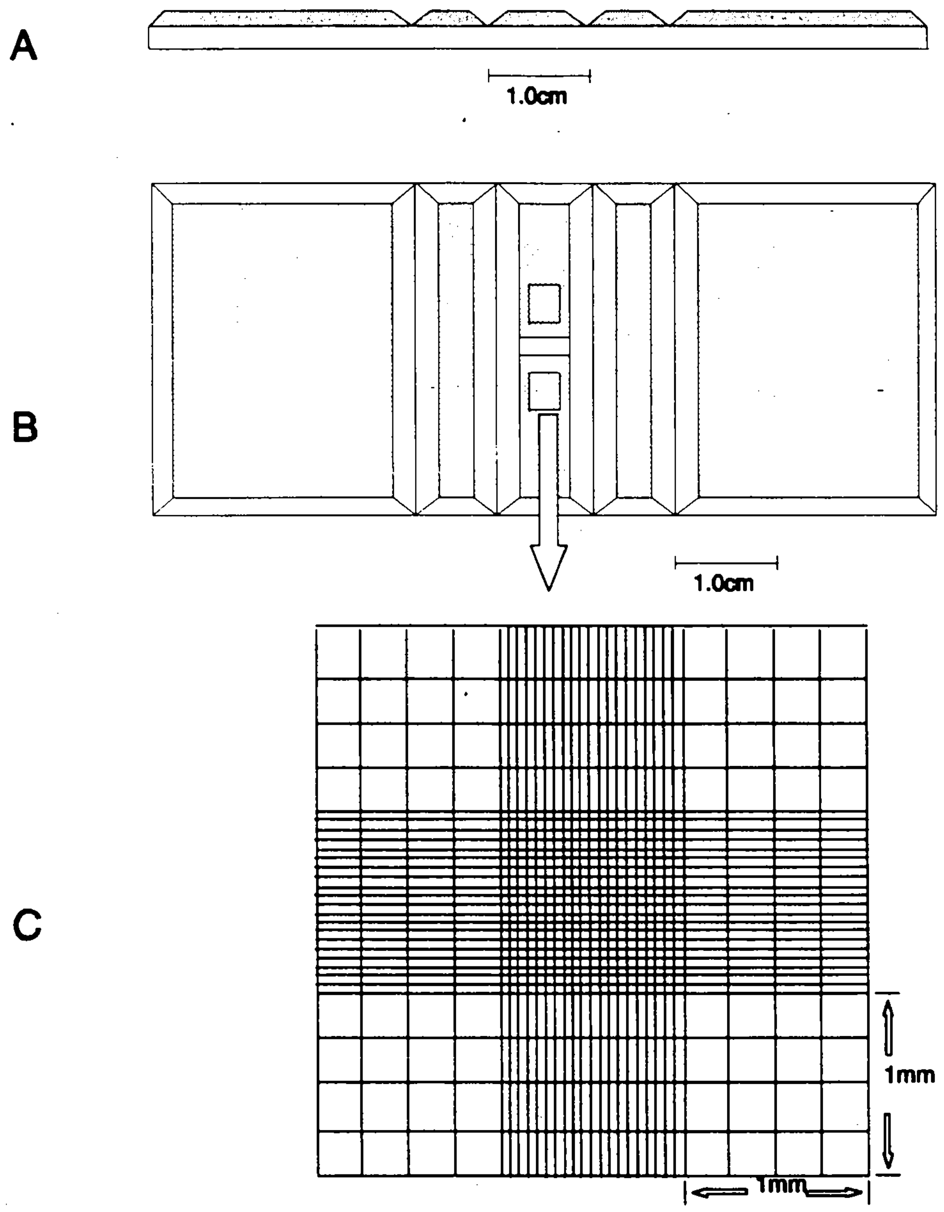


Figure 6.4. Diagram of an improved Neubauer counting chamber.

(A) Lateral view
(B) Dorsal view
(C) Detail of the middle part of the chamber showing grid lines

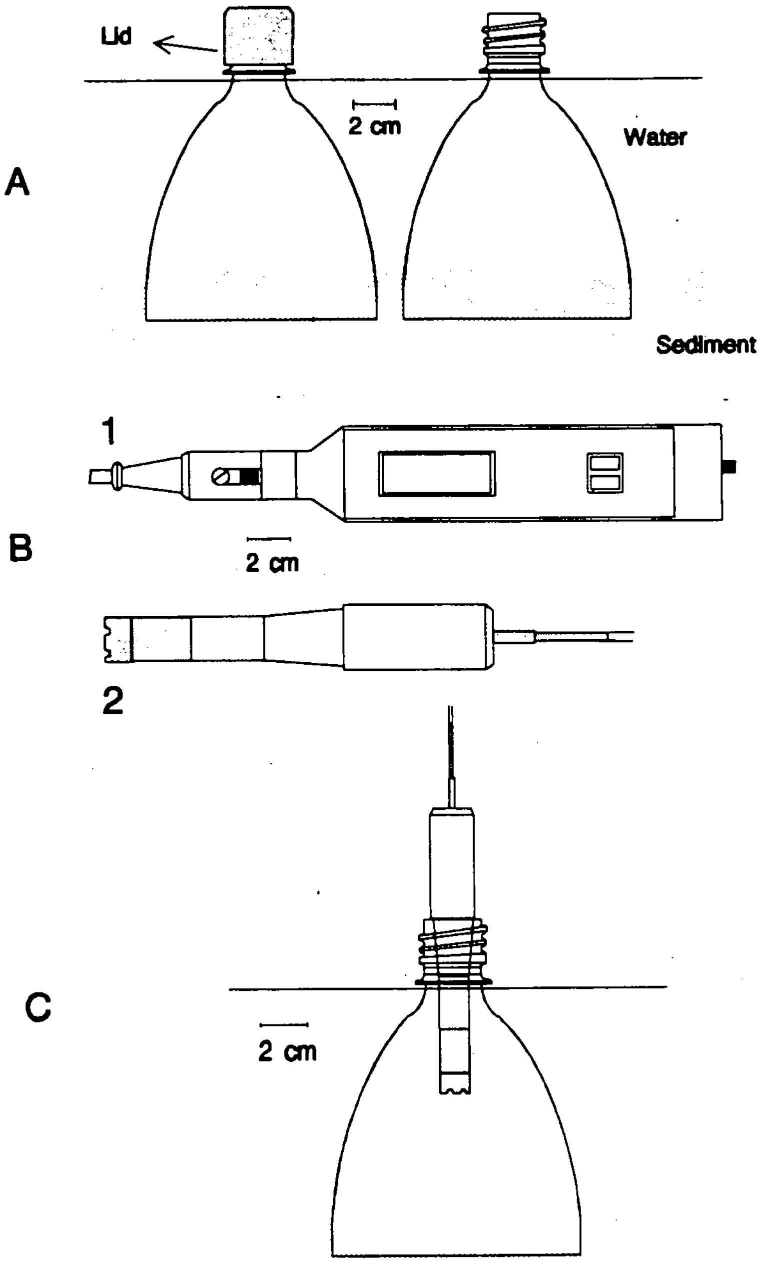


Figure 6.5. Diagram of equipment used for measurement of oxygen production.

(A) Position of jars on substratum
(B) The Oxygen-meter unit consisting of a meter (1) and an oxygen probe (2).
(C) Positon of the probe to measure dissolved oxygen in the water inside the jar.

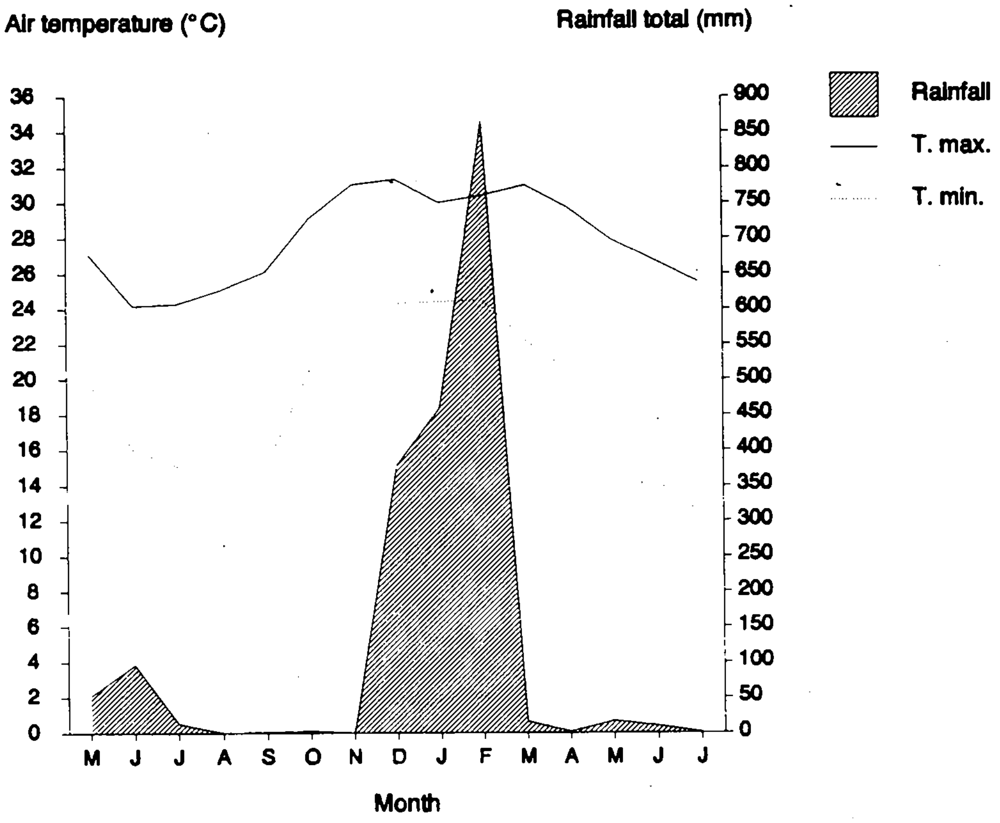


Figure 6.6. Average monthly maximum and minimum air temperatures and monthly total rainfall for Townsville and surrounding areas, from May 1990 to July 1991.

Data were collected from Commonwealth Bureau of Meteorology.

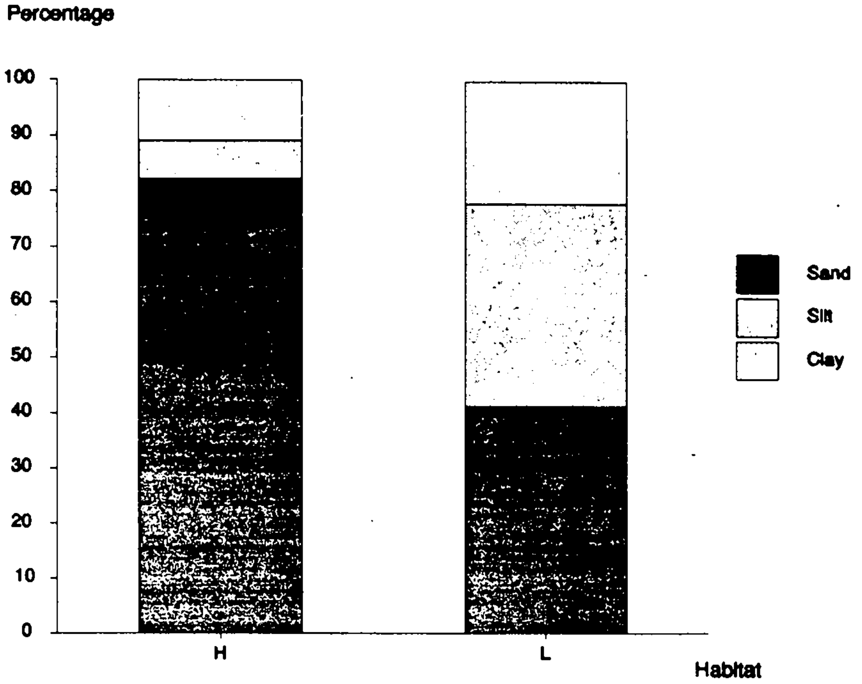


Figure 6.7. Sand, silt and clay content (expresed as a percentage) of soils in high (habitat H) and low (habitat L) intertidal mangrove areas at Chunda Bay, North Queensland.

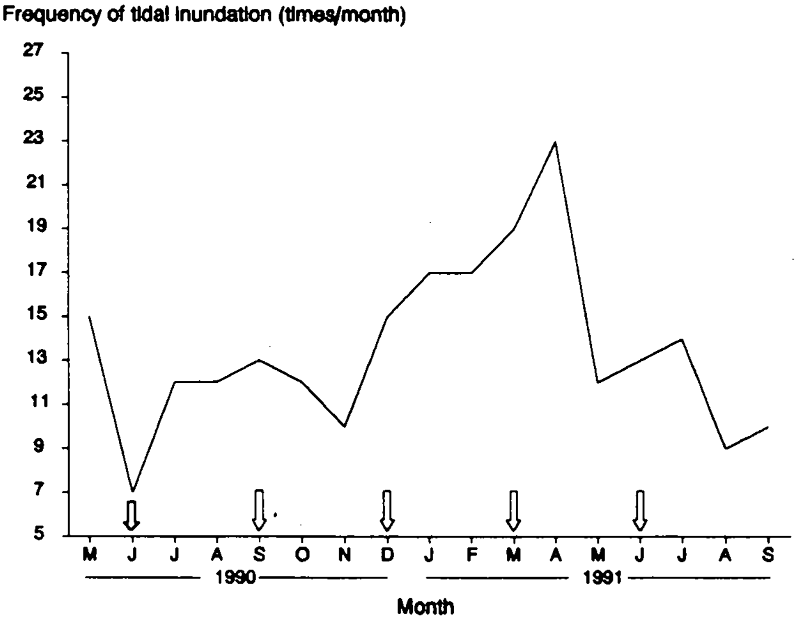


Figure 6.8. Frequency of tidal inundation during periods of the field based experiment.
Arrows show the three monthly sampling times for benthic diatoms.

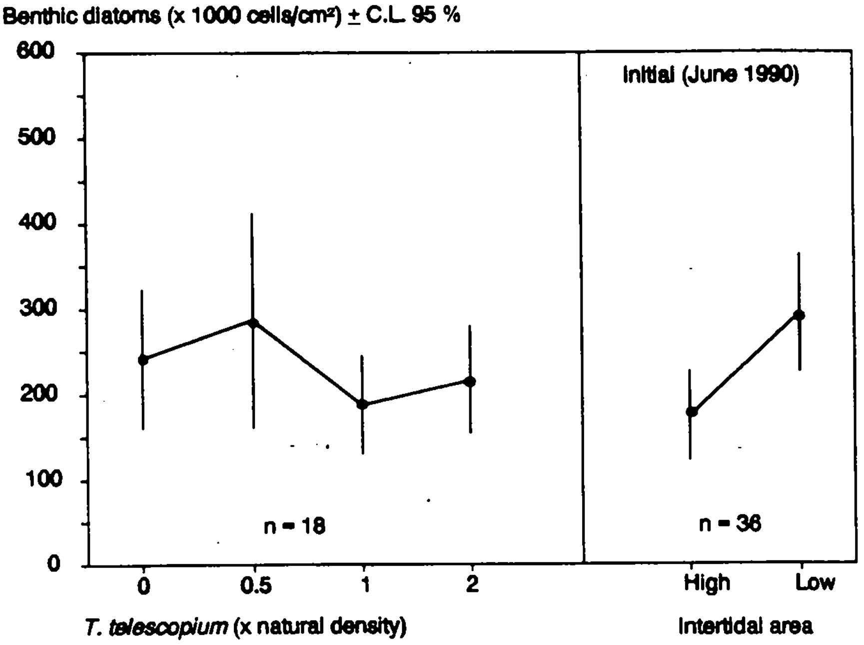


Figure 6.9. Abundance of benthic diatoms in four density treatments of *T. telescopium* and in two different habitats at the initial sampling period (June 1990)

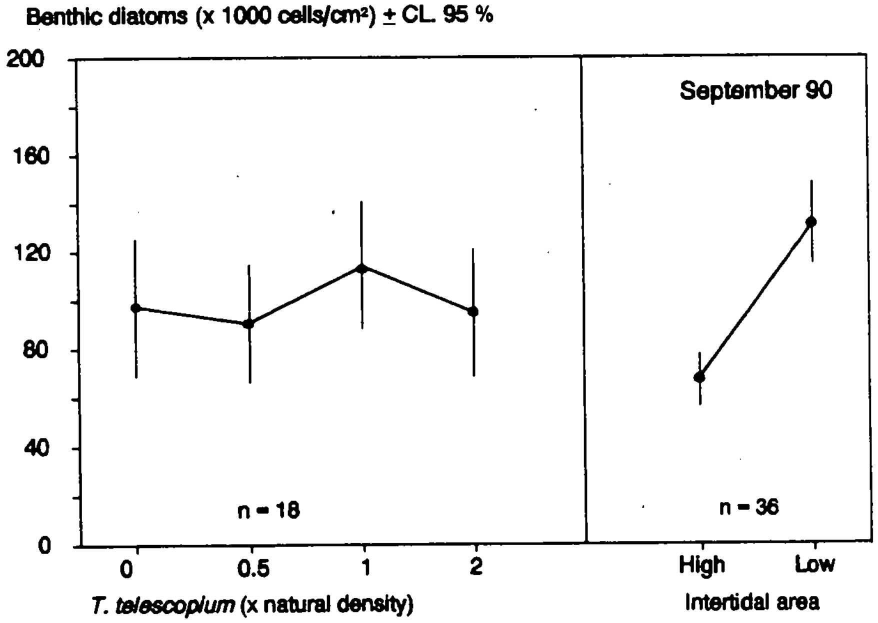


Figure 6.10. Abundance of benthic diatoms in four density treatments of *T. telescopium* and in two different habitats in September 1990.

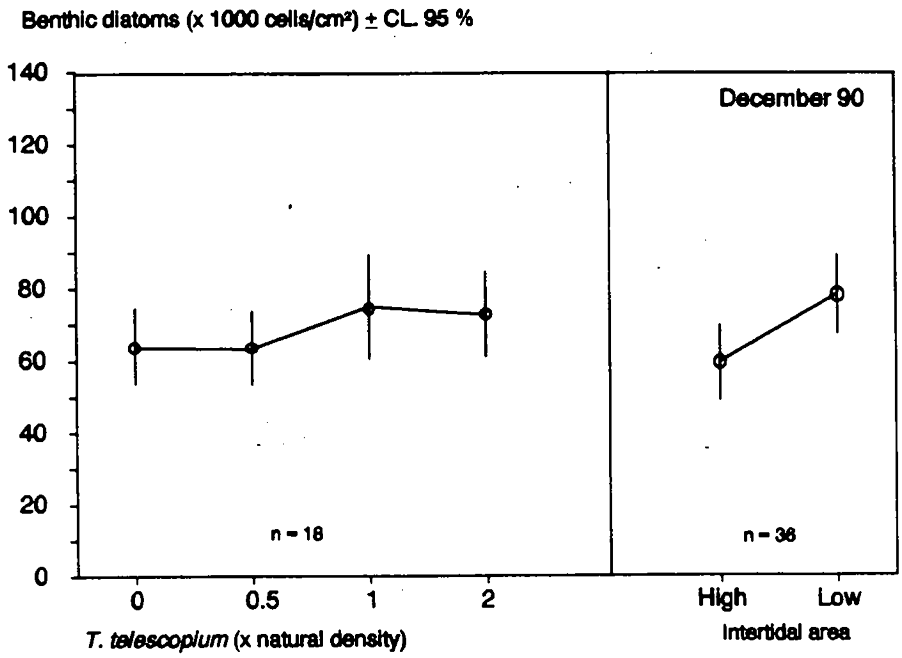


Figure 6.11. Abundance of benthic diatoms in four density treatments of *T. telescopium* and in two different habitats in December 1990.

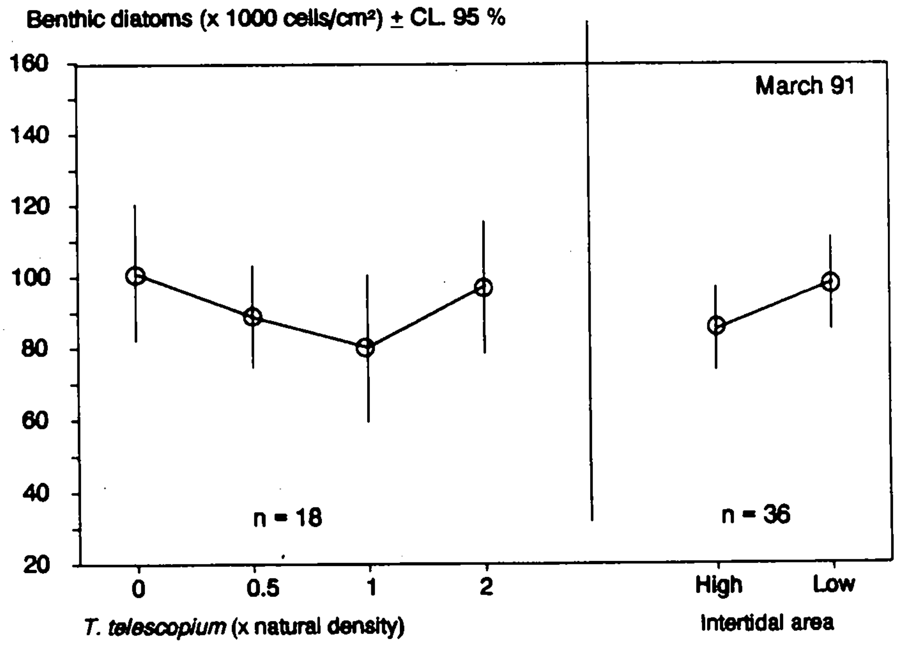


Figure 6.12. Abundance of benthic diatoms in four density treatments of *T. telescopium* and in two different habitats in March 1990.

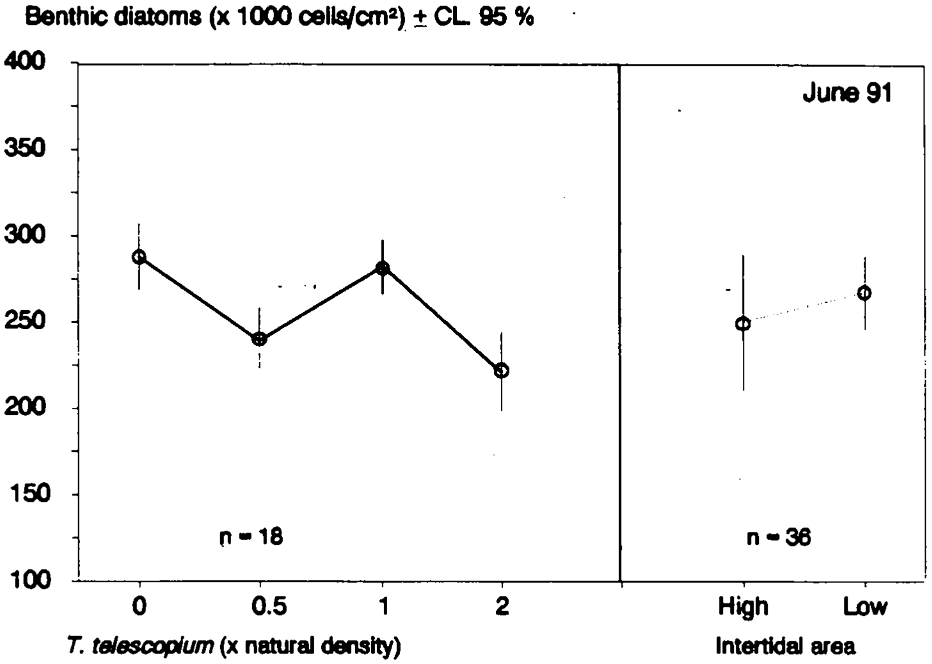


Figure 6.13. Abundance of benthic diatoms in four density treatments of *T. telescopium* and in two different habitats in June 1991

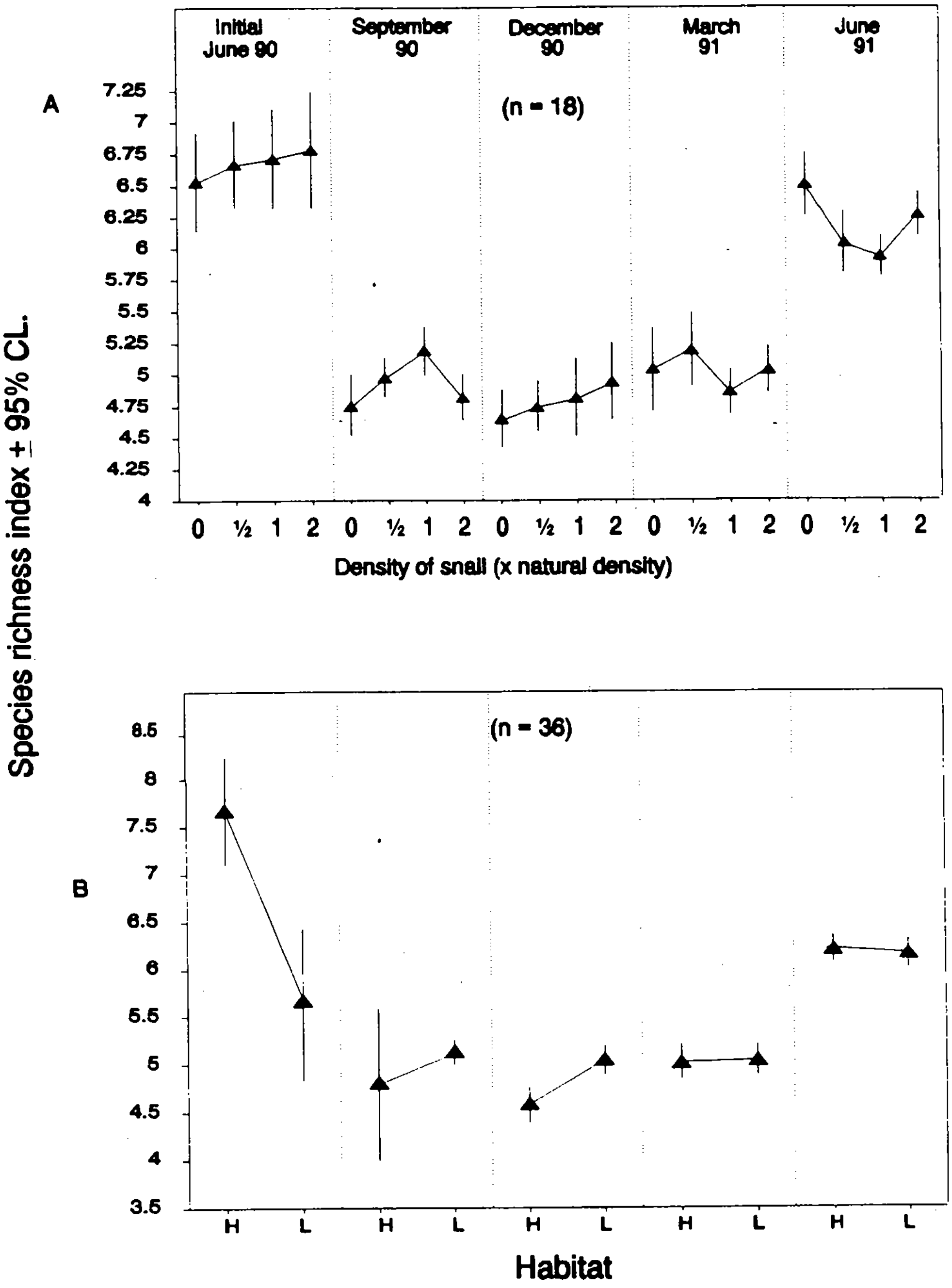


Figure 6.14. Graphs showing the species diversity index (Margalef's index) as a function of T. telescopium density (A) and of intertidal habitats (B) at every period of sampling.

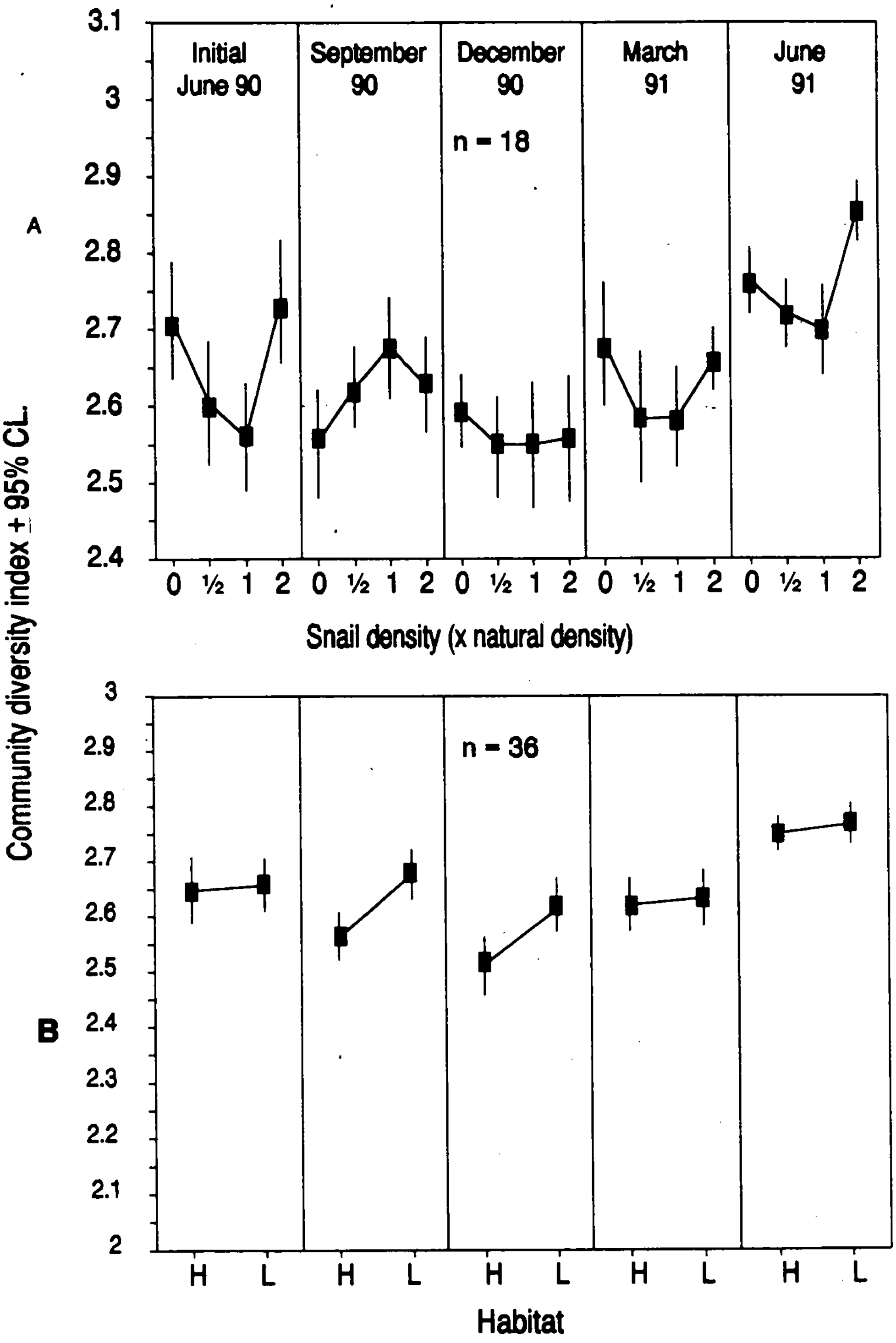


Figure 6.15. Community diversity index (Shannon-Weaver index) as a function of *T. telescopium* density (A) and of intertidal habitats (B) at every period of sampling.

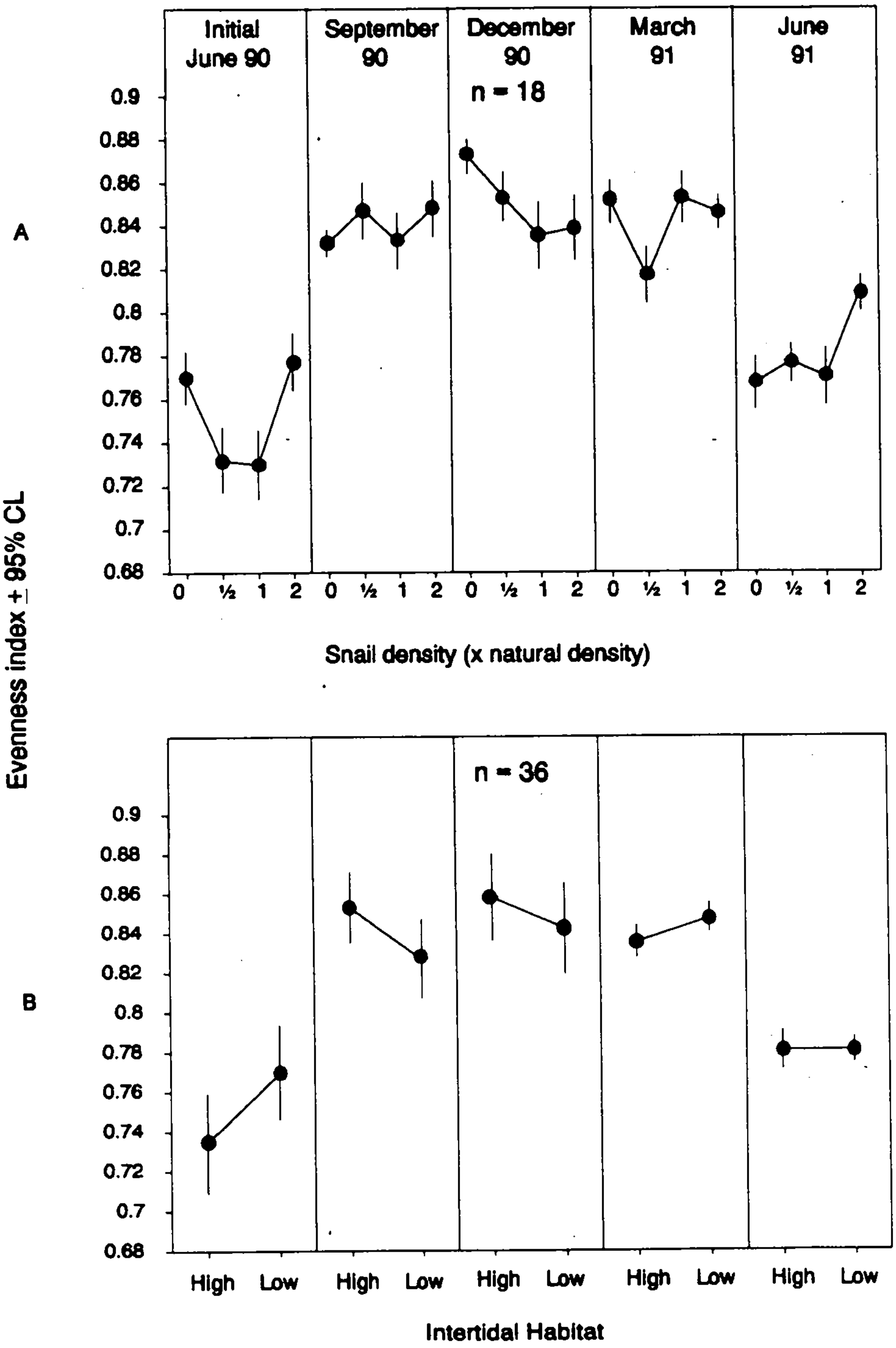
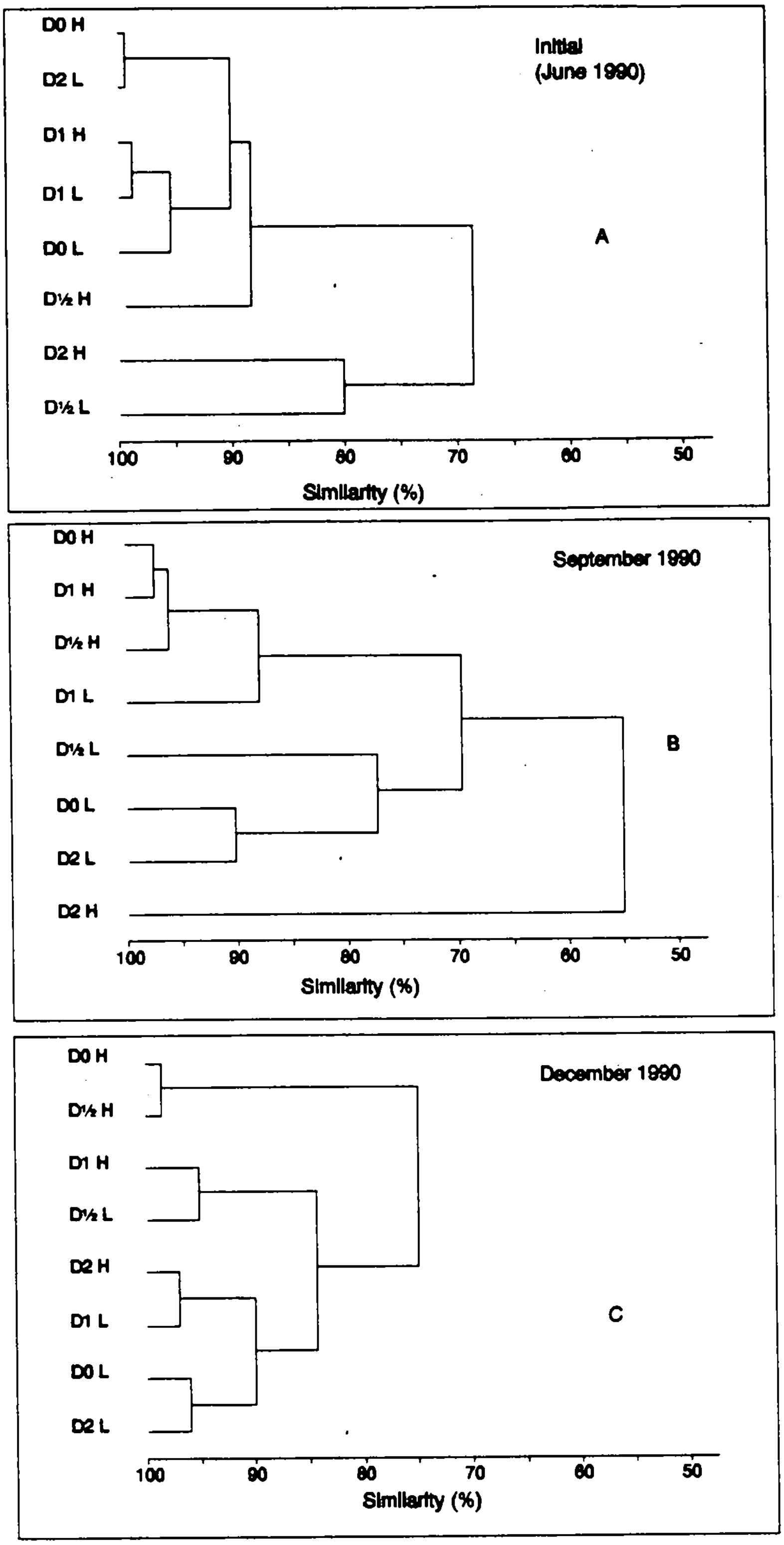


Figure 6.16. Evenness index of benthic diatom communities as a function of *T. telescopium* density (A) and of intertidal habitats (B) at every period of sampling.



No patter

Habitat

Habitat

Figure 6.17. ....

Continued ⟶

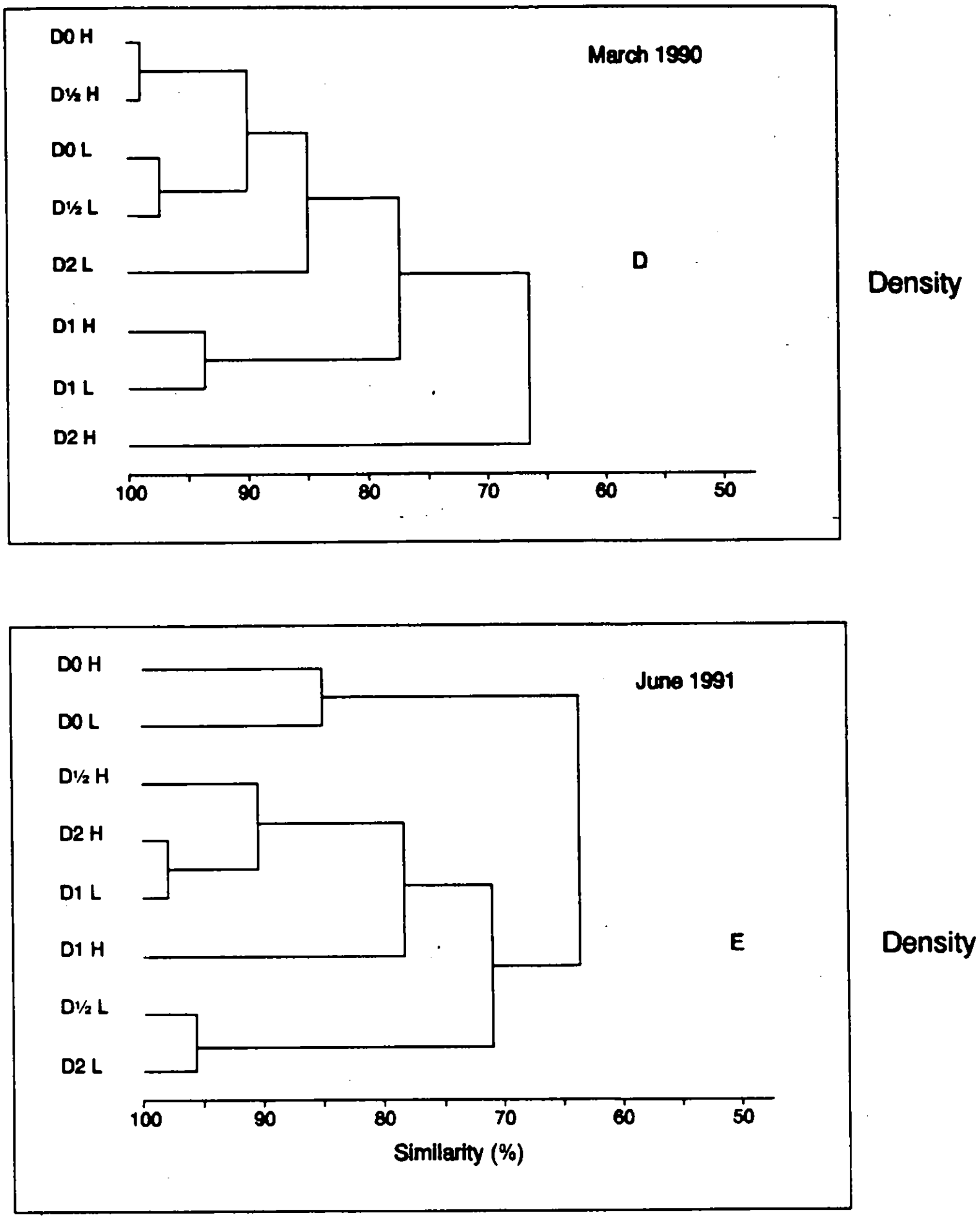


Figure 6.17. Dendrograms showing the relationships of benthic diatom communities in the four density treatments of *T. telescopium* in the high (H) and low (L) intertidal habitats.

The Bray-Curtis index of similarity was based on standardised data. Group average sorting was applied. Dn in n times natural snail density. Sampling periods were initial - June '90 (A),, September '90 (B), December '90 (C) (at previous page) and March '91 (D), June '91 (E).

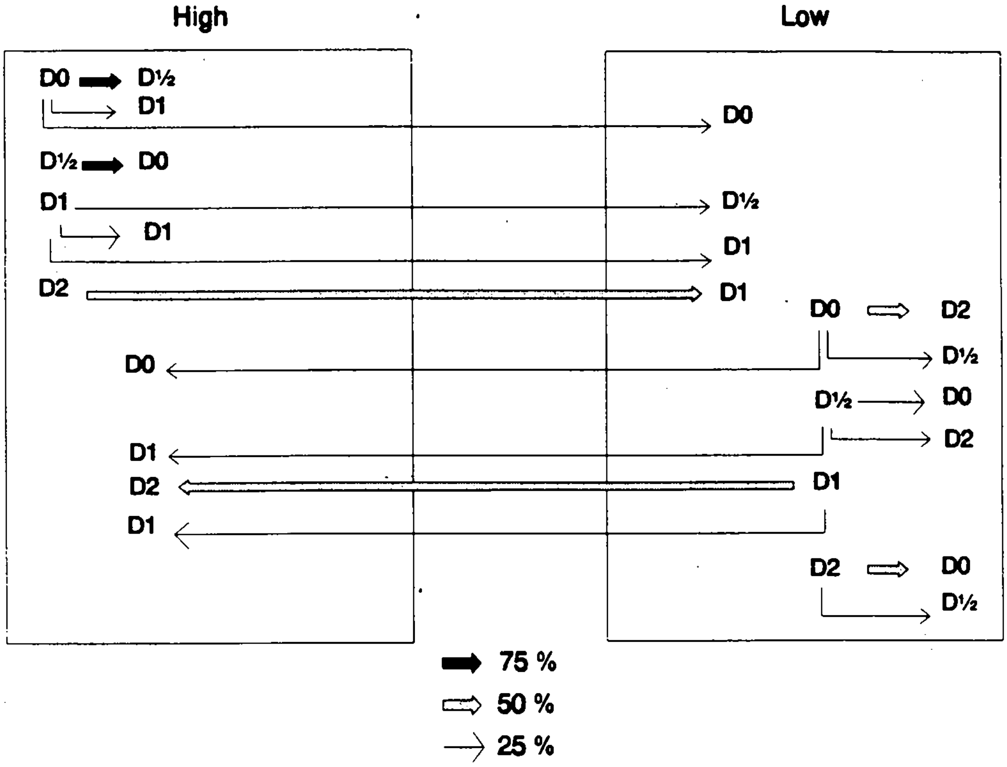


Figure 6.18. Diagram summarizing the relationships of diatom communities in different density treatments of *T. telescopium* and in different habitats (high and low intertidal areas).

Data based on the similarities of benthic diatom communities in Figures 6.17B to 6.17E. Dn is n times natural density. Arrows indicate where one density/habitat combination clustered closely to another (in terms of diatom community composition) from one sampling period to the next. The thickness of the arrow indicates the percentage of occasions (out of a total of 4 transitions) with which the density/habitat treatments clustered. No clear pattern of affinities of diatom communities is apparent as a function of *T. telescopium* density. However, there was a much stronger tendency for diatom community affinities within habitats (arrows inside boxes) than between habitats (arrows crossing between boxes).

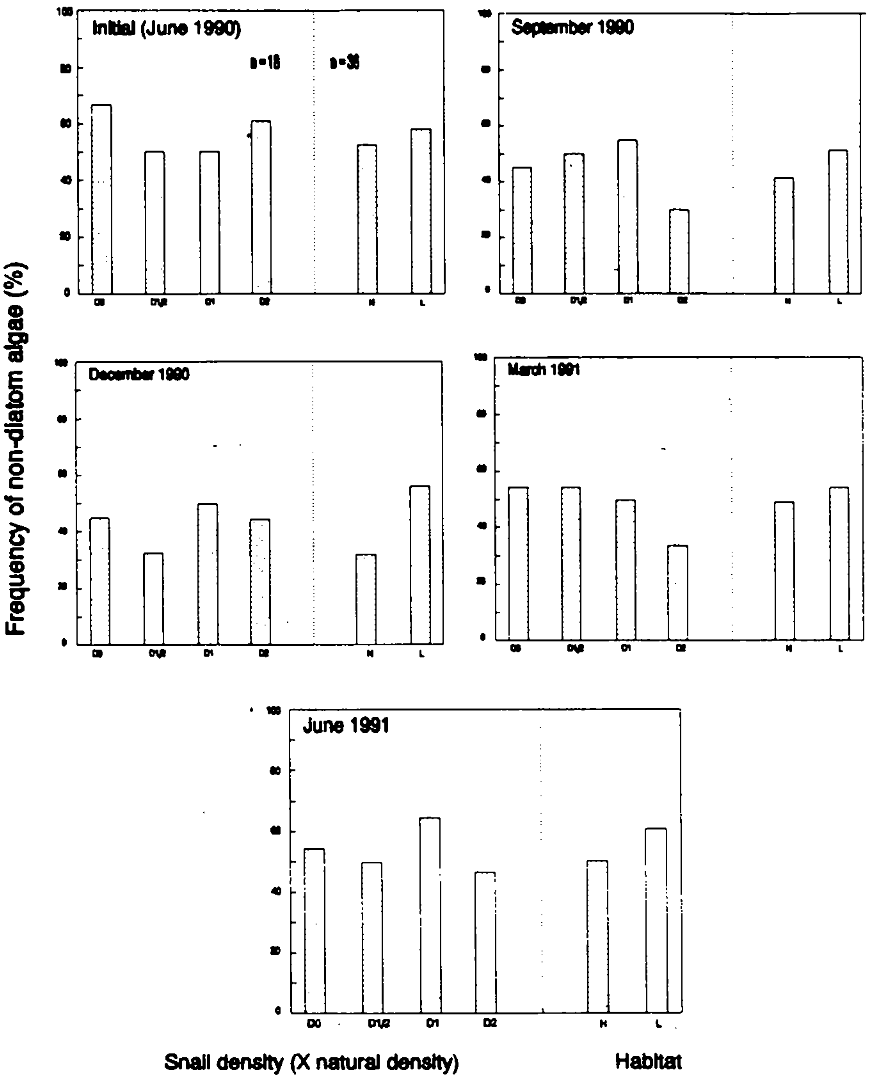


Figure 6.19. Frequency distribution (in percentages) of non-diatom algae at different densities of *T. telescopium* and in different areas within mangroves in each period of sampling.

Frequency was based on the % of times each category was recorded in samples (n = 18 for the snail density and n = 36 for area treatments, respectively). H = Lanward and L = Seaward areas.

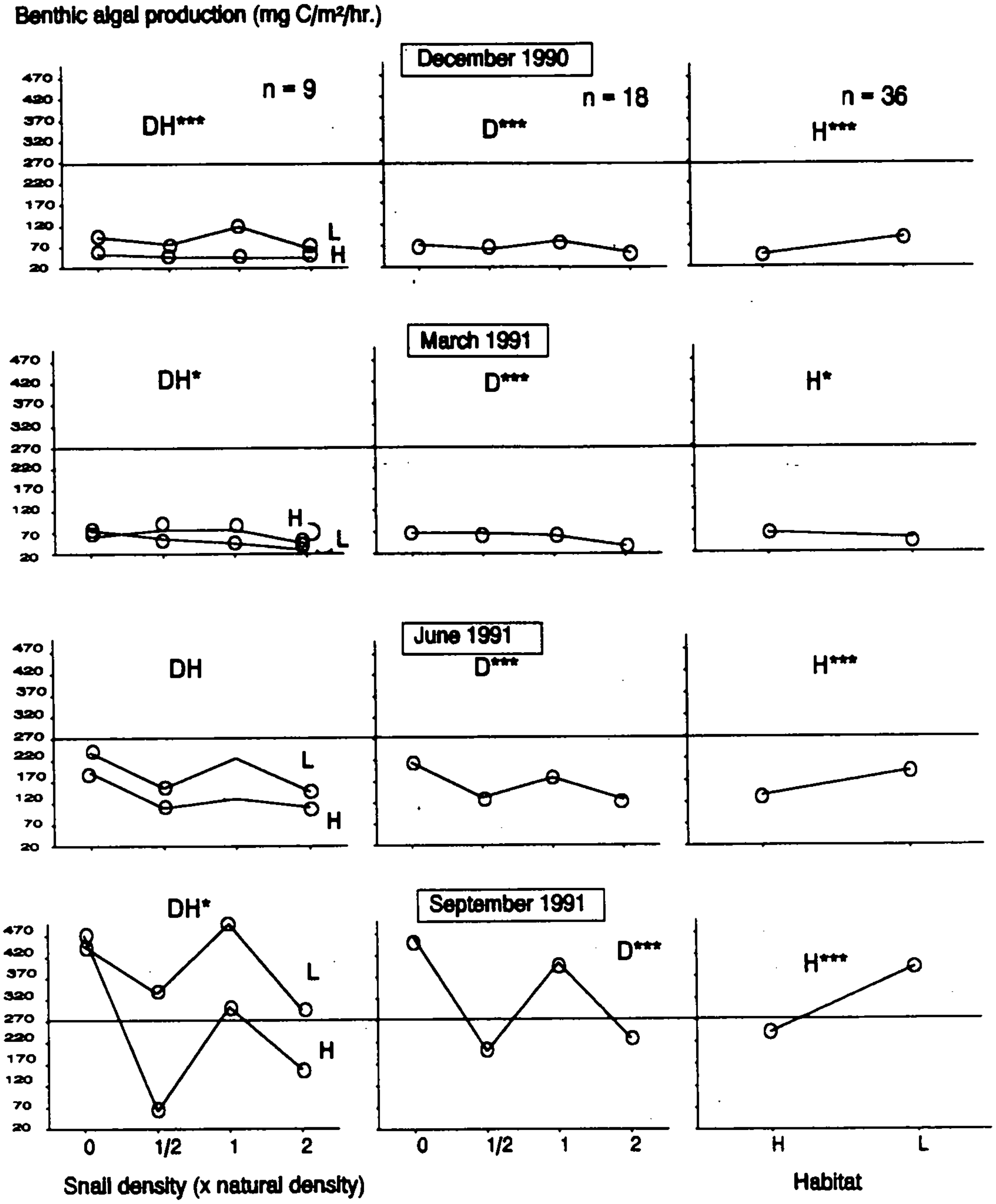


Figure 6.20. Effects of *T. telescopium* density (D), habitat (H) and the interaction of density-habitat (DH) on carbon production of benthic algae in three monthly periods of sampling.

H and L represent higher and lower intertidal habitats in the mangroves.. ***, ** and * indicate that differences were significant at the 0.001, 0.01 and 0.05 levels respectively.

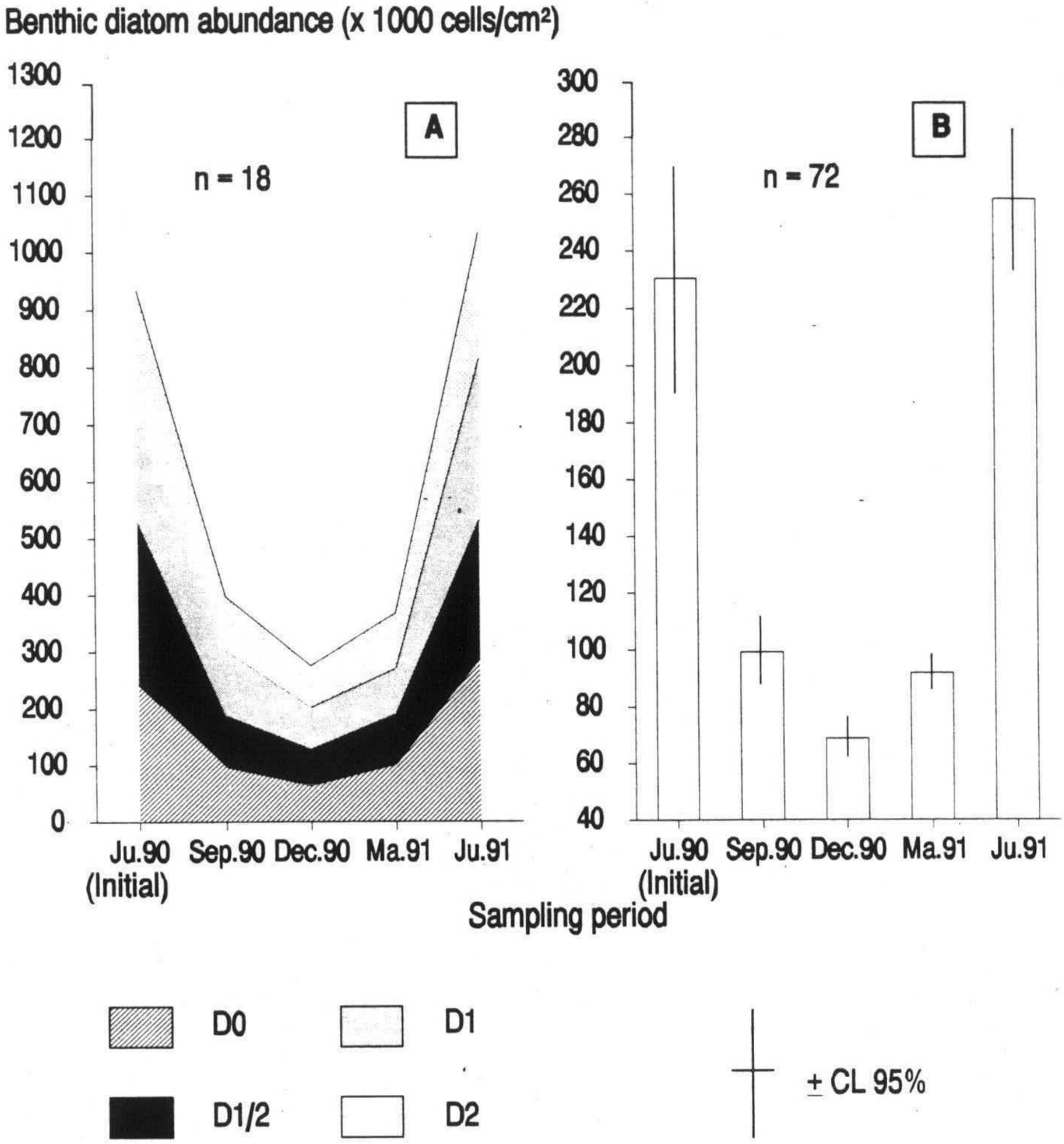
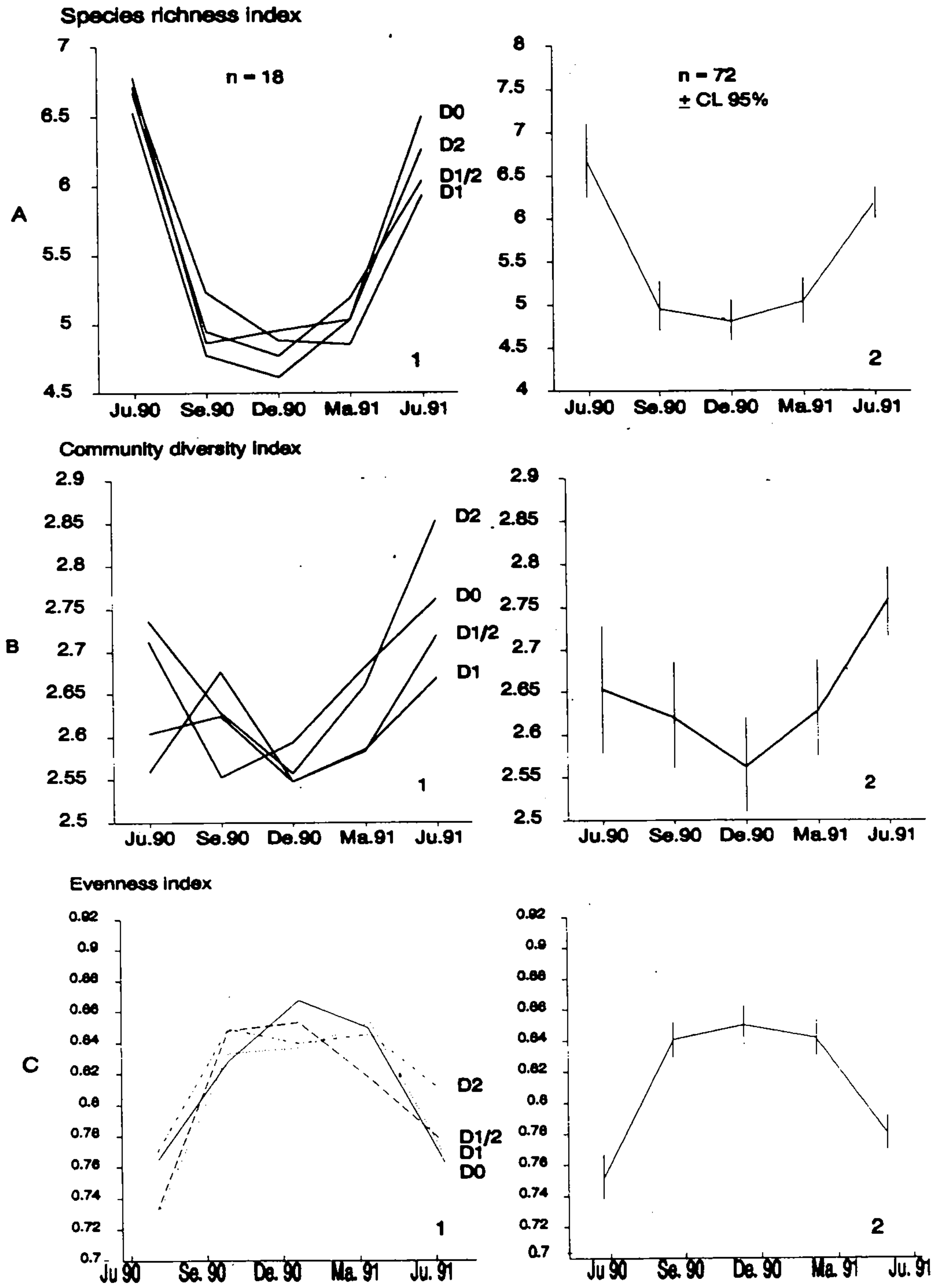


Figure 6.21. Seasonal variation of abundance of benthic diatoms.

The area-graph (A) shows the seasonal patterns of abundance in different density treatments of *T. telescopium*. Error bars were omitted for clarity. The bar-graph (B) shows the mean abundance in each season.



Sampling periods

Figure 6.22. The seasonal fluctuation of (A) species richness (Margalef index), (B) community diversity (Shannon-Weaver index) and (C) evenness indices of benthic diatom communities.

(1) shows these indices in each density treatment of *Telescopium telescopium*. Error bars were omited for clarity.
(2) shows the average of these indices ± C.L 95% .

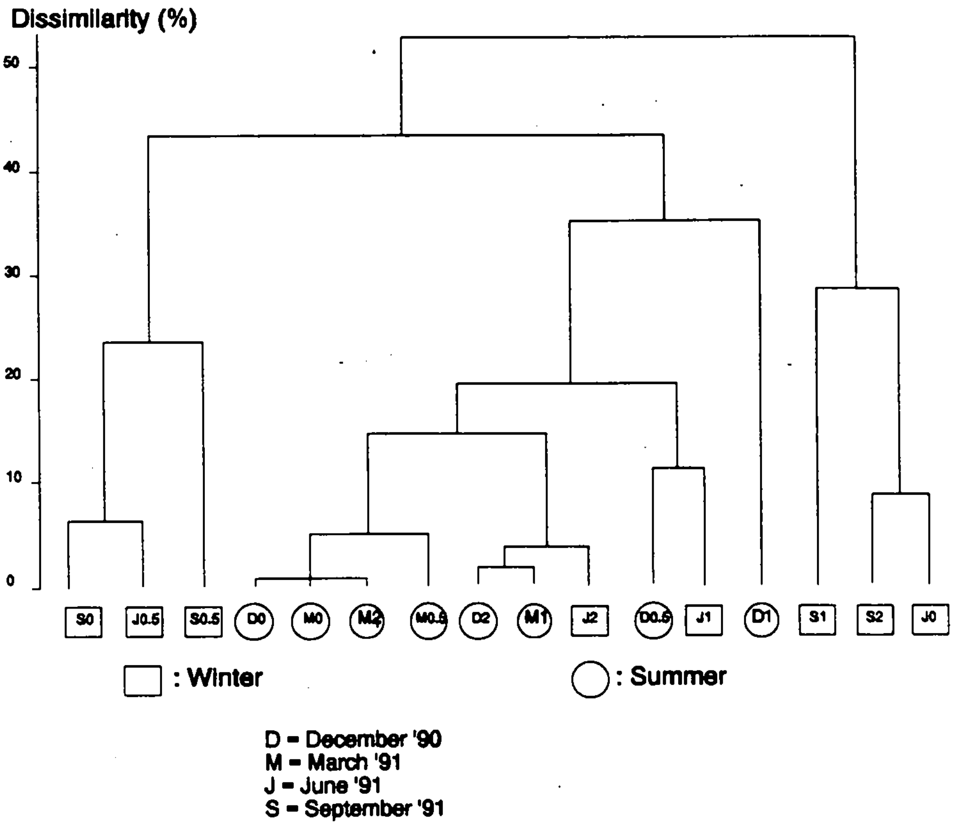


Figure 6.23. A dendrogram showing the relationship of productivity of benthic algae in the four density treatments of *T. telescopium* at different seasons.

The Bray-Curtis index of similarity was used based on standardised data. The densities of *T. telescopium* were 0, 0.5, 1 and 2 times natural density.

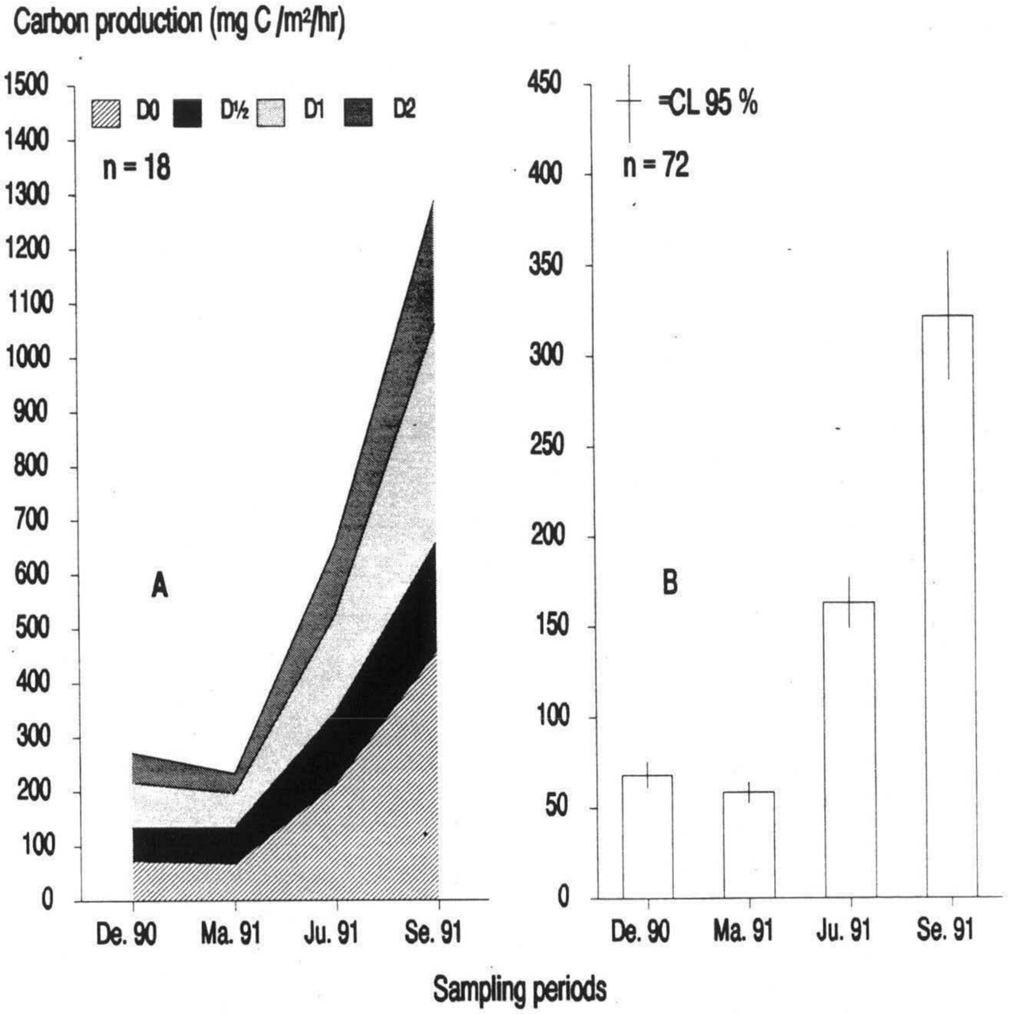


Figure 6.24. Seasonal fluctuation in the productivity of benthic algae.

The area-graph (A) shows the seasonal patterns of productivity in each density treatment of *T. telescopium*. Error bars were omitted for clarity.
The bar-graph (B) shows the average productivity in each season.

Table 6.2. Results of the three way ANOVAs of numbers of benthic diatom cells for each period of sampling.

Factors investigated were density of *T. telescopium* (De); mangrove intertidal habitat (Ha) and sites nested in habitat (St(Ha)).
SNK is the result of Student-Newman-Keuls multiple comparison tests. Underlines show non significant differences (P < 0.05).
Sn = site number; H and L = landward and seaward areas respectively.
(*), (**) and (***) indicate that the differences are significant at tha 95 %, 99% and 99.9 % levels respectively.

Month	Source of variation	Df.	Df. of F	F ratio	P	SNK
Initial	Density-De	3	3,12	1.8676	> 0.10	
(June 90)	Habitat-Ha	1	1,4	1.4560	> 0.10	
	Site-St(Ha)	4	4,48	42.3259	< 0.001***	HS1 HS2 LS3 LS1 LS2 HS3
	De x Ha	3	3,12	1.4885	> 0.25	
	De x St(Ha)	12	12,48	0.6867	> 0.25	
September 90	De	3	3,60	2.0574	>0.25	
	Ha	1	1,4	19.7574	< 0.01**	
	St(Ha)	4	4,48	2.7924	< 0.05*	HS2 HS1 HS3 LS1 LS2 LS3
	De x Ha	3	3,12	1.4702	> 0.10	
	De x St(Ha)	12	12,48	0.7525	> 0.25	
December 90	De	3	3,12	0.8403	> 0.25	
	Ha	1	1,4	5.6847	> 0.05	
	St(Ha)	4	4,48	2.5589	> 0.05	
	De x Ha	3	3,12	0.1984	> 0.25	
	De x St(Ha)	12	12,48	1.0030	> 0.25	
March 91	De	3	3,12	1.1587	> 0.25	
	Ha	1	1,4	2.2867	> 0.25	
	St(Ha)	4	4,48	1.0358	> 0.25	
	De x Ha	3	3,12	0.4252	> 0.25	
	De x St(Ha)	12	12,48	0.0771	> 0.25	
June 91	De	3	3,12	3.5568	< 0.05*	D2x D½x D1x D0x
	Ha	1	1,4	0.0852	> 0.25	
	St(Ha)	4	4,48	13.7130	> 0.001***	HS1 HS2 LS3 LS1 LS2 HS3
	De x Ha	3	3,12	0.1338	> 0.25	
	De x St(Ha)	12	12,48	1.2931	> 0.25	

Table 6.3. Results of three way ANOVAs of the species richness index (*i.e.* Margalef index) in each period of sampling.

Factors were density of *T. telescopium* (De), habitat (Ha) and Site nested in habitat (St).
(*), (**) and (***) indicate that the differences are significant at tha 95 %, 99% and 99.9 % levels respectively.

Source of variation	Df.	Df. of F	F ratio	P
A. Initial				
Density (De)	3	3,12	0.1520	>0.25
Habitat (Ha)	1	1,4	4.078	>0.1
Site (St)	4	4,48	21.5050	<0.0005***
De x Ha	3	3,12	0.4577	>0.25
De x St	12	12,48	1.6347	>0.1
B. September 90				
Density (De)	3	3,12	0.7662	> 0.25
Habitat (Ha)	1	1,4	0.4960	> 0.25
Site (St)	4	4,48	7.3468	< 0.0005***
De x Ha	3	3,12	0.4297	> 0.25
De x St	12	12,48	1.6408	> 0.1
C. December 90				
Density (De)	3	3,12	0.4245	> 0.25
Habitat (Ha)	1	1,4	0.7593	> 0.25
Site (St)	4	4,48	5.6835	< 0.001***
De x Ha	3	3,12	0.6535	> 0.25
Da x St	12	12,48	1.0693	> 0.25
D. March 91				
Density (De)	3	3,12	0.4171	> 0.25
Habitat (Ha)	1	1,4	0.0019	> 0.25
Site (St)	4	4,48	9.9038	< 0.01**
De x Ha	3	3,12	1.9364	> 0.25
De x St	12	12,48	1.03762	> 0.25
E. June 91				
Density (De)	3	3,12	1.6557	> 0.25
Habitat (Ha)	1	1,4	0.0151	> 0.25
Site (St)	4	4,48	6.8709	< 0.0005***
De x Ha	3	3,12	0.3852	> 0.25
De x St	12	12,48	1.0935	> 0.25

Table 6.4. Results of three way ANOVAs of the Shannon-Weaver diversity index in each period of sampling.

Factors were density of *T. telescopium* (DE), habitat (HA) and Site nested in habitat (ST).
(*), (**) and (***) indicate that the differences are significant at tha 95 %, 99% and 99.9 % levels, respectively.

Source of variation	Df.	Df. of F	F ratio	P
A. <u>Initial</u>				
Density (DE)	3	3,12	1.6757	>0.25
Habitat (HA)	1	1,4	0.0018	>0.25
Site (ST)	4	4,48	22.7369	<0.0005***
DE x HA	3	3,12	0.2750	>0.25
DE x ST	12	12,48	1.7452	>0.25
B. <u>September 90</u>				
Density (DE)	3	3,12	0.0446	>0.25
Habitat (HA)	1	1,4	0.5320	>0.25
Site (ST)	4	4,48	8.9720	<0.0005***
DE x HA	3	3,12	0.7623	>0.25
DE x ST	12	12,48	1.0439	>0.25
C. <u>December 90</u>				
Density (DE)	3	3,12	0.09030	>0.25
Habitat (HA)	1	1,4	0.3318	>0.25
Site (ST)	4	4,48	9.3478	<0.0005***
DE x HA	3	3,12	0.5604	>0.25
DE x ST	12	12,48	1.50423	>0.25
D. <u>March 91</u>				
Density (DE)	3	3,12	0.5484	>0.25
Habitat (HA)	1	1,4	0.0016	>0.25
Site (ST)	4	4,48	4.7849	<0.05*
DE x HA	3	3,12	1.1514	>0.25
DE x ST	12	12,48	1.0211	>0.25
E. <u>June 91</u>				
Density (DE)	3	3,12	3.3071	>0.05
Habitat (HA)	1	1,4	0.0463	>0.25
Site (ST)	4	4,48	3.4063	<0.025*
DE x HA	3	3,12	1.0262	>0.25
DE x ST	12	12,48	0.7001	>0.25

Table 6.5. Results of three way ANOVAs of the evenness index in each period of sampling.

Factors were density of *T. telescopium* (DE), habitat (HA) and Site nested in habitat (ST).
(*), (**) and (***) indicate that the differences are significant at the 95 %, 99% and 99.9 % levels, respectively.

Source of variation	Df.	Df. of F	F ratio	P
A. Initial				
Density (DE)	3	3,12	2.2194	>0.10
Habitat (HA)	1	1,4	1.8192	>0.25
Site (ST)	4	4,48	4.8134	>0.25
DE x HA	3	3,12	0.0378	>0.25
DE x ST	12	12,48	1.8863	>0.05
B. September 90				
Density (DE)	3	3,12	1.3962	>0.25
Habitat (HA)	1	1,4	3.7960	>0.10
Site (ST)	4	4,48	1.5653	>0.10
DE x HA	3	3,12	3.0113	>0.05
DE x ST	12	12,48	0.5289	>0.25
C. December 90				
Density (DE)	3	3,12	2.0283	>0.10
Habitat (HA)	1	1,4	0.4808	>0.25
Site (ST)	4	4,48	3.5438	<0.05*
DE x HA	3	3,12	0.7734	>0.25
DE x ST	12	12,48	0.8553	>0.25
D. March 91				
Density (DE)	3	3,12	2.1434	>0.10
Habitat (HA)	1	1,4	3.6326	>0.10
Site (ST)	4	4,48	0.3099	>0.25*
DE x HA	3	3,12	0.2284	>0.25
DE x ST	12	12,48	1.0121	>0.25
E. June 91				
Density (DE)	3	3,12	3.6031	<0.05*
Habitat (HA)	1	1,4	0.0001	>0.25
Site (ST)	4	4,48	6.6853	<0.01**
DE x HA	3	3,12	1.2102	>0.25
DE x ST	12	12,48	1.1681	>0.25

Table 6.6. Dominant benthic diatom species in density treatments of *Telescopium telescopium* in different habitats in June 1990 (initial sampling).

Dn H/L indicates densities of the snail (n times natural density) in certain habitats (H = landward, L = seaward mangrove areas).
Data were standardised using general relativization $(X_{ij}/\Sigma X_j) \times 100\%$.

SPECIES	D0 H	D½ H	D1 H	D2 H	D0 L	D½ L	D1 L	D2 L
Achnanthes delicatula	3.36	4.15	5.87	5.69	4.31	2.28	6.15	4.40
Amphora coffeaeformis	21.77	17.31	17.76	18.06	22.67	24.05	26.39	26.92
Amphora ovalis	5.91	3.08	5.75	2.06	8.72	9.75	10.48	5.73
Amphora ventricosa	5.69	4.64	3.00	4.03	2.47	1.81	2.32	2.96
Gyrosigma scalproides	1.68	1.59	0.69	0.94	1.07	2.33	1.11	1.20
Mastogloia exigua	0.96	0.01	0.10	0.01	5.36	2.40	0.92	1.40
Navicula cincta	1.52	3.50	1.08	2.93	1.91	1.51	2.06	2.15
Navicula halophila	7.43	12.21	7.70	11.66	11.31	11.14	10.96	10.71
Navicula tripunctata	11.60	20.25	23.83	17.82	13.95	20.04	14.87	13.52
Nitzschia closterium	6.30	2.49	2.04	4.46	2.83	0.33	0.79	2.36
Nitzschia granulata	2.47	3.79	8.20	2.68	3.64	3.21	1.85	4.10
Nitzschia punctata	12.35	7.88	9.70	8.89	7.72	6.04	7.64	7.69
Nitzschia sigma	1.81	2.55	1.26	3.01	1.11	1.38	2.40	1.97
Rhophalodia musculus	1.12	1.27	0.85	3.03	1.52	1.61	1.43	2.32
Navicula sp.	16.04	15.26	12.17	14.72	11.42	12.11	10.62	12.58
TOTAL	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

Table. 6.7. Dominant benthic diatom species in density treatments of *Telescopium telescopium* in different habitats in September 1990.

Dn H/L indicates densities of snail (n times natural density) in certain habitats (H = landward, L = seaward mangrove areas). Data were standardised using general relativization $(X_{ij}/\Sigma X_j) \times 100\%$.

Species	DO H	D½ H	D1 H	D2 H	D0 L	D½ L	D1 L	D2 L
Achnanthes delicatula	4.14	4.56	4.91	4.33	5.32	3.28	5.18	4.73
Amphora acutiuscula	3.98	2.44	2.53	2.72	3.43	3.28	5.07	4.94
Amphora coffeaeformis	13.67	10.71	10.30	11.07	9.41	10.13	9.80	10.10
Amphora ovalis	6.86	9.99	7.02	7.70	7.06	6.53	7.34	7.43
Amphora subturgida	6.45	4.72	4.83	6.13	5.49	5.23	5.61	4.91
Amphora veneta	1.61	3.56	2.08	3.55	2.34	3.12	3.48	2.55
Amphora ventricosa	1.41	1.00	1.92	4.15	3.43	2.99	4.79	3.89
Bacillaria paradoxa	3.88	4.32	1.89	2.31	2.89	3.28	2.32	0.90
Gyrosigma scalproides	6.10	5.36	4.91	3.04	4.35	3.12	2.61	3.98
Mastogloia exigua	4.89	4.76	2.53	4.98	4.89	5.03	3.20	5.54
Navicula cincta	1.97	4.88	10.30	2.95	2.49	3.12	3.40	2.46
Navicula gregaria	5.04	5.64	7.02	7.19	0.00	0.00	0.00	0.00
Navicula halophila	0.00	0.00	4.83	0.00	6.89	7.18	6.32	6.05
Navicula tripunctata	7.92	5.56	2.08	5.62	4.63	4.35	4.70	5.63
Nitzschia cocconeiformis	2.17	1.04	1.92	1.75	1.52	2.76	2.01	3.74
Nitzschia granulata	3.38	4.16	1.89	1.89	4.12	4.12	2.86	4.64
Nitzschia obtusa	0.00	0.76	0.98	0.78	4.12	3.28	4.65	2.46
Nitzschia punctata	7.26	6.71	7.70	9.22	5.97	6.69	6.01	5.99
Nitzschia sigma	3.78	2.44	3.58	2.31	2.63	3.12	4.08	2.97
Rhopalodia gibberula	1.46	2.56	2.08	0.32	2.89	4.12	1.50	3.39
Rhopalodia musculus	3.33	4.24	4.91	6.18	5.06	4.32	3.20	2.88
Trachyneis aspera	0.71	2.36	1.85	2.49	3.43	3.28	4.39	3.68
Navicula sp.	9.98	8.27	7.96	9.31	7.66	7.69	7.48	7.13
TOTAL	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

Table. 6.8. Dominant benthic diatom species in density treatments of *Telescopium telescopium* in different habitats in December 1990.

Dn H/L indicates densities of snail (n times natural density) in certain habitats (H = landward, L = seaward mangrove areas). Data were standardised using general relativization $(X_{ij}/\Sigma X_j) \times 100\%$.

Species	D0 H	D½ H	D1 H	D2 H	D0 L	D½ L	D1 L	D2 L
Achnanthes delicatula	0.67	1.30	3.58	3.26	3.83	5.36	2.74	2.01
Amphora coffeaeformis	12.25	15.28	12.75	12.43	11.01	11.50	11.23	12.02
Amphora ovalis	4.33	2.35	5.70	4.53	7.85	7.00	7.11	6.21
Amphora subturgida	6.89	6.75	4.99	5.30	3.11	3.73	5.28	5.55
Amphora turgida	0.00	2.35	1.14	0.61	3.61	4.36	5.99	4.77
Amphora veneta	2.80	5.07	1.14	2.93	3.47	3.95	2.45	3.10
Bacillaria paradoxa	8.78	10.15	8.25	5.58	9.56	3.23	7.44	10.41
Gyrosigma scalproides	2.32	3.65	5.91	2.10	2.53	2.82	3.83	1.66
Mastogloia exigua	4.69	2.35	2.50	4.25	4.74	2.09	3.20	2.89
Navicula cincta	3.60	1.86	2.88	4.25	2.07	3.36	2.95	3.80
Navicula cuspidata	3.23	4.39	4.45	5.08	5.32	5.05	4.82	5.82
Navicula gregaria	0.00	0.00	0.00	0.00	8.89	9.41	8.32	8.31
Navicula halophila	5.30	6.50	6.67	7.35	0.00	0.00	0.00	0.00
Navicula ramosissima	2.07	3.28	0.00	1.16	5.14	5.91	3.41	2.89
Navicula tripunctata	8.29	10.46	6.51	7.96	5.73	8.77	7.44	9.44
Nitzschia granulata	4.02	3.65	3.85	4.25	2.53	2.55	4.37	3.10
Nitzschia hungarica	6.64	3.65	7.05	6.24	3.47	3.64	0.87	2.32
Nitzschia obtusa	1.83	0.68	2.06	2.54	3.20	3.64	4.53	2.89
Nitzschia sigma	5.00	2.85	3.85	4.53	2.07	2.68	3.83	2.32
Surirella gemma	4.33	2.35	4.99	4.81	1.71	0.95	1.58	1.31
Navicula sp.	12.98	11.08	11.72	10.83	10.15	10.00	8.61	9.18
TOTAL	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

Table. 6.9. Dominant benthic diatom species in density treatments of *Telescopium telescopium* in different habitats in March 1991.

Dn H/L indicates densities of snail (n times natural density) in certain habitats (H - landward, L - seaward mangrove areas). Data were standardised using general relativization $(X_{ij}/\Sigma X_j)$ x 100%.

Species	D0 H	D½ H	D1 H	D2 H	D0 L	D½ L	D1 L	D2 L
Achnanthes delicatula	2.32	1.93	2.40	4.40	2.99	3.66	3.52	3.40
Amphora coffeaeformis	9.51	11.40	10.84	8.51	9.51	10.81	11.07	10.43
Amphora ovalis	2.71	2.47	3.22	3.19	3.38	4.89	5.71	3.95
Amphora veneta	2.32	3.23	3.95	3.38	3.11	3.81	4.25	2.31
Bacillaria paradoxa	1.62	6.16	3.22	1.10	5.28	3.66	4.33	5.20
Cocconeis directa	2.71	0.88	2.68	2.17	2.06	4.49	2.83	2.58
Mastogloia exigua	7.61	4.23	2.99	3.01	2.68	3.06	1.63	2.58
Navicula cincta	3.24	1.93	3.95	5.69	5.05	3.06	4.85	2.77
Navicula cryptocephala	4.79	3.86	5.26	3.71	4.66	1.19	2.83	4.96
Navicula cuspidata	4.23	4.74	5.76	7.45	6.79	4.49	5.96	5.63
Navicula halophila	5.46	6.58	6.81	7.05	6.09	5.84	5.58	7.35
Navicula tripunctata	10.32	11.27	10.57	8.88	8.97	9.61	8.97	8.05
Nitzschia closterium	5.07	7.80	4.17	7.49	5.16	3.81	2.66	2.07
Nitzschia granulata	4.09	4.02	3.22	2.42	4.85	5.40	5.45	5.08
Nitzshia hungarica	2.71	2.47	3.22	3.71	5.51	3.06	0.47	5.86
Nitzschia longissima	4.47	5.32	3.72	4.77	4.43	6.95	10.25	6.84
Nitzschia lorenziana	6.48	4.02	4.36	6.42	3.38	2.34	1.07	2.58
Nitzschia sigma	4.90	4.02	5.13	4.15	2.06	2.82	3.17	1.48
Nitzschia tryblionella	5.78	4.40	4.17	4.15	1.32	1.19	0.00	2.31
Rhopalodia gibba	0.74	0.00	0.00	0.00	3.45	6.36	5.58	4.26
Navicula sp.	8.91	9.26	10.34	8.37	9.28	9.50	9.82	10.32
Total	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

Table. 6.10. Dominant benthic diatom species in density treatments of *Telescopium telescopium* in different habitats in June 1991.

Dn H/L indicates densities of snail (n times natural density) in certain habitats (H = landward, L = seaward mangrove areas). Data were standardised using general relativization $(X_{ij}/\Sigma X_j) \times 100\%$.

Species	DO H	D½ H	D1 H	D2 H	D0 L	D½ L	D1 L	D2 L
Achnanthes delicatula	0.90	1.58	2.21	3.20	5.90	4.17	5.87	5.70	
Amphora coffeaeformis	12.26	11.20	9.28	9.37	11.06	11.66	11.57	11.26	
Amphora ovalis	0.00	5.73	5.50	6.11	6.91	7.86	7.32	8.04	
Amphora turgida	5.16	3.01	1.51	3.37	4.19	3.86	4.68	3.80	
Amphora veneta	3.83	4.85	3.01	4.56	7.93	8.08	8.18	7.13	
Amphora ventricosa	4.45	2.88	2.21	2.22	4.29	4.25	4.74	5.95	
Mastogloia exigua	9.11	4.92	7.11	5.88	3.26	2.83	3.77	3.49	
Navicula cincta	2.78	4.78	3.64	2.14	4.91	4.17	4.16	4.08	
Navicula cuspidata	4.90	4.16	5.45	5.35	4.03	3.91	4.30	4.65	
Navicula halophila	7.82	5.98	7.60	7.66	7.46	7.78	8.01	8.49	
Navicula inserata	8.33	8.54	8.41	8.06	1.01	1.75	0.58	0.33	
Navicula tripunctata	11.03	11.24	11.24	10.40	9.93	10.02	9.41	10.44	
Nitzschia granulata	5.41	6.80	7.40	6.24	8.62	9.33	8.60	8.16	
Nitzschia punctata	7.63	8.77	9.53	8.84	7.50	7.85	7.22	7.09	
Rhopalodia gibberula	7.27	6.20	6.38	7.76	4.93	4.70	3.51	3.38	
Navicula sp.	9.14	9.37	9.51	8.84	8.08	7.79	8.09	7.99	
Total	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	

Table 6.11. Chi square goodness of fit tests on the frequency of occurrence of non-diatom algae as a function of density of *Telescopium telescopium* and of habitat in each period of sampling.

(***) indicates that the differences are significant at the 99.9 % level.

Factor	Period of sampling	Chi square	D.F.	P
Density. (k = 4)	Initial (June 1990)	1.8560	3	0.6028
	September 1990	55.6300	3	< 0.0001***
	December 1990	0.0911	3	0.9929
	March 1991	0.1767	3	0.9813
	June 1991	0.8662	3	0.9934
Habitat (k = 2)	Initial (June 1990)	0.0059	1	0.9390
	September 1990	0.0193	1	0.8894
	December 1990	0.1300	1	0.7184
	March 1991	0.0018	1	0.9655
	June 1991	0.0335	1	0.8547

Table 6.12. Results of three way ANOVAs of productivity of benthic algae in each period of sampling.

Factors were density of *T. telescopium* (D), habitat (H) and Site nested in habitat (S).
(*), (**) and (***) indicate that the differences are significant at the 95 %, 99% and 99.9 % levels respectively.

Periods of sampling	Source of variation	Df.	Df of F	F ratio	P
December 90	Density (D)	3	3,12	28.53	< 0.0005***
	Habitat (H)	1	1,4	1021.3	< 0.0005***
	Site (S)	4	4,48	0.18	> 0.25
	Interaction (DxH)	3	3,12	26.73	< 0.0005***
	Interaction (DxS)	12	12,48	0.53	> 0.25
March 91	D	3	3,12	12.86	< 0.0005***
	H	1	1,4	10.10	< 0.05*
	S	4	4,48	1.78	> 0.10
	D x H	3	3,12	5.64	< 0.025*
	D x S	12	12,48	1.73	> 0.05
June 91	D	3	3,12	24.41	< 0.0005***
	H	1	1,4	74.54	< 0.001***
	S	4	4,48	0.43	> 0.25
	D x H	3	3,12	2.68	> 0.05
	D x S	12	12,48	0.64	> 0.25
September 91	D	3	3,12	21.82	< 0.0005***
	H	1	1,4	232.38	< 0.0005***
	S	4	4,48	0.56	> 0.25
	D x H	3	3,12	5.33	< 0.025*
	D x S	12	12,48	4.73	< 0.0005***

Table 6.13. Kruskal-Wallis non-parametric tests by ranks on the effects of season on abundance of benthic diatoms in different density treatments of *T. telescopium*.

Dn is density of the snail (n times natural density). H is the Kruskal-Wallis statistic. P is the probability of rejecting Ho using a chi-squared approximation. SNK is the result of the non-parametric Student-Newman-Keuls test. Underlines indicate no significant difference between mean ranks (P < 0.05). JU1, SE, DE, MA, JU2 are periods of sampling *i.e.* Initial (June 1990), September 1990, December 1990, March 1991 and June 1991 respectively.

(**) and (***) indicate that the differences are significant at the 99% and 99.9 % levels respectively.

Treatment	n	H	P	SNK
D0	18	42.3044	< 0.0001***	DE SE MA JU1 JU2
D½	18	44.2150	< 0.0001***	DE SE MA JU1 JU2
D1	18	42.4730	< 0.0001***	DE MA SE JU1 JU2
D2	18	39.5412	< 0.0001***	DE MA SE JU1 JU2
Average	72	164.0518	< 0.0001***	DE MA SE JU1 JU2

Table 6.14. Kruskal-Wallis non-parametric tests by ranks on the effects of season on the species richness index of benthic diatoms in different density treatments of *T. telescopium*.

See caption for Table 6.13 for details of other abbreviations.

Treatment	n	H	P	SNK
D0	18	27.9800	< 0.0001***	DE SE MA JU1 JU2
D½	18	25.7026	< 0.0001***	DE SE MA JU1 JU2
D1	18	22.9319	< 0.0001***	DE MA SE JU2 JU1
D2	18	27.6807	< 0.0001***	SE DE MA JU1 JU2
Average	72	99.9660	< 0.0001***	DE MA SE JU2 JU1

Table 6.15. Kruskal-Wallis non-parametric tests by ranks on the effects of season on the Shannon-Weaver index of benthic diatoms in different density treatments of *T. telescopium*.

See caption for Table 6.13 for details of other abbreviations.

Treatment	n	H	P	SNK
D0	18	7.3327	0.1193	
D½	18	3.4504	0.4855	
D1	18	2.9275	0.5700	
D2	18	13.3198	0.0098 **	DE SE MA JU1 JU2
Average	72	17.7746	0.0014 **	DE SE MA JU1 JU2

Table 6.16. Kruskal-Wallis non-parametric test by ranks on the effects of season on the evenness index of benthic diatoms in different density treatments of *T. telescopium*.

See caption for Table 6.13 for details of other abbreviations.

Treatment	n	H	P	SNK
D0	18	48.6275	< 0.0001 ***	JU2 JU1 SE MA DE
D½	18	37.7052	< 0.0001 ***	JU1 JU2 MA SE DE
D1	18	34.6532	< 0.0001 ***	JU1 JU2 SE DE MA
D2	18	24.8401	< 0.0001 ***	JU1 JU2 DE MA SE
Average	72	132.1403	< 0.0001 ***	JU1 JU2 SE MA DE

Table 6.17. Dominant benthic diatom species in density treatments of *T. telescopium* in different seasons (n = 18).

(0), (½), (1) and (2) indicate densities of snails (n times natural density). Data were standardised using general relativization ($X_{ij}/\Sigma X_{ij}$ x 100%).

SPECIES	Relative frequency of occurrence (%)															
	September 90				December 90				March 91				June 91			
Density	0	½	1	2	0	½	1	2	0	½	1	2	0	½	1	2
Ach. delicatula	4.68	2.85	4.87	3.95	1.75	3.23	2.02	1.42	1.56	1.67	1.74	2.84	1.46	0.92	1.91	2.22
Am. coffeaeformis	27.8	25.9	27.8	27.6	12.5	14.9	15.1	13.4	18.2	22.8	19.5	17.3	25.8	24.1	19.8	18.5
Am. ovalis	9.53	13	11.0	11.0	6.92	5.33	6.93	4.51	1.9	2.6	3.38	2.4	4.73	5.02	4.24	5.93
Am. subturgida	5.85	4.61	5.48	5.05	3.7	4.21	4.41	4.27	1.43	1.11	0.82	0.62	0.67	0.6	0.6	0.25
Am. veneta	1.15	2.25	1.96	1.81	2.1	3.46	1.13	1.78	1.6	2.22	2.71	1.78	4.61	4.85	4.5	3.9
Am. ventricosa	1.84	1.31	3.14	3	1.26	1.58	1.01	1.42	1.3	0.56	0.26	0.18	1.58	1.14	1.28	2.15
B. paradoxa	2.02	2.71	1.19	0.72	12.7	6.76	9.32	11.8	2.59	3.89	2.46	2.4	0.94	0.42	0.71	0.93
G. scalproides	4.15	3.25	3.01	2.7	1.61	2.18	3.78	0.95	0.56	1.95	1.13	1.24	0.77	0.81	0.63	0.51
M. exigua	4.29	4.41	2.71	5.33	3.63	1.35	1.89	2.14	6.44	2.32	1.23	1.69	4.61	1.48	3.11	2.44
N. cincta	1.3	2.95	2.18	1.58	1.68	1.88	1.89	2.61	3.11	1.39	3.07	3.64	1.36	1.84	1.36	1.15
N. cuspidata	0.57	0.94	1.43	0.71	3.56	3.98	3.78	4.39	5.27	3.34	4.91	7.56	1.63	1.51	2.21	2.54
N. halophila	0	0	0	0	1.68	2.4	2.64	2.85	5.62	5.75	5.42	8.71	5.99	5.06	6.78	8.13
N. inseriata	0	0	0	0	0	0	0	0	0	0	0	0	3.19	4.34	4.06	4.07
N. tripunctata	5.49	4.3	5.42	5.77	6.57	13.3	7.93	11.1	19.9	19.2	14.4	13.1	16.8	18.4	17.5	18.3
Ni. granulata	2.93	3.22	1.69	3.06	2.03	2.03	0	2.25	3.5	3.61	3.17	2.76	6.41	8.21	7.8	6.2
Ni. punctata	7.18	8.25	8.64	9.26	14.6	12.1	17	17.0	6.09	7.04	14.7	12.5	5.87	8.1	8.85	8.13
Ni. sigma	1.83	1.81	3	1.69	2.24	1.8	2.77	2.02	2.76	2.13	2.81	1.96	0.72	0.36	0.71	0.68
R. gibberula	1.45	2.54	0.89	1.57	0.21	1.13	1.64	0.83	1.25	3.15	2.35	1.51	3.32	2.83	2.43	4.24
R. musculus	4.05	3.42	2.95	3.22	1.89	1.35	0.88	1.42	0.82	0.74	0.1	0.89	0.92	0.74	1.52	0.44
Navicula sp.	13.8	12.2	12.5	11.8	19.2	16.8	15.8	13.6	16.0	14.4	15.6	16.8	8.49	9.11	9.92	9.22
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100

Table 6.18. Kruskal-Wallis non parametric test by ranks on the effects of season on production of carbon of benthic microalgae in different densities of *T. telescopium*.

Dn is density of the snail (n times natural density). H is the Kruskal-Wallis statistic. P is the probability of rejecting Ho using the Chi-squared approximation. SNK is the result of the non-parametric Student-Newman-Keuls test. Underlines indicate no significant difference between mean ranks ($P > 0.05$). DE, MA JU and SE are periods of sampling *i.e.* December 1990, March 1991, June 1991 and September 1991, respectively.

(***) indicate that the differences are significant at the 99.9 % level .

Treatment	$\underline{n}$	H	$\underline{P}$	SNK
D0	18	59.8757	< 0.0001***	$\underline{\text{DE MA}}$ JU SE
D½	18	18.1543	0.0004 ***	$\underline{\text{DE MA}}$ $\underline{\text{SE JU}}$
D1	18	56.4824	< 0.0001***	$\underline{\text{MA DE}}$ JU SE
D2	18	58.4133	< 0.0001***	MA DE JU SE
Average	72	175.5922	< 0.0001***	$\underline{\text{MA DE}}$ JU SE

Table 6.19. Correlation between productivity of benthic algae and abundance of benthic diatoms.

Statistical test used was the non-parametric Spearman's rank correlation coefficient test. $\underline{P}$ is the probability of accepting H_o (non-significant correlation).

(*) indicates that the differences are significant at the level of 95 % .

Correlation (n = 72)	Spearman's correlation coefficient (rs)	P
1. December 1990	+ 0.3281	< 0.05 *
2. March 1991	+ 0.0837	> 0.05
3. June 1991	+ 0.2344	< 0.05 *

Chapter 7.

General Discussion.

7. General Discussion.

This thesis has investigated several inter-related aspects of the ecology of both benthic diatoms and *T. telescopium* within a natural, undisturbed mangrove ecosystem. These aspects were distribution and abundance of the benthic diatoms, *T. telescopium* principal food (diatoms), feeding and growth of the gastropod and it's grazing impact on diatom communities.

Some conclusions, can be extracted from the results in Chapters 3 to 6:

1. Mangrove sediments adjacent to Chunda Bay supported 223 taxa of benthic diatoms belonging to 18 families and 48 genera. The most dominant family was the Naviculaceae. Higher similarity occurred among benthic diatom assemblages from sites in areas of running water (*i.e.* wet areas) than in standing water areas. Assemblages of benthic diatoms in the seaward and landward habitats showed more similarity than dissimilarity.

2. The abundance of *T. telescopium* differed significantly between locations within the mangrove system (locations separated by distances of 0.35 to 2.00 km), but not between intertidal habitats and sites within combinations of habitat and location.

3. The lengths and weights of *T. telescopium* in the seaward habitat were generally greater than those in the landward habitat. The length of the shell was a good predictor of the fresh weight.

4. The rate of growth of *T. telescopium* in the seaward habitat was slightly higher than that in the landward habitat.

5. *T. telescopium* fed on benthic diatoms, detritus and microalgae in combination. During it's foraging movements, the gastropod decreased population density of benthic diatoms significantly on the scale of individual foraging tracks. This appeared to be due to the actual feeding process of the gastropod, as opposed to mechanical disturbance as the snail moved across the substratum.

6. The different experimental densities of *T. telescopium* used in these investigation did not affect the abundance, number of species and community diversity of benthic diatom nor the abundance of non-diatom microalgae significantly.

7. Grazing by *T. telescopium* affected the productivity of benthic algae significantly. Lower primary productivity was often recorded in the half and twice natural density treatments of *T. telescopium.* The natural density treatment consistently had a relatively high primary production.

8. The effect of season on abundance of benthic diatoms was significant. The highest abundance of benthic diatoms was in winter. This seasonal effect was most apparent when the densities of *T. telescopium* were experimentally reduced to zero and half normal density.

9. Primary productivity of benthic algae was lower during summer (December to March) than during winter (June, September). The effect of grazing of *T. telescopium* was more significant during winter. The primary productivity in the high density treatment of *T. telescopium* was always the lowest of the treatments in all periods.

10. The primary productivity of benthic microalgae was highly correlated with the abundance of benthic diatoms in the winter/spring periods. During summer this correlation was not significant.

It is likely that the distribution and abundance of *T. telescopium* in this mangrove ecosystem are not limited by abundance of benthic diatoms. Furthermore the relatively flat mangrove intertidal area might not physically restrict the spatial distribution of the mangrove whelk. This may allow *T. telescopium* to migrate from one habitat to another even if food ever became limited in one habitat. Green (1968) and Green and Hobson (1970) suggested also that access to food may be a more critical factor limiting abundance then food itself for animals in an intertidal environment.

The difference in the rate of growth of *T. telescopium* in the two different habitats may influence the size attained by this animal significantly. The values of length and fresh weight (including shell) of *T. telescopium* were significantly higher in the seaward than in the landward habitat (Chapter 5). Several factors that may influence these differences have been discussed in Chapter 5. Results in Chapter 5, however, implied strongly that the growth rate was relatively higher in the seaward habitat than in the landward habitat. The seaward habitat would appear to provide greater opportunity for growth of *T. telescopium.* The size and weight of this gastropod in this habitat, therefore, were significantly greater than those in the landward habitat. McLachlan and Lombard (1981) reported that one habitat may have provided a better physical conditions for growth of a rocky shore gastropod, *Turbo sarmaticus.* The growth of this gastropod was slightly lower in the habitat exposed in fairly heavy wave action than the habitat partly protected from the swell.

The primary productivity of benthic microalgae (Chapter 6) may be correlated with the rate of growth, size and biomass of *T. telescopium.* The values of the morphometrics and rate of growth of *T. telescopium* were significantly higher in the low than in the high intertidal habitats (see Chapters 3, 4 and 6). In Chapter 6, it was shown that the productivity of benthic algae living on mangrove sediments was higher in the lower than in the higher intertidal habitat. This suggested therefore, that the size of *T. telescopium* may be higher in an environment of higher productivity of benthic algae. The gastropod may grow better where "a good quality" of food is available. Branch (1974) suggested that the growth rate of a rocky shore gastropod *Patella longicosta* was determined by food value. A study by Bodoy and Plante-Cuny (1984, cited by Navarro *et al.*, 1992) on the shellfish, *Ruditapes decussatus*, indicated that its growth rate was correlated significantly with primary production of microphytobenthos.

The present study on distribution and abundance of *T. telescopium* was limited to sites occupied by this gastropod only. These sites always contained standing water during low tide, but during long periods of exposure (especially during hot, sunny days) this water in the landward (or high intertidal) habitat was evaporated. *T. telescopium* tends to cluster in sites close to standing water. Results in Chapter 3, however, showed that benthic diatom assemblages in dry sites differed from those in wet sites. Thus the clustering pattern of *T. telescopium* may be related to the spatial patterns of benthic diatom assemblages. This contention requires further study, since the clustering behaviour of *T. telescopium* adjacent to the wet sites may be influenced more strongly by physical factors such as heat stress and desiccation (see discussion in Chapter 4). The animals need to conserve body fluid to avoid desiccation. The effects of composition of benthic diatom assemblages and this physical stress may act synergistically to affect the clustering behaviour of the snail. McLachlan and Lombard (1981) suggested that both food and physical stress (*i.e.* temperature) were major factors affecting the growth of *Turbo sarmaticus*, a large, edible rocky shore gastropod. This may explain why *T. telescopium* was often very abundant in small ponds in open and unshaded areas, such as in Location 3 (see Chapter 4) and in similar specific habitats in Maluku, Indonesia (Budiman, 1988).

In tropical mangrove areas, *T. telescopium* is rarely found inside dense forests (see Lasiak and Dye, 1986 and Budiman, 1988). This may be due to differences in the benthic diatom assemblages within the mangrove areas and a certain degree of dependence of *T. telescopium* on benthic diatoms as food. In Chapter 3, species richness of diatoms was lowest in the areas with greatest coverage of mangrove trees. In Chapter 5, it was found that *T. telescopium* consumed benthic diatoms. Limitation of good quality food may, to a certain extent, impede this animal from existing in shady, darker places such as dense mangrove forests. Kristensen *et al.* (1988) suggested that the low productivity of algae on sediments inside mangrove forests of Thailand was due to the effect of shading. To support this contention, a laboratory or field study on the effects of shading on both *T. telescopium* and the benthic diatom community, is required.

Both the distribution and abundance, and the difference in morphometrics of *T. telescopium* in landward and seaward habitats (in Chapters 4 and 5, respectively) may be determined also by factors such as age and reproduction of this species. *T. telescopium* in the seaward habitat may reach maturity more quickly than in the landward habitat. The juvenile snails in the landward habitat may migrate to the seaward habitat as they mature. The snails may then spawn in the seaward habitat. Such a situation occurs in a natural habitat in Porto Novo, India. In this area *T. telescopium* has been found spawning at the low water mark from April to July (Ramamoorthi and Natarajan, 1973). Robertson *et al.* (1988) also recorded that gastropod larvae as well as polychaete larvae were more abundant in the mangrove main stream compared to abundance in the streams inside mangrove forests of Alligator Creek, North Queensland, Australia.

The effects of season may also influence the rate of growth of *T. telescopium*. It has been suggested above that size and growth of this mangrove whelk can be correlated with benthic microalgal primary productivity. However, the primary productivity itself was strongly affected by season as well as by the abundance of benthic diatoms (see Chapter 6). Therefore it is possible that the rate of growth of *T. telescopium* also varied with season. This contention requires further study. Many authors have reported seasonal growth in molluscs including Branch (1974) working on *Pattela longicosta*, McLachlan and Lombard (1981) on *Turbo sarmaticus* and Cockcroft and Forbes (1981) working on *Cerithidea decollata*. All of these studies recorded the lowest growth rate in the winter months.

From the results above, aspects of the ecology of *T. telescopium* may be generalised:

(1) The mangrove whelk does not control abundance/species richness of benthic diatoms nor vice versa.
(2) Growth rates of the whelk are greater in a lower intertidal habitat where diatom availability may be greater.
(3) The grazing by the whelk does affect productivity, more so in winter.

Results from Chapter 6 suggest that removal of a large number of *T. telescopium* from natural tropical mangrove habitats may affect the flow of energy (carbon) within the ecosystem. Productivity of benthic algae measured on semi-open sediments of mangroves was relatively high and highest at natural densities of *T. telescopium*. If abundance of the snail were decreased, results in Chapter 6 suggest that the productivity may decrease significantly. This may influence the oxygen content of mangrove waters significantly, thus affecting other organisms in the ecosystem indirectly.

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Appendix 1

A photograph showing *Telescopium telescopium* in a natural habitat at a mangrove area adjacent to Chunda Bay, North Queensland.

A photograph of one of the enlosures (1 m x 1 m) used to retain *Telescopium telescopium* during the field based experiment.

Appendix 3

A photograph showing *Telescopium telescopium* (approximately 9 cm total shell length) inside the enclosure and tracks created by natural foraging movement of *T. telescopium*.

A photograph showing the measurement of dissolved oxygen concentration in seawater inside the light and dark jars using a digital oxymeter.