UNIVERSITY OF SOUTHAMPTON

THE ECOLOGY OF A *Zostera noltii* BED ECOSYSTEM IN THE SOLENT

by

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ABSTRACT

FACULTY OF SCIENCE
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There is a scarcity of seagrass bed studies along the British coast inspite of numerous works conducted in the subtropics and temperate regions. This study observed the biological and chemical aspects of seagrass, sediment pigment production and macrozoobenthos dynamics of *Zostera noltii* bed on the Isle of Wight during September 1997 to October 1999 from the dense and sparse sites.

Seasonal patterns occurred in all studied seagrass biology aspects. Average values of shoot density (276-1020 stands·m^{-2}), shoot height (13-23.2 cm), shoot leaf number (2.4-5.7) were maximum in the summer and autumn, whilst shoot biomass (2.1-22.3 g DW·m^{-2}) had the highest values in the autumn. *Z. noltii* growth continued through April-October in each year. Reproduction was mainly through rhizomal growth, although flowering was recorded. Except for shoot leaf number per plant and shoot height, all variables were in higher values at the dense site.

Of the chemical constituents measured, only protein did not vary. There were no clear differences in the contents of total carbohydrate, phenolics and protein of *Z. noltii* between the two different sites.

Bed pigment production varied according to the season and site, and was mainly derived from the microphytobenthos chl-*a* in the sediment. The dense site always had higher average concentartions of chl-*a* than the sparse site, both through spectrophotometer (3.25-14.24μg·g^{-1} Vs 2.76-10.20 μg·g^{-1}) and HPLC (0.81-5.32 μg·g^{-1} Vs 0.66-4.24 μg·g^{-1}) analyses. Fucoxanthin values correlated with that of chl-*a*, indicating the main source of pigment was generated from diatoms. To a lesser extent, *Z. noltii* detritus contributed to the bed pigment production. Other pigments resulting from HPLC measurements were chl-*c1*+*c2*, lutein/zeaxanthin, *ß*-carotene, diatoxanthin and diadinoxanthin. Phaeopigment species, phaeophorbide *a* and phaeophytin *a* were also detected by HPLC, indicates the occurrences of macrozoobenthos grazing. The causes for higher values of chl-*a* and phaeopigment at the dense site were discussed.

The macrozoobenthos variables measured varied seasonally and most of them varied temporally. All trophic levels in the food chain were represented. Of 124 species found, the polychaetes (49 species), amphipods (29 species) and gastropods (15 species) composed the three most dominant groups accordingly. Macrozoobenthic abundance, biomass, species number and species richness decreased from the dense to the sparse sites, and from the warmer months to the winter periods, also species number was higher in comparison with many other seagrass beds. The higher degrees of species similarity occurred among the samples from the same season and between the spring and autumn samples. The possible reasons for these were presented.

This study emphasised the importance of seagrass bed in supporting the complexity of the food web within the system.

I dedicate this thesis
to my beloved wife, son and parents.

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Chapter I:
General Introduction

1.1. Seagrass and Seagrass Bed Ecosystem

A commonly found characteristic of shallow nearshore bays and inlets throughout the tropical and temperate regions is the presence of the seagrass beds. The seagrass bed ecosystem plays an important role in the coastal processes by: (1) Providing food and facilitating shelter for a great diversity of plant and animal species, including juvenile commercial fishes; (2) Trapping and recycling nutrients; (3) Increasing primary production of inshore waters; (4) Stabilising sediments and shorelines (Zieman and Wetzel, 1980; Orth *et al.*, 1984; Phillips and Meñez, 1988; Kennish, 1996). Of the seagrass meadows, seagrasses are known to be the main feature of vegetation (Barnes and Hughes, 1988; Bortone, 2000). In some cases there are associated alga species (Kennish, 1996; Tomaschik *et al.*, 1997) or salt marsh grasses (Dring, 1992; Junoy and Viéitez, 1992) found within the seagrass bed ecosystems.

Seagrasses are the only representative group of angiosperms found in the ocean (Dawson, 1960; Dahl, 1998). They evolved from terrestrial angiosperm ancestors that returned to the sea in the Cretaceous, ~100 million years B.P. (Klap *et al.*, 2000 and papers therein). Seagrasses are unique in their ability to achieve vegetative and reproductive cycles completely submerged in the marine environment. This group of vascular plant grows well particularly in shallow waters and retains effective leaves, flowers, roots and rhizomes (den Hartog, 1970). Morphologically, seagrass leaves are thin in general and have an elongate-ribbon type shape with a monopodial growth (Barnes and Hughes,

1988; Bortone, 2000). In comparison with most other marine vegetation, seagrass flowers eventually give rise to fruits and seeds. Seagrasses also effectively utilise root and rhizome for vegetative reproduction. The roots have fine hairs and they have an internal system in which gases and nutrients are translocated (Phillips and Meñez, 1988; Fortes, 1994). Taxonomically, seagrasses are comprised of 2 families, 12 genera and 48 species (Dawson, 1960; den Hartog, 1970; Phillips and Meñez, 1988; Dahl, 1998). The first family, the Hydrocharitaceae, consists of three genera: *Enhalus, Halopohlia* and *Thalassia*. In the second, the Potamogetonaceae, there are nine genera: *Amphibolis, Cymodocea, Halodule, Phyllospadix, Posidonia, Ruppia, Syringodium, Thalassodendron* and *Zostera*.

The centre of seagrass species distribution and bed existence appears to be in the Indo-Malaysian region; a second area of importance occurrence is in the Caribbean Sea (Tomascik *et al.*, 1997; Kennish, 1996; Barnes and Hughes, 1988). There are no seagrasses found in the polar regions (Valentine and Heck, 1999), and surprisingly, they are rare in South American coastal waters (Dawson, 1960; Phillips and Meñez, 1988). The *Phyllospadix* and *Zostera* genera are strictly temperate in distribution (Kennish, 1996; Dahl, 1998), whereas *Posidonia* may be found throughout warm-temperate to subtropical coastal waters (Mazella *et al.*, 1989, 1992; Dahl, 1998). The remaining members of the Potamogetonaceae are truly tropical species (den Hartog, 1970; Kennish, 1996; Phillips and Meñez, 1988; Bortone, 2000).

Zostera is known as the most widely distributed seagrass genus in the temperate coastal areas of North America as well as in the European intertidal and sublittoral zones, whereas *Thalassia* is the commonest genus found in tropical waters (Carter, 1993; Kennish, 1996; Mann, 1996; Dahl, 1998;). Of the *Zostera* species, *Zostera marina* and *Z. noltii* are the most widespread (Phillips and Meñez, 1988; Dahl, 1998; Reise, 1998-personal communication; Schramm, 1998-personal communication; Mattila *et al.*, 1999).

In Great Britain, *Zostera* biotopes are found throughout the shallow coastal regions (Davison and Hughes, 1998). Locally, *Zostera* species have been reported growing in the Solent region (an area covering the coasts of Dorset, Hampshire and the Isle of Wight) (Tubbs and Tubbs, 1983; Al-Suwailem, 1991; Aspinall and Tasleer, 1992; Barne *et al.*, 1996; Davidson, 1996; Jones, 1998; Sheader, 1998-personal communication; Ganter, 2000), Devon and Cornwall (Webster *et al.*, 1998), East Anglia (Stewart *et al.*, 1994; Hughes, 1998-personal communication) and the eastern coast of Scotland (Stewart *et al.*, 1994; Raffaelli, 1998-personal communication). Small patches of *Zostera* meadow have also been recorded along the shores of Wales, Northern Ireland and Southwest Scotland (Dahl, 1998; Davison and Hughes, 1998).

The size of the beds along with the number of seagrass species found within the bed can vary greatly. Seagrass communities range in size from a small patch of less than a square metre in area to vast meadow of hundreds of square kilometers (Phillips and Meñez, 1988; Reise, 1992; Philippart, 1994a; Davison and Hughes, 1998). The number of component species in one particular bed can range between one and twelve seagrass species (Brix *et al.*, 1983; Kirkman, 1990; Philippart, 1994a). The variations in the bed size and seagrass species have been attributed to different stages of meadow formation, from newly established patches to fully developed meadows (Cebrián *et al.*, 2000), though maximum area must be determined by the local availability of suitable condition for seagrass bed formation, and the maximum number of species determined by the number of species available in a given area.

In general, seagrasses grow in the mid-intertidal zone (Barnes and Hughes, 1988) in relatively protected coastal waters where there is enough light penetration to support their life cycle (Mann, 1996). Stands of seagrass generally occupy intertidal flats with a high-water depth of 4 - 5 m and the best growths are usually performed at 0.5 - 1.5 m deep (Carter, 1993). However, seagrass species distribution varies greatly according to the species, as well as local environmental characteristics (Phillips and Meñez, 1988; Kennish, 1996). *Zostera marina* and

Thalassodendron ciliatum both have been recorded at 30 m depths, *T. pachirhizum* was found at 40 m, *Posidonia oceanica* has been seen at 60 m, and *Halophilla* sp. was reported at as deep as 90 m (den Hartog, 1970).

1.2. The Ecological Importance of Seagrass Bed Ecosystems

During the past 50 years, and particularly in the last decade, there has been ever increasing interest in the ecological study of seagrasses and seagrass bed ecosystems in both tropical and temperate coastal waters (de Jonge and Schramm, 1998-personal communications; also see Bortone, 2000). The presence of seagrass bed ecosystems has been recognised as of major importance amongst the factors considered to be of significance in the dynamics of intertidal soft bottom macrofauna (Castel *et al.*, 1989; Junoy and Viéitez, 1992). Seagrass bed ecosystems are known to house some substantial numbers of marine organisms, particularly the benthic fauna (Randal, 1967; Parker, 1975; den Hartog, 1977; Davison and Hughes, 1998). A great number of animals may be found resident within seagrass meadows, since the ecosystem is able to provide a wide range of microhabitats for animals according to their complexity (Sardá *et al.*, 1995; Çinar *et al.*, 1998).

Seagrass bed ecosystems are considered as one of the most productive ecosystems in the world ocean (Barnes and Hughes, 1988; Phillips and Meñez, 1988; Mann, 1996; Raffaelli and Hawkins, 1996). In many cases, the standing stock and productivity of seagrass bed ecosystems can rival cultivated tropical agriculture (Zieman and Wetzel, 1980; Meñez, 1987; Tomaschik *et al.*, 1997) and may exceed that of adjacent plankton-dominated ecosystems (Phillips and Meñez, 1988; Dring, 1992; Sze, 1993; Bortone, 2000) as well as benthic alga communities (Dring, 1992; Sze, 1993). The high productivity is mainly attributable to the ability of this vegetation to fix organic carbon that later enters the marine food chain through direct herbivory and detrital decomposition (Carter, 1993; Barnes and

Hughes, 1988). The other factor contributing to the high productivity of the seagrass bed ecosystems is as a result of the bed accumulating fine sediments containing large amount of organic matter (Junoy and Viéitez, 1992). This organic matter provides an addition to the growing medium as well as nutrient resources for the primary producers of the bed.

Another ecological function of seagrass bed ecosystems is that the materials derived from the seagrass bed are not only utilised within the system but some of these materials are exported to the peripheral ecosystems in considerable amounts and over surprising distances (Kennish, 1996; Mann, 1996; Tomaschik, 1997). Only ca. 5 % annual production of seagrass is believed to be used directly by *in situ* consumers (Barnes and Hughes, 1988). The export of decomposed seagrass materials can vary; one study found that approximately 50 % of seagrass production in a North Carolina bed might was distributed to the surrounding ecosystems (Thayer *et al.*, 1975), whilst the study by Suchanek *et al.* (1985) indicated great variability with export estimates ranging from 1% to 100 %. From short-term measurements, it has been estimated that somewhere between ~3 and 100 % of seagrass net primary production enters the food webs through the grazing pathway (Nienhaus and Groenendijk, 1986; Greenway, 1995).

In some cases, seagrass material can be exported beyond the continental shelf. Substantial drift of seagrasses, mainly from *Thalassia,* have been reported in the deep sea off the North Carolina coast, 550 – 1100 km away from its known source region. Abundant seagrass detritus has also been reported in the deep sea in the Cayman Island and Puerto Rican trenches, the Virgin Islands basins (Suchanek *et al.*, 1985) as well as the Caribbean deep sea floor (Barnes and Hughes, 1988).

The water dynamics of the coastal region mainly determine the transport of seagrass materials to the outer ecosystems. Suchanek *et al.* (1985) noted that detrital segrasses often escape from the coastal environments, particularly during the winter storms, and are exported into the outer seagrass bed ecosystem as far as the deep sea. Also, rafts of drifting *Thalassia* ca. 50 m in diameter were noted in the Florida currents following a hurricane (Barnes and Hughes, 1988). Both

fragmented leaves and uprooted shoots, for example, were very often carried offshore by the currents and found to be significant in the diet of many herbivores (Tubbs and Tubbs, 1982, 1983; Alongi and Tenore, 1985; Aspinall and Tasleer, 1992; Green and Cade, 1997; Ganter, 1998-personal communication; Nacken and Reise, 2000).

Few investigators have speculated on the role of seagrass detritus and fresh seagrass materials as nutrition sources for marine organisms outside of seagrass bed ecosystems (Barnes and Hughes, 1988; Loneragan *et al.*, 1997; Sheridan, 1997; Bortone, 2000). One such study concluded that the abundance of commercially important gadoid (*Macruronus novazelandica*) larvae off the coast of Tasmania correlated not with the phytoplankton production, but somewhat surprisingly with the arrival of winter storms (Thresher *et al.*, 1992). $\delta^{13}C$ analyses showed gadoid larvae to feed mainly on the buoyant seagrass detritus transported by the storms, rather than phytoplankton. Direct seagrass consumption by fishes has long been established, particularly for the Carribean species. Herbivorous fishes seek shelter on coral reefs at night, commonly foraging in nearby seagrass meadows by the day (Zieman *et al.*, 1984; McAfee and Morgan, 1996). Two species of parrotfish, *Scarus guacamaia* and *S. coelestinus*, have been reported to move up 500 m inshore from their coral reefs to feed on seagrass (Valentine and Heck, 1999).

1.3. Research on the Faunistic Richness of Seagrass Beds

Seagrass bed ecosystems are considered as useful environments for investigating the role of habitat heterogeneity in structuring animal communities in the marine environments (Mazella *et al.*, 1992). In addition to providing rich sediment communities, the seagrasses themselves may be regarded as the major structural species in the community. Indeed, each part of the seagrass shoot actually provides a microhabitat for the animals and plants to live on.

As has been noted, a distinguishing characteristic of the seagrass bed ecosystem is the significantly greater abundance of animals and number of species as compared with adjacent unvegetated systems (Mazzella *et al.*, 1992; Davison and Hughes, 1998 and papers therein). In many cases seagrass beds also contain more species of benthic fauna compared with nearby vegetated environments (Sheridan, 1997). The faunistic richness of seagrass bed was first described by Petersen through his works in 1913 and 1918 in Danish waters (Zieman and Wetzel, 1980; Phillips and Meñez, 1988). Peterson's studies have inspired marine ecologists worldwide, and the studies on the benthic fauna associated with seagrass bed ecosystems have continued.

From the studies on European coasts, it can be summarised that the faunal richness of seagrass bed ecosystems declined sharply in the 1930s following a notorious 'wasting-disease' phenomenon of *Z. marina* and *Z. noltii* in the North Atlantic in 1931-1932 (Christiansen *et al.*, 1981; Phillips and Meñez, 1988; Davison and Hughes, 1998; Reise, 1998-personal communication; Bortone, 2000). In the 1950s and 1960s faunal research focused around European and Japanese studies describing communities or associations in seagrass bed habitats. There are many studies that have described the faunal assemblages of seagrass beds. These include works by the following authors: Thayer *et al.* (1975), Heck and Westone (1977), Withers (1979), Junoy and Viéitez (1992), Mazzella *et al.* (1992), Currás *et al.* (1993), Nelson and Virnstein (1996), Boström and Bondorff (1997; 2000), Bach *et al.* (1998), Çinar *et al.* (1998) and Webster *et al.* (1998). However, there is a scarcity of information on benthic animals associated with seagrass bed ecosystems in the British Isles coastal waters, though published studies from Northern European waters may provide useful comparitors.

1.4. Objectives of the Study

This study aimed to observe the interrelationships between the seagrass population, sediment bed pigment production and benthic macrofauna in order to gain an understanding of how the seagrass bed ecosystem functions in a UK site. The site, Ryde Beach, is situated on northern coast of the Isle of Wight on the south coast of England, and is located within the Solent, a channel separating the island from the mainland.

The first objective of the study was to follow the seasonal cycle of biological complexities and variations in the chemical constituents of the seagrass itself. The main reason for doing this was to provide a baseline data for an understudied geographic area (in terms of seagrass composition), namely the Isle of Wight and the Southern English coasts. This study, therefore, is the first attempt to describe the biological and chemical aspects of a seagrass community through regular sampling in English coastal waters. The study by Webster *et al.* (1998) on a Devon coast, Southwest England, determined shoot density and mean leaf number per shoot only. There are many other important biological parameters of the seagrass that need to be investigated. The present study assessed those two factors together with shoot height and aboveground biomass as well as total phenolic, carbohydrate and protein contents.

The second objective of the study was to observe the pigment dynamics of the seagrass bed sediment and to understand how the seagrass bed sediment influences the benthic macrofaunal community structure. Indeed, the relationships between the faunistic patterns and the pigment production of the seagrass bed sediment have been reported in many studies (see Levinton and McCartney, 1991; Underwood and Paterson, 1993; Cariou-LeGall and Blanchard, 1995; Karakassis and Eleftheriou, 1997). Until now no such study has been carried out on the south coast of England or for British seagrass bed ecosystems. In the present study, seagrass bed pigment dynamics were observed through the measurements of chlorophyll, seagrass associated pigments, microphytobenthos related pigments and phaeopigment species concentrations of the sediments.

The third objective was to investigate the dynamics of macrobenthic fauna in the seagrass bed. There has only been a single study in the area describing the faunal community at Ryde some 3 decades ago (Withers, 1979). Thus, there was a need to update the macrozoobenthic data from this marine ecosystem-rich island. Indeed, in spite of the rich body of literature on the animals associated with seagrass beds worldwide, there is only one other study reported on the macrobenthos fauna living among the seagrasses in the British Isles (Webster *et al.*, 1998). Although many attempts have been made to observe the animal communities of the seagrass beds worldwide (see the references in part 1.4. in this chapter), one study reported a scarcity of appropriate data on the overall zoobenthos of the seagrass (Çinar *et al.*, 1998). Thus, detailed studies are required in order to understand how the seagrass ecosystem functions. To follow the macrozoobenthic dynamics, this study observed the species composition, species number, abundance, biomass and diversity.

The present study was conducted over a-26 month period in order to follow the seasonal patterns of the observed variables. The samples for all aspects studied were collected from two different densities of seagrass population, i.e. the dense stands and sparse stands, allowing spatial pattern to be determined. In fact such changes in macrovegetation may also be accompanied by structural changes in associated faunal communities (Isakson and Pihl, 1992). Indeed, many studies have tried to relate faunal parameters of seagrass bed ecosystems from different densities of the seagrass (e.g. Edgar *et al.*, 1994; Webster *et al.*, 1998).

1.5. Hypotheses

This study proposed that:

1. Seagrass densities will influence the spatial patterns of macrozoobenthos dynamics.

2. The dynamics of seagrass bed pigment production and chemical constituents of seagrass are related to shoot densities and the season.
3. Seasonal variations in seagrass bed pigment production influence the temporal pattern of macrozoobenthos dynamics.

Chapter II:
Materials and Methods

2.1. Study Site

This study was carried out in the intertidal area of Ryde Beach, Isle of Wight, Southern England (Figure 2.1.). Ryde Beach is located in the eastern approach of the Solent, one of the busiest shipping areas in the English Channel. This small and biologically rich estuary has an intertidal area of approximately 466 ha with 18.5 km of shore length and geomorphologically falls into the coastal plain category (Davidson, 1996; Jones, 1998). It is a relatively protected environment and has a semi diurnal tide with the spring tidal range of 3.8 m (Barne *et al.*, 1996). Ryde Beach was chosen for the study area because it is the most accessible extensive intertidal seagrass bed to be found in the region. The site also has been studied intermittently over several decades.

The seagrass bed of the study area stretches along the mid-intertidal zone, approximately 400 m from MLWS and between 700 and 1400 m west of Ryde pier (Figure 2.2.). A dwarf eelgrass (*Zostera noltii* Hornem.) community dominates the area. Scattered patches of common eelgrass (*Z. marina*) occur at ELWS. The other macrophytes found in the study area are *Ceramium rubrum, Chaetomorpha* sp., *Chondrus crispus, Cystoclonium pefurien, Enteromorpha intestinalis, Fucus vesiculosus* and *Laminaria saccharina* (Abbott and Dawson, 1978; Hiscock, 1991; I. Tittley, 1997-personal communication).

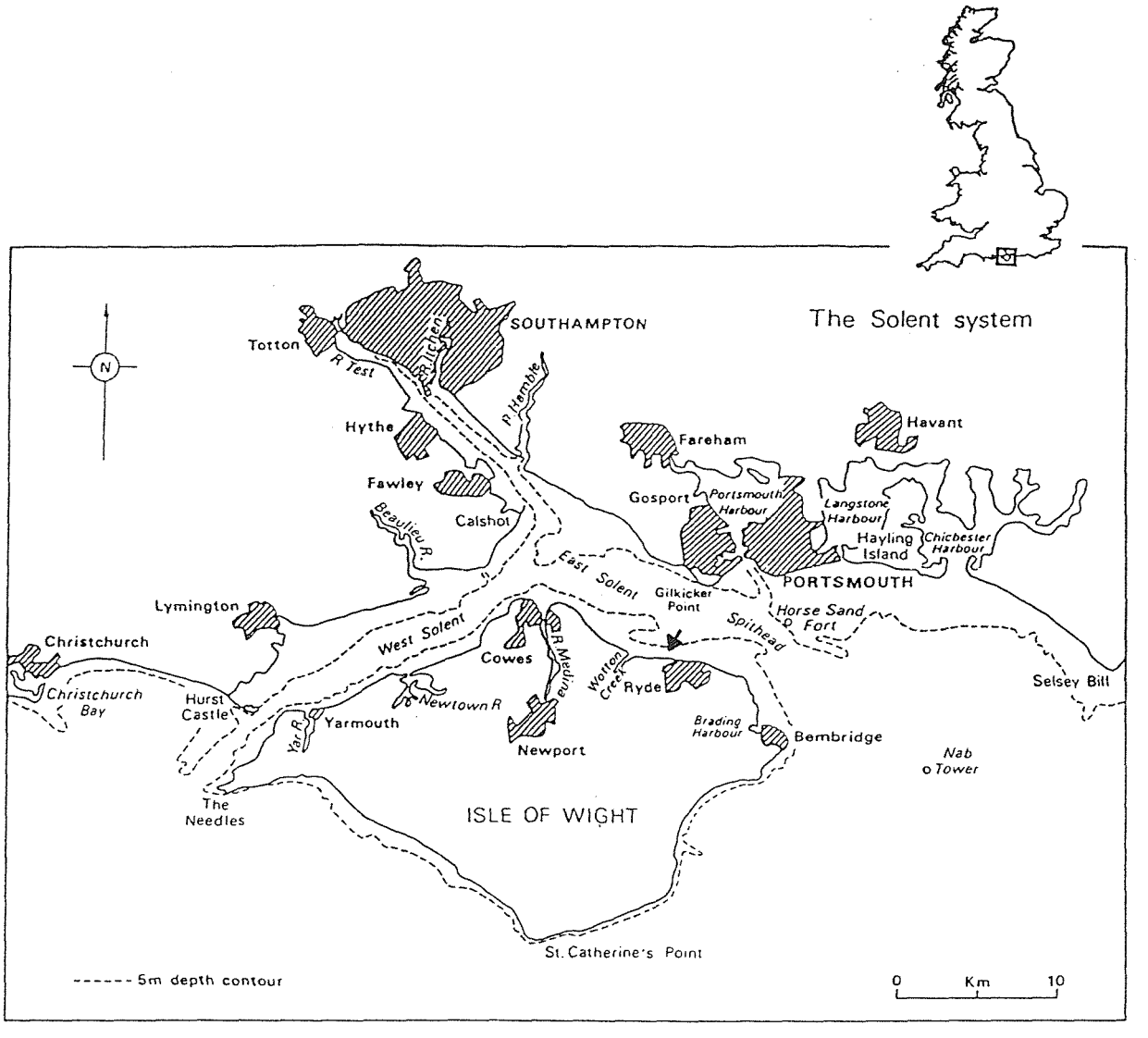

Fig. 2.1. A map showing the area of study. The arrow indicates the site where the samples were collected). (Modified from Thorp, 1980).

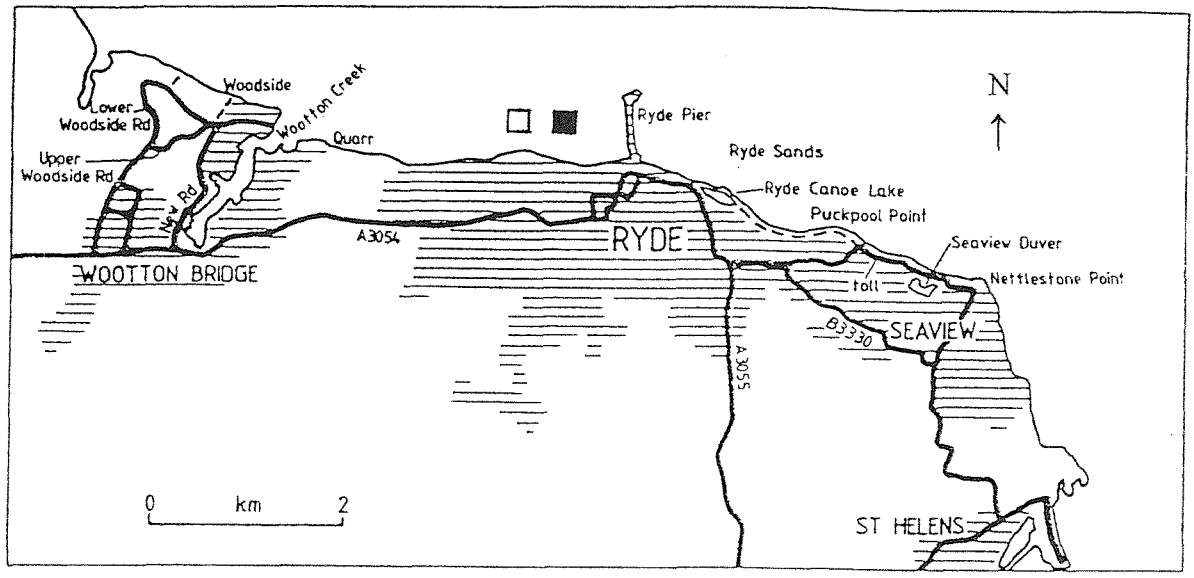

Fig. 2.2. A map of Ryde Beach with squares showing the sites.
(■ the dense site; □ the sparse site). (Source: Aspinall and Tasleer, 1992).

The upper intertidal zone of the study area is characterized by a sandy beach with tubeworms (*Lanice conchilega*) and lugowrms (*Arenicola marina*) mats on the western side and pebble beach that is inhabited by two species of brown algae, *Fucus vesiculosus* and *Ascophyllum nodusum*, on parts of area on the eastern side. Pebble and gravel are found in furthest intertidal reaches of the upper shore. In this region the green algae, *Enteromorpha intestinalis,* grows robustly in some months. Concrete wall is bordering between the area of study and the land along the coastline. From September to the early spring (March) in each year the filamentous algae and other epiphytes grow on the *Z. noltii* leaves, particularly on the old ones. Bare sand with small patches of mussel bed is found in the lower intertidal zone.

2.2. Seagrass Species of Ryde Beach

Three species of *Zostera* have been recorded to grow in the Solent shallow waters (Tubbs and Tubbs, 1983; Aspinall and Tasleer, 1992; Green and Cade, 1997; Davison and Hughes, 1998). It is difficult to distinguish between *Z. noltii* and the other two locally occurring members of the genus, i.e. common eelgrass (*Z. marina* L.) and narrow-leaved eelgrass (*Z. angustifolia* (Hornem.) Reichb.), especially in the field. Morphological features used to separate the three species of *Zostera* are given in Table 2.1.

Table 2.1. Comparison features of *Zostera* species. (summarized from Nature Conservancy Council, 1960 and Davison and Hughes, 1998).

Features	*Z. noltii*	*Z. marina*	*Z. angustifolia*
Leaf width	0.5-1.5 mm	4.0-10.0 mm	1.0-3.0 mm
Leaf apex	emarginate	rounded mucronate	rounded becoming emarginate
Number of veins in the leaf	3	5-11	3-5
Shoot height	~22 cm	~50-120 cm	~30 cm
Seed size	1.5-2.0 mm	3.0-3.5 mm	2.5-3.0 mm

Phytogeographically, *Z. noltii* is found throughout British Isles waters (Stewart *et al.*, 1994, Figure 2.3.). The Solent waters are among the most important habitats for *Z. noltii* in the United Kingdom. Tubbs and Tubbs (1983) recorded *Z. noltii* and *Z. marina* from Ryde Beach (Figure 2.4.). The centres of distribution of this seagrass include southern England, East Anglia and northeast Scotland (Stewart *et al.*, 1994). In the World, *Z. noltii* is distributed in the European continent waters, from the Mediterranean to the coast of Sweden and southwestern Norway (Loques *et al.*, 1988; Dahl, 1998), in Northwest African waters and in the Black Sea (Phillips and Meñez, 1988; Kennish, 1996). Study on the ecological aspects of eelgrass becomes very important particularly because *Z. noltii* and the other two species of *Zostera* have been given conservation status as scarce marine macrophytes in the United Kingdom (Stewart *et al.*, 1994; Davison and Hughes, 1998).

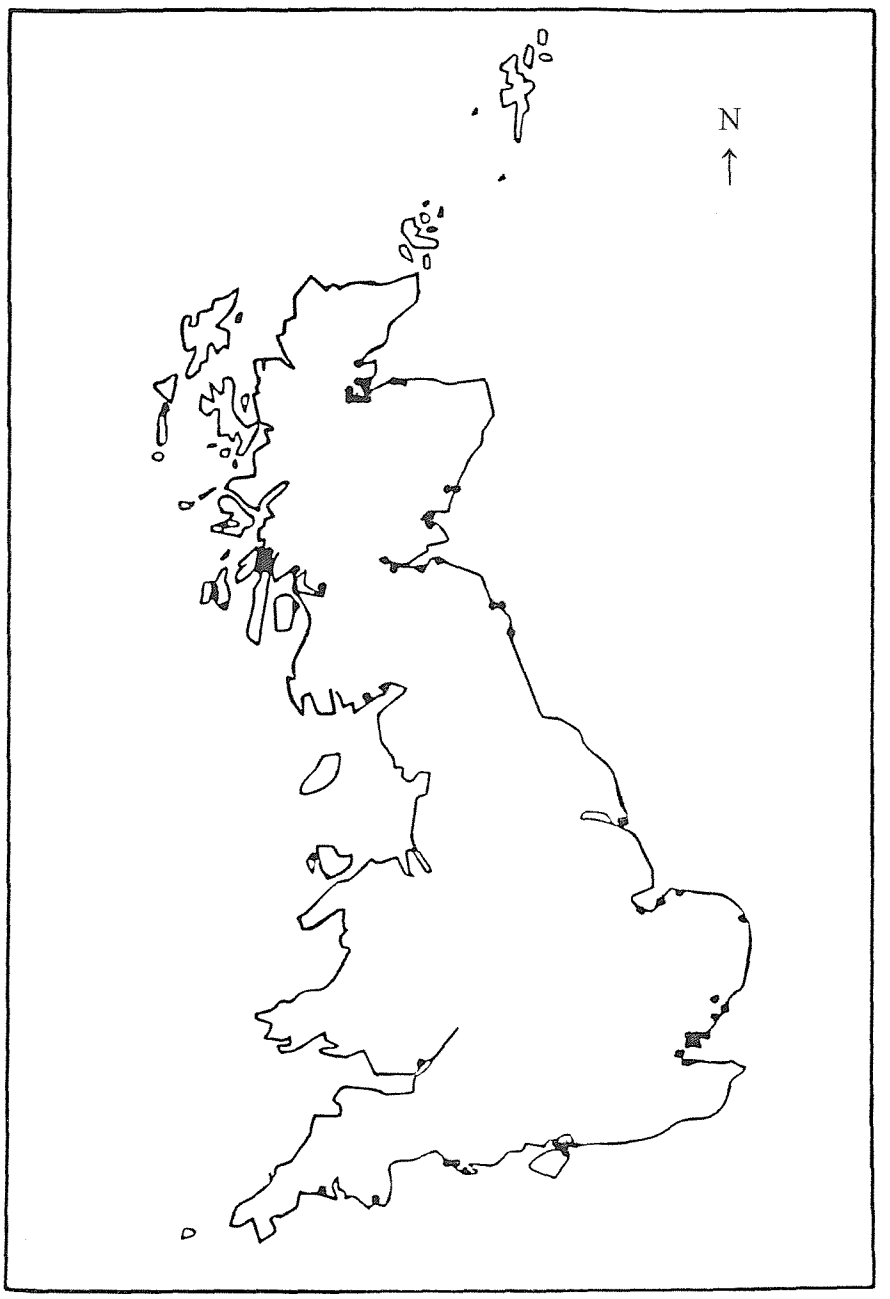

Fig. 2.3. Phytogeography of *Z. noltii* on the coasts of mainland Britain. (● indicating the major areas). (Source: Stewart *et al.*, 1994).

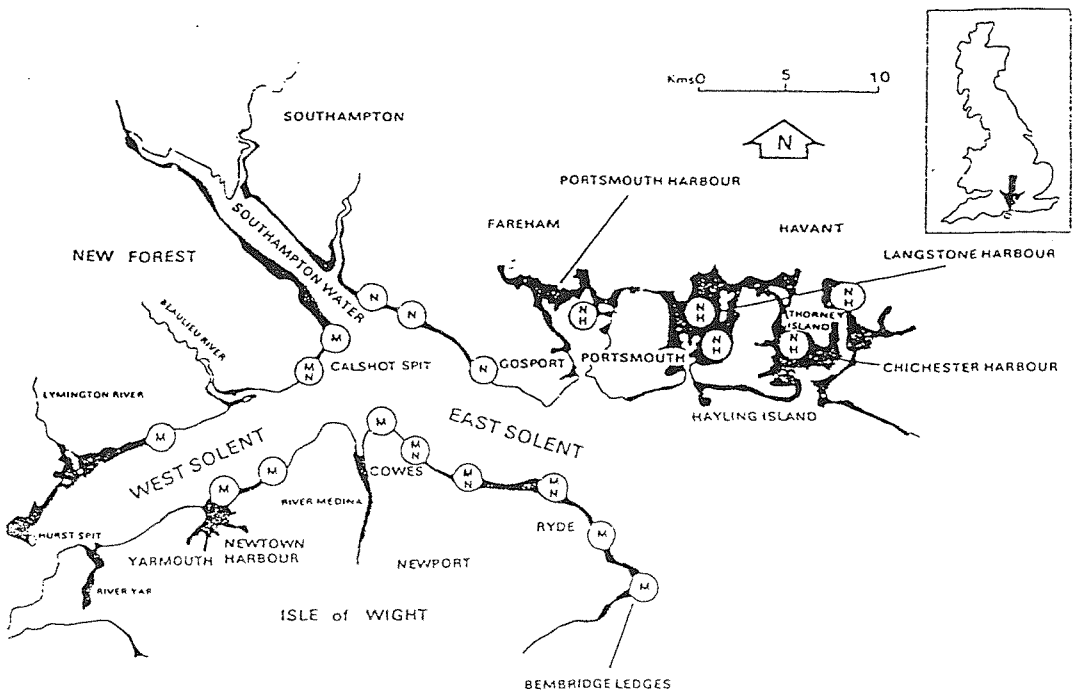

Fig.2.4. The Solent waters and *Zostera* distribution within it in 1980's. (M) *Zostera marina*; (N) *Z. noltii*; (H) *Z. marina* intertidal populations. (Adapted from Tubbs and Tubbs, 1983).

2.3. Field Sampling

Field sampling was carried out over a 26 months period, from September 1997 to October 1999. In the first 18 months the site was visited on a monthly basis. After this period, sampling was done on a seasonal basis, i.e. spring, summer and autumn 1999. Spring fieldwork was conducted in May 1999, summer fieldwork was done in July 1999 and autumn fieldwork was conducted in October 1999. Field sampling was always carried out at low tide. Depending on the weather conditions, some field sampling was completed on a single day, while others required two days. Two site locations were selected at mid-shore level. One site (to the west), the 'sparse bed', supported a low density of seagrass shoots (< 500 shoots·m^2), whereas the other site, the 'dense bed', supported a high density

of seagrass shoots (> 500 shoots·m^2). The two sites were retained throughout the study and remained 'sparse' and 'dense' throughout the sampling period.

On each visit seagrasses were counted for the shoot density study and some were taken for biological studies and various chemical analyses in the laboratory. Sediments were obtained for studies of the macrozoobenthos, chlorophylls and phaeopigments, total organic matter and granulometry. Samples for all analyses were collected from two different densities of seagrass beds, the sparse and the dense, in which five plots were deployed from each type of density. The sampling sites were chosen inside the seagrass bed. The sites were located each time using pier supporting columns (numbers 40-44) as a marker. A GPS model 38 from Garmin Inc. was used to locate the site positions.

2.4. Study of Seagrass Biology

The study of the biology of *Z. noltii* included determinations of shoot density, shoot height, number of leaves per shoot and above-ground biomass. In addition, the reproductive status of *Z. noltii* was determined.

For the studies of shoot height, shoot leaf number and shoot above-ground biomass, the seagrasses were collected from the field by uprooting individual shoots very carefully. These were returned to the laboratory. Prior to analysis in the laboratory, all shoots were gently rinsed with tap water several times enable to remove salt and sediments. The epiphytic and filamentous algae were removed from shoot surfaces by careful scraping. When these adhering epiphytic and filamentous algae were still attached after scraping, the shoots were then dipped and bathed in 5 % phosphoric acid, as suggested by Zieman and Wetzel (1980). Finally, the shoots were once again rinsed with the water.

2.4.1. Shoot Density

The density of *Z. noltii* was determined directly in the field by counting the number of the seagrass shoots within a 50 x 50 cm^{-2} frame randomly thrown 5 times into each of the bed types, dense and sparse. Obtaining an estimate of the number of seagrass shoots in a given area of the seafloor is necessary for the calculation of many plant parameters. The method used in this study was derived from Dennison (1990) and was nondestructive. The advantage of this method is that it reduces perturbation of the seagrass bed and is therefore useful for repeated sampling. To facilitate the counting, the frame was subdivided into four sections. This technique was found very efficient during fieldwork. Boström and Bonsdorff (1997) also applied this method, though they divided the frame into five sections.

2.4.2. Shoot Height

To determine the height of the seagrass, precleaned shoots were first placed into a tray. The measurement was then obtained from the most basal part of the shoot to the tip of the longest leaf was. Similar methods have been applied to shoot height measurements of *Z. capricorni* (Udy and Dennison, 1997). The measurement was expressed to the nearest millimeter.

2.4.3. Shoot Leaf Number

The dynamics of leaf number may reflect the health status of the seagrass over time and the environmental dynamics of the seagrass bed itself (Davidson and Hughes, 1998). To obtain seagrass leaf numbers, at each visit 50 plants were chosen randomly for each bed type. All attached leaves were included in the enumeration.

2.4.4. Shoot Biomass

As has been applied in other studies (see Ott, 1990; Lee, 1997; Terrados *et al.*, 1998), the aboveground biomass was assessed by determining ash free dry weight (AFDW) of the shoots collected from each quadrat. Prior to the process, precleaned shoots were first spread over a thick layer of tissue paper, leaving them for about 30-60 minutes (depending on the sample condition) until the adherent water was lost (Al-Suwailem, 1991). The shoots were then dried in an oven at 60 °C for 48 hours. The shoots were later weighed and this weight was considered as the dry weight. These dried samples were then combusted in a muffle furnace at 500 °C for 24 hours (Ott, 1990) to obtain the ash free dry weight (AFDW).

2.4.5. Reproductive Period

Data on flowering and seed presence were obtained during the above studies in order to follow the reproductive cycle of the *Z. noltii*. This type of data on seagrass reproduction in the British Isles is limited, but can be very useful in supporting conservation and restoration programmes of *Zostera* biotopes (Davison and Hughes, 1998).

2.5. Seagrass Chemical Constituents Analyses

The measured compounds were total protein, total phenolics and total carbohydrate from the live plants. The reason for selecting these chemicals for measurement is that they have been shown to be important in inducing settlement of infaunal invertebrates in the vegetated marine ecosystem (Morse, 1992). Many works revealed that the chemical cues of seagrass play either as attractant or repellant for the animal settlement in the seagrass bed ecosystem (Orth, 1990; Mazzella *et al*, 1992). Moreover, the chemical constituents indicate food quality of

seagrass leaves and are related to the maturation and decay process of seagrass shoots (Klap *et al.*, 2000).

2.5.1. Total Phenolics

To extract total phenolics from *Z. noltii* shoot, 100 mg of dried seagrass powder was extracted twice with 5 ml of 50 % methanol (95 °C, 25 minutes). The extracts were combined and the final volume was readjusted to 10 ml; 0.5 ml of the extract was mixed with 0.5 ml of distilled water and 5 ml of 2 % Na_2CO_3 in 0.1 N NaOH. After 10 minutes, 0.5 ml of Folin and Ciocaltaeu's solution was added and the absorbance read at 725 nm in a spectrophotometer (Martin and Martin, 1983). Tannic acid (Sigma 0125) was used as standard.

2.5.2. Total Carbohydrate

The phenol-sulphuric acid method from Dubois *et al.* (1956) was used for determination of total carbohydrate of the seagrass shoot. This is a simple, colorimetric procedure for dissolved carbohydrates. The procedure was as follows (Dawes and Kenworthy, 1990): 5 mg homogenized dried plant material was weighed out into a 10-ml centrifuge tube; the tube was then filled with 10 ml 5% TCA (trichloroacetic acid) in water. It was then heated in a hot-water bath (80 - 90 °C) for 3 hours and shaken gently at least twice to ensure adequate extraction. This step was standardized for all runs. The tubes were removed from the bath, cooled, returned to volume (mark) with distilled water. They were then centrifuged for 10 minutes at the highest speed on a standard table top centrifuge. A sum of 0.2 ml aliquot was then taken and placed into a test tube (a finger was placed over a pipette and the tube was inserted through the surface before taking samples to avoid scum), 1 ml of 5% phenol was then added and mixed by tapping test tube, 5

ml concentrated H_2SO_4 was added rapidly and then mixed by tapping, this was an exothermic reaction. The tube was allowed to cool for 30 minutes and then read at 490 nm. Glycogen was used as a standard. Calculation was done as follows:

$$\text{Percent carbohydrate} = \frac{\text{mg carbohydrate}}{\text{mg tissue used}}$$

note: mg of carbohydrate = (mg carbohydrate in 0.2 ml)(50)*. The mg carbohydrate in 0.2 ml is obtained from the standard curve. *Dilution of an original sample.

2.5.3. Total Protein

Total protein content of the live seagrass plant was determined by using a modification of the Lowry procedure (Dawes and Kenworthy, 1990). This is probably the most simple and rapid method for measuring the total amount of protein in seagrass. The technique was as follows: a quantity of 10 mg of homogenized, freeze dried seagrass powder was weighed and placed in a 15-ml test tube, it was then mixed with 5 ml of 1N NaOH and capped with a marble. The tube was allowed to stand at room temperature for 24 hours, 0.5 ml of the aliquot was pipetted into a second test tube; it was then added to 5 ml alkaline copper tartrate reagent (prepared fresh each day) and mixed with 0.5 ml 1N Folin-Ciocaltaeu phenol reagent. The aliquot was transferred into a cuvette, placed in a spectrophotometer and read at 660 nm. Bovine Serum Albumin (BSA) was used as standard (Jones *et al.*, 1989). Calculations were expressed in percent of protein as follows:

$$\% \text{ protein} = \frac{(\text{mg protein from std curve})\ (10)^*}{\text{mg of tissue}}$$

note:*dilution of original sample

2.6. Study of Seagrass Bed Sediment Pigment Dynamics

The use of photosynthetic pigments as tracers for sources of macrophyte organic matter (Levinton and McCartney, 1991 and the papers therein) and fingerprints of primary producers (Mantoura and Llewellyn, 1983; de Jonge and Colijn, 1994; Cariou-LeGall and Blanchard, 1995) in the coastal ecosystems has been widely accepted. The observations commonly determine the chlorophyll-*a*, accessory pigments and phaeopigments (Mantoura and Llewellyn, 1983; Shaffer and Onuf, 1983; Riaux-Gobin *et al.*, 1987; Boon *et al.*, 1998). The measurements normally observe the top few centimetres of the sediment where the pigments are concentrated (see Fielding *et al.*, 1988; Levinton and McCartney, 1991; Klein and Riaux-Gobin, 1991; Bianchi *et al.*, 1993; Lucas and Holligan, 1999).

2.6.1. Sample Collection and Preservation

In the present study, the top centimetre of the sediment was collected by using a small corer modified from a plastic syringe. The corer has a diameter of 1.5 cm. This collection method has been used by several studies with a variety of core sizes. The collected sediment was then transferred into a pre-labeled polyethylene bag and placed in the ice-box for transport back to the laboratory.

Before the analyses were carried out, the sediments were freeze-dried for approximately 24 hours until dry. During this process the freeze drier was covered tightly with two layers of black polyethylene in order to prevent light penetration into the sediment. The dried sediments was stored frozen till ready for analyses. The storage method does not significantly influence sediment pigment concentration (Gieskes and Kraay, 1983; Klein and Riaux-Gobin, 1991). Chlorophyll and phaeopigment measurements in the sediments were carried out by using spectrophotometric and HPLC (high performance liquid chromatography) methods.

2.6.2. Spectrophotometric Analyses

The spectrophotometric analyses of chlorophyll-*a* and phaeopigment concentrations were carried out by using a modification of chlorophyll-*a* and phaeopigment determinations for seawater (Parsons *et al.*, 1984). The objective of this method is to give the total chlorophyll-*a* and phaeopigment concentrations of the seagrass bed system. The procedure of measurement was as follows: a gram of dried sediment was transferred to a 15-ml test tube; 10 ml of 90 % acetone was then added and ultrasonicated for 30-60 seconds; this mixture was left to stand at 4°C until ready for analysis. Prior to analyses the mixture was centrifuged at 3000 rpm for 5 minutes. The supernatant was then poured into a fresh test tube to prevent concentration stratification. The spectrophotometer was zeroed with 90 % acetone and the supernatant was transferred into a silica cuvette and the extinction was measured at 665 nm. Two drops of 10 % HCl was added into cuvette; aluminum foil was placed over and the cuvette was inverted to mix. Measurements were carried out at the extinction wavelength of 665 nm. The used cuvette was rinsed with 90 % acetone before re-use, to ensure no acidification occurred. The amount of chlorophyll-*a* was calculated by using the following formula:

$$\text{chlorophyll-}a = \frac{26.7\,(665_o - 665_a) \times V}{W \times l}$$

where:
- 665_o = extinction before acidification
- 665_a = extinction after acidification
- V = volume of acetone extract
- W = weight of dried sediment (g)
- l = path length (cm) of cuvette

Chlorophyll-*a* standard (Sigma) was used as a standard. The concentration of chlorophyll-*a* was expressed as μg chlorophyll-*a* g^{-1} dry weight sediment.

The total phaeopigment content of the sediment was calculated by using the following formula:

$$\text{Total phaeopigment} = \frac{26.7\,(1.7\{665_a\} - 665_o) \times V}{W \times 1}$$

where:
- 665_o = extinction before acidification
- 665_a = extinction after acidification
- V = volume of acetone extract
- W = weight of dried sediment (g)
- l = path length (cm) of cuvette

The total concentration of phaeopigment was expressed as μg phaeopigment g^{-1} dry weight sediment.

2.6.3. HPLC Analyses

The sediment pigment content analyses were also done by using the HPLC method. The aim of these analyses was to provide information as to the source of the pigment of the seagrass bed, i.e. whether the pigment production was contributed solely by the benthic algae or both by the benthic algae and seagrass detrital materials. The HPLC measurements have successfully identified a diverse variety of pigments found from different sources in the marine environments, whereas spectrophotometer only measures the total concentration of chlorophyll and phaeopigment (Mantoura and Llewellyn, 1983). Table 2.2. presents the pigments found in different groups of marine plants detected by HPLC.

Table 2.2. Pigments found in different groups of marine plants detected by HPLC. (summarized from Kennish, 1996).

Pigments	CHLO	EUGL	CHRY	XANT	BACI	DINO	CRYP	CYAN	SEAG
Chlorophyll-*a*	+	+	+	+	+	+	+	+	+
Chlorophyll-*b*	+	+	-	-	-	-	-	-	+
Chlorophyll-*c*	-	-	+	-	+	+	-	-	-
Chlorophyll-*e*	-	-	-	+	-	-	-	-	-
α-Carotene	-	-	-	-	-	-	+	-	-
β-Carotene	+	+	+	+	+	+	-	+	+
γ-Carotene	+	-	-	-	-	-	-	-	-
ε-Carotene	-	-	-	-	+	-	-	-	-
Lutein	+	+	+	+	-	-	-	-	+
Zeaxanthin	+	-	-	-	-	-	+	+	+
Violaxanthin	+	-	-	+	-	-	-	-	-
Neoxanthin	+	+	-	+	-	-	-	-	-
Fucoxanthin	-	-	+	+	+	-	-	-	-
Diatoxanthin	-	-	-	-	+	-	+	-	-
Diadionoxanthin	-	-	-	-	+	+	-	-	-
Dinoxanthin	-	-	-	-	-	+	-	-	-
Neodinoxanthin	-	-	-	-	-	+	-	-	-
Diadinoxanthin	-	-	-	-	-	+	-	-	-
Neodiadinoxanthin	-	-	-	-	-	+	-	-	-
Peridinin	-	-	-	-	-	+	-	-	-
Neoperidinin	-	-	-	-	-	+	-	-	-
Myxoxanthin	-	-	-	-	-	-	-	+	-
Oscilloxanthin	-	-	-	-	-	-	-	+	-
Phycoerythrin	-	-	-	-	-	-	-	+	-
Phycocyanin	-	-	-	-	-	-	-	+	-

CHLO = Chlorophyceae, EUGL = Euglenophyceae, CHRY = Chrysophyceae, XANT = Xanthophyceae, BACI = Bacillariophyceae, DINO = Dinophyceae, CRYP = Cryptophyceae, CYAN = Cyanophyceae, SEAG = Seagrass

All sediments for HPLC measurements were first freeze-dried and stored in various length of time until ready for analyses. Procedures of pigment measurements were made as follows: between 0.5-1.0 g of freeze-dried sediment was transferred into a 15-ml plastic test tube; 5 ml of 90 % acetone HPLC grade was then added and ultrasonicated for 20 seconds; this mixture was left to stand at

4 °C in the fridge until ready for analysis; prior to analyses the mixture was centrifuged at 3000 rpm for 10 minutes; 1 ml of the supernatant was then transferred into HPLC analysis tube through a 0.2 µm Nyaflo membrane filter (Gellman) to prevent any contamination; pigments were determined by ion-impairing, reverse-phase HPLC, modified from Mantoura and Llewellyn (1983) and as described by Lucas and Holligan (1999).

The mobile phase consists of a binary eluant system consisting of eluant A (80 % methanol, 20 % 1M ammonium acetate), and eluant B (60 % methanol, 40% acetate). Ammonium acetate acts as an ion-impairing agent. For the analyses, 700 µl of 1M ammonium acetate was mixed with 500 µl of pigment extract for 12 seconds. 100 µl of the resulting mixture was then injected into a Perkin Elmer 5µm C-18 column (25 cm x 46 mm i.d.). A linear gradient from 0 to 100 % eluant B was created for 10 minutes, followed by an isocratic stop at 100 % eluant B for 7.5 minutes. A second gradient of 2.5 minutes was used to return to the initial condition of 100 % eluant A. Separation of the pigments was achieved within 17 minutes. Dual channel detection was achieved with Spectra-System UV1000 detector set to 440 nm for absorbance, and a Spectra-System FL3000 fluoerescence detector set at excitation 410 nm and emission 670 nm.

Pigments were identified by comparing their peaks and retention times with either commercially available standards or monocultures with well-documented accessory pigment markers, such as *Phaeodactylum tricornutum* (Bacillaripohyceae), *Amphidinium carterae* (Dinophyceae), *Synechococcus* sp. (Cyanophyceae), *Euglena* sp. (Euglenophyceae) and *Emiliania huxleyi* (Prymnesiophyceae). The main pigments and their retention times (Rt) used in this study were chlorophyll *c1+c2* (chl *c1+c2*) (2.2 min), peridinine (2.9), fucoxanthin (4.3), 19'hexanoyloxyfucoxanthin (4.6), diadinoxanthin (5.6), diatoxanthin (6.6), zeaxanthin/lutein (6.8), chlorophyll *b* (chl-*b*) (9.3), chlorophlyll-*a* (chl-*a*) (10.3) and *β*-carotene (12.0) was identified. Breakdown products of chl-*a* were identified as chlorophyllide *a* (Rt 2.0 min), phaeophorbides (elute before chl-*a*) and phaeophytins (elute after chl-*a*). The phaeophorbides and phaeophytins were

numbered in order of elution as phaeophorbide *a*1 (2.9), phaeophorbide *a*2 (4.7), phaeophytin *a*1 (11.7) and phaeophytin *a*2 (12.5) in accordance with Barlow *et al.* (1993) and Lucas and Holligan (1999). The '*a*2' phaeopigments correspond to the 'a-like' phaeopigments of Hawkins *et al.* (1986) and Klein and Riaux-Gobin (1991). Copepod faecal pellets were used to identify retention times. Peak areas were converted to concentrations using response factors calculated from standards and published extinction coefficients (Mantoura and Llewellyn, 1983). The following equation was used for the quantification of chl-*a* and other detected pigments:

$$\text{Pigment concentration } (\mu g/g) = \frac{A \times V \times 10}{0.5 \times RF \times 1000 \times W}$$

where: A = peak area from HPLC chromatogram
V = volume of acetone extract (ml)
RF = response factor (see Table 2.3.)
W = weight of sample (g DW)

Table 2.3. Response factors used in the calculation for each pigment measured by the HPLC method (Barlow *et al.*, 1990).

Pigment Species	Response Factor
chl-*a*	3514
chl-*b*	3405.4
chl-*c1+c2*	12378.69
β-carotene	8818.79
fucoxanthine	10258.69
lutein/zeaxanthine	14388.95
diadinoxanthine	16963.81
diatoxanthine	10637.6

The phaeopigment concentration in the sediment was calculated by using this equation:

$$\text{Phaeopigment concentration } (\mu g/g) = \frac{CA \times V \times RF}{0.5 \times EC \times W}$$

where: CA = calibrated peak area of HPLC chromatogram (see Table 2.4.)
V = volume of acetone extract (ml)
RF = response factor (see Table 2.4.)
EC = extinction coefficient (see Table 2.4.)
W = weight of sample (g DW)

Table 2.4. Calibrated peak area, extinction coefficient and response factor used in the calculation for each species of phaeopigment measured by the HPLC method (Barlow *et al.*, 1990).

Phaeopigment Species	Calibrated Peak Area	Extinction Coefficient	Response Factor
Phaeophorbide *a1*	PA : 15.531	69.8	0.00187
Phaeophorbide *a2*	PA : 12.501	69.8	0.00187
Phaeophytin *a1*	PA : 14.831	49.5	0.00187
Phaeophytin *a2*	PA : 13.201	49.5	0.00187

2.7. Study of Seagrass Bed Macrozoobenthos

The macrozoobenthos has been regarded as an important ecological indicator for marine ecosystems in general (Pearson and Rosenberg, 1978, Barnes and Hughes, 1988; Mann, 1996) and for seagrass beds in particularly (Heck and Wilson, 1990; Orth, 1992). This research studied macrozoobenthos dynamics by

following the number of species, the number of individuals, biomass, diversity indices and similarity indices.

2.7.1. Sample Collection and Preservation

The benthic macrofauna were sampled from the seagrass bed sediment by using a hand-operated plastic corer with an interior diameter of 6.0 cm (covering an area of 28.27 cm^2). Five replicates were applied for each type of seagrass density. Core samplers are known as the most appropriate means of collecting the benthic macrofauna in shallow-water seagrass beds (Baden and Pihl, 1984; Heck and Wilson, 1990). The only disadvantage of this method is it does not collect the large, highly mobile crustaceans or large low abundance organisms effectively. The other possible collection devices, i.e. dredges and grabs, are not deemed suitable since they normally require large boats for deployment and frequently do not make quantitative collections (Heck and Wilson, 1990). Additionally, they may significantly impact on small seagrass beds.

During sample collections, the corer was pushed into the sediment to a depth of 10 cm. The collected materials were then transferred into pre-labeled polyethylene bags. In the laboratory, the sediments were sieved gently through a 500-µm sieve under a gentle flow of sea water and preserved in 7 % of formaldehyde in sea water. A small quantity of Rose Bengal was added to stain all organic matter red, thus making sorting and identification easier. The sorting of preserved materials was done using the methods given by Eleftheriou and Holme (1984). The fixed materials were carefully washed through a-500 µm sieve with tap water to remove excess formaldehyde, stain and any remaining sediment. The cleaned material was then transferred to a white tray. All visible organisms were picked out and preserved in labeled vials containing 7 % of formaldehyde in sea water according to group.

2.7.2. Species Identification and Composition

To follow the composition and species number of macrozoobenthos, the preserved sediment samples from five replicates were first identified under a low power binocular microscope. Identifications of macrozoobenthos were carried out according to the following keys: Day (1967a and 1967b), Fauchald (1977), George and Hartmann-Schröder (1985), Pleijel and Dales (1991) and Hartmann-Schröder (1996) for polychaetes; Eisenberg (1981), Graham (1988), Dance (1990) and Hayward and Ryland (1990b) for gastropods and bivalves; Lincoln (1979) for gammarids; Holdich and Jones (1983) for tanaids; Jones (1976) for cumaceans; Huys *et al.* (1996) for harpacticoids; Naylor (1972) for isopods; Picton (1993) for echinoderms. In addition, Abbott (1991) was used to identify the molluscs, whilst Hayward and Ryland (1990a) was also used for identification of nematodes together with polychaetes, isopods, cumaceans, decapods, gammarids, tanaids, and harpacticoids.

2.7.3. Abundance

The identified species in each core were then counted. To assess the macrozoobenthos abundance counting for each species was conducted at the same time during identification. The macrozoobenthos numbers were expressed as individuals per core.

2.7.4. Biomass

To obtain the macrozoobenthos biomass, first the dry weight of sorted and identified animals were measured. This was accomplished by drying the fauna in an oven at 100 - 150 °C for at least 48 hours until three consecutive weightings were equal (Hecks and Wilson, 1990). Five replicates from each seagrass bed type were

used in this study. Fresh weight of the animals is not recommended as it is highly variable and gives a very poor estimation of the biomass. Ash free dry weights, which give an estimate of inorganic material included in the sample, were then obtained by ashing known quantities of each macrozoobenthos group in a muffle furnace at 450 °C for 6 hours (Hecks and Wilson, 1990 and the papers therein).

2.7.5. Species Diversity

The objective for using diversity indices in ecological studies is mainly to compare and contrast between communities and within a single community on a temporal basis and in relation to the environmental conditions in the ecosystem (Odum, 1971). This study employed three of the most commonly used indices to analyze the macrozoobenthic diversity. These were Shannon-Wiener Index (Parsons *et al.*, 1984), Pielou's Eveness Index (Gray, 1981) and Margalef's Index (Odum, 1971).

The Shannon-Wiener Index (H) can be defined as "the degree of uncertainty involved in predicting the species identity of randomly selected individuals". Parsons *et al.* (1984) explained that when the H value is large uncertainty is great and therefore diversity is considered high and *vice versa.* The H index has the advantage of combining both species abundance and evenness when calculating diversity. H value also reflects the two components of the community structure, i.e. number of species and distribution of the individuals among the constituent species. H was calculated by using the following equation:

$$H = - \sum_{n_i=1}^{s} p_i \log_2 p_i$$

where S = total number of species
n_i = total number of individuals of the ith species
p_i = the proportion of individuals that belong to the ith species (n_i/N)
N = total number of individuals

Index of eveness (J) measures how evenly the individuals are distributed among species in the community (Odum, 1971). The higher value of J indicates the more even of the community (Pielou, 1975). The J index is considered as a useful method in identifying the changes in the value of H as being due to either the increase in the species richness or in species dominance or in evenness of individuals in a sample (Gray, 1981). This index was as follows:

$$J = \frac{H(\text{observed})}{H_{max}} = \frac{H}{\log S}$$

where H = calculated Shannon-Wiener Index
H_{max} = maximum possible diversity which would be achieved if all species were equally abundant (= log S)
S = number of species in the sample

Margalef's index (d) estimates species richness and assumes that there is a linear relationship between the number of species (S) and the logarithm of the total number of individuals (N) (Odum, 1971). This index ignores the details of distribution of individuals between species, however it gives an equal weight to both the dominant and rare species. The value of d can be calculated by using the following formula:

$$d = \frac{S - 1}{\ln N}$$

where S = total number of species
N = total number of individuals

2.7.6. Species Similarity

Faunal community studies often produce a large set of data. A clear view of the communities and species associations in the surveyed areas is not usually easy to establish by looking at the data sets from these studies. More often, the data are subjected to numerical classification methods which employ statistical criteria to identify population and evaluate the frequency of occurrence and abundance of species in quantifying associations through various types of similarity analyses (Warwick and Clarke, 1991). Sometimes the results are presented in the form of a similarity matrix or more frequently in the form of a dendrogram (Warwick *et al.*, 1987).

This study applied an coefficient, the Bray-Curtis index, which is commonly used in benthic faunal studies (Clarke and Warwick, 1994). The Bray-Curtis index (CN) considers the species composition as well as the individuals abundance of each species in a sample. The CN value is more likely affected by the abundance of the sample where the community is strongly dominated by a single species. This index can be defined by using the following equation:

$$CN = \frac{2jN}{aN + bN} \times 100$$

where jN = the sum of lesser values for the species common to both samples
aN = the total individuals in sample 1
bN = the total individuals in sample 2

2.8. Data Analyses

All data were statistically analysed by using a "Microsoft Excel" version 5.0 package. Macrozoobenthic diversity and similarity indices were calculated by using the PRIMER (Plymouth Routines In Multivariate Ecological Research) programme developed at the Plymouth Marine Laboratory (Clarke and Warwick, 1994).

Multidimensional scaling (MDS) analysis from PRIMER was used to analyse the results from similarity tests. A t-test was used to interpret the level of difference of mean macrozoobenthic abundance and pigment production, as well as other parameters measured in the biological and chemical studies in both types of seagrass densities. Moreover, multiple linear regression followed by forward stepwise regression using the Sigma Stat package was applied to examine interrelationships between variables and faunal data.

Chapter III

Environmental Parameters of the Site

The selected environmental parameters recorded in this study were water temperature, salinity, sediment organic matter and sediment granulometry.

3.1. Method

3.1.1. Water Temperature and Salinity

Water temperature and salinity are considered as among the most important environmental parameters of seagrass beds (Fonseca, 1990; Brey, 1995). In this study, water temperature and salinity of the site were recorded *in situ* by using a mercury thermometer (accuracy ± 0.5 °C) and a field refractometer (accuracy ± 0.5 ‰) monthly following the field work.

3.1.2. Sediment Organic Matter

The sediment samples for total organic matter study were collected by using the corer as employed for benthic macrofauna collection (Chapter II). The study used five replicates from each seagrass density type. For total organic matter (TOM) analyses sediment was first sieved through a 2-mm sieve to remove shells, large plant fragments and large fauna. A small quantity of sediment was then oven-dried to a constant weight at 60 °C and combusted in a muffle furnace at 500 °C for 24 hours. After cooling in a dessicator, the sediment was weighted and the loss

in weight was taken to be due to the combustion of all organic material from the sediment. The percentage of TOM was counted as:

$$\% \text{ TOM} = \frac{\text{Loss in dry weight on combustion}}{\text{Initial dry weight before combustion}} \text{ X } 100\%$$

3.1.3. Sediment Granulometry

The aim of granulometric study was to observe the sediment type of the sites and to determine whether season or different seagrass density influenced grain size composition. The sediment was wet-sieved as outlined by Buchanan (1984). The sediment was dried in the oven at 70 °C for 24 hours following field collection. The next step is adding 250 ml of tap water and 10 ml of aqueous sodium hexametaphosphate (6.2 g l^{-1}) to 50 - 100 g of dried sediment to desegregate the silt/clay particles in the sediment. The sediment was then stirred mechanically for 15 minutes and left to soak overnight. Prior to sieving the sediment was stirred again for 15 minutes and passed immediately via a-63 μm sieve. The remaining material was then dried at 70 °C for 24 hours. The dried sediment on the 63 μm sieve was then agitated over a large sheet of white paper until no further material was seen to pass the sieve. The remaining material in the 63 μm sieve was transferred into the largest pore size sieve in a stack of graded sand sieves arranged in decreasing order of pore size (2.00, 1.40, 1.00, 0.71, 0.50, 0.355, 0.25, 0.18, 0.125 and 0.063 mm). The stack column of sieves was then shaken for 30 minutes until the sieving was completed. The material left on each sieve was carefully removed and weighed. The percentage of each fraction was calculated and plotted to show the frequency distribution of particle sizes.

3.2. Results

3.2.1. Water Temperature and Salinity

The water temperature and salinity of the site ranged between 3 - 19 °C and 29 - 32 ‰ respectively (Figure 3.1.). These variables were in the range of the values have been reported for the Solent area (Davidson, 1996; Jones, 1998).

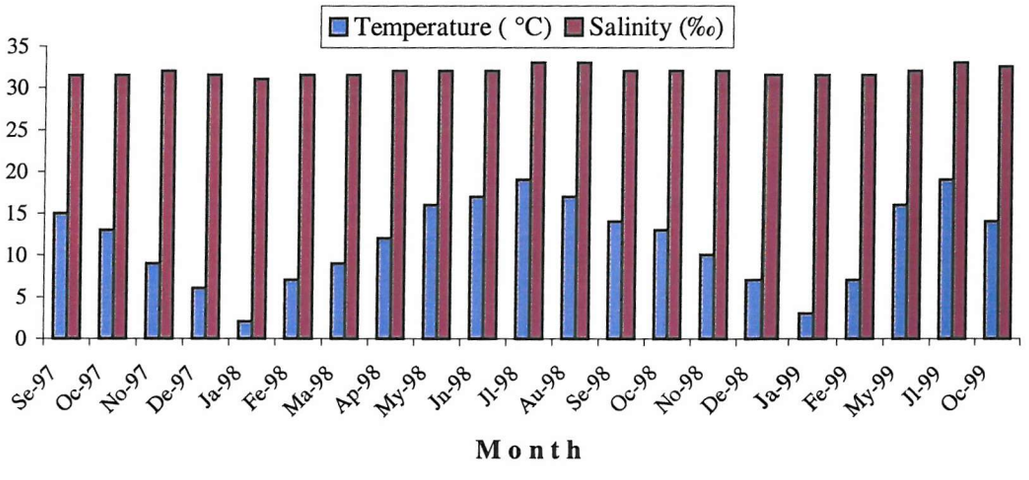

Fig.3.1. Water temperature and salinity of the Seagrass Bed at Ryde Beach.

3.2.2. Sediment Organic Matter

The seagrass bed had an average of sediment organic matter of 0.48 (± 0.03) – 1.17 % (± 0.06) at the dense site and 0.38 (± 0.04) – 0.96 % (± 0.05) at the sparse site respectively (Figure 3.2.). These sediment organic contents were significantly different when they were tested (t-test, $P < 0.0001$). Sediments from the dense site always had higher values than those of the sparse site.

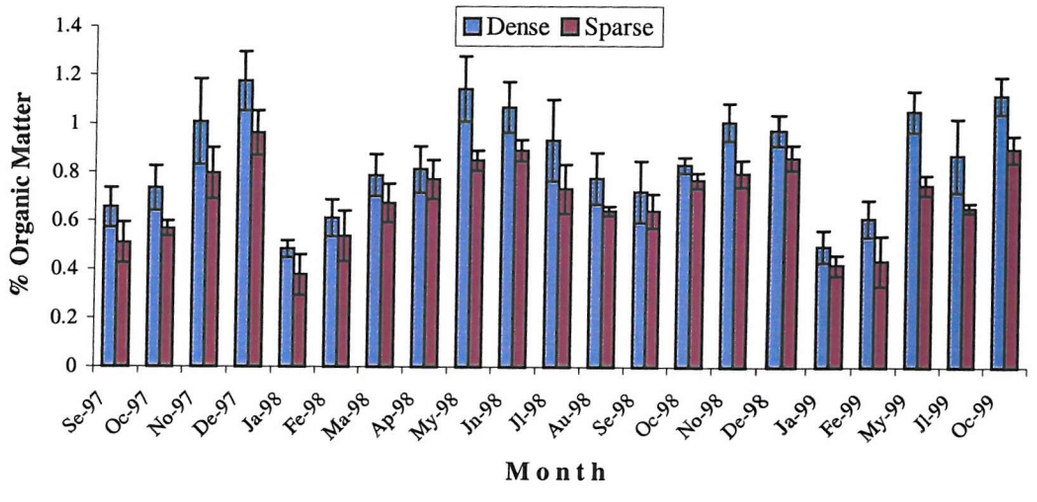

Fig. 3.2. Sediment Organic Matter Content of the Seagrass Bed at Ryde Beach (n = 5; ± SD).

3.2.3. Sediment Granulometry

The sediment samples from both sites fell into the category of sandy sediments in which fine sand (Phi value 2 – 3) composed the highest percentage of sediment fractions (Figure 3.3. and 3.4.). A similar type of sediment was reported from an adjacent area (Henderson, 1997). Since there were no significant difference results between the sites, granulometric analyses were not carried out in the second year of study.

Gravel (Phi value (-1) – (-2)) and coarse silt (Phi value 4 – 5) were found as the coarsest and finest fractions respectively throughout the study. The samples from the sparse site were clearly coarser since they possessed higher percentages in low phi value than that of the dense site (t-test, $P = 0.025$). Meanwhile the sediments from the dense site had higher percentages in fine sand (Phi value 2 – 3) (t-test, $P = 0.018$), very fine sand (Phi value 3 – 4) (t-test, $P = 0.025$) and coarse silt fractions (Phi value 4 – 5) (t-test, $P = 0.010$).

Although the sediments at both sites fell into the category sandy sediments throughout the year, the seasonal variations in particular grain sizes were observed. The sediments in the winter and spring periods were coarser compared to the other seasons. Figures 3.3. and 3.4. show fine sand sediment (Phi value 2 – 3) reached the lowest percentages in January – May 1998, indicates the sediments in these months possesed the highest sand contents. These higher sand contents perhaps correlate with the dynamics of *Z. noltii* population. Indeed, the highest shoot density in both sites, which in general occurred during the summer and autumn months (Figure 4.1. in Chapter IV), might have added the silt content to the sediment. In addition, strong wave actions experienced by the site during the winter possibly did not able to retain silt fraction in the upper layer of sediment.

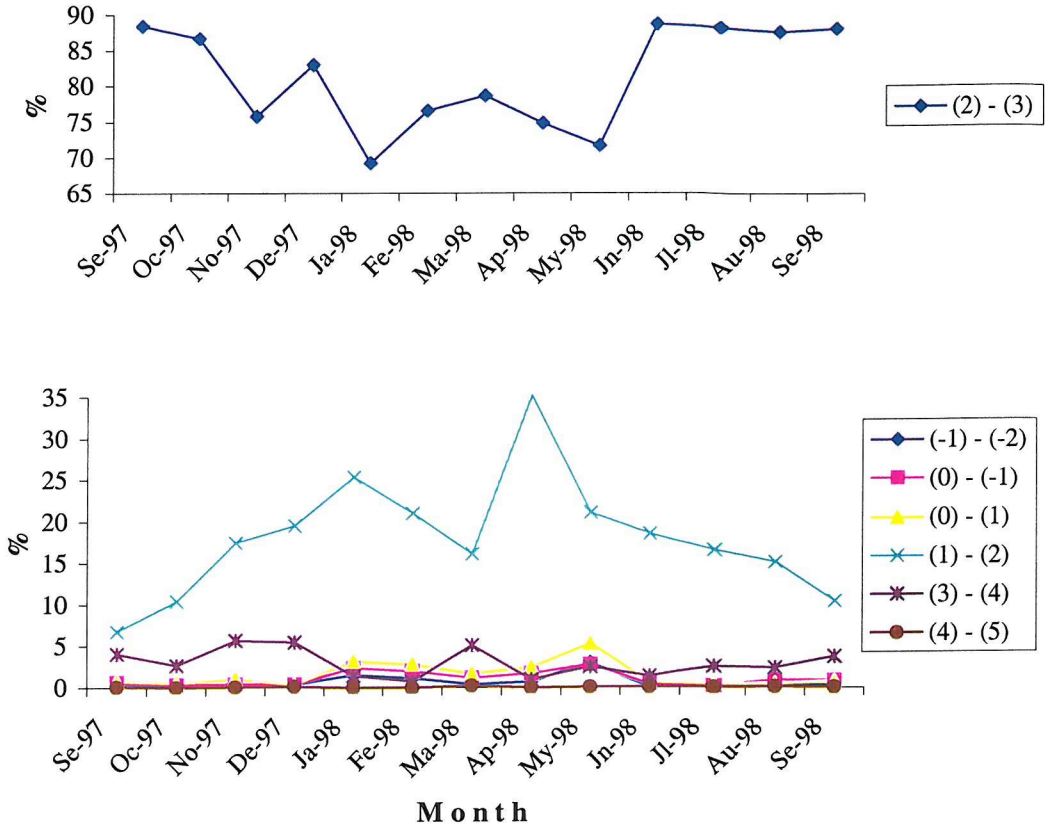

Fig. 3.3. Percentage of Phi value distribution of the sediments collected from the dense site (n = 5).

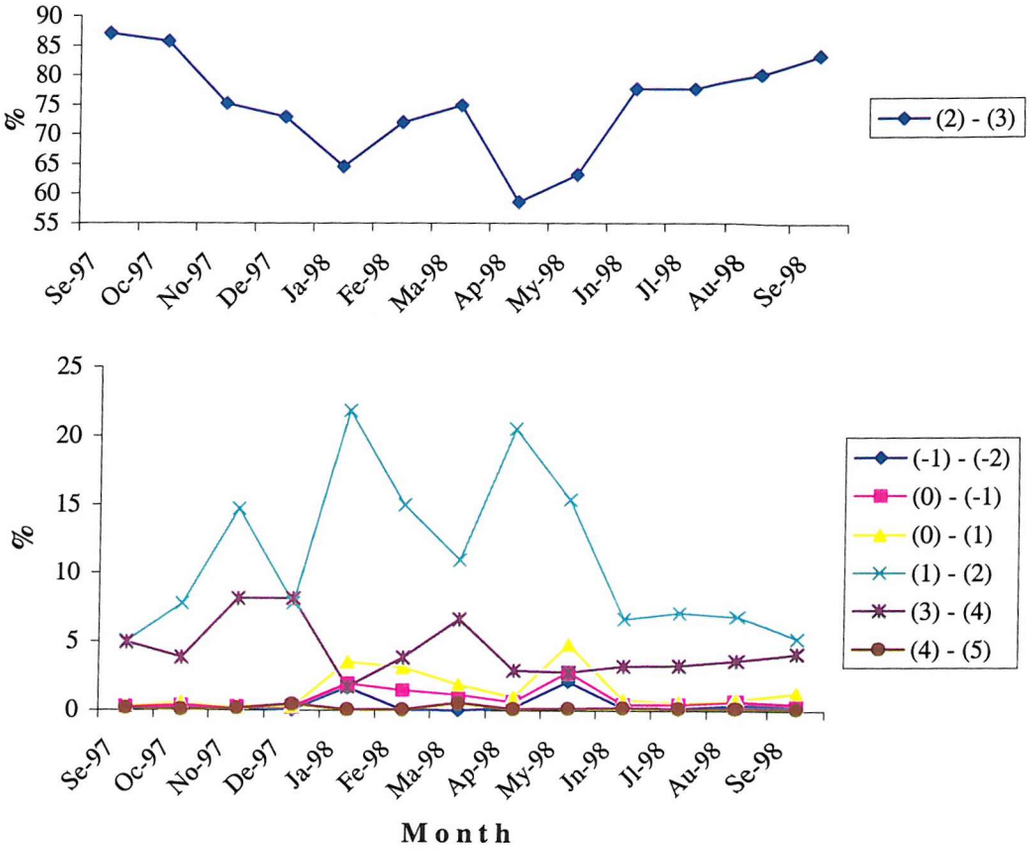

Fig. 3.4. Percentage of Phi value distribution of the sediments collected from the sparse site (n = 5).

Chapter IV:
Seagrass Biology and Chemical Constituents

4.1. Introduction

The significant roles of seagrass bed ecosystems in the marine environment have been reported in many studies (Dawes, 1998; also see Chapter I), although, for most species and most areas there is a scarcity of information on their basic biology and life cycle (Phillips and Meñez, 1988). Of the species studied, perhaps *Zostera marina* is the most well and intensively studied among the temperate and cold species, whereas *Thalassia testudinium* is the best studied of the tropical species (Zieman and Wetzel, 1980; Phillips and Meñez, 1988; Fortes, 1994; Kennish, 1996; Tomascik *et al.*, 1997; Dahl, 1998).

Biological studies of seagrasses are important because they are essential if seagrass ecosystems are to be fully understood and can reveal the status of the health of the seagrass bed ecosystem itself (Phillips and Meñez, 1988; Davison and Hughes, 1998; Bortone, 2000). Also, such studies may allow an interpretation of how biotic and abiotic parameters interact (Brix *et al.*, 1983; Mann, 1996; Dawes, 1998). On a larger scale, seagrass beds may be important features within coastal ecosystems and reflect the general health of such systems (Bortone, 2000).

In European waters most seagrass biology studies have been either concentrated in the northwestern mainland Europe or in the Mediterranean regions (Dawson, 1960; Zieman and Wetzel, 1980; Phillips and Meñez, 1988; Terrados *et al.*, 1998). Until 1999, studies of seagrass biology from the British Isles generally were less comprehensive (see Webster *et al.*, 1998). In fact, many aspects of *Zostera* biology in the UK are still relatively poorly understood (Davison and Hughes, 1998). Thus, further information on these would make an important

contribution to the biological knowledge as well as the conservation management of eelgrass biotopes.

The chemical composition of marine vegetation in general and seagrasses in particular is poorly understood despite the acknowledged importance of these organisms as primary producers (Dawes and Kenworthy, 1990). As has been observed in the marine algae, the chemicals of the seagrass can function as either deterrents or attractants for marine animals (Hay *et al.*, 1992). The following important functions of seagrass chemicals include: indicators of growth, plant condition, food storage, nutrient availability and microbial inhibitors (Zapata and MacMillan, 1971; Quakenbush *et al.*, 1990 and papers therein; Klap *et al.*, 2000).

Surprisingly, no single study of chemical constituents of the seagrass has ever been conducted in British Isles waters. One study considering relationships between benthic fauna and vegetation indicated the potential importance of chemical cues from seagrass in the settlement of marine fauna (see Mazella *et al.*, 1992). Therefore information in the chemical constituents of the seagrass will be useful for studying the seagrass bed ecosystem in general, and of the seagrass bed benthic fauna in particular.

This part of study aims to present detailed biological data as well as selected chemical constituents data for *Z. noltii* from Ryde Beach, Isle of Wight. For the study of the seagrass biology, the research was directed to the following aspects: shoot density, shoot height, leaf number, shoot biomass and reproduction condition. For the selected chemical constituents, the study was targeted at the measurements of total phenolics, carbohydrate and protein concentrations. Though the presence of *Zostera* in the Solent waters have been documented in several works (see Tubbs and Tubbs, 1983; Al-Suwailem, 1991; Bamber, 1993; Irving, 1996; Dahl, 1998; Davison and Hughes, 1998; Jones, 1998), a comprehensive investigation of *Z. noltii* this type has never been previously undertaken.

4.2. Results

4.2.1. Seagrass Biology

4.2.1.1. Shoot Density

There was a distinctive seasonal fluctuation in shoot density for both seagrass densities during the first year of study. The seasonal pattern was repeated in the following year. In general, the average of the *Z. noltii* population at the dense site reached between 420 (± 23) – 1020 (± 69) shoots·m^{-2}, whereas at the sparse site the average density ranged between 276 (± 30) – 477 (± 21) shoots·m^{-2} (Figure 4.1). The lowest densities were found in March 1998 for the dense site and in February 1998 for the sparse site respectively. At both sites, shoot densities reached maximum values in the autumn months, i.e. October – November 1997 and 1998 and October 1999. Increasing shoot densities were recorded throughout summer (June – August 1998, July 1999), early autumn (September 1997 and 1998) and early winter (December 1997 and 1998). Statistically, the shoot density between the two sites was very different (t-test, $P < 0.001$). These differences were not surprising, since these are selected as high and low density sites.

The greatest decline of shoot population happened in between January and February months for dense and sparse sites both in 1998 and 1999. Again for both type of densities, the shoot numbers started to increase by April 1998 and May 1999. The process of shoot addition then occurred until mid autumn, i.e. November 1997 and 1998. Although the *Z. noltii* vegetation reached its peak in November, the highest rates of shoot addition occurred during the May and August period in 1998 and between spring (May) and summer (July) in 1999.

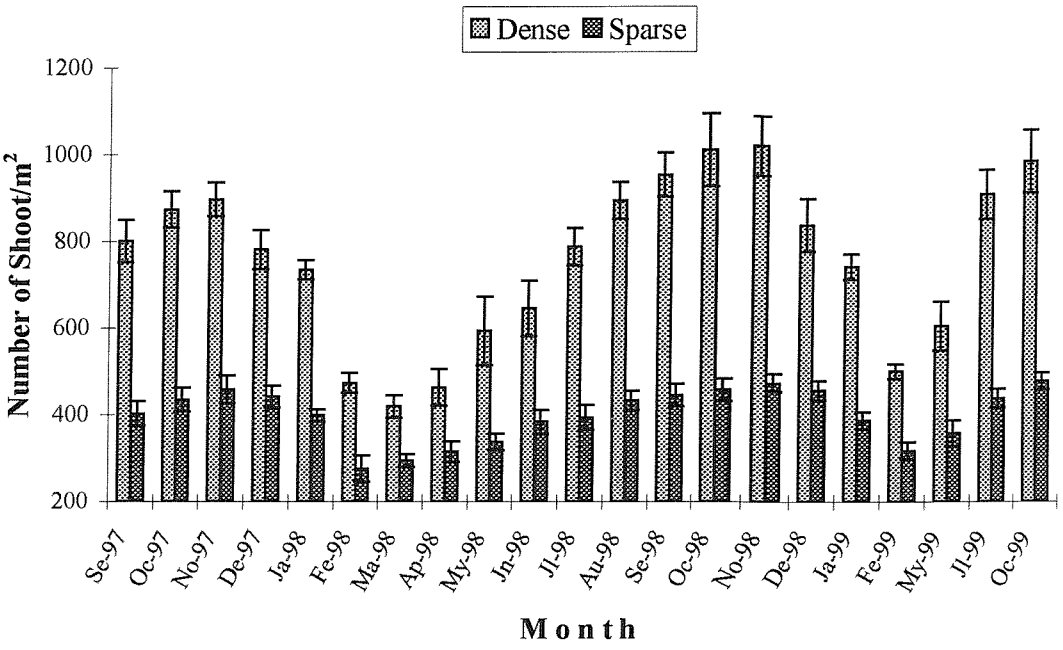

Fig.4.1. Shoot density of *Z. noltii* from Ryde Beach seagrass bed (n = 5; ± SD).

4.2.1.2. Shoot Height

There was great seasonal variations recorded in shoot height. Figure 4.2. illustrates the mean height of *Z. noltii* shoots measured throughout the study. There was a similar pattern between the two different densities. In both types, the shortest shoots were recorded during the winter to early spring months, i.e. February – March 1998 and February 1999; while the tallest stands were recorded in late autumn, i.e. November 1997 and 1998. From September to November 1997 the shoots were still elongating, then apparently they stopped growing until March 1998. From April 1998 the shoots started to grow and reached the maximum height in November 1998. Though in December 1998 the plants were still relatively tall, yet they started to loose their height toward February 1999. Observation in

spring (May) 1999 indicated the shoots were starting to grow and the maximum heights were obtained by the autumn (October) 1999 cohort.

Statistically the shoots height were not different between the two type of shoot densities (t-test, $P = 0.044$). The average heights of *Z. noltii* shoots at the dense site ranged from 14.6 (± 3.6) – 23.2 (± 4.1) cm, whereas those of the sparse site fell between 13.1 (± 3.9) – 23.0 (± 3.7) cm. Moreover, though there was no significant difference, the maximum heights of shoot in autumn months (September – November) 1998 were higher compared to that of the 1997 autumn samples. Also the summer (July) 1999 samples had taller shoot sizes compared to that of 1998 summer (June – August) samples.

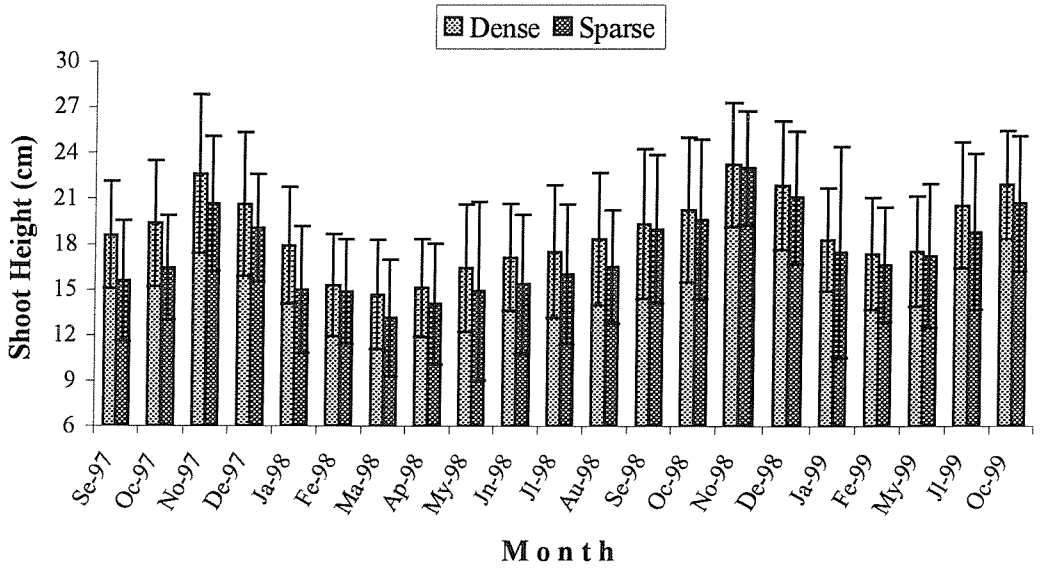

Fig.4.2. Height of *Z. noltii* shoots in Ryde Beach seagrass bed (n = 50; ± SD).

4.2.1.3. Leaf Number

As with shoot density and shoot height, the leaf number per shoot varied greatly according to the season (Figure 4.3). However, as has been observed in shoot height, shoot leaf number did not vary between the sites. The number of leaves per shoot followed the growth period of the shoots. The average leaf number fell between 2.5 (± 0.6) – 5.7 (± 0.6) leaves per shoot for the dense bed and 2.4 (± 0.5) – 5.5 (± 0.7) leaves per shoot for the sparse bed respectively. There was no difference in number of leaves between the dense and sparse sites (t-test, $P = 0.023$).

For both seagrass densities, the lowest values for leaf number were found in February 1998, whereas the highest values were found in August and September 1998. The detailed data showed the *Z. noltii* shoots to possess between 2 and 8 leaves at one time. The highest mean of leaf number was shown from the late summer to early autumn in each year. This study has also seen that by the end of winter all shoots have lost more than half of their leaves.

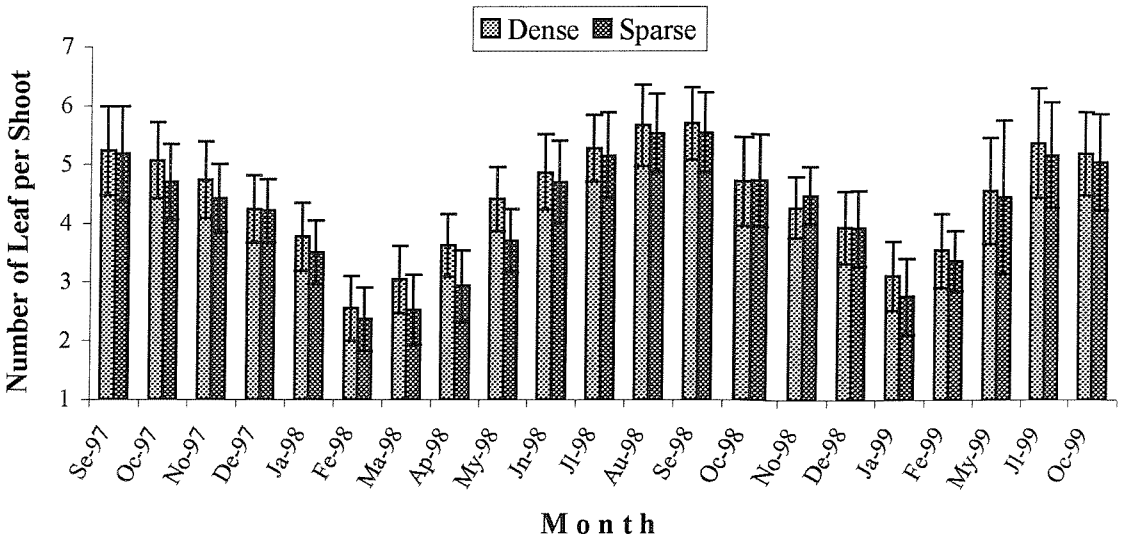

Fig. 4.3. Average leaf number of Z. noltii from Ryde Beach seagrass bed (n = 50; ± SD).

4.2.1.4. Shoot Biomass

The AFDW shoot biomass per square metre of *Z. noltii* also varied greatly with season as well as between the sites in each year (Figure 4.4.). The values for the dense site were always very significantly higher compared to that of the sparse site (t-test, $P < 0.001$).

Shoot biomass was high in September 1997 with mean aboveground biomass values of 21.57 (± 3.42) $g \cdot m^{-2}$ and 8.39 (± 1.39) $g \cdot m^{-2}$ for the dense and sparse density respectively. In the early winter each year, i.e. December 1997 and 1998, the biomass values decreased rapidly and reached a minimum in the months of February and March 1998 and February 1999 in both sites. Statistically, there was a significant difference between the shoot biomass of the dense and sparse sites (t-test, $P = 0.010$) in which the dense site always possessed the higher values.

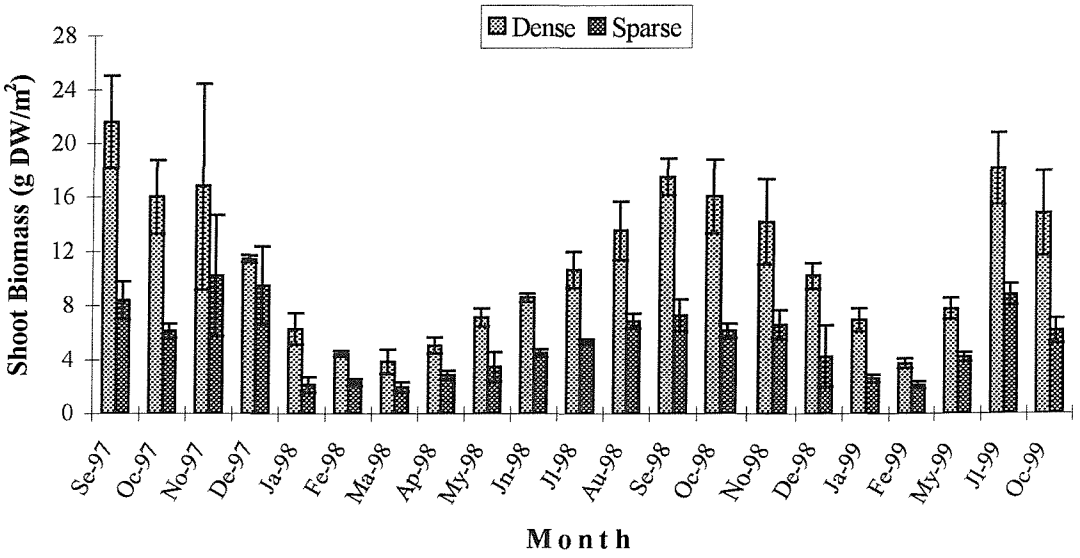

Fig.4.4. Aboveground biomass of *Z. noltii* in Ryde Beach (n = 5; ± SD).

4.2.1.5. Reproductive Condition

In September 1997, relatively few shoots (24 % from the dense site and 19 % from the sparse site) were found in flower, and throughout the study no more than 29 % of shoots were in flower at any time (Figure 4.5). There was a clear seasonal pattern, with flower shoots developing rapidly from July to August 1998 reaching maximums of 28 % and 29 % for dense and sparse site respectively in August 1998. A steady decline in flowering shoots occurred throughout autumn and winter 1997 and 1998.

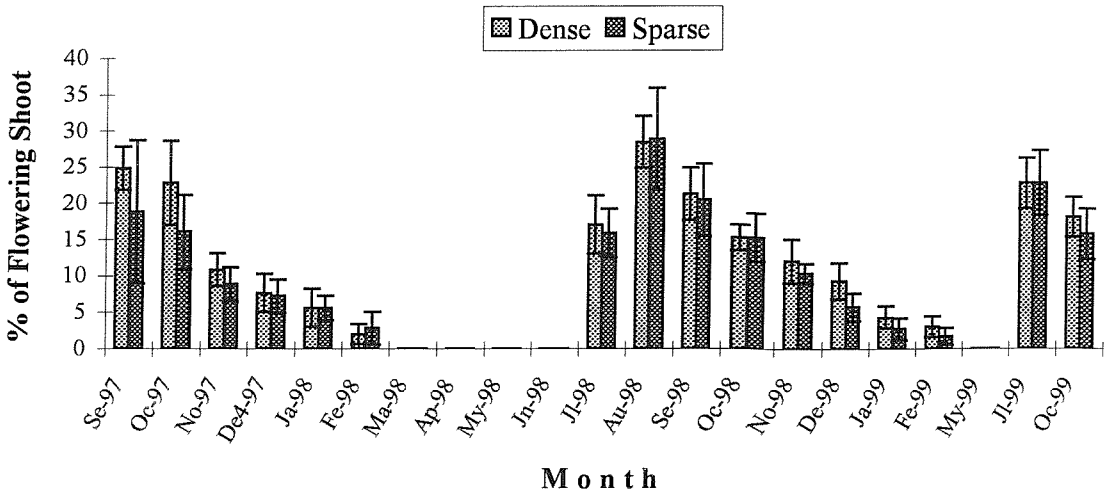

Fig. 4.5. Percentage of *Z. noltii* shoots with the flower from Ryde Beach (n = 5; ± SD).

By using the data on shoot density and percentage of flowering shoots, there were 198 shoots·m^{-2} and 76 shoots·m^{-2} at the dense and sparse sites respectively in flower (Figure 4.6.). The lowest number of flowering shoots at the dense site was recorded in February 1998 (9 shoots·m^{-2}), whereas that at the sparse site was found in February 1999 (5 shoots·m^{-2}). In both seagrass densities, the highest number of flowering shoots were recorded in August 1998 (253 shoots·m^{-2} at the dense site and 124 shoots·m^{-2} at the sparse site respectively). The number of flowering shoots maintained high numbers during the early autumn (September – October) in each year.

Surprisingly, this study found evidence for flowering continuing into winter, i.e. from December 1997 to February 1998 and from December 1998 to February 1999. The flowering shoots in these periods were seeding and ranged between 2 and 9 % of shoots for the dense site and between 2 and 7 % for the sparse site. There were no shoots found with flowers from the spring and early summer of 1998 (March – June) and spring 1999 (May) samples. Statistically there

is no significant difference between the dense and sparse site in term of the proportion of shoots that flower (t-test, $P = 0.328$).

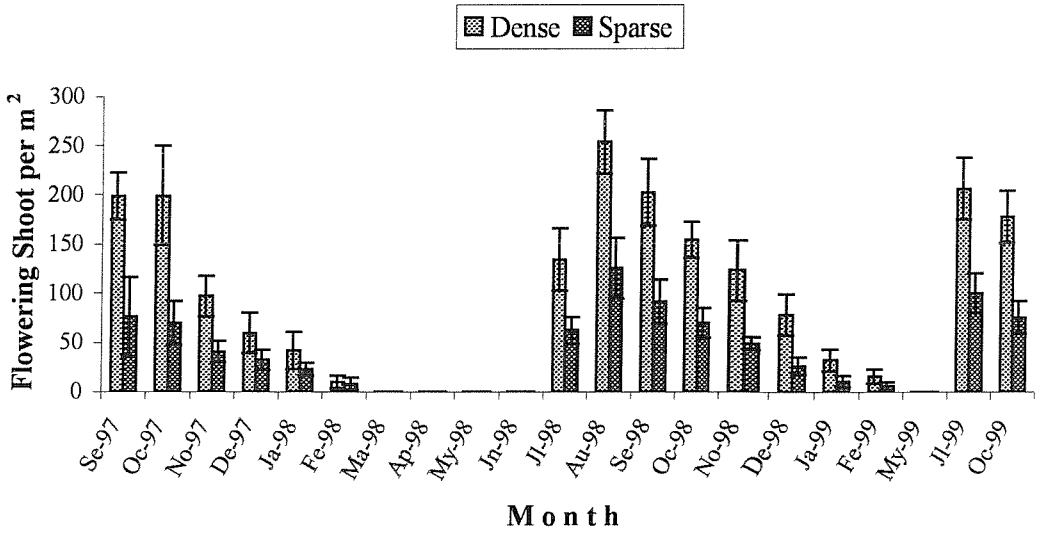

Fig. 4.6. Number of *Z. noltii* shoots in flower from Ryde Beach (n = 5; ± SD).

This study was not able to record the seed production of *Z. noltii*. Nonetheless seeds were seen in the bed sediment. The sediments taken from the autumn (November 1997 and 1998) towards the early spring (March and April 1998) occasionally contained seeds. In the laboratory the seeds were measured and the sizes ranged between 1.4 – 1.9 mm in length and 0.9 – 1.1 in width, corresponding to values for this species in the literature (Table 2.1.).

4.2.2. Seagrass Chemical Constituents

4.2.2.1. Total Phenolics

In general, the total phenolics concentrations of *Z. noltii* shoots varied temporally but not between the sites (Figure 4.7.). In September 1997 the phenolics value was high, then declined during the autumn and reached the lowest values in January – March 1998. Significant increases occurred from April to August 1998. In 1998, the maximum value was shown in September and there was no clear decrease until December. After low concentrations in January – February 1999, the phenolics increased in the last three 1999 seasonal samples.

Statistically, the total phenolics contents of *Z. noltii* shoots were not significantly different (t-test, $P = 0.798$) between the two sites. The more densely populated site had the mean values of 0.44 (± 0.06) – 0.81 (± 0.08) % AFDW, while the less populated area ranged from 0.40 (± 0.02) – 0.82 (± 0.09) % AFDW.

4.2.2.2. Total Carbohydrate

As has been found in the phenolics contents, seasonal variations were also observed for the total carbohydrate concentrations of *Z. noltii* shoots, and there was no variation shown between the sites (Figure 4.8.). Regardless of the site type, carbohydrate concentrations declined at the beginning of the study in the autumn 1997 (September – November) and then decreased more rapidly into winter and early spring (December 1997 – March 1998). A steady increase of carbohydrate occurred during the spring to early autumn (April – September) in 1998 and from May to October 1999.

Statistically there were no significant differences in the carbohydrate contents between the two sites (t-test, $P = 0.370$). The mean concentrations were in the range of 0.70 (± 0.07) – 1.20 (± 0.24) % AFDW for the dense site and 0.73 (± 0.11) – 1.23 (± 0.021) % AFDW for the sparse site.

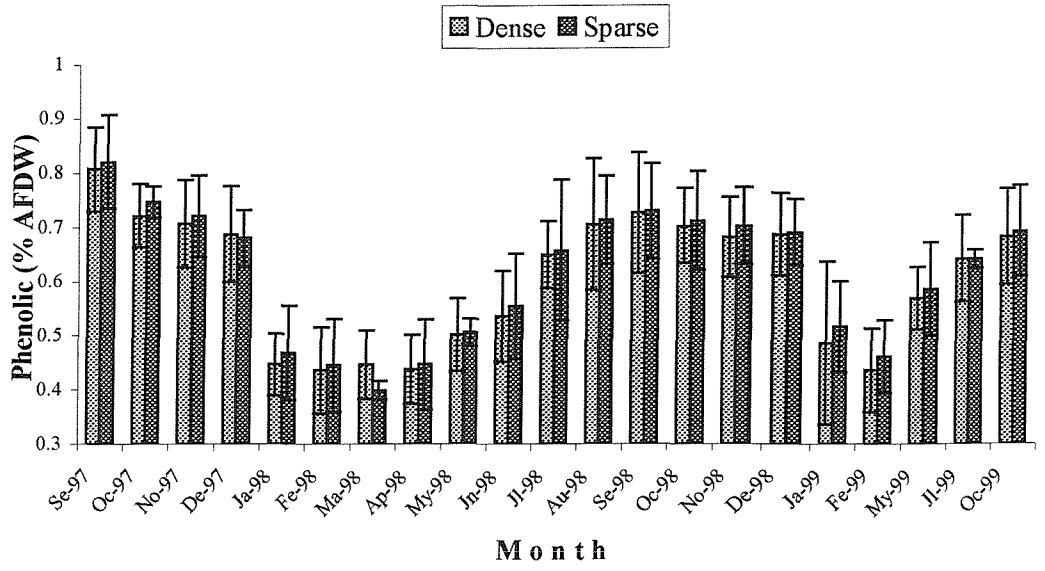

Fig.3.7. Total phenolic content of *Z. noltii* shoots from Ryde Beach seagrass bed (n = 15; ± SD).

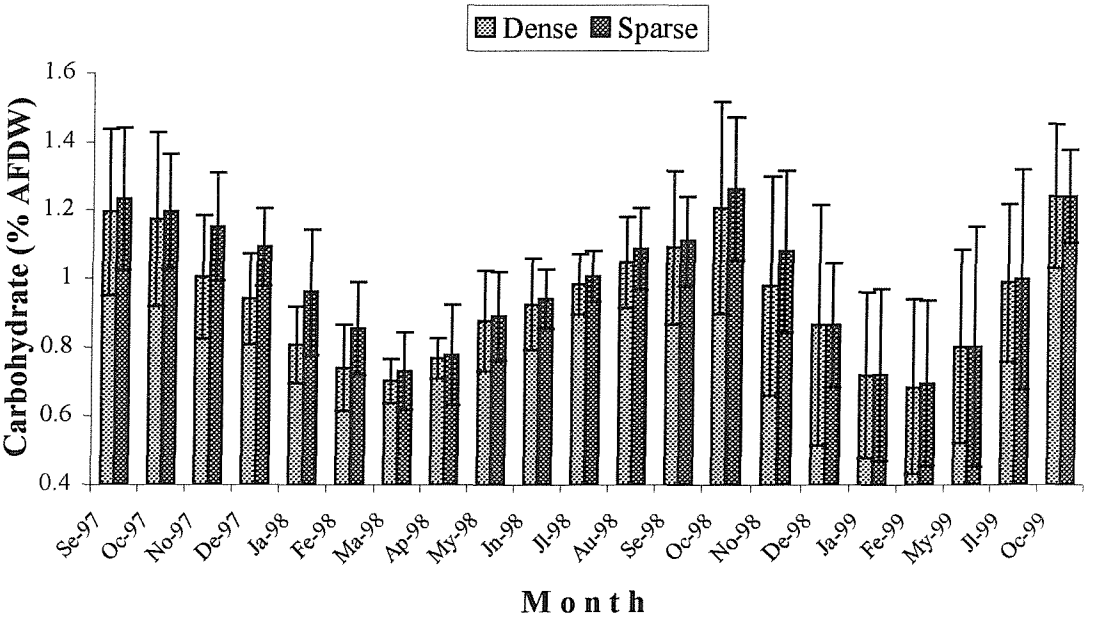

Fig.4.7. Total carbohydrate content of *Z. noltii* shoots from Ryde Beach seagrass bed (n = 15; ± SD).

4.2.2.3. Total Protein

As with the total phenolics and total carbohydrate results, the total protein content between the two sites did not differ significantly (Figure 4.9.; t-test, P = 0.186). The mean total protein content fell between 0.62 (± 0.07) – 0.88 (± 0.11) % AFDW and 0.57 (± 0.008) – 0.83 (± 0.10) % AFDW for dense and sparse sites respectively. The seasonal variation of protein was less apparent than for sugars and phenolics, with highest values in October - November 1997 and 1998 and lowest values from the winter to early spring in both years.

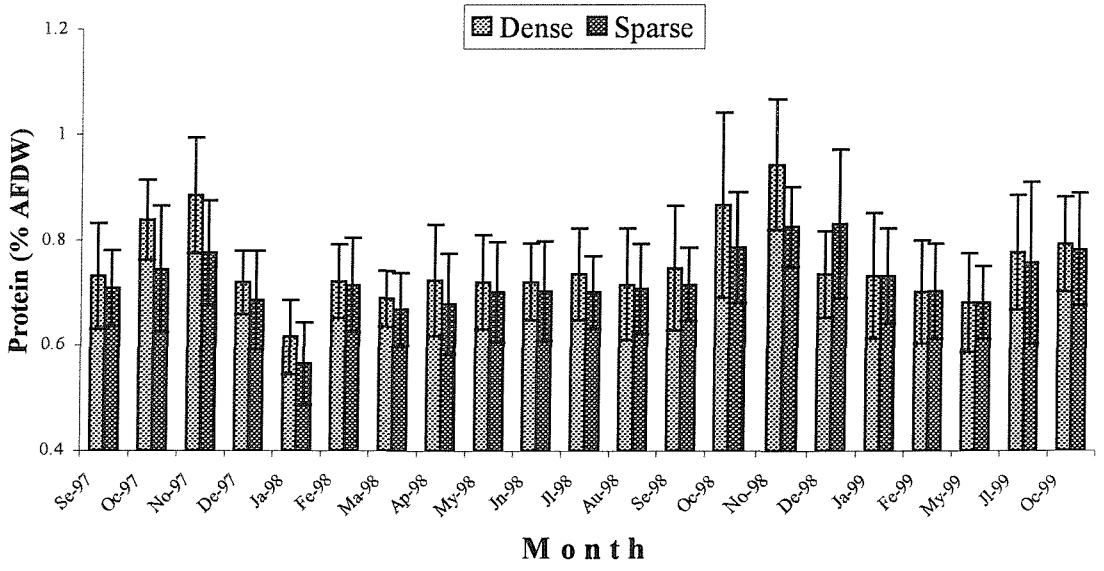

Fig.4.9. Total proteins content of *Z. noltii* shoots from Ryde Beach seagrass bed (n = 15; ± SD).

4.2.3. Statistical Analyses

Multiple linear regression for the dense site showed that the variables in general were positively correlated with seagrass shoot density ($F_{8,12} = 19.4$; $P < 0.0001$; Table 4.1). There were six variables, i.e. shoot height, shoot aboveground biomass, shoot leaf number, total carbohydrates and phenolics, and sediment organic matter content, that significantly correlated with the shoot density. Shoot leaf number was also positively correlated with the other variables measured ($F_{8,12} = 19.6$; $P < 0.0001$; Table 4.2). Besides shoot density, five other variables correlated with the shoot leaf number, these were shoot aboveground biomass, shoot height, carbohydrate and phenolic contents, and water temperature. Together with shoot density and shoot leaf number, shoot height showed positive correlation with shoot aboveground biomass, phenolic and carbohydrate contents, and water temperature ($F_{8,12} = 22.6$; $P < 0.0001$; Table 4.3). As for the shoot aboveground biomass, it not only correlated with shoot density, shoot leaf number and shoot height, but also with all three chemical constituents and water temperature ($F_{8,12} = 22.1$; $P < 0.0001$; Table 4.4).

Table 4.1. ANOVA of multiple linear regression between shoot density and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	8	661233.8	82654.2	19.4	< 0.0001
Residual	12	51256.5	4271.4		
Total	20	712490.3	35624.5		

Table 4.2. ANOVA of multiple linear regression between shoot leaf number and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	8	15.03	1.8786	19.6	< 0.0001
Residual	12	1.15	0.0961		
Total	20	16.18	0.8091		

Table 4.3. ANOVA of multiple linear regression between shoot height and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	8	112.03	14.003	22.6	< 0.0001
Residual	12	7.43	0.619		
Total	20	119.46	5.973		

Table 4.4. ANOVA of multiple linear regression between shoot aboveground biomass and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	8	535.9	66.98	22.1	< 0.0001
Residual	12	36.3	3.03		
Total	20	572.2	28.61		

For the study of seagrass chemical constituents at the dense site, a positive correlation was observed between seagrass phenolic content and all biological variables measured as well as with carbohydrate and protein contents ($F_{8,12} = 13.1$; $P < 0.0001$; Table 4.5). Total carbohydrate also correlated with all variables, except sediment organic matter and water temperature ($F_{8,12} = 12.2$; $P = 0.0001$; Table 4.6). Protein did not correlate with all biology variables in general ($F_{8,12} = 4.18$; $P = 0.0133$; Table 4.7), although as has been explained, it correlated with shoot aboveground biomass, phenolics and carbohydrate contents ($F_{1,19} = 17.1$; $P = 0.0006$; Table 4.8).

Table 4.5. ANOVA of multiple linear regression between total phenolics and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	8	0.2631	0.03289	13.1	< 0.0001
Residual	12	0.0301	0.00251		
Total	20	0.2932	0.01466		

Table 4.6. ANOVA of multiple linear legression between total carbohydrate content and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	8	0.5493	0.06866	12.2	0.0001
Residual	12	0.0674	0.00562		
Total	20	0.6167	0.03083		

Table 4.7. ANOVA of multiple linear regression between total protein and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	8	0.0839	0.01048	4.18	0.0133
Residual	12	0.0301	0.00251		
Total	20	0.1140	0.00570		

Table 4.8. ANOVA of forward stepwise regression between total protein and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	1	0.0539	0.05392	17.1	0.0006
Residual	19	0.0600	0.00316		

The stepwise regression test indicated that shoot density had the strongest correlation with shoot height ($P < 0.0001$; F- value = 56.39) and shoot aboveground biomass ($P < 0.0001$; F-value = 40.42). These were then followed by carbohydrate, phenolic, shoot leaf number and sediment organic matter respectively. The highest correlation level for the shoot leaf number was observed with shoot aboveground biomass ($P < 0.0001$; F-value = 31.70), followed closely by three variables, i.e. phenolic, carbohydrate and water temperature. In the test for shoot height, water temperature was found to be the second most correlated variable ($P = 0.0006$; F-value = 17.07) after shoot density. Besides being strongly correlated with shoot density and shoot leaf number, carbohydrate was the variable from the chemical constituents which had the highest correlation with shoot

aboveground biomass ($P < 0.0001$; F-value = 77.97). As among the chemical constituents, phenolic had stronger correlation to carbohydrate ($P < 0.0001$; F-value = 59.52) than with protein ($P = 0.0102$; F-value = 8.14). Table 4.9 summarises the observed correlation among the variables at the dense site.

Table 4.9. Summary of Pearson product moment correlation test for the biological aspects and chemical constituents of seagrass of the dense site.

Group of Test	*P*-Value	Correlation Coefficient
Shoot Density v Shoot Height	< 0.001	0.865
Shoot Density v Shoot Aboveground Biomass	< 0.001	0.825
Shoot Density v Shoot Leaf Number	< 0.001	0.682
Shoot Density v Carbohydrate	< 0.001	0.760
Shoot Density v Phenolic	< 0.001	0.737
Shoot Density v Sediment Organic Matter	0.0014	0.649
Shoot Leaf Number v Shoot Height	0.048	0.503
Shoot Leaf Number v Shoot Abvgr. Biomass	< 0.001	0.791
Shoot Leaf Number v Carbohydrate	< 0.001	0.755
Shoot Leaf Number v Phenolic	< 0.001	0.757
Shoot Leaf Number v Water Temperature	< 0.001	0.750
Shoot Height v Shoot Aboveground Biomass	< 0.001	0.679
Shoot Height v Phenolic	< 0.001	0.617
Shoot Height v Carbohydrate	0.005	0.588
Shoot Height v Water Temperature	< 0.001	0.688
Shoot Abvgr. Biomass v Water Temperature	0.005	0.504
Shoot Abvgr. Biomass v Phenolic	< 0.001	0.644
Shoot Abvgr. Biomass v Carbohydrate	< 0.001	0.896
Shoot Abvgr. Biomass v Protein	0.006	0.582
Phenolic v Carbohydrate	< 0.001	0.871
Phenolic v Protein	0.010	0.548
Carbohydrate v Protein	0.008	0.562

For the sparse site, all the biological variables in general correlated with each other as have been observed at the dense site. Only shoot aboveground biomass had a different result. Multiple linear regression test for the shoot density concluded this variable correlated with shoot leaf number, shoot height, shoot aboveground biomass, phenolic and carbohydrate contents, as well as with sediment organic matter ($F_{8,12} = 22.7$; $P < 0.0001$; Table 4.10). As with the dense site, apart from shoot density, shoot leaf number in the sparse site showed correlation with shoot height, shoot aboveground biomass, phenolics and carbohydrate concentrations, and water temperature ($F_{8,12} = 54.0$; $P < 0.0001$; Table 4.11). Again, shoot height also showed a similar pattern of correlation to those found in the dense site, it also correlated to shoot density, shoot leaf number, shoot aboveground biomass, phenolics and carbohydrate contents, as well as water temperature ($F_{8,12} = 18.7$; $P < 0.0001$; Table 4.12). Aboveground biomass did not correlate with all variables ($F_{8,12} = 13.1$; $P < 0.0001$; Table 4.13). It correlated with shoot height, phenolics, carbohydrate and protein contents ($F_{1,19} = 31.7$; $P < 0.0001$; Table 4.14).

Table 4.10. ANOVA of multiple linear regression between shoot density and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	8	71187.1	8898.4	22.7	< 0.0001
Residual	12	4710.3	392.5		
Total	20	75897.4	3794.9		

Table 4.11. ANOVA of multiple linear regression between shoot leaf number and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	8	18.913	2.3641	54.0	< 0.0001
Residual	12	0.525	0.0438		
Total	20	19.439	0.9719		

Table 4.12. ANOVA of multiple linear regression between shoot height and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	8	106.63	13.329	18.7	< 0.0001
Residual	12	8.55	0.713		
Total	20	115.19	5.759		

Table 4.13. ANOVA of multiple linear regression between shoot aboveground biomass and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	8	376.6	47.07	7.25	< 0.0001
Residual	12	78.0	6.50		
Total	20	454.5	22.73		

Table 4.14. ANOVA of forward stepwise regression between shoot aboveground biomass and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	1	284.3	284.28	31.7	< 0.0001
Residual	19	170.3	8.96		

Overall multiple linear regression tests for the chemical constituents at the sparse site indicated that the correlation was also observed between seagrass phenolic contents and all biological variables measured, as well as with carbohydrate and protein contents, as has been found for the dense site ($F_{8,12}$ = 16.5; $P < 0.0001$; Table 4.15). Carbohydrate content did not correlate with all variables ($F_{8,12} = 4.97$; $P = 0.0068$; Table 4.16), but further tests showed it correlated with shoot density, shoot leaf number, shoot aboveground biomass and phenolic content ($F_{1,19} = 4.76$; $P < 0.0001$; Table 4.17). Seagrass protein did not correlate with all variables ($F_{8,12} = 11.4$; $P = 0.0002$; Table 4.18), although it did correlate with shoot aboveground biomass, and phenolic content ($F_{1,19} = 27.9$; $P <$ 0.0001; Table 4.19).

Table 4.15. ANOVA of multiple linear regression between total phenolic and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	8	0.2778	0.03473	16.5	< 0.0001
Residual	12	0.0253	0.00211		
Total	20	0.3031	0.01516		

Table 4.16. ANOVA of multiple linear regression between total carbohydrate and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	8	0.506	0.0632	4.97	0.0068
Residual	12	0.153	0.0127		
Total	20	0.659	0.0329		

Table 4.17. ANOVA of forward stepwise regression between total carbohydrate and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	1	0.471	0.47080	47.6	< 0.0001
Residual	19	0.188	0.00990		

Table 4.18. ANOVA of multiple linear regression between total protein and the other variables at the sparse site.

Source of Variance	DF	SS	MS	F	P
Regression	8	0.06090	0.007612	11.4	0.0002
Residual	12	0.00801	0.000667		
Total	20	0.06890	0.003445		

Table 4.19. ANOVA of forward stepwise regression between total protein and the other variables at the dense site.

Source of Variance	DF	SS	MS	F	P
Regression	1	0.0410	0.04101	27.9	< 0.0001
Residual	19	0.0279	0.00147		

Results of the stepwise regression test at the sparse site shown that shoot density also had the strongest correlation with the shoot height ($P < 0.0001$; F-value = 31.14) and shoot aboveground biomass ($P < 0.0001$; F-value = 28.07). Carbohydrate and phenolic contents and shoot leaf number followed closely. The shoot leaf number was observed to be correlated highly with shoot density ($P < 0.0001$; F-value = 21.68), followed by water temperature (P = 0.0006; F-value = 16.87). Shoot aboveground biomass ($P < 0.0001$; F-value = 31.73) and water temperature ($P < 0.0001$; F-value = 27.93) were found to be the next two variables mostly correlated with the shoot height. Being strongly correlated with shoot density, shoot leaf number and shoot height, shoot aboveground biomass correlated closely with all three chemical constituents. Of the chemical constituents, phenolics content was most strongly correlated with carbohydrate ($P < 0.0001$; F-value = 47.58) compared with protein ($P = 0.0102$; F-value = 7.99). Correlation was not observed between the content of carbohydrate and protein. The summary of variables observed to be correlated at the sparse site is presented in Table 4.20.

Table 4.20. Summary of Pearson product moment test for the biological aspects and chemical constituents of seagrass of the sparse site.

Group of Test	P-Value	Correlation Coefficient
Shoot Density v Shoot Height	< 0.001	0.788
Shoot Density v Shoot Aboveground Biomass	< 0.001	0.772
Shoot Density v Shoot Leaf Number	< 0.001	0.730
Shoot Density v Carbohydrate	< 0.001	0.760
Shoot Density v Phenolic	< 0.001	0.737
Shoot Density v Sediment Organic Matter	0.009	0.558
Shoot Leaf Number v Shoot Height	0.049	0.503
Shoot Leaf Number v Shoot Abvgr. Biomass	0.009	0.558
Shoot Leaf Number v Carbohydrate	< 0.001	0.655
Shoot Leaf Number v Phenolics	< 0.001	0.639
Shoot Leaf Number v Water Temperature	< 0.001	0.686
Shoot Height v Shoot Aboveground Biomass	< 0.001	0.791
Shoot Height v Phenolics	0.003	0.620
Shoot Height v Water Temperature	< 0.001	0.772
Shoot Abvgr. Biomass v Water Temperature	0.005	0.620
Shoot Abvgr. Biomass v Phenolics	0.002	0.644
Shoot Abvgr. Biomass v Carbohydrate	0.006	0.579
Shoot Abvgr. Biomass v Protein	< 0.001	0.771
Phenolics v Carbohydrate	< 0.001	0.845
Phenolics v Protein	0.011	0.544

4.3. Discussion

Overall, the seagrass density in the present study ranged between 276 – 1020 shoots·m^{-2}. As it has been stated in the beginning of this chapter, this is the first study solely concerned with the monitoring of *Z. noltii* density at Ryde Beach, therefore it is not possible to present a historical account of the seagrass community of this site. Nevertheless, shoot density data collected from the recent study was relatively high compared with that from *Zostera* population studies conducted in the neighbouring English Channel areas. For example a *Z. marina* bed at Roscoff, France and the Yealm Estuary, Southwest England had densities of 500 – 800 shoots·m^{-2} (Jacobs, 1980) and 12 – 144 shoots·m^{-2} (Webster *et al.*, 1998) respectively.

This study found that *Z. noltii* at Ryde Beach persisted throughout the year. This finding is in the agreement with former observations that concluded the seagrass beds of the Solent coast remain wintergreen (Tubbs and Tubbs, 1983). *Zostera* spp. was thought to exhibit a winter-dormant condition, but is now known to remain active all winter along a broad latitudinal gradient in North America (Phillips and Meñez, 1988; Dawes, 1998). Statistical analysis between shoot density and water temperature indicated that there was no correlation between these two variables, meaning the production of *Z. noltii* in the site was not dependant on the water temperature, as it was shown to be more closely correlated with the sediment organic matter.

It has been observed that the density of *Z. noltii* (276 – 1020 shoots·m^{2}) varied according to the season. Overall, the peak population was reached in autumn, while in the winter months the numbers of shoots fell drastically to less than 50 % of the peak values (Figure 4.1.). The fluctuation in seagrass density is common (Dawes, 1998; Bortone, 2000), this varying seasonally (Marba and Duarte, 1997) and with depth (Zieman and Wetzel, 1980). It was reported that subtidal eelgrass may be 3 – 4 times denser in summer than in winter (Phillips and Meñez; 1988). Since the statistical tests indicated no correlation between shoot density and water temperature, thus other factors, i.e. natural disasters (particularly

winter storm), shoot ageing and herbivory, are to be suggested as influencing the shoot dynamics of *Z. noltii* in this study.

The natural processes have indeed been reported as the main causes for the shoot mortality. Burial in the sediment (Terrados, 1997), wave action (den Hartog, 1971; Dawes, 1998), tidal currents (Townsend and Fonseca, 1998; Bortone, 2000) and light reduction (de Jonge and de Jonge, 1992; Terrados, 1997; Townsend and Fonseca, 1998; Bach *et al.*, 1998; Moore and Wetzel, 2000) have been identified as causes of shoot mortality that lead to the decline of seagrass populations. It is suggested that environmental disturbances were also experienced by *Z. noltii* bed at Ryde Beach during the winters. The severe weather in both winter seasons in 1997/1998 and 1998/1999 experienced by the site, as occurred widely throughout coastal southern England, resulted in strong wave action and currents, resulting in the burial of many shoots. Many others had their roots and rhizome exposed to the air. Under the condition of reduced light availability due to very short daytime, these phenomena are thought to contribute in the decline of the *Z. noltii* population during the winter. Indeed, the evidence of the *Zostera* declining due to multiple physical factors has been reported from a North Carolina seagrass bed (Townsend and Fonseca, 1998).

The higher silt and organic matter content of the sediment of the dense site (though was not different significantly) probably contributed to the higher density of the seagrass shoots compared to the sparse one. The positive effect of organic mud on the robust development of the plant is documented, as is the need for a more well-developed nutrient absorptive system in the coarser sediments, which generally tend to be lower in nutrients and organic matter (Zieman and Wetzel, 1980). Shoot density and sediment organic matter at both sites (Tables 4.9 and 4.20) provided evidence of this correlation.

Shoot height of *Z. noltii* in this study showed a clear seasonal pattern. Changes in shoot height are oftenly used as the determinant for the growing periodicity (Phillips, 1990). Results from this study concluded that the growing period lasted from early spring (March - April) to early winter (December).

Increase in both shoot length (Figure 4.2.) as well as the number of the leaves per shoot (Figure 4.3.) provided indications of the growing season. Shoot height correlated with leaf number (see statistical analyses) indicating that increase in the height of shoots occurs simultaneously with increase in leaf number.

The shoot height of *Z. noltii* at Ryde Beach fell in the range of 13.1 – 23.7 cm. This is much higher than *Z. noltii* studied from the other side of the English Channel (i.e. Golfe Juan, France, 11 cm, see Loques *et al.*, 1988), but fell within the range of the values recorded in the British Isles (up to 20 – 22 cm, Nature Conservancy Council, 1960 and Davison and Hughes, 1998) as well as for the same species in other European waters (up to 25 cm, den Hartog, 1971).

The peaks of growing period and shoot density appear to correlate with day length; that is peak growth reached its high values during the summer and early autumn months when the site received the longer period light. This has also been reported for other studies (see Loques *et al.*, 1988; Phillips, 1990; de Jonge and de Jonge, 1992; Beer *et al.*, 1998).

This study found a seasonal pattern in the leaf number of *Z. noltii*. The highest leaves per shoot was shown by the summer shoots compared to that of winter shoots, as was found in a report on North Atlantic eelgrass (Phillips, 1972). Perhaps, the burial of the shoots in the sediment during winter months leads to a decline in the shoot population and the leaf number, as has been suggested by Terrados (1997). By using field experiment, Terrados' study concluded that the number of new leaves tended to decrease when the shoots were buried and illuminated. Additionally, low temperatures throughout the winter, particularly in January – February 1998 and 1999, have possibly prevented *Z. noltii* at the site from producing new leaves. It has been reported that freezing condition can cause defoliation to the temperate seagrasses, and this phenomenon has been recorded for all three *Zostera* species in the UK (Davison and Hughes, 1998).

Figure 4.3. shows that the *Z. noltii* shoots started into growth, adding new leaves, soon after the winter ended. However, numbers increased sharply in spring (April 1998 and May 1999) when the shoots start to grow. The leaf numbers

increased to reach maximum values in September – October of each year. The finding in this study was in concordance with the leaf growth season of other members of the *Zostera* genus around the British Isles, which in general takes place during spring and summer (Davison and Hughes, 1998) when the water temperature is still warm. Indeed, statistical analyses provided a strong relationship between water temperature with either leaf number or shoot height (Tables 4.9 and 4.20). A study from the Solent reported that regrowth of *Zostera* began in late February, while the leaf cover increased from March to achieve a maximum by August - September (see Tubbs and Tubbs, 1983). Thus, the observations in this study found that there was a slight delay in the onset of the leaf production period. Perhaps the spring seasons of 1998 and 1999 may have come rather late or maybe the summers of 1997 – 1999 were a little longer and warmer than 20 years ago.

The decline in shoot densities with shorter shoot length and fewer numbers of the leaves at the end of winter were not only brought about by a reduction in growth rate. There are at least two other factors that may responsible for this phenomenon. Firstly, the site suffered badly from storms and strong waves during the months of January and February both in 1998 and 1999. Together with low temperatures (Figure 3.1., Chapter III) and minimum day length, these two physical disturbances could have reduced the growth of *Zostera*. There were plenty of freshly broken *Z. noltii* leaves drifting and deposited on the shore during those two visits. Secondly, the decline will also result from bird grazing pressure. Hundreds (or perhaps thousands) of waterfowl flock to the site during winter and seem to select to feed on the young *Zostera* leaves from shoots rather than on the broken floating leaves. Many of the coastal habitats in the Solent have ecological importance as the grazing destination for migratory bird populations, especially dark-bellied brent geese (*Branta bernicla bernicla*), and many other wildfowl and wader species (see Gee, 1996; Ganter, 1998 personal communication). The disturbances of seagrass beds by birds in the South England coastal systems have been addressed in several studies (Aspinall and Tasleer, 1997; Green and Cade, 1997; Tubbs and Tubbs, 1982, 1983; Dawes, 1998 and papers therein; Ganter,

2000). One comprehensive study of *Zostera* biotopes of the United Kingdom reported that although *Z. marina* was known as the most important food source for species such as brent geese in the UK coastal habitats, it had currently been supplanted by *Z. noltii* in this role (Davison and Hughes, 1998).

Overall the average leaf number of each shoot ranged between 2.4 – 5.7. No other study has ever recorded the dynamics of leaf number of *Z. noltii*. However, *Thalassia* shoots from Florida were reported as having 3 – 5 leaves each shoot at a time (Patriquin, 1973). In regions and times of high turnover, a new leaf is produced by a shoot as frequently as every 10 days, with a rate of one new leaf per 14 – 16 days per shoot being the average (Patriquin, 1973).

Throughout the study, the biomass of *Z. noltii* fluctuated widely but showed clear seasonal patterns. Many studies reported that biomass of seagrasses exhibit seasonal variation, which has been attributed to periodic fluctuations of environmental factors such as light, nutrient availability, salinity, water temperature, herbivore grazing and hydrological conditions (see Erftemeijer and Herman, 1994; Philippart, 1994b; Stapel *et al.*, 1997; Dawes, 1998; Bortone, 2000).

The maximum values of shoot biomass in this study occurred at the end of autumn, in the month of November each year. Biomass values were high for the summer and autumn shoots, whereas the minimum values were seen from the winter samples. The high values during the autumn and summer months are likely to be predominantly the result of high shoot densities. The strong correlation between shoot density and shoot aboveground biomass in both sites (see Statistical Analyses of this chapter) supported this suggestion. During the autumn the shoots had reached their growth maximum; on the other hand decaying had just begun and thus was a key factor in the high biomass values. In the winter a considerable number of shoots either carried fewer leaves or they had leaves decomposed and or lost. Therefore this may reflect the decline in biomass. The decline in leaf biomass related to the decline in shoot density was also reported in *Thalassia hemprichii* by

Stapel *et al.* (1997). The reduction in leaf biomass from peak values in their study reached as great as 61%.

Following the appearances of new shoots in the spring biomass increased. As in the summer months, the addition of biomass was possibly accelerated by the onset of optimal growth conditions for *Zostera*, i.e. the extension of daylight exposure (de Jonge and de Jonge, 1992; Terrados, 1997). Seasonal pattern in aboveground biomass has been reported from *Z. japonica* in Hong Kong waters in which the peaks were found in March – April (Lee, 1997). In a study of seasonal variation, Sand-Jensen (1975) found the biomass of living *Z. marina* leaves increasing from 60 $g \cdot m^{-2}$ in March to 225 $g \cdot m^{-2}$ in September.

The higher values of aboveground biomass in the dense area are clearly influenced by shoot density. Contribution of high aboveground biomass in the more densely populated beds has been reported from the south-west English coast (Webster *et al.*, 1998). The values from the Ryde study (range 1.94 – 21.57 g $DW \cdot m^{-2}$) were lower compared to those for aboveground biomass of other *Zostera* species. A study on *Z. japonica* found the aboveground biomass of 8 - 34 g $DW \cdot m^{-2}$ (Lee, 1997); while the average value for *Z. marina* was 56.2 g $DW \cdot m^{-2}$ (Mattila *et al*, 1999). The biomass values of seagrass can vary greatly depending on the biological and environmental conditions (see Ott, 1990; Stapel *et al.*, 1996; Phillips and Meñez, 1988) as well as on the methods of measurement used. Therefore it is difficult to compare results. However, it is proposed that the lower values found in this study are possibly the result of shoot size. The *Zostera* stands from Maine were far higher (shoot length 7 – 124 cm with an average of 53 cm, Mattila *et al*, 1999) compared to the ones from the Isle of Wight (shoot length 13.1 – 23.8 cm). The other factor is possibly the scraping method which was applied to *Z. japonica* from Hong Kong (see Lee, 1997) which may not have cleaned all the adherent materials on the leaves; thus this method may over-estimate the biomass. Seagrass leaves contain 19 – 26 % ash, with tropical species generally being higher than temperate species (McRoy, 1970; Birch, 1975; Zieman and Wetzel, 1980; Stapel *et al.*, 1997). Because of the variety of habitats, the

differences in sample times, the number of replicate samples taken and the diverse purposes of the investigators when taking these collections, it is difficult to draw meaningful patterns from the published results (Dawes, 1998). The evidence is ample that when conditions are optimal, the seagrass will produce dense, continuous meadows over large areas.

The reproduction season of *Z. noltii* in the study area began in July until November. This was indicated by shoots flowering and producing seeds (Figures 4.5. and 4.6.). In Great Britain, the record of reproduction cycles of *Z. noltii* is very scarce. The only information of *Zostera* reproduction in the Solent was from Langstone and Chicester Harbours (Tubbs and Tubbs, 1983). Though the information on the reproduction cycles of *Z. noltii* in the United Kingdom is inadequate, there are a few valuable studies from Europe. In the eastern Scheldt, The Netherlands, *Z. noltii* influorescences have been reported as occurring from late June to September (Hootsman *et al.*, 1987). The second study from Golfe Juan, France, recorded the flowering season of *Z. noltii* beginning at the end of May and continuing until late August (Loques *et al.*, 1988). The differences in the timing of the *Z. noltii* reproduction season in Ryde Beach compared with other studies may relate to water temperature and day length. As part of the Mediterranean, Golfe Juan normally experiences an earlier summer than the English Channel.

As a local comparison, it was found that the time of onset of reproduction was delayed by approximately a month later in the present study in comparison to nearly 20 years ago, i.e. between July and September (Tubbs and Tubbs, 1983). This delay may have a connection with the change of the climate or reflect normal year to year variability. The summers in Southern England in the last two years had been either warmer or more extended compared with that of two decades earlier.

The timing of flowering for Ryde Beach seagrass was within the period of flowering recorded for the members of the genus *Zostera*, which falls during the summer and extends into the autumn. However, one study in New Zealand found an exceptional flowering period of *Z. marina* that started at the end of winter and

occurred during the whole spring through early summer (Ramage and Schiel, 1998).

Based on the seed observation it is suggested that *Z. noltii* shoots in the Ryde Beach do not entirely depend on seed for propagation. The state of seed propagation of *Z. noltii* is less clear in the literature. However, there is a suggestion that though seed production may be high, that seeds did not seem to be important in shoot propagation in some seagrasses (den Hartog, 1970; Dawes, 1998). In addition, a report from Terschelling, the Dutch Wadden Sea described *Z. noltii* reproduces mainly vegetatively (Jacobs *et al.*, 1979). Though seagrasses in general depend on both vegetative and sexual reproduction for the maintenance of existing beds and colonization of new areas (Orth *et al.*, 1984), nevertheless vegetative development is the main mechanism for seagrass proliferation (Marba and Duarte, 1998). Of the Ryde Beach *Z. noltii* case, seeds produced by the seagrass possibly do not play an important function in the year to year survival of the population. Of the 3 species of *Zostera* found in the United Kingdom, *Z. marina* and *Z. noltii* are considered to rely mainly on vegetative reproduction, whereas *Z. angustifolia* populations are maintained by a combination of vegetative means and seed set (Davison and Hughes, 1998). *Z. noltii* reported by those authors was recorded from the meadows in Moray and Cromarty Firths, Argyll, and Thames Estuary.

This study observed that phenolics and carbohydrate concentrations of *Z. noltii* shoots both declined at the beginning of the sampling programme. After reaching the lowest values in February, March and April 1998 and in the winter season of 1998/1999, these two compounds then increased toward the end of the study. In the end of autumn, i.e. November, the tips on some leaves started to blacken, indicating that decomposition had begun. The decline of phenolics and carbohydrate is probably correlated with age and the stage of decomposition (Drew, 1983). Those two compounds are water-soluble (see Zapata and MacMilan, 1979 for phenolics and Drew, 1983 for carbohydrate) and therefore are susceptible to leaching (Blum and Mills, 1991), i.e. rapid, abiotic removal during

the early stages of decomposition. Indeed, the rates of loss were generally highest in the first few months. The lowest values were seen at the end of winter until the beginning of spring and may be caused by the increasing number of old dead leaves. Carbohydrates, particularly the water soluble ones, become more rapidly depleted from senescent leaf tissue (Velimirov, 1986, 1987). As for the total phenolics of *Zostera* leaves, it has been assessed that the value varies with season. The low concentrations were normally found throughout the winter, whereas the high values occurred in spring when the shoots have young and actively growing leaves (Ravn *et al.*, 1994; Harrison and Durance, 1989). In addition, it was found that during the winter months the *Z. noltii* shoots in the Isle of Wight possessed a lower number of the leaves (see Fig. 4.2). This would explain the lower concentrations of chemical constituents measured.

In addition, the fluctuations in both phenolics and carbohydrate contents were probably also affected by microbial activity. Some marine fungi can utilize polysaccharide (possibly causing leaching), and can metabolise *p*-coumaric and ferulic acids (Bergbauer and Newell, 1992). One study concluded that seagrasses are similar to terrestrial plants in their phenolics content, and it is known from previous investigation that *p*-coumaric and ferulic acids are among the major phenolic forms found in *Zostera* (Zapata and MacMilan, 1979). These two phenolic compounds were successfully detected in old leaves of *Zostera* with the probabilities of 80 % and 64 % for *p*-coumaric and ferulic acids, respectively (Zapata and MacMilan, 1979). Fungal activity is more pronounced when the shoots are bearing more dead leaves. This helps in the interpretation of the lower total phenolic and carbohydrate concentrations during the winter. The decrease of phenolic and carbohydrate contents may also result in part from translocation of material from the leaves to the rhizome prior to leaf death, as found in other estuarine vascular plants (Samiaji and Baerlocher, 1996; Baerlocher and Moulton, 1999). Nonetheless, more direct investigations comparing overall chemical constituents of seagrass would be worthwhile.

There was no marked change in the total protein contents during the study and the values were relatively low. Protein content in leaves tends to remain stable particularly in the early stages of the decaying process. It has been reported that detritus derived from vascular plant material is usually low in nitrogen content (Tenore, 1983). This study found a slight increase of total protein concentrations following the ageing period of the *Z. noltii* shoots. One study reported that ageing is one of the most important parameters influencing the nutritional values of living seagrass tissues (Mazzella *et al.*, 1992). They reported that young leaves have a low value in C/N ratio; during the decay this ratio tends to increase.

The higher concentrations of protein in particular months may also be the result of the appearances of the microflora on the seagrass leaves (Alongi and Hanson, 1985), in which once again this phenomenon was more clearly seen during the end of autumn to the winter period when the leaves reached their maturity. A clear correlation between bacterial production and leaf age was found in *Z. marina* of Roskilde Fjord, Denmark (Tornblom and Sondergaard, 1999 and the papers therein). Fungal mycelia are also a common component of the microflora that are very obviously seen in the ageing seagrass leaves (Kohlmeyer and Kohlmeyer, 1979; Blum and Mills, 1991). Indeed, fungal mycelia can increase the proteinaceous nitrogen content of vascular plants (Cuomo *et al.*, 1982; Baerlocher, 1994-personal communictaion). Bacterial activities possibly contribute to the increase of protein concentrations in seagrass leaves from Ryde Beach. It has been found that dissolved organic carbon leached from seagrass (*Thalassia testudinum, Syringodium filiforme* and *Zostera marina*) leaves is rapidly converted to bacterial biomass, which lends support to the concept that these soluble materials are readily available to microorganisms (Blum and Mills, 1991). Thus, in addition to representing a major portion of the primary production, the leached material also has the potential to be converted quickly and possibly very efficiently via bacterial secondary production to a form that is available to higher tropic levels.

Chapter V:

Pigment Dynamics of Seagrass Bed Sediment

5.1. Introduction

Seagrass bed ecosystems have been widely recognised as one of the richest and most productive ecosystems in the marine environment (Wood *et al.*, 1969; Thayer *et al.*, 1975, Barnes and Hughes, 1988; Davison and Hughes, 1998). Seagrass beds can rival cultivated tropical agriculture in productivity (Phillips and Meñez, 1988). The net annual production of a temperate seagrass meadow is comparable with that of a temperate forest, whereas the tropical seagrass bed production can be as high as that of tropical rain forest (Dring, 1992). The high primary production of seagrass bed is essential in maintaining the productivity and stability of many near shore marine and estuarine ecosystems (Zieman and Wetzel, 1980), and in particular the macrozoobenthos of such systems.

Seagrass beds are classified as part of the benthic ecosystem (Duarte, 1991; Bortone, 2000 and the works therein). The productivity of the benthic ecosystem of shallow coastal waters has often been characterised by the measurement of the production of the microphytobenthos by determining the levels of chlorophylls and degradation products (Barranguet *et al.*, 1997; Santos *et al.*, 1997; Schlüter *et al.*, 2000). As has been explained previously in Chapter II, measuring the chlorophyll and phaeopigment concentrations of the sediment is also applicable to the understanding of seagrass bed productivity (Levinton and McCartney, 1991) because it may track the fate of the aquatic macrophyte production (Bianchi and Findlay, 1991; Bianchi *et al.*, 1993). Indeed, the determination of photosynthetic chlorophyll pigments and their

degradation products is one of the most frequently performed analyses in marine ecology (Mantoura and Llewellyn 1983; Hawkins *et al.*, 1986). Chlorophyll-*a* concentrations are routinely used to estimate phytoplankton biomass and productivity (Riaux-Gobin *et al.*, 1987; de Jonge and Colijn, 1994; Wear *et al.*, 1999 and the papers therein) as well as to quantify biomass of intertidal microphytobenthos (Cariou-Le Gall and Blanchard, 1995; Barranguet *et al.*, 1997). In addition, the degradation products of chlorophyll (chloropyllide *a*, phaeophytins *a* and phaeophorbides *a*) are diagnostic indicators of physiological status, detrital content and grazing processes in phytoplankton communities (Mantoura and Llewellyn, 1983; Plante-Cuny *et al.*, 1993).

The commonly used methods for determination of the three chlorophylls, *a*, *b* and *c* are based on spectrophotometric or fluorometric measurements of acetone extracts of particulate matter (Strickland and Parsons, 1968; Riaux-Gobin *et al.*, 1987). Such methods are able to determine the total quantity of plant pigments and are simple in practice (Parsons *et al.*, 1984). However, as has been pointed out in many works (see Mantoura and Llewellyn, 1983 and the papers therein; Hawkins *et al.*, 1986), spectrophotometric and fluorometric methods are often incomplete. This is because they suffer from several drawbacks: (i) absorption and emission bands of chlorophyll *b* and *c* and even bacteriochlorophyll overlap with those of chlorophyll *a*, giving rise to less precision and on occasions even negative concentrations; (ii) chlorophyll degradation products, which at times constitute a major fraction of green pigments, are either not detected or are determined along with their parent chlorophyll; (iii) the different spectrophotometric formulae reported in the literatures often yield different apparent concentrations of individual chlorophylls; (iv) the spectrophotometric method is relatively insensitive, and requires large volumes of samples; (v) individual carotenoids (carotenes and xanthophylls) are not determined, even though these pigments may be better indicators of algal biomass and of different taxonomic groups. Furthermore, it

has been reported that, by using chromatographic techniques, it is not only the individual chlorophyll concentration that can be detected but also those of other light-harvesting pigments such as carotenoids, fucoxanthin, peridinin and lutein (Gieskes and Kraay, 1983; Jeffrey *et al.*, 1999; Wear *et al.*, 1999; Schlüter *et al.*, 2000).

It has been postulated that particulate organic matter (POM) derived from decomposing phytoplankton and seaweeds is of major trophic importance in marine ecosystems (Thrush, 1986; Levinton and McCartney, 1991). In fact an examination of the quality and quantity of chlorophyll degradation pigments facilitates the understanding of the main degradation pathways (Bianchi *et al.*, 1993; Barranguet *et al.*, 1997; Boon *et al.*, 1998). Indeed, measurements of chlorophylls, pigments and chlorophyll derivatives may indicate the deposition of macrophyte in water samples (Gieskes and Kray, 1983; Wright and Jeffrey, 1987; Jeffrey *et al.*, 1999) as well as in marine sediments (Riaux-Gobin *et al.*, 1987; Abele-Oeschger, 1991; Jeffrey *et al.*, 1999). This concept can be applied to tracking of decomposed seagrass materials.

The aim of the present study is to assess the pigment production of the seagrass bed of Ryde Beach by measuring the chlorophyll, accessory pigments, seagrass associated pigments and phaeopigment concentrations of the bed sediment. The dynamics of pigment production were followed continuously at two seagrass densities, dense and sparse sites (see Chapter II for site definition) over a 28-month sampling period. Though pigments have been used successfully to identify the sources of the phytodetritus in aquatic ecosystems (Abele-Oeschger, 1991 and papers therein; Bianchi and Findlay, 1991; Bianchi *et al.*, 1993; de Jonge and Colijn, 1994; Duarte and Cebrian, 1996), such investigations have never been conducted before at the study site. The total chl-*a* and phaeopigment concentrations in this work were determined by using two methods, the conventional method i.e. spectrophotometric, and through HPLC analyses. Besides measuring chl-*a* and phaeopigment, the HPLC method was

also used to analyse seagrass associated pigments, accessory pigments and all species of phaeopigments in the sediment. HPLC not only can be used to measure the total chlorophyll concentration, but also gives some indication as to whether the detritus of the bed was derived from the seagrass vegetation or from other sources such as higher marine algae and microphytobenthos.

5.2. Results

5.2.1. Spectrophotometric Method

5.2.1.1. Chlorophyll-*a*

Chl-*a* of the seagrass bed showed fluctuations, both temporally and between sites. Spectrophotometric measurements in the sediment samples from November – December 1997, May – June 1998, September – November 1998, May 1999 and October 1999 gave highest values in the chl-*a* concentration (Figure 5.1.). Relatively high chl-*a* contents occurred in September – October 1997, July – August 1998, December 1998 and July 1999; whereas the lowest values were shown by January – March 1998 and January – February 1999 samples.

The average concentrations of chl-*a* in the dense and sparse sites ranged between 3.25 (± 0.98) – 14.24 (± 4.46) $\mu g \cdot g^{-1}$ DW and 2.76 (± 1.25) – 10.20 (± 1.36) $\mu g \cdot g^{-1}$ DW respectively. Statistically the chl-*a* contents were very significantly different when the samples from two sites were compared (t-test, $P < 0.001$). The dense site clearly did contain the higher values of chl-*a*.

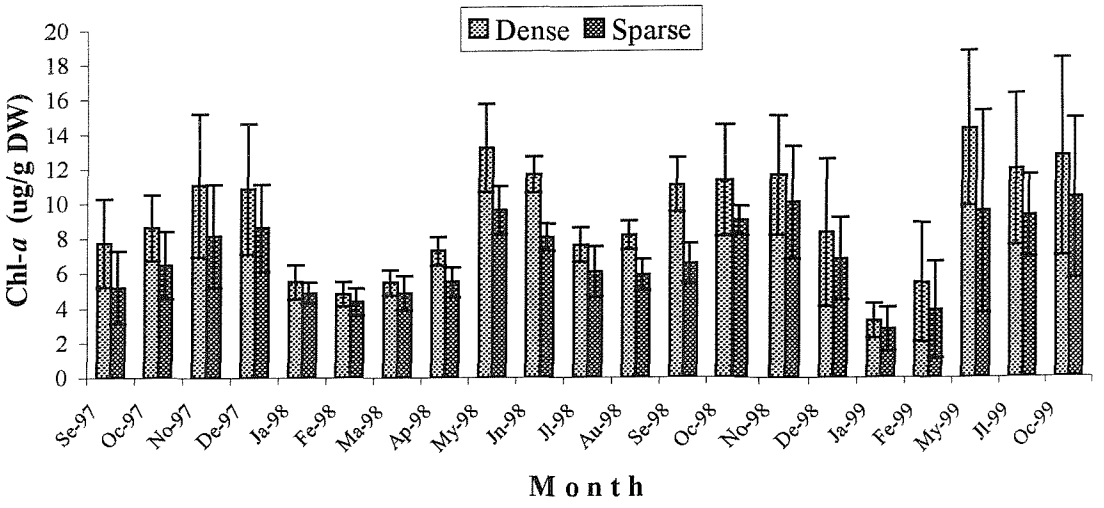

Fig.5.1. Spectrophotometric measurement of sediment chl-*a* concentration collected from Ryde Beach seagrass bed (n = 15, ± SD).

5.2.1.2. Phaeopigments

The sediments collected from *Z. noltii* bed contained phaeopigments. There were very clear variations of phaeopigment concentrations throughout the study, both temporally and between the sites (Figure 5.2.). The low concentrations of phaeopigment were found in January – February 1998 and 1999, whereas the highs were recorded in September – December 1997, May – August 1998, October – December 1998 and May, July and October 1999 samples. As has been observed for the chl-*a*, the dense site of the seagrass bed had the higher range of phaeopigment compared to that of the sparse one (15.12 (± 4.30) – 32.80 (± 5.01) $\mu g \cdot g^{-1}$ DW Vs 10.50 (± 1.72) – 25.20 (± 5.28) $\mu g \cdot g^{-1}$ DW). When these values were tested, they were very significantly different (t-test, $P < 0.001$).

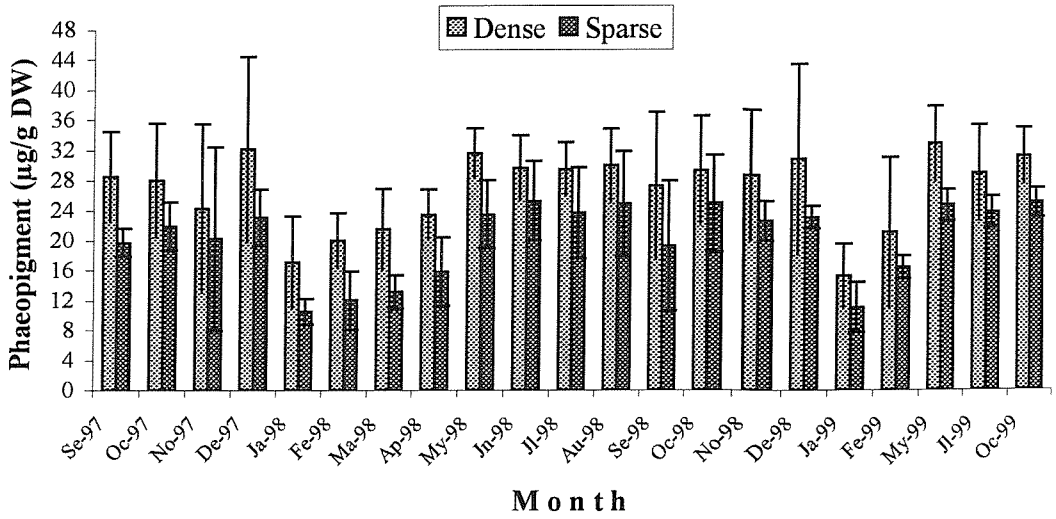

Fig.5.2. Spectrophotometric measurement of sediment phaeopigment concentration collected from Ryde Beach seagrass bed (n = 15, ± SD).

5.2.2. HPLC Method

There was great variability in the HPLC analyses results throughout the study as well as between the samples. There were nine pigments detected from the HPLC method, i.e. chlorophyll-*a*, chlorophyll-*b*, chlorophyll-*c1+c2*, zeaxanthin/lutein, fucoxanthin, *ß*-carotene, 19-hexanoyloxyfucoxanthin, diadinoxanthin and diatoxanthin. In general, all samples in all months contained phaeopigments. The phaeopigments observed were phaeophorbide *a1*, phaeophorbide *a2*, phaeophytin *a1* and phaeophytin *a2*. In one sampling period some samples had a wide variety of pigments as well as phaeopigments, while in the other many pigments were absent. Figures 5.3. and 5.4. each presents an example of readings of all detected pigments and phaeopigments performed by HPLC analyses in the dense and sparse site respectively. The examples of peak area values and real contents of each pigment are given in Appendices 1 and 2.

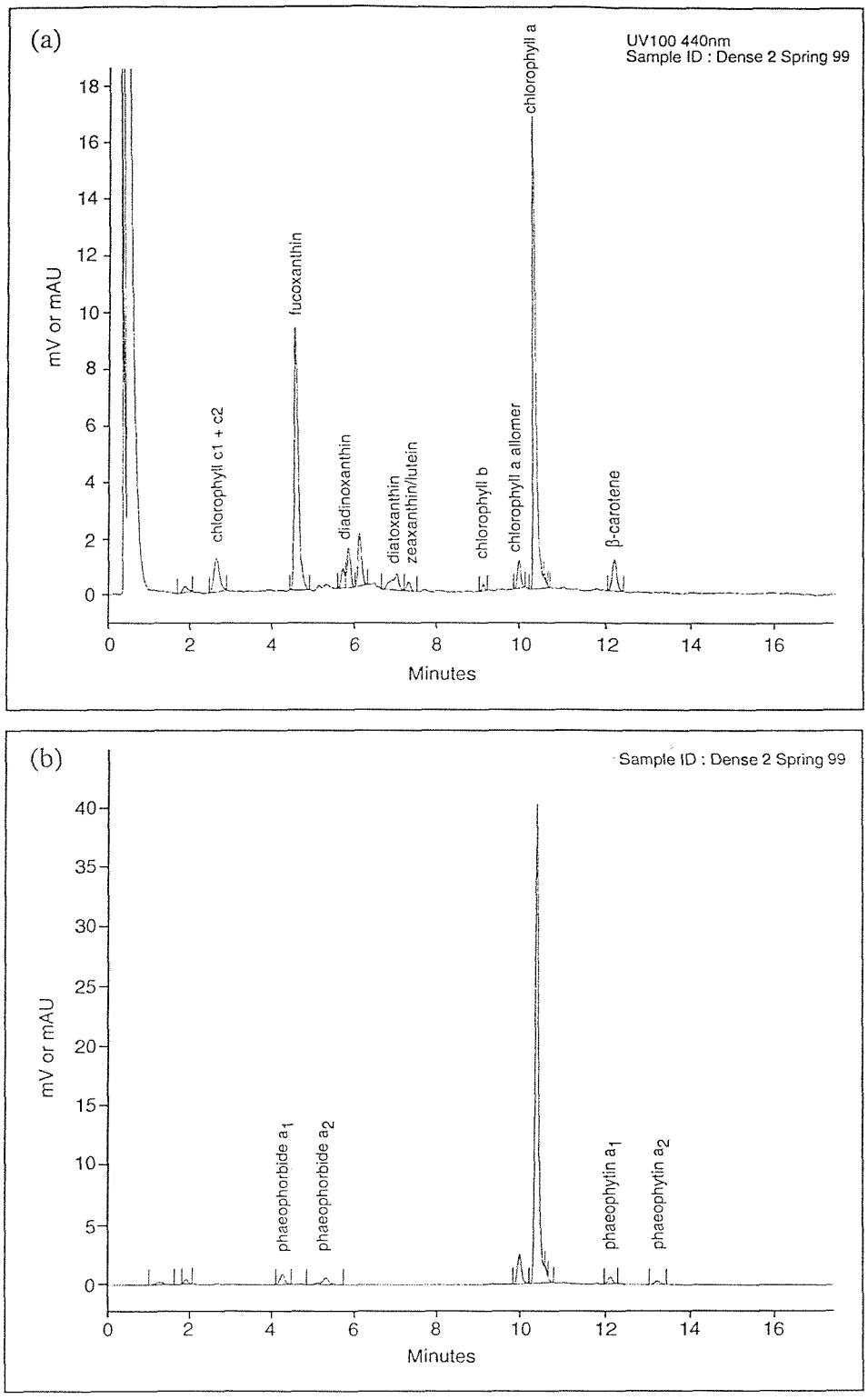

Fig. 5.3. Results of HPLC reading for chl-*a* and other pigments (a), and phaeopigments (b) of sediment from the dense site.

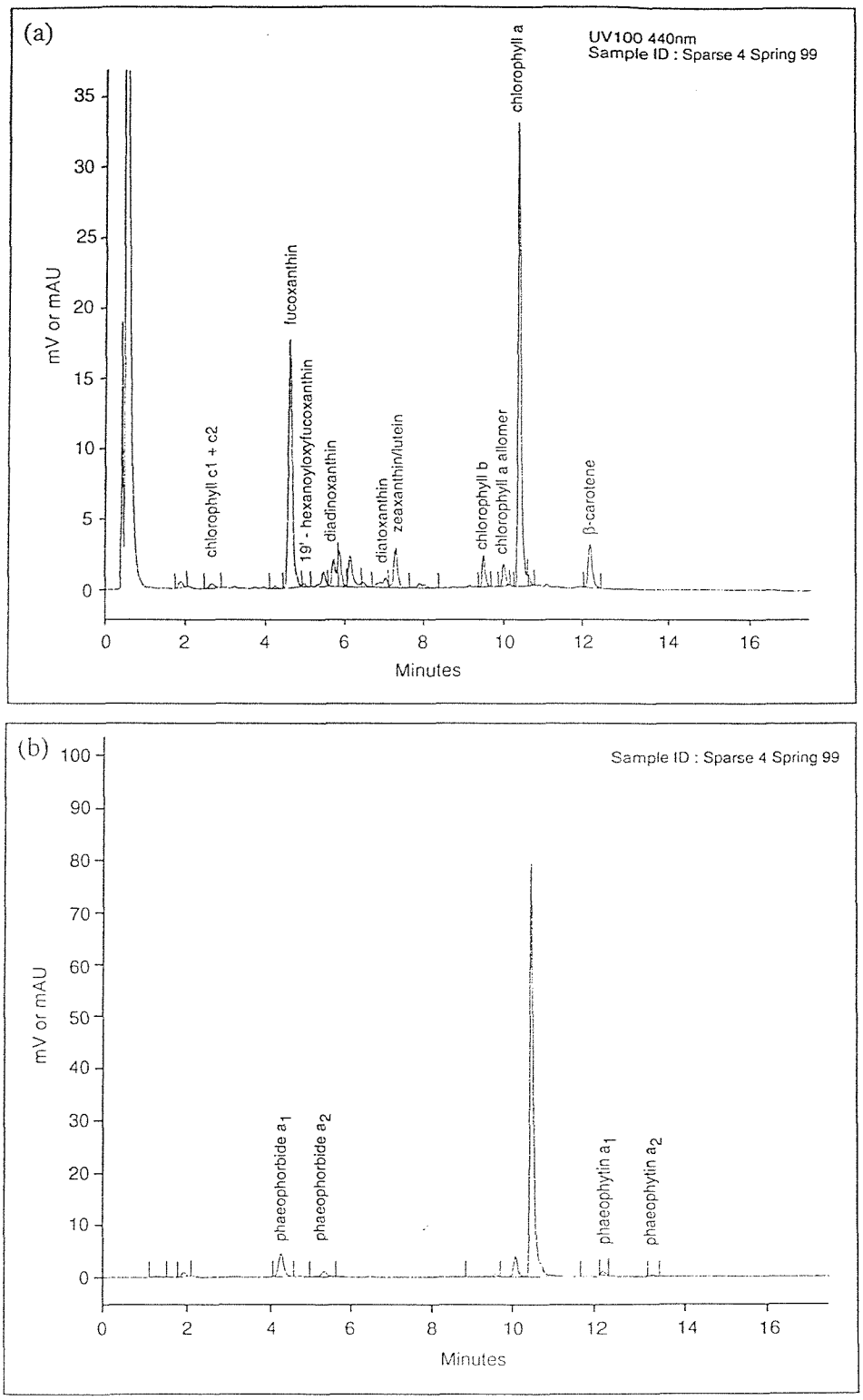

Fig. 5.4. Results of HPLC reading for chl-*a* and other pigments (a), and phaeopigments (b) of sediment from the sparse site.

5.2.2.1. Chlorophyll-*a*

The sediment chl-*a* concentrations showed distinctive temporal variations, with the highest values occurring in September – December 1997, May 1998, August – December 1998 and May, July and October 1999 samples. The minimum concentrations of chl-*a* were shown by the winter samples with the lowest values reached in January – February 1998 and January 1999. Compared to the spectrophotometric measurement, overall the values from HPLC method gave lower results. Nevertheless, the chl-*a* concentrations derived from HPLC measurements did show the same pattern of variations found in the data from spectrophotometric measurement. In general, all sediments collected in 1999 possessed higher concentrations of chl-*a* than comparable periods of samplings in 1997 and 1998.

Chl-*a* of the dense site averaged between 0.81 (± 0.05) – 5.32 (± 1.55) $\mu g \cdot g^{-1}$ DW, whereas those of the sparse site fell between 0.66 (± 0.17) – 4.24 (± 0.87) $\mu g \cdot g^{-1}$ DW (Figure 5.5.). There was a significant difference in the chl-*a* contents when the two sites were compared (t-test, $P < 0.001$). The dense site had always much higher chl-*a* levels.

5.2.2.2. Chlorophyll *b*, Lutein/Zeaxanthin and *ß*-carotene

The results for chlorophyll *b* (chl-*b*), lutein/zeaxanthin and *ß*-carotene are presented first, because among the detected pigments in the samples these three pigments are recognised as the most common signatures of the detrital products derived from the vascular aquatic macrophytes as seagrass (Bianchi and Findlay, 1991; Levinton and McCartney, 1991). The remaining pigments are common signatures of the microphytobenthos in the sediment and later are grouped into accessory pigments.

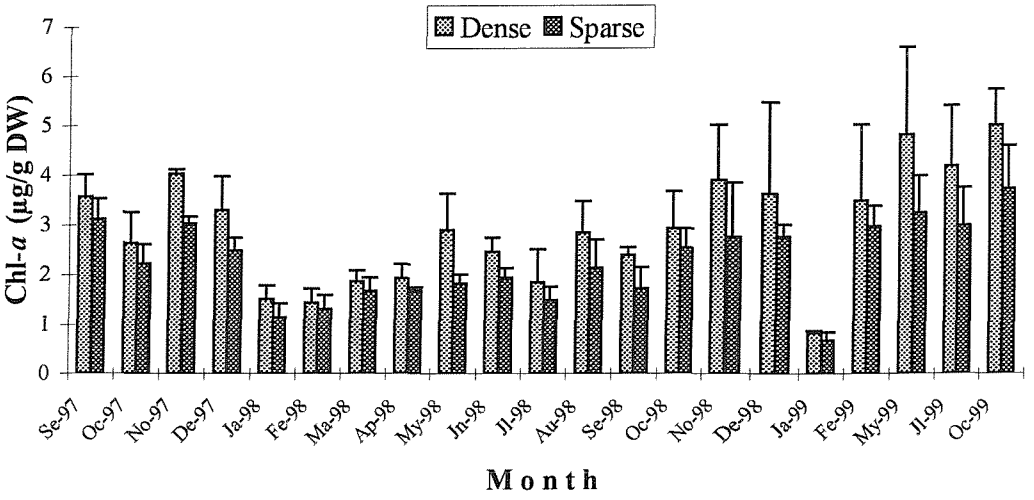

Fig.5.5. Chl-*a* concentration of the sediments measured by HPLC collected from Ryde Beach seagrass bed (n = 15, ± SD).

Overall, the concentration of chl-*b* of the study site fluctuated according to the season as well as site type (Figure 5.6a.). In January 1998 and 1999 the bed sediment of both sites did not contain chl-*b*. In February 1999 this pigment was also absent in the sparse site. The high values of chl-*b* were shown in September – October 1997, April 1998, June 1998, August – December 1998 and October 1999. The average values of chl-*b* from the dense site ranged between 0 – 0.78 (± 0.71) $\mu g \cdot g^{-1}$ DW. As for the sparse site the contents fell between 0 – 0.35 (± 0.11) $\mu g \cdot g^{-1}$ DW. Statistically the dense site had significantly higher content in chl-*b* compared to that of sparse site (t-test, P = 0.0087).

Lutein/zeaxanthin was detected at low concentration and it did not fluctuate as clearly as chl-*a* and chl-*b* concentrations (Figure 5.6b.). However, the higher values were found in September 1997, August 1998 and November 1998. The sediment samples from September 1998 and January 1999 did not

contain lutein/zeaxanthin. Overall, the mean values of this pigment ranged between 0 – 0.13 (± 0.07) $\mu g \cdot g^{-1}$ DW and 0 – 0.13 (± 0.12) $\mu g \cdot g^{-1}$ DW for the dense and sparse site respectively. There was no significant difference when these values were statistically compared for the two sites (t-test, $P = 0.0779$).

Figure 5.7. presents the detected values of *ß*-carotene. Except for an absence in January 1999, it seems that this pigment was always present throughout the year. This is not surprising, because *ß*-carotene is found in all marine vegetations. Overall, the mean concentrations of *ß*-carotene in the dense site ranged between 0 – 0.33 (± 0.24) $\mu g \cdot g^{-1}$ DW whereas from the sparse site fell between 0 – 0.24 (± 0.18) $\mu g \cdot g^{-1}$ DW. These levels were statistically very different when they were tested (t-test, $P < 0.001$).

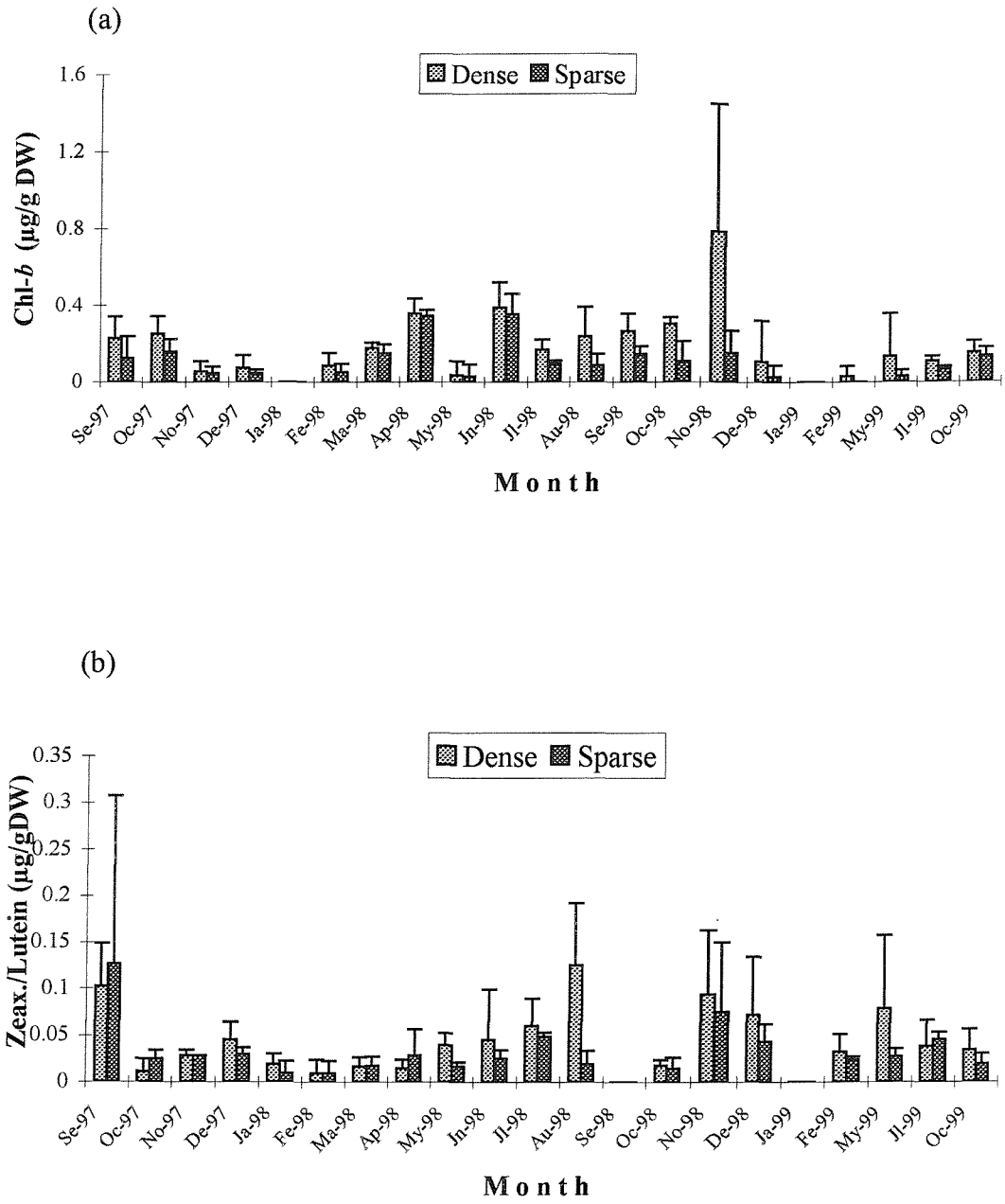

Fig.5.6. Concentrations of chl-*b* (a) and lutein/zeaxanthin (b) of the sediments measured by HPLC collected from Ryde Beach seagrass bed (n = 15, ± SD).

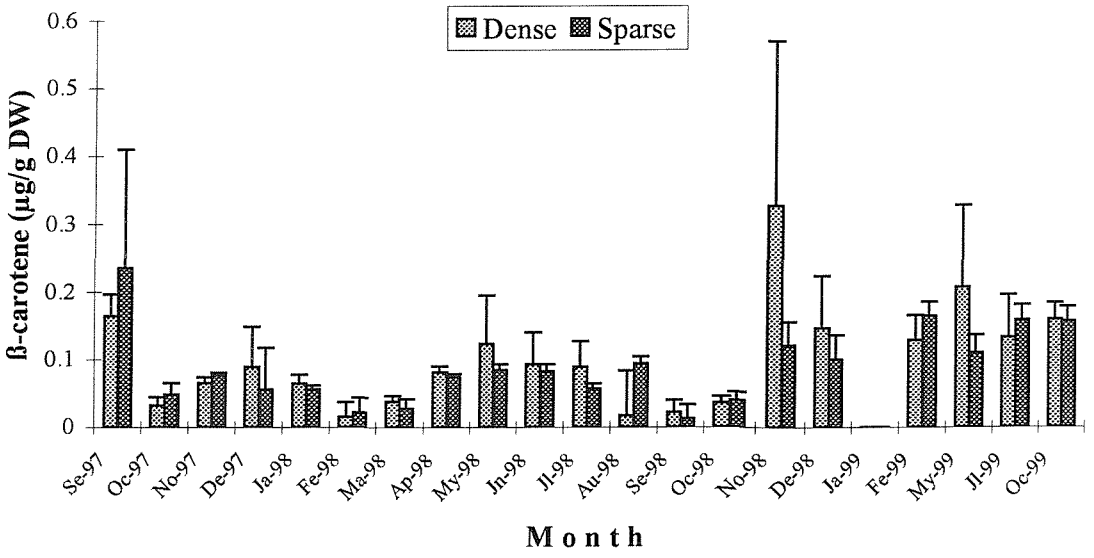

Fig.5.7. *ß*-carotene concentration of the sediments measured by HPLC collected from Ryde Beach seagrass bed (n = 15, ± SD).

5.2.2.3. Accessory Pigments

The accessory pigments in this study consisted of the remaining four pigments detected from the sediments through the HPLC measurements, i. e. chlorophyll-*c1+c2* (chl-*c1+c2*), fucoxanthin, diadinoxanthin and diatoxanthin. These pigments are common in diatoms (see Fielding *et al.*, 1988, Cariou-Le Gall and Blanchard, 1995; Lucas, 1999-personal communication). Overall, the concentrations of these pigments were higher compared with that of chl-*b* and lutein/zeaxanthin. It means that diatoms contributed a greater amount of pigment production in the bed sediment compared than seagrass or algae. The concentration patterns of these four pigments were in general following the seasonal fluctuation of chl-*a* contents.

Chl-*c1+c2* was always present in the sediment, except in January 1999 samples (Figure 5.8.). The average values of chl-*c1+c2* were in the range of 0 – 0.18 (± 0.10) $\mu g \cdot g^{-1}$ DW and 0 – 0.16 (± 0.03) $\mu g \cdot g^{-1}$ DW for the dense and sparse site respectively. Those concentrations did not different statistically (t-test, $P = 0.4193$).

The overall concentrations of fucoxanthin were relatively low with the samples collected in January 1999 in both sites resulted the lowest values (Figure 5.9.). There was no clear seasonal pattern of this pigment, although the higher concentrations were shown in the last four samplings in 1999. Statistically, fucoxanthin concentrations between the dense and sparse sites were not different (t-test, $P = 0.9383$). The averages of this pigment ranged between 0.16 (± 0.03) – 1.32 (± 0.18) $\mu g \cdot g^{-1}$ DW at the dense site and 0.11 (± 0.02) – 1.56 (± 0.11) $\mu g \cdot g^{-1}$ DW ± at the sparse site.

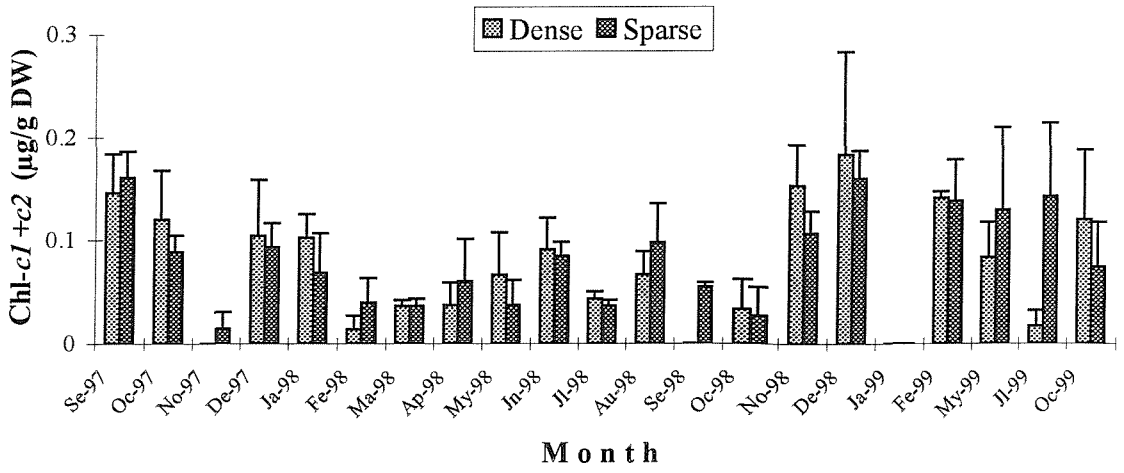

Fig.5.8. Concentrations of chl-*c1+c2* of the sediments measured by HPLC collected from Ryde Beach seagrass bed (n = 15; ± SD).

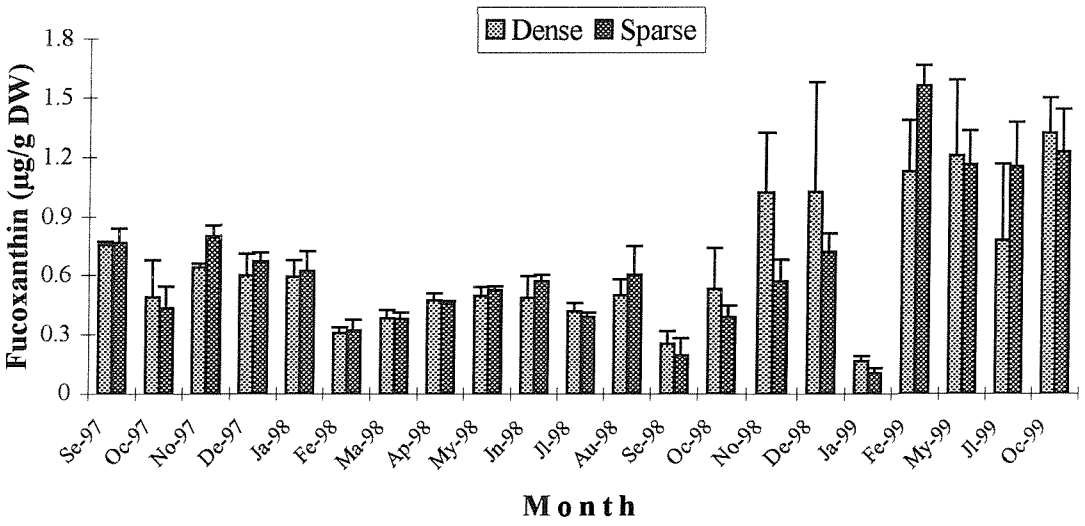

Fig.5.9. Concentrations of fucoxanthin of the sediments measured by HPLC collected from Ryde Beach seagrass bed (n = 15, ± SD).

Although diadinoxanthin contents did fluctuate during the study, there was no clear seasonal pattern observed (Figure 5.10.). This pigment was detected in all sediment collections except in January 1999. As has been observed in fucoxanthin values, the sediments from the last four samplings, i.e. February, May, July and October 1999, had the highest diadinoxanthin contents. The mean values fell between 0 – 0.12 (± 0.04) $\mu g \cdot g^{-1}$ DW and 0 – 0.14 (± 0.03) $\mu g \cdot g^{-1}$ DW for the dense site and sparse site respectively in which these values were not different significantly (t-test, $P = 0.001$). The average contents of diatoxanthin varied according to the period of sampling (0 – 0.08 (± 0.01) $\mu g \cdot g^{-1}$ DW for the dense site and 0 – 0.12 (± 0.02) $\mu g \cdot g^{-1}$ DW for the sparse site). In general, the concentrations were much lower compared to diadinoxanthin (Figure 5.11.). This pigment was often not detected, thus make difficult to draw the meaningful comparisons. However, on the last four sampling occasions it was higher in the spring (May 1999) and autumn (October 1999) seasons. Additionally, these last seasonal collections gave significantly higher values at the sparse site (t-test, $P = 0.0023$).

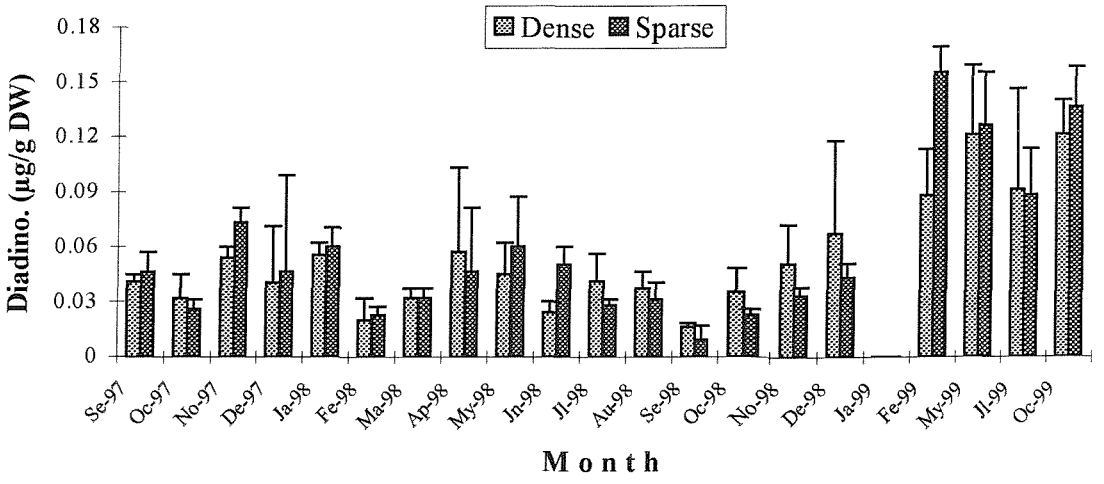

Fig.5.10. Concentrations of diadinoxanthin of the sediments measured by HPLC collected from Ryde Beach seagrass bed (n = 15, ± SD).

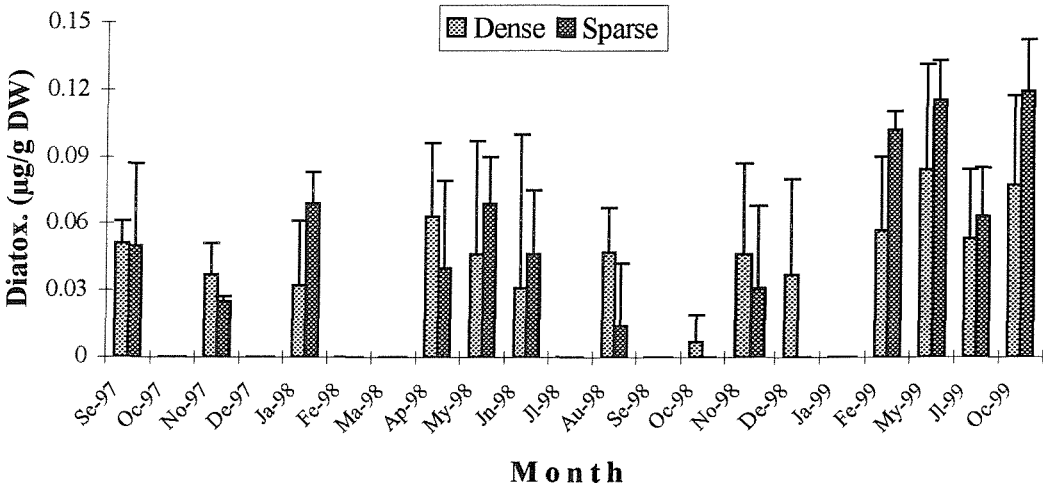

Fig.5.11. Concentrations of diatoxanthin of the sediments measured by HPLC collected from Ryde Beach seagrass bed (n = 15, ± SD).

5.2.2.4. Phaeopigment

5.2.2.4.1. Total Phaeopigment

Figure 5.12. presents the total contents of sediment phaeopigment resulting from the HPLC measurement. The mean values from the dense site ranged between 3.54 (± 0.43) – 28.35 (± 5.00) $\mu g \cdot g^{-1}$ DW, meanwhile the sparse site contained 3.32 (± 1.38) – 24.38 (± 1.91) $\mu g \cdot g^{-1}$ DW. Although in particular months the average values were close, overall the dense seagrass bed had very significantly higher levels of phaeopigment (t-test, $P < 0.001$). The seasonal pattern of phaeopigment was not clear, however samples from December 1997, June 1998 and November – December 1998 had the highest contents of phaeopigment.

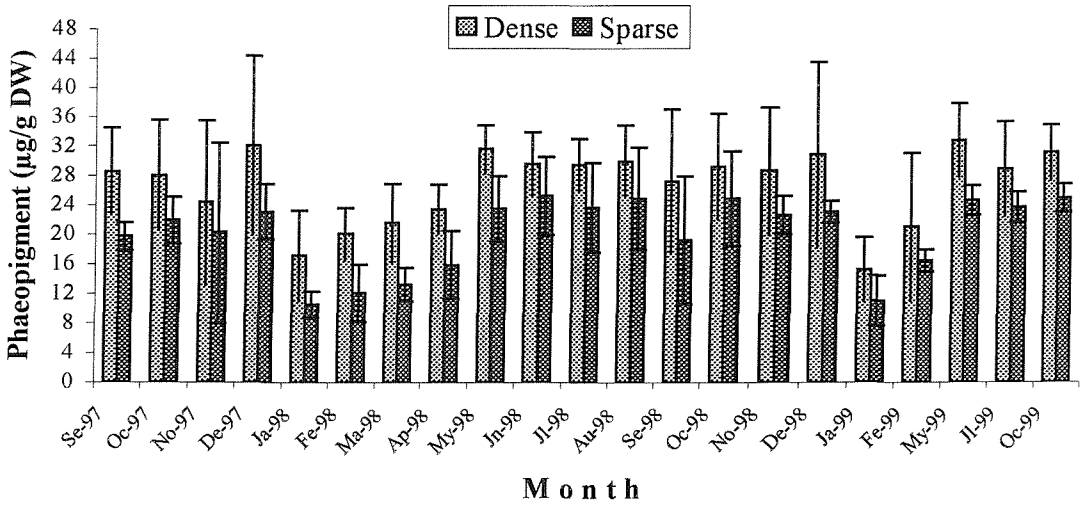

Fig. 5.12. Total phaeopigment of the sediments measured by HPLC collected from Ryde Beach seagrass bed (n = 15, ± SD).

5.2.2.4.2. Phaeophorbide

The contents of phaeophorbide also varied according to the season and between the sites (Figures 5.13. and 5.14.). In the dense site, the lowest mean value for phaeophorbide *a1* (0.87 $\mu g \cdot g^{-1}$ DW $\pm$ 0.02) was found in January 1999, whereas the highest mean value (7.16 $\mu g \cdot g^{-1}$ DW $\pm$ 5.29) was given from December 1998 samples. The samples collected in January 1999 also contained the lowest amount of phaeophorbide *a2* (2.12 $\mu g \cdot g^{-1}$ DW $\pm$ 0.41), while the highest values (17.35 $\mu g \cdot g^{-1}$ DW $\pm$ 9.22) was performed by December 1997 collection.

In the sparse site, the average content of phaeophorbide *a1* ranged between 0.57 $\mu g \cdot g^{-1}$ DW $\pm$ 0.49 (January 1999) and 6.19 $\mu g \cdot g^{-1}$ DW $\pm$ 2.74 (December 1998). The phaeophorbide *a2* concentration fell in the values of 2.12 $\mu g \cdot g^{-1}$ DW $\pm$ 0.50 (January 1999) and 12.69 $\mu g \cdot g^{-1}$ DW $\pm$ 2.94 (November 1997). The phaeophorbide contents between two sites were different significantly (t-test, $P = 0.0033$ for phaeophorbide *a1*; t-test, $P < 0.001$ for phaeophorbide *a2*). In both tests the dense site was always possessed the higher level concentration of both phaeopigments.

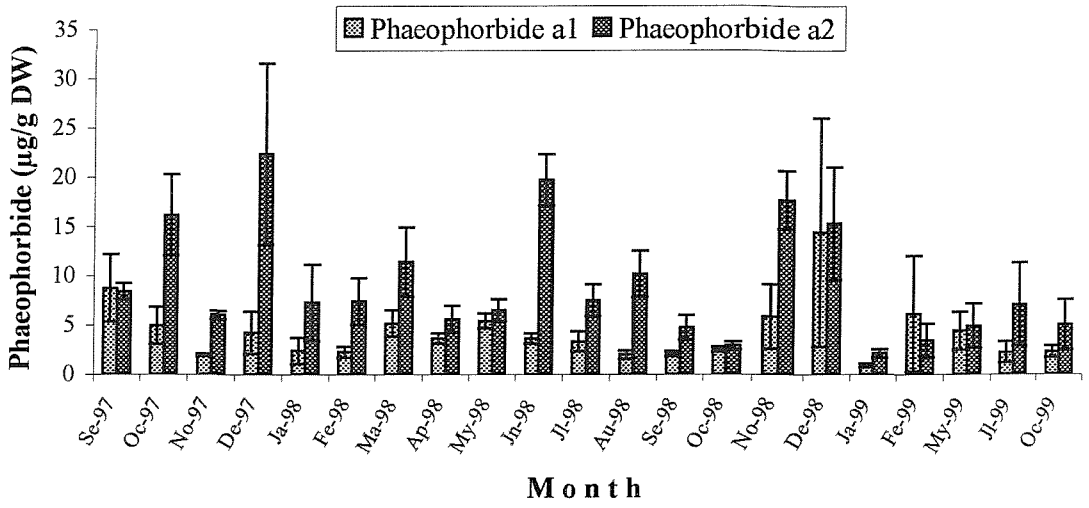

Fig.5.13. Phaeophorbide of the sediments measured by HPLC collected from the dense site of Ryde Beach seagrass bed (n = 15, ± SD).

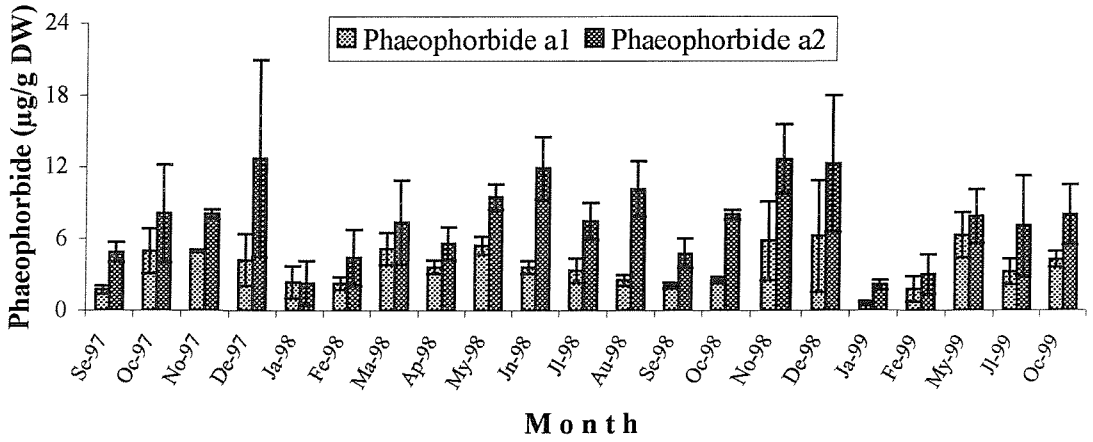

Fig.5.14. Phaeophorbide of the sediments measured by HPLC collected from the sparse site of Ryde Beach seagrass bed (n = 15, ± SD).

5.2.2.4.3. Phaeophytin

The phaeophytin *a1* and phaeophytin *a2* concentrations of the sediments showed clear seasonal variations as well with January 1999 samples giving the lowest values for both phaeophytin types at the two different sites (Figures 5.15. and 5.16.). In the dense site, the average content of phaeophytin *a1* ranged between 0.55 $\mu g \cdot g^{-1}$ DW (± 0.21) (January 1999) and 5.12 $\mu g \cdot g^{-1}$ DW (± 0.52) (May 1999), whereas the phaeophytin *a2* concentration ranged from the undetected level (January 1999) to 4.67 (± 0.45) $\mu g \cdot g^{-1}$ DW (August 1998).

For the sparse site, the mean concentrations of phaeophytin *a1* ranged between 0.49 (± 0.17) $\mu g \cdot g^{-1}$ DW (January 1999) and 4.29 (± 1.05) $\mu g \cdot g^{-1}$ DW (November 1998). As for phaeophytin *a2,* the mean values ranged between undetected level (January 1999) and 3.49 (± 0.74) $\mu g \cdot g^{-1}$ DW (December 1998). When the values of these two phaeophytins were compared to that of the dense site, they both differed significantly, with values for phaeophytin *a1* and phaeophytin *a2* at the dense site significantly higher ((t-test, $P < 0.001$ for phaeophytin *a1*), (t-test, $P < 0.001$ for phaeophytin *a2*)).

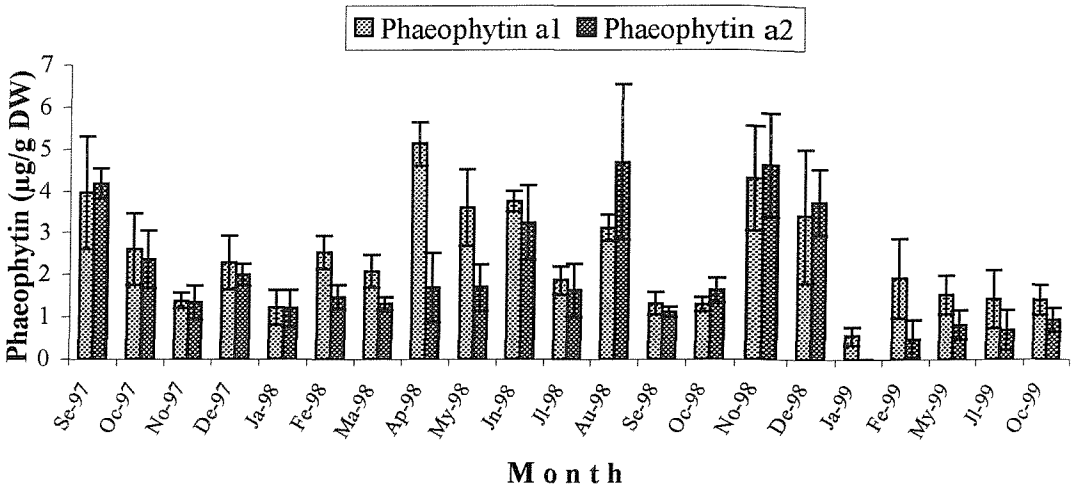

Fig.5.15. Phaeophytin of the sediments measured by HPLC collected from the dense site of Ryde Beach seagrass bed (n = 15, ± SD).

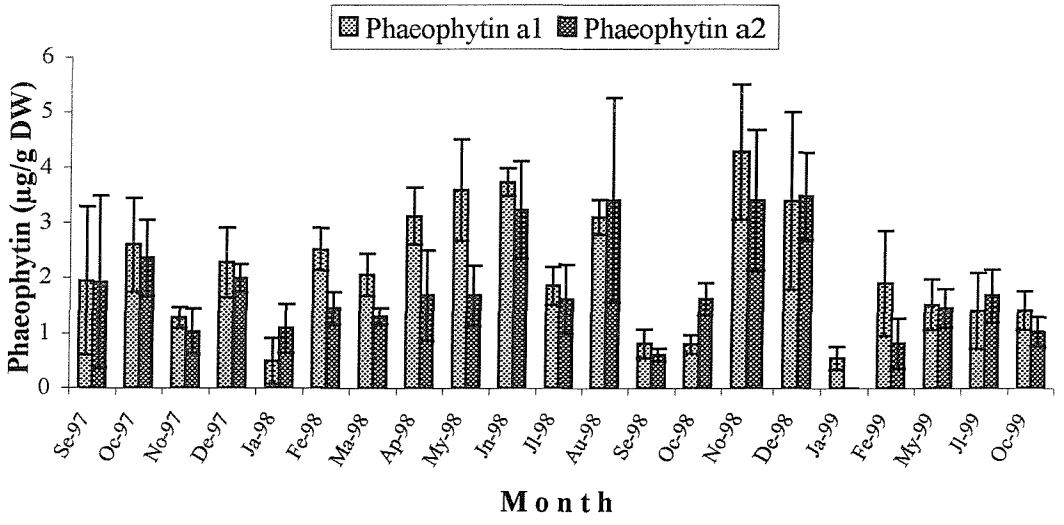

Fig.5.16. Phaeophytin of the sediments measured by HPLC collected from the sparse site of Ryde Beach seagrass bed (n = 15, ± SD).

5.2.3. Statistical Analyses

The multiple linear regression test for the dense site showed that overall sediment chl-*a* was not correlated to all seagrass biological and environmental parameters ($F_{9,11} = 5.82$; $P = 0.0041$; Table 5.1.). However, the stepwise forward regression test indicated that the contents of sediment chl-*a* did correlate with a few variables ($F_{1,19} = 40.1$; $P < 0.0001$; Table 5.2.). The closest correlations were given between sediment chl-*a* and sediment organic matter as well as with phaeopigment. Following these, shoot leaf number and water temperature also indicated strong correlation with sediment chl-*a*. No variables had significant correlation with sediment chl-*b* contents ($F_{9,11} = 0.603$; $P = 0.7714$; Table 5.3.) nor with lutein/zeaxanthin concentrations ($F_{9,11} = 1.39$; $P = 0.2977$; Table 5.4.). Further tests gave similar results (for chl-*b* and 8.27; $F_{1,19} = 8.27$; $P = 0.0097$; Table 5.5. for lutein/zeaxanthin).

Table 5.1. ANOVA of multiple linear regression tests for the chl-*a* and the other variables of the dense site.

Source of Variance	DF	SS	MS	F	*P*
Regression	9	156.3	17.37	5.82	0.0041
Residual	11	32.8	2.98		
Total	20	189.1	9.46		

Table 5.2. ANOVA of forward stepwise regression tests for chl-*a* and the other variables of the dense site.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	128.3	128.31	4.01	<0.0001
Residual	19	60.8	3.20		

Table 5.3. ANOVA of multiple linear regression tests for chl-*b* and the other variables of the dense site.

Source of Variance	DF	SS	MS	F	*P*
Regression	9	0.207	0.0230	0.603	0.7714
Residual	11	0.420	0.0382		
Total	20	0.627	0.0314		

Table 5.4. ANOVA of multiple linear regression tests for lutein/zeaxanthin and the other variables of the dense site.

Source of Variance	DF	SS	MS	F	*P*
Regression	9	0.0129	0.00143	1.39	0.2977
Residual	11	0.0113	0.00103		
Total	20	0.0242	0.00121		

Table 5.5. ANOVA of forward stepwise regression tests for lutein/zeaxanthin and the other variables of the dense site.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	0.00734	0.007340	8.27	0.0097
Residual	19	0.01685	0.000887		

Overall correlations were not observed also when the multiple regression test was applied to the sediment phaeopigment and other variables ($F_{9,11} = 9.16$; $P = 0.0006$; Table 5.6.). However, the stepwise regression test resulted in correlation of sediment phaeopigment with the other variables at the dense site ($F_{1,19} = 40.1$; $P < 0.0001$; Table 5.7.). In addition to sediment chl-*a*, sediment phaeopigment correlated with sediment organic content, water temperature and shoot leaf number. The magnitude of correlation between sediment chl-*a* and other variables at the dense site is summarised in Table 5.8.

Table 5.6. ANOVA of multiple linear regression tests for sediment total phaeopigment and the other variables of the dense site.

Source of Variance	DF	SS	MS	F	*P*
Regression	9	455.3	50.59	9.16	0.0006
Residual	11	60.7	5.52		
Total	20	516.1	25.80		

Table 5.7. ANOVA of forward stepwise regression tests for sediment total phaeopigment and the other variables of the dense site.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	350.1	350.15	40.1	< 0.0001
Residual	19	165.9	8.73		

Table 5.8. Summary of Pearson product moment tests for chl-*a* and phaeopigment of the dense site.

Group of Test	*P*-Value	Correlation Coefficient
Total Chl-*a* v Sediment Organic Matter	< 0.001	0.822
Total Chl-*a* v Shoot Leaf Number	0.018	0.6
Total Chl-*a* v Shoot Aboveground Biomass	0.019	0.541
Total Chl-*a* v Water Temperature	0.011	0.583
Sediment Phaeopigment v Total Chl-*a*	< 0.001	0.824
Sediment Phaeopigment v Sediment Org. Matter	< 0.001	0.792
Sediment Phaeopigment v Water Temperature	0.012	0.681
Sediment Phaeopigment v Shoot Leaf Number	< 0.001	0.691

As was observed at the dense site, the multiple linear regression test for the sparse site showed that overall the sediment chl-*a* was not correlated to other variables measured ($F_{9,11} = 4.87$; $P = 0.0083$; Table 5.9.). However, the stepwise forward regression test indicated that chl-*a* at the sparse site did correlate with a greater number of variables than at the dense site ($F_{1,19} = 31.3$; $P < 0.0001$; Table 5.10.). Significant correlations were found between sediment chl-*a* and sediment organic matter and sediment total phaeopigment. Shoot aboveground biomass, shoot density, shoot leaf number and shoot height also were strongly correlated. A weaker correlation with water temperature was also indicated.

Neither chl-*b* ($F_{9,11} = 1.12$; $P = 0.4231$; Table 5.11.) nor lutein/zeaxanthin ($F_{9,11} = 0.346$; $P = 0.9390$; Table 5.12.) concentrations in the sediment correlated with other variables in the seagrass bed.

Table 5.9. ANOVA of multiple linear regression tests for chl-*a* and the other variables of the sparse site.

Source of Variance	DF	SS	MS	F	*P*
Regression	9	77.9	8.66	4.87	0.0083
Residual	11	19.6	1.78		
Total	20	97.5	4.87		

Table 5.10. ANOVA of forward stepwise regression tests for chl-*a* and the other variables of the sparse site.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	60.7	60.9	31.3	< 0.0001
Residual	19	36.8	1.94		

Table 5.11. ANOVA of multiple linear regression tests for chl-*b* and the other variables of the sparse site.

Source of Variance	DF	SS	MS	F	*P*
Regression	9	0.0908	0.01009	1.12	0.4231
Residual	11	0.0992	0.0092		
Total	20	0.1901	0.00950		

Table 5.12. ANOVA of multiple linear regression tests for lutein/zeaxanthin and the other variables of the sparse site.

Source of Variance	DF	SS	MS	F	*P*
Regression	9	0.00343	0.000381	0.346	0.9390
Residual	11	0.01210	0.001100		
Total	20	0.01553	0.000776		

As with the dense site, no overall correlation was observed when the multiple regression test was applied to the sediment phaeopigment and other variables at the sparse site ($F_{9,11} = 11.7$; $P = 0.0002$; Table 5.13.). Nevertheless, as found at the dense site, stepwise regression tests indicated the correlation of sediment phaeopigment with the other variables ($F_{1,19} = 31.3$; $P < 0.0001$; Table 5.14.). A greater number of variables correlated with sediment phaeopigment at the sparse site than at the dense site. In addition to those variables recorded as correlating for the dense site (sediment chl-*a*, sediment organic content, water temperature and shoot leaf number), sediment phaeopigment also correlated with shoot density and shoot aboveground biomass. Table 5.15. shows the level of correlation between sediment chl-*a* and other variables as well as between sediment phaeopigment and other variables at the sparse site.

Table 5.13. ANOVA of multiple linear regression tests for sediment total phaeopigment and the other variables of the sparse site.

Source of Variance	DF	SS	MS	F	*P*
Regression	9	449.2	49.91	11.7	0.0002
Residual	11	46.9	4.27		
Total	20	496.1	24.81		

Table 5.14. ANOVA of forward stepwise regression tests for sediment total phaeopigment and the other variables of the sparse site.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	308.8	308.84	31.3	< 0.0001
Residual	19	187.3	9.86		

Table 5.15. Summary of Pearson product moment tests for chl-*a* and phaeopigment of the sparse site.

Group of Test	***P*-Value**	**Correlation Coefficient**
Total Chl-*a* v Sediment Organic Matter	< 0.001	0.768
Total Chl-*a* v Shoot Leaf Number	0.017	0.515
Total Chl-*a* v Shoot Aboveground Biomass	0.001	0.651
Total Chl-*a* v Shoot Density	0.015	0.523
Total Chl-*a* v Shoot Height	0.019	0.504
Total Chl-*a* v Water Temperature	0.029	0.475
Sediment Phaeopigment v Total Chl-*a*	< 0.001	0.789
Sediment Phaeopigment v Sediment Org. Matter	< 0.001	0.707
Sediment Phaeopigment v Shoot Leaf Number	< 0.001	0.77
Sediment Phaeopigment v Shoot Density	0.0076	0.565
Sediment Phaeopigment v Shoot Abvgr Biomass	0.0067	0.573
Sediment Phaeopigment v Phenolics	0.0018	0.639
Sediment Phaeopigment v Water Temperature	< 0.001	0.721

Since the results showed the main source of pigment production of the bed came from the diatoms, a test was applied to understand the correlation between fucoxanthin and chl-*a* concentrations. Fucoxanthin was chosen among four accessory pigments because its concentration was much higher compared

with the other three, also it was present in every month sample. It is also the major accessory pigment in diatoms. The test showed a positive correlation in which the increase of chl-*a* was followed by the increase of fucoxanthin, both at the dense ($R^2 = 0.8489$) and sparse sites ($R^2 = 0.8156$) (Figure 5.17).

Further analyses were also carried out to follow the fate of *Z. noltii*, whether the production was retained in the bed sediment. The analyses were done by testing two important signatures of seagrass detritus, i.e. chl-*b* and zeaxanthin/lutein of the sediment, each against seagrass biomass. The tests showed that chl-*b* concentrations did not follow the shoot biomass pattern, both in the dense ($R^2 = 0.0200$) and sparse sites ($R^2 = 0.0051$) (Figure 5.18.). Shoot biomass also did not correlate with the zeaxanthin/lutein contents of the sediment, neither at the dense site ($R^2 = 0.0874$) nor at the sparse site ($R^2 = 0.1673$) (Figure 5.19.).

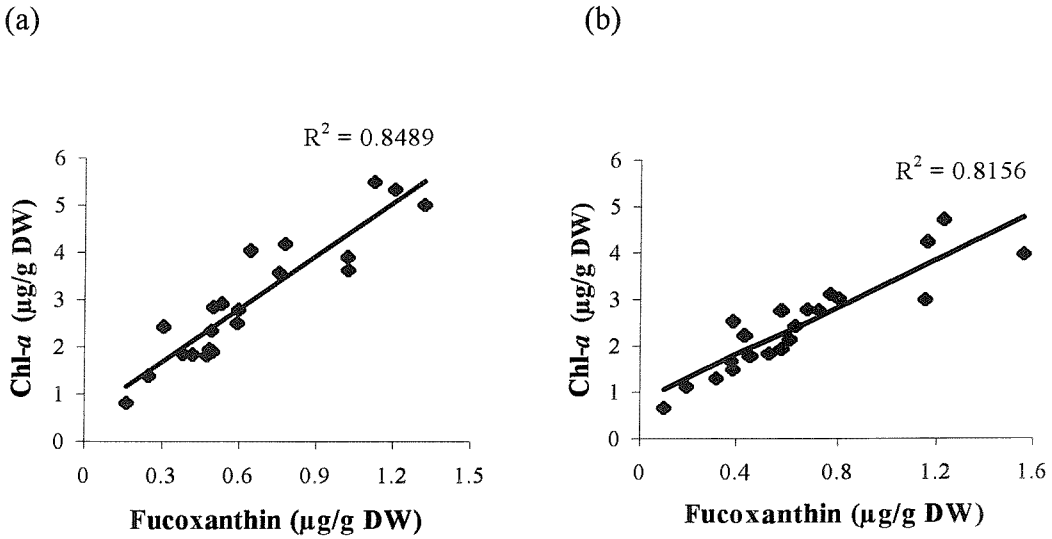

Fig. 5.17. Correlation tests between sediment chl-*a* and fucoxanthin concentrations of the dense site (a) and sparse site (b).

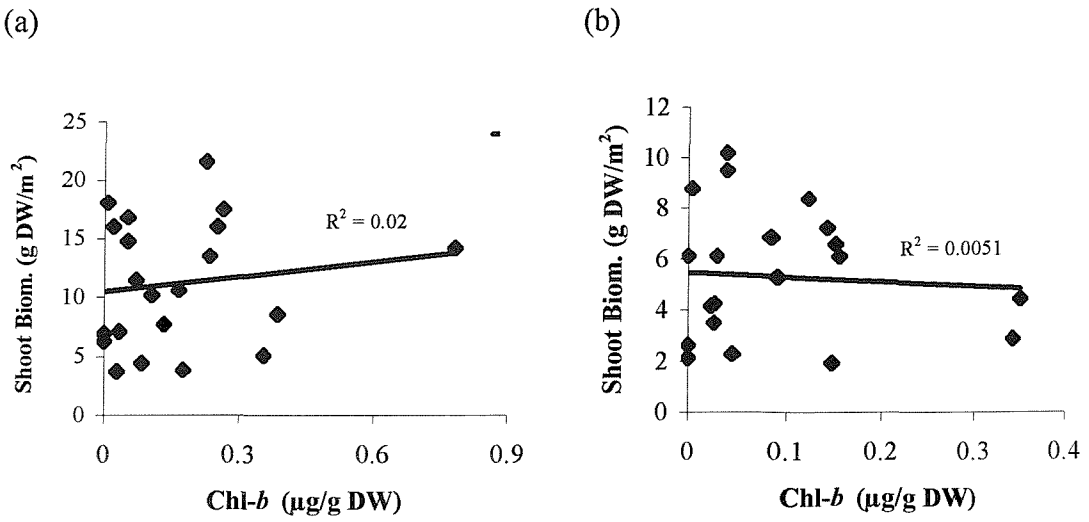

Fig. 5.18. Correlation tests between sediment chl-*b* concentrations and seagrass shoot biomass of the dense site (a) and sparse site (b).

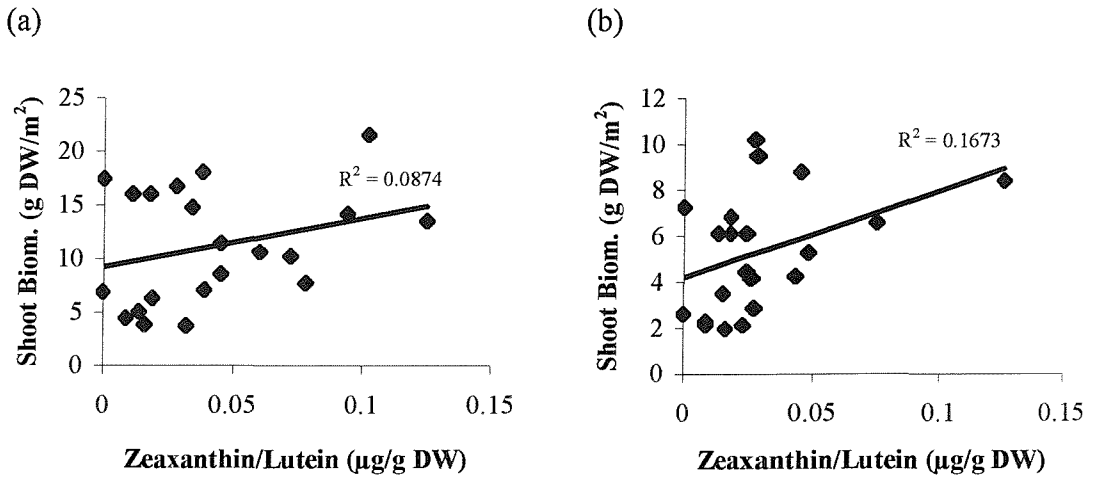

Fig. 5.19. Correlation tests between zeaxanthin/lutein concentrations and seagrass shoot biomass of the dense site (a) and sparse site (b).

5.3. Discussion

Seasonal variations in the seagrass bed pigment dynamics of Ryde Beach could be detected as distinctive fluctuations of chlorophyll, accessory pigments and phaeopigment concentrations in the sediments. In general, the fluctuations observed were both seasonal and between the sites. Although annual variations in the parameters have not been found in several studies (see Rizzo and Wetzel, 1985; Brotas *et al.*, 1995), in most cases the seasonal cycles of shallow benthic ecosystems studied in the subtemperate and temperate waters were very clear (Jacobs and Noten, 1980; Colijn and Dijkema, 1981; Riaux-Gobin *et al.*, 1987; Underwood and Paterson, 1993; de Jonge and Colijn, 1994; Pickney *et al.*, 1995; Santos *et al.*, 1996; Barranguet *et al.*, 1997; Beukema and Cadée, 1997; Boon *et al.*, 1998; Lucas and Holligan, 1999; Dransfield, 2000).

The high concentrations of chl-*a* and other pigments during the spring and autumn months found in this study can be attributed mainly to the microphytobenthic blooms on the site. It is widely reported that the sediment chl-*a* of coastal shallow systems often increases significantly following the blooms of the microphytobenthic population (Pickney and Zimarck, 1991; Barranguet *et al.*, 1997; Beukema and Cadée, 1997; Babichenko *et al.*, 1999). The other main source of bed sediment pigment production on the site is the contribution from *Z. noltii* vegetation itself. Though the concentration of seagrass detrital products were always small (as indicated by relatively low contents of chl-*b*, lutein/zeaxanthin and *ß*-carotene, Figures 5.5 and 5.6.) they contribute the maintenance of sediment bed pigment production. It is believed that the chl-*b*, lutein/zeaxanthin and *ß*-carotene found originate from certain species of phytobenthos (e.g. euglenoid and blue-green algae, see Fielding *et al.*, 1988 and Klein and Riaux-Gobin, 1991) and the end products of decaying *Z. nolti.* It is very unlikely that the sources of were derived from the higher algae. This is because although they were present, they were relatively rare at the study site (Chapter II). The retention of nutrients from the water column

when the seagrass bed is submerged entirely by the water perhaps also adds to the pigment production within the sediment. This process has been known as one of the most important factors in driving the productivity of seagrass bed sediment in particular (Zieman and Wetzel, 1980), and marine benthic vegetation in general (De Vries *et al.*, 1996; Fletcher, 1996a; Schramm and Nienhuis, 1996).

In some months, the sediment of the site had low pigment concentrations. The decline of alga biomass in the nearshore environment could be caused by a range of factors, such as nutrient limitations, consumption by grazers, desiccation by exposure, or removal by adverse weather conditions (Underwood and Paterson, 1993; De Vries *et al.*, 1996). At Ryde Beach, the lower sediment alga biomass (as indicated by reduced pigment concentrations) observed in the seagrass bed during the winter months may have been connected to the weather conditions as nutrient limitation is unlikely in estuarine and semi-enclosed coastal situations (Admiraal *et al.*, 1982; Fletcher, 1996b; Nienhuis, 1996). Desiccation and grazing by fish and invertebrates are possible causes for summer decline in standing stock (Montagna, 1984). This situation does not apply to the seagrass bed at Ryde Beach. Throughout the field visits it was seen that the site was never completely dry for more than an hour during the lowest tide of the month. Indeed, personal communications with Ryde Harbour Master (October 1997) and local residents (November 1997 and May 1998) also concluded that the *Z. noltii* bed at the study site was always submerged by the water. However, short photo-period together with the low temperatures, as has been suggested by several works (de Jonge and Colijn, 1994; Cariou-Le Gall and Blanchard, 1995; Bortone 2000), may have reduced the microphytobenthos growth rate and thus their pigment production in the site.

Besides affecting shoot density (as explained in Chapter IV), strong storm and wave action experienced by the seagrass bed in December 1997 –

January 1998 and during January – February 1999 may have resulted in transport of microphytobenthos away from the bed (this is in an agreement with Underwood and Paterson, 1993). The severe weather in winter often creates more powerful water movements with high turbidity, which may result in reduced primary production and resuspension of sediments and algae (de Jonge, 1985; de Jonge and de Jonge, 1995). Most of the decomposition process of *Z. noltii* occurs from the autumn through the winter (see discussion of Chapter IV), and storm conditions will aid in the dispersion of seagrass detrital product, as has been suggested by Harrison (1989). Thus the consequence is that seagrass products such as chl-*b* and lutein/zeaxanthin are low (Figure 5.5.) as is total chlorophyll concentration (Figure 5.4.).

It is not surprising that measurements from the spectrophotometric method yielded the higher values of chl-*a* and pheopigment compared to HPLC analyses (between 208 – 386 % and 170 – 381 % for chl-*a* at the dense and sparse site respectively; between 114 – 306 % and 102 – 332 % for phaeopigment at the dense and sparse site respectively). Those findings are not surprising since the spectrophotometric method actually measures the total chlorophyll as well as phaeopigment concentrations (Strickland and Pearson, 1968). The error in prediction of algal biomass by the spectrophotometric procedure can be too high by 400 % in sediments (see Mantoura and Llewellyn, 1983). The findings of the chl-*a* contents from the more traditional method in this study did not highly overestimate the chl-*a* concentrations as yielded from HPLC measurements. Although the accuracy of methods for determination and quantification of sediment phaeopigments is still in open to debate, in general spectrophotometric measurements give higher values compared those obtained by HPLC analyses (see Plante-Cuny *et al.*, 1993 and the papers therein). Occasional studies obtain higher values using HPLC in comparison to the spectrophotometric method (Barlow *et al.*, 1990).

Comparison of chlorophyll concentrations between two different densities of *Z. noltii* bed showed that the dense site always had the higher values. This finding is in concordance with the study observed by Santos *et al.* (1996). They proposed that the siltier sediment of the dense site had helped in supporting the microphytobenthos population as it may have had a higher nutrient content. However, the difference of sediment organic matter found in this study was small and the dense site of the bed contained less sand and had higher values of organic content (see Chapter III). Similar interpretations have been put forward in three previous studies (see de Jonge and de Jonge, 1995; Mackey *et al.*, 1996; Barranguet *et al.*, 1997). By having a denser population of seagrass (Fig. 4.1. Chapter IV) it is possible for the dense site to generate higher detrital outputs, not only from the seagrass itself but also from the epiphytic algae attached to the seagrass. In this area, the epiphytes may have contributed to the concentration of benthic chlorophyll. The addition of epiphytic organisms to the bed pigment production has been reported previously by a study from *Z. noltii* bed on the Dutch Wadden Sea (within the range of 20 – 50 %; see Philippart, 1995). The water flow in the bed presumably also influenced the pigment values. The higher number seagrass stands in the dense site may diminish the water movement and create the lower chance to wash away the algae from the seagrass bed sediment.

The lower values of the pigments in the sparse site can be related to increased exposure to the wave action and current. Lower densities of *Z. noltii* give rise to more exposed sediments, more easily resuspended, thus lowering microphytobenthic retention and survival. Fielding *et al.* (1988) has studied the correlation between chlorophyll contents and the site exposure. They reported that very low chl-*a* concentrations (0.49 – 1.03 μg chl-*a* g^{-1} sand) were found in the more exposed conditions.

It has been proposed that the seagrass bed pigment production at the site was also generated from the *Z. noltii* derived detritus. The findings of chl-*b*

and lutein/zeaxanthin from the sediment strongly supported this evidence. These pigments are normally found in macrophytes such as *Zostera* but are absent in diatoms (Levinton and MacCartney, 1991). As well as only being found at low concentrations, lutein/zeaxanthin levels in Ryde Beach seagrass bed did not fluctuate greatly. One study reported that the addition rate of lutein to the sediment was slow and this pigment was relatively stable in the sediment (Abele-Oescheger, 1991). Bianchi and Findlay (1991) have also identified the stability of lutein and zeaxanthin throughout the time in the other study. The higher levels of chl-*b* and lutein/zeaxanthin at the dense site may be the results of two factors. The first is due to a higher input of *Z. noltii* detritus (Bianchi *et al.*, 1993) at the dense site. This becomes more evident over the period of study when the site had higher shoot densities (from summer to autumn) and the contents of chl-*b* and lutein/zeaxanthin increased. Secondly, in the sparse site the level of sediment resuspension was higher and the chance of detrital retention reduced.

This study indirectly observed diatoms as the main group of microphytobenthos that contributed to the sediment pigment production. The positive correlation between sediment fucoxanthin, the main signature of diatoms, and chl-*a* (Figure 5.17.) explains this finding. Diatom dominance in the sandy sediments is common in the features of intertidal sediment microphytobenthos in general (Riaux-Gobin *et al.*, 1987; Klein and Riaux-Gobin, 1991; Boon *et al.*, 1998; Lucas and Holligan, 1999; Lucas, 2000-personal communication) and of seagrass bed in particular (Jacobs and Noten, 1980; Coleman and Bulkholder, 1994; Trautman and Borowtizka, 1999). The higher contribution of diatoms compared to that of *Z. noltii* detritus to the sediment pigment was shown by the concentration ranges of fucoxanthin and three seagrass associated pigments, i.e. chl-*b*, lutein/zeaxanthin and *ß*-carotene. Fucoxanthin was detected in the range of 0.16 – 1.32 μg·g DW at the dense site and 0.11 – 1.56 μg·g DW at the sparse site respectively (Figure 5.9.).

Compared with seagrass associated pigments, these values are higher although all three chl-*b*, lutein/zeaxanthin and *ß*-carotene concentrations are combined (0 – 1.24 µg·g DW for the dense site and 0 – 0.72 µg·g DW for the sparse site; Figures 5.6. and 5.7).

An interesting phenomenon was seen in the fate of *Z. noltii* production. The analyses between two main seagrass associated pigments and shoot biomass showed that neither chl-*b* nor lutein/zeaxanthin concentrations correlated with shoot biomass dynamics (Figures 5.18. and 5.19.). This may explain that seagrass detritus did not retain entirely within the seagrass bed, most of the detritus might have been exported to the outer ecosystems. Although the site is located in a semi-enclosed area, the dynamics of tide and water currents are high. The site also persistently received the additional waves created from the nearby sea traffics and adjacent ferry terminal. These make possible for *Z. noltii* detritus to be carried away from the site in more frequently basis.

It has been presented that in general, with the HPLC measurements all sediments collected in 1999 possessed higher concentrations of chl-*a* (Figure 5.5.) than the comparable period of samplings in 1997 and 1998. Meanwhile chl-*a* measured by spectrophotometer in those comparable periods showed similar patterns (Figure 5.1.). Although in many cases sediment preservation did not give clear effect to chl-*a* readings in the HPLC (Chapter II, Gieskes and Kraay, 1983; Klein and Riaux-Gobin, 1991), the present study found much lower chl-*a* concentrations from the stored samples. Preserving and freeze-drying samples may cause the differences of the chl-*a* values as has been reported in several studies (Riaux-Gobin, 1987; Barlow *et al.*, 1990). Indeed, the HPLC analyses were only started in January – February 1999, after 1.5 years the study was begun. Thus, some pigments perhaps have degraded and or their concentrations were too low to detect.

Interestingly, the trends for fucoxanthin, diadinoxanthin and diatoxanthin (Figures. 5.9., 5.10. and 5.11. respectively), were also similar to that of chl-*a* values. In 1999 these three pigments also showed higher concentrations than that of comparable periods in 1997 and 1998. Diadinoxanthin and diatoxanthin both are protecting photo-pigments and mostly found in diatoms within sandy sediments (Riaux-Gobin *et al.*, 1987; Lucas, 2000-personal communication). This similarity provides more evidence that seagrass bed sediment pigment production at the site is mainly derived from the diatoms. Moreover, the prolonged storage of the sediment samples showed not only decreased concentrations of chl-*a* but also of fucoxanthin, diadinoxanthin and diatoxanthin.

Overall, this study found clear seasonal variations of phaeopigment concentration in the sediment. The variations of phaeopigment were also reported from other studies (Shaffer and Onuf, 1983; Santos *et al.*, 1996). Fluctuations of phaeopigment in the shallow benthic ecosystems could be caused by several factors, such as faunal biomass (Webb and Montagna, 1993) and season (Boon *et al.*, 1998). Two modes of faunal action can produce phaeopigment: through the acidification of chl-*a* via ingestion; and by the burial of plant materials by bioturbation. In the case of the seagrass bed of Ryde Beach it was clear that the level of phaeopigment became higher following the addition of its chl-*a* contents, particularly during the spring, end of summer and end of autumn. Throughout these times, macrozoobenthos species richness and biomass were also high (see later in Chapter VI), thus macrozoobenthos activities may have contributed to the phaeopigment increase.

It is believed that the extreme weather conditions gave rise to the low phaeopigment values during the winter. As has been explained earlier in this discussion, the high dynamics of water movement and low water temperature reduced the generation of chl-*a* in the bed, thus there was little chance for the macrozoobethos to consume the pigment over the winter. The result is that the

production of phaeopigment derived from ingestion became reduced. As for the burial process itself, it was clear that there was only a little chance of *Z. noltii* detritus being retained in the system owing to the winter storm conditions prevailing during the time of maximum detritus generation.

Though the variations of their concentrations were obvious, in this study both phaeophorbide and phaeophytin were detected for all months of observation. The regularity of phaeophytin in the coastal sediments of seagrass beds has been reported in the earlier studies (Barranguet *et al.*, 1997 and papers therein). The existence of phaeophorbide indicates grazing activity (Bianchi *et al.* 1993). Thus, it can be explained that the evidence of phaeophorbide throughout the study did support the existence and richness of the macrozoobenthos in the Ryde Beach seagrass bed.

Chapter VI:
Macrozoobenthos of the Seagrass Bed

6.1. Introduction

The fauna associated with seagrass bed ecosystems has been reported in the literature only over the last few decades (Mazella *et al*, 1990), relatively late compared with studies of the marine fauna of other submerged marine macrophyte ecosystems (Boaden *et al.*, 1992). The realization that seagrass beds are highly productive and diverse habitats has played a major role in attracting attention to them in recent decades (Young *et al.*, 1976; Heck and Orth, 1980; Zieman and Wetzel, 1980; Bortone, 2000).

As already mentioned in Chapter I, seagrass bed ecosystems are known to support abundant fauna. One reason for this is that they provide a wide range of microhabitats (Thayer *et al.*, 1975a). Infauna occur within root-rhizome bound sediments. The leaves and canopy support both sessile and mobile fauna as the settlement, spawning and nursery grounds (see Lenanton *et al.*, 1982; Heck and Thoman, 1984; Jenkins *et al.*, 1995; Perkins-Visser *et al.*, 1996). In addition, the water column within the seagrass beds are regularly used as feeding grounds by many species. Some invertebrates and fish, both demersal and pelagic species, are also known to use the seagrass meadow as a refuge from predators (Heck and Orth, 1980; Jenkins *et al.*, 1996). Seagrass bed also able to modify environmental hydrodynamic processes, since both the shoot and root-rhizomal systems have been observed to reduce the impact of current and wave actions. These mechanisms are very important in determining the settlement of fauna in general, and larvae in particular (Orth, 1992).

Faunistic study of the seagrass bed ecosystem, particularly macrofaunal dynamics, has become very important in terms of monitoring programmes to

determine the quality and disturbance levels of not only the seagrass bed ecosystems themselves, but also as an indicator for the wider marine ecosystem in general (Houston *et al.*, 1983; Davison and Hughes, 1998). Many attempts have been made to correlate the quality status of coastal ecosystems with that of the seagrass beds it contains (Houston *et al.*, 1983; Nelson and Virnstein, 1996 and papers therein; Alfonso *et al.*, 1998).

The studies of the fauna of seagrass beds have been conducted worldwide. However, studies have been concentrated on north-west Europe (particularly the Wadden Sea and Baltic Sea regions), the Mediterranean Sea (especially the Spanish and French coasts), North American waters and Australian shores. Somewhat surprisingly, there has only been a single detailed study in Britain. The important works from the Baltic Sea and the Wadden Sea are from Rasmussen (1973), Baden and Pihl (1984), Möller *et al.* (1985), Isakson and Pihl (1992), Böstrom and Bonsdorff (1997 and 2000). The examples of significant contributions from the Mediterranean Sea are reported by Bell and Westboy (1986), Mazzella *et al.* (1989), Gambi *et al.* (1991), Štévçic (1991), Currás *et al.* (1993), Sardá *et al* (1995) and Çinar *et al.* (1998). The works of North American studies are found from Young *et al.* (1976), Heck and Orth (1980), Orth *et al.* (1984), Orth and Montfrans (1990), Durako (1994) and Sheridan (1997). In the Australian waters, studies have been reported by Watson *et al.* (1984), Robertson (1984), Edgar (1990), Edgar *et al.* (1994) and Jenkins *et al.* (1995). As for the British Isles, a recent study was reported from the Yealm Estuary, southwestern England by Webster *et al.* (1998).

On a local scale, benthic studies have been limited in the Solent coastal waters (Thorp, 1980). Faunistic data from many areas of the Solent coastal regions are still poorly understood; most effort has been concentrated in either Langstone Harbour or Southampton Water (see Oyenekan, 1981 and papers therein; Houston *et al.*, 1983; Al-Suwailem, 1991). For the Isle of Wight, in particular, a species list for the macrobenthic fauna was compiled by Morey nearly a century ago (Thorp, 1980). The majority of intertidal macrobenthic fauna studies were concentrated on

the southern shores of the island from Bembridge to Freshwater, with studies focussing on spatial and faunistic distributions rather than seasonal dynamics or biomass variability.

The aim of this section of the study was to follow the dynamics of the benthic macrofauna of Ryde Beach seagrass bed. The site was chosen because, first, it is easily accessible, and secondly only few macrofaunal observations have been conducted at the site. The other studies applied in this area were conducted more than 35 years ago by Crisp and Southward (see Thorp, 1980) and in the mid 1970's by Withers (1979). Thus there is a need to validate these earlier results, since within such a dynamic ecosystem, the structure of macrofaunal communities may well have changed over the decades. The seagrass bed was selected for the area of study in order to test the worldwide hypothesis that generally considers seagrass bed ecosystems to support both a high species richness and high abundance of macrozoobenthos (Orth *et al.*, 1984).

In order to follow the macrozoobenthic dynamics, this research documented the seasonal and temporal changes in species composition, abundance, biomass, diversity and similarity. The macrobenthic faunas were collected from two different sites of seagrass bed, i.e. sparse and dense sites, to test the hypothesis that the denser seagrass bed supports higher species number and abundance of macrozoobenthos. Such an approach has been used in only a few studies (Kenworthy *et al.*, 1982; Orth *et al.*, 1984; Castel *et al.*, 1989; Webster *et al.*, 1998). Sampling was conducted over a 26 month period enabling an understanding on the role of the seagrass bed in supporting the seasonal patterns of macrozoobenthic community structure and composition, and to observe the life cycles of the dominant macrozoobenthic invertebrates.

6.2. Results

6.2.1. Macrozoobenthos Species Number

Overall, 124 species of macrozoobenthos were identified from the *Z. noltii* bed of Ryde Beach. The dense seagrass bed supported 112 species, whereas the sparse bed contained 92 species. Amongst 124 recorded macrozoobenthic species, 80 species were found at both the dense and sparse sites. The number of species from the dense site not found at the sparse site was 33, whereas the sparse site possessed 11 species that were not found at the dense site.

The macrozoobenthic species number showed distinctive seasonal and temporal variations (Figure 6.1.). At both sites, the peaks of species number occurred in the spring, i.e. May and June 1998 and May 1999, and autumn, i.e. October 1999, whereas the lowest values were found in February 1998 and January 1999. High species numbers were also found in the samples from October and November 1997 and 1998, as well as July 1999. As was expected, the dense site always had the higher number of species compared to those of the sparse site. Statistically, the difference in the species number was very significant (t-test, $P < 0.001$). In the dense site, the calculated averages of species number per core were in the range 11.0 (± 1.0) to 26.6 (± 5.2), whereas those for the sparse site fell between 9.2 (± 3.7) and 22.4 (± 1.9).

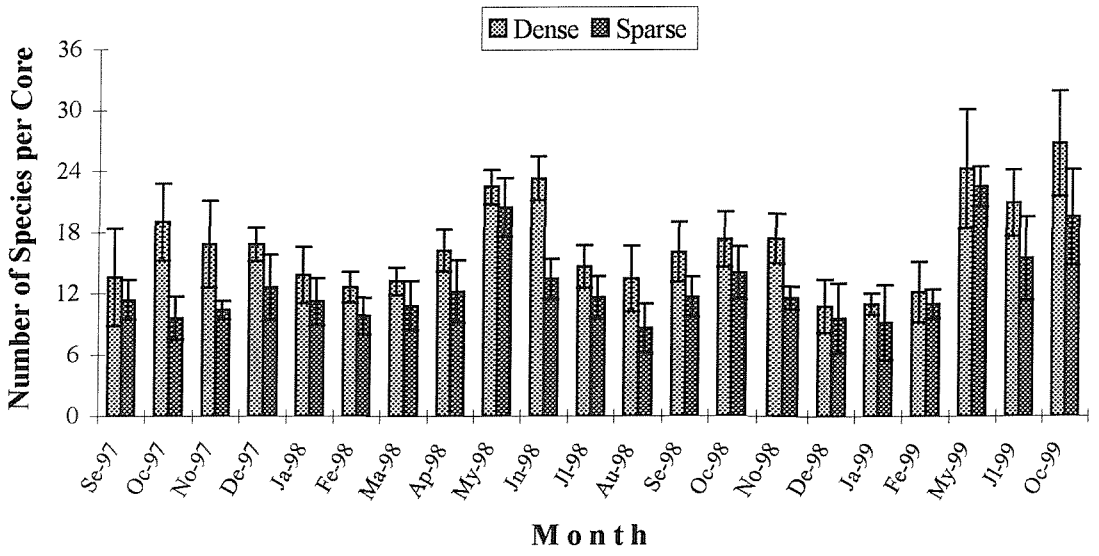

Fig. 6.1. Species number of macrozoobenthos collected from Ryde Beach seagrass bed (± SD; n = 5; core area = 28.27 cm^2).

6.2.2. Species Composition of Macrozoobenthos

The macrozoobenthic figures recorded in this study were composed of 16 orders from 5 phyla. Altogether, the order of polychaetes, with 49 species, was the group most frequently sampled throughout the sampling programmes. This was followed by the amphipods with 29 species and gastropods with 15 species respectively. The next groups which had few representatives on the species list were cumaceans (6 species), tanaids (5 species), bivalves (5 species), decapods (4 species) and isopods (4 species). The rest of the groups, i.e. nematodes, oligochaetes, copepods, caprellids, harpacticoids, mysids, palaemonids and ophiuroids, were only represented by one or two taxa. Only one echinoderm species, *Amphipolis squamata*, was recorded from the present study. It was only sampled once at both sites. More details of the species of macrozoobenthos

composition in the dense and sparse sites are presented in Appendices 1 and 2 respectively.

As was mentioned earlier, the polychaetes were represented by the highest number of species. At the dense site, they were represented by 47 species (41.97 % of total species). The amphiphods and gastropods each had 28 and 15 species respectively, each composing 25.00 % and 13.39 % of total species number. At the sparse site, the polychaetes were represented by 37 species or 40.21 % of total species number. Whereas the amphipods and gastropods each consisted of 20 and 10 species respectively, or 21.73 % and 10.87 % of total species number. Table 6.1. summarizes the details of the species composition of macrozoobenthos found in this study.

The composition of the most dominant species between the two sites was different. At the dense site, Nematoda, *Capitella capitata* and *Pygospio elegans* were always present on each sampling programme. These three were then followed by, in ranked order, *Aricidea minuta, Exogene hebes, Ericthonius punctatus, Scoloplos armiger, Phyllodoce mucosa, Euclymene lumbricoides* and *Hydrobia ulvae.* At the sparse site, no single species occurred on all sampling occasions. *C. capitata* was the most frequently recorded species. It was recorded on twenty sampling visits. The following were the next most frequently sampled species in ranked order at the sparse site: *E. hebes, P. elegans, E. punctatus, A. minuta, Typosyllis prolifera* and Nematoda. Table 6.2. presents the list for the top 20 most frequently found species at each site.

Table 6.1. Species composition of macrozoobenthos identified from Ryde Beach seagrass bed.

Group of Macrozoobenthos	Dense Site		Sparse Site	
	Species Number	%	Species Number	%
NEMATODA				
Nematoda	1	0.89	1	1.09
ANNELIDA				
Polychaeta	47	41.97	37	40.21
Oligochaeta	1	0.89	1	1.09
ARTHROPODA				
Amphipoda	28	25.00	20	21.73
Caprellidae	1	0.89	1	1.09
Copepoda	1	0.89	-	-
Cumacea	2	1.79	5	5.44
Decapoda	2	1.79	3	3.26
Harpacticoida	1	0.89	1	1.09
Isopoda	2	1.79	3	3.26
Mysidacea	-	-	1	1.09
Palaemonidae	1	0.89	2	2.17
Tannaidacae	4	3.58	4	4.35
MOLLUSCA				
Bivalvia	5	4.46	2	2.17
Gastropoda	15	13.39	10	10.87
ECHINODERMATA				
Ophiuridae	1	0.89	1	1.09
Total	112	100	92	100

Table 6.2. Top 20 macrozoobenthos species found most often at the Ryde Beach seagrass bed.

Dense Site		Sparse Site	
Species	Frequency*	Species	Frequency*
Nematoda	21	*Capitella capitata*	21
Capitella capitata	21	*Exogene hebes*	18
Pygospio elegans	21	*Pygospio elegans*	18
Aricidea minuta	20	*Typosyllis prolifera*	17
Exogene hebes	20	*Aricidea minuta*	17
Ericthonius punctatus	20	*Ericthonius punctatus*	17
Phyllodoce mucosa	19	Nematoda	16
Euclymene lumbricoides	18	*Euclymene lumbricoides*	15
Scoloplos armiger	18	*Malacoceros fuliginosus*	15
Malacoceros fuliginosus	17	*Scoloplos armiger*	15
Hydrobia ulave	17	*Syllis gracilis*	14
Euclymene oerstedii	15	*Euclymene oerstedii*	13
Leptochelia savignyii	15	*Hydrobia ulvae*	13
Corophium arenarium	15	*Arenicola marina*	12
Typosyllis prolifera	14	*Leptochelia savignyii*	12
Gammarus finmarchicus	14	*Corophium arenarium*	11
Syllis gracilis	12	*Ampithoe rubricata*	10
Urothoe poseidonis	12	*Urothoe brevicornis*	10
Clymenura clypeata	11	*Urothoe poseidonis*	10
Urothoe marina	11	*Gammarus finmarchicus*	10

*Frequency of species occurrence in 21 field visits.

It was found that relatively few species were exclusively found at a particular site only. The dense site did clearly have more representatives of the polychaetes, amphiphods and molluscs. On the other hand, the sparse site supported more species of crustaceans, except from the order of amphipods (28 at the dense site vs 20 at the sparse site). The list of species that occurred in either the dense or sparse site only is presented in Table 6.3.

Table 6.3. Macrozoobenthos species recorded only from either dense or sparse site of Ryde Beach seagrass bed.

Occur only at the Dense Site	Occur only at the Sparse Site
Polychaeta	**Polychaeta**
Amphitritides gracilis	*Orbinia sertulata*
Eulalia aurea	
Euphrosyne foliosa	***Amphipoda***
Lanice conchilega	*Apherusa jurinei*
Nepthys caeca	
Perinereis cultrifera	**Caprellidae**
Phyllodoce longipes	*Caprella linearis*
Pista cristata	
Polydora giardi	**Cumacea**
Sabellidae sp.	*Pseudocuma longicornis*
Terebellidae sp.	*P. similis*
Amphipoda	**Decapoda**
Ampithoe gammaroides	*Crangon crangon*
Chaetogammarus marinus	*Palaemon adspersus*
Cheirocratus intermedius	
C. sundevalli	**Mysidacea**
Corophium crassicorne	*Siriella jaltensis*
Hyale nilssoni	
Iphimedia spatula	**Isopoda**
Jassa pusilla	*Cirolana cranchii*
Melita obtusata	
Microprotopus maculatus	**Tannaidacae**
	Apseudes latreilli
Copepoda	
Hersilioides latericeus	**Gastropoda**
	Lacuna vincta
Caprellidae	
Caprella erithizon	
Tannaidacae	
Apseudes talpa	
Bivalvia	
Venerupis aurea	
V. pullastra	
V. saxatilis	
Gastropoda	
Crepidula fornicata	
Hydrobia neglecta	
Mytilus edulis	
Parvicardium exiguum	
Rissoa sarsi	
Tornus sp.	

6.2.3. Macrozoobenthos Abundance

The abundance of macrozoobenthos showed clear variations according to the season. The figures also varied greatly between the two sites. As has been observed for the species number, the average individual numbers in each core were very significantly higher for the dense site (t-test, $P < 0.001$). In both types of seagrass density, the lowest macrozoobenthic population was found in January 1999 samples, whereas those of the highest numbers were recorded from May, October and November 1998, and May and October 1999 collections. The high values of macrozoobenthic abundance were also recorded in December 1997. Overall, the mean of macrozoobenthic abundance at the dense site ranged between 33.6 (± 11.9) and 118.2 (± 14.9) individuals per core (12,000 to 42.214 individuals per m^2). At the sparse site the average values were between 13 (± 7.4) and 70.6 (± 19.3) individuals per core (4,642.8 and 25,214.1 individuals per m^2). Figure 6.2. illustrates the seasonal and temporal variations of macrofaunal abundance at each seagrass bed density.

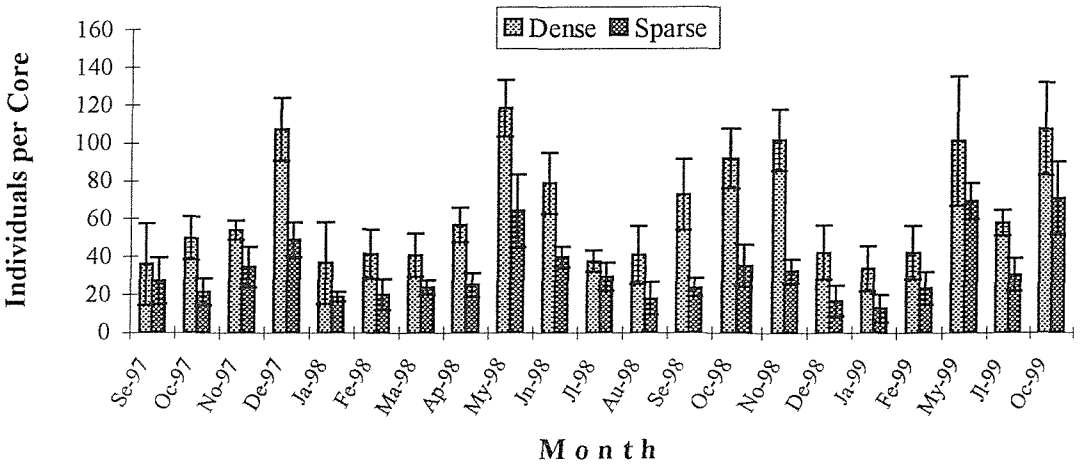

Fig.6.2. The abundance of macrozoobenthos from Ryde Beach seagrass bed (± SD, n = 5; core area = 28.27 cm^2).

6.2.4. Macrozoobenthos Biomass

This study observed clear temporal variations in macrozoobenthic biomass. The average biomass values at the dense site ranged from 12.28 to 38.51 mg DW per core (4.38 to 13.75 g DW m^{-2}; Figure 5.3.), whilst those of the sparse site fell between 7.389 – 28.590 mg DW per core (1.97 to 10.21 g DW m^{-2}; Figure 6.4.). Overall, the pattern of temporal variation in macrozoobenthic biomass at both sites was similar. At the dense site, biomass values reached their maximum and minimum in May 1998 and January 1999 respectively. Relatively high values for macrozoobenthic biomass were also recorded in November and December 1997, June, August, September, October and November 1998, and May, July and October 1999. At the sparse site, the highest and lowest biomass levels were also reached in May 1998 and January 1999 respectively. High values of biomass were also recorded in December 1997, June, October and November 1998, and May,

July and October 1999. When the monthly mean values of biomass were tested, they were significantly different (t-test, $P = 0.0031$). The dense site had always the higher value compared to those of the sparse one.

The macrozoobenthic biomass values were also presented as percentage composition by phylum (Figures 6.5. and 6.6. for the dense and sparse sites respectively). The results did not follow the patterns found for species composition (see Table 6.1.). Although the polychaetes were always dominant in the species composition, they did not always contribute the highest proportion of the total biomass. On the contrary, the crustaceans and molluscs were often dominant.

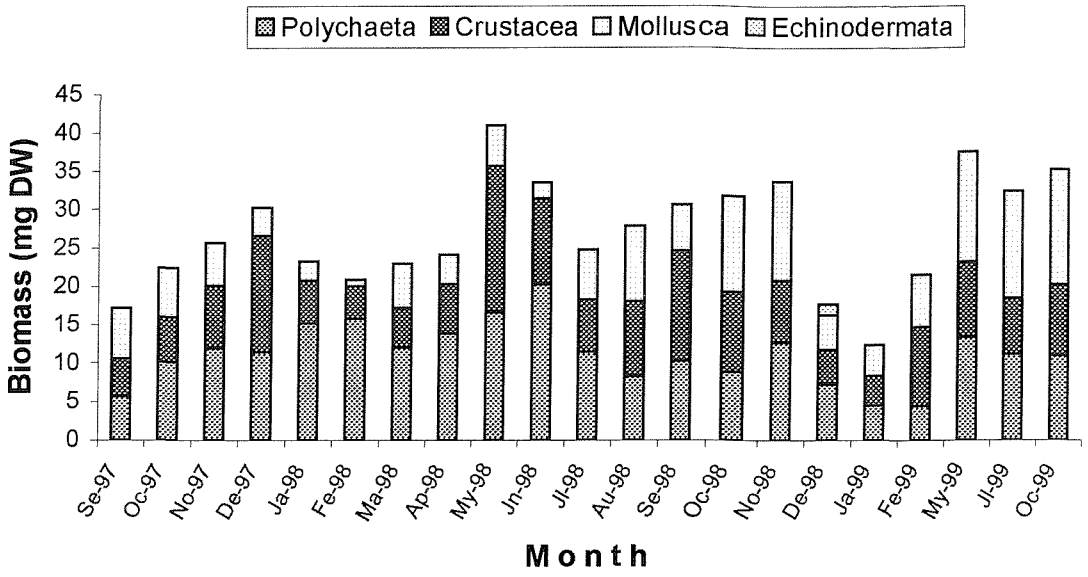

Fig.6.3. Macrozoobenthos biomass per core collected from the dense seagrass bed of Ryde Beach (n = 5; core area = 28.27 cm^2).

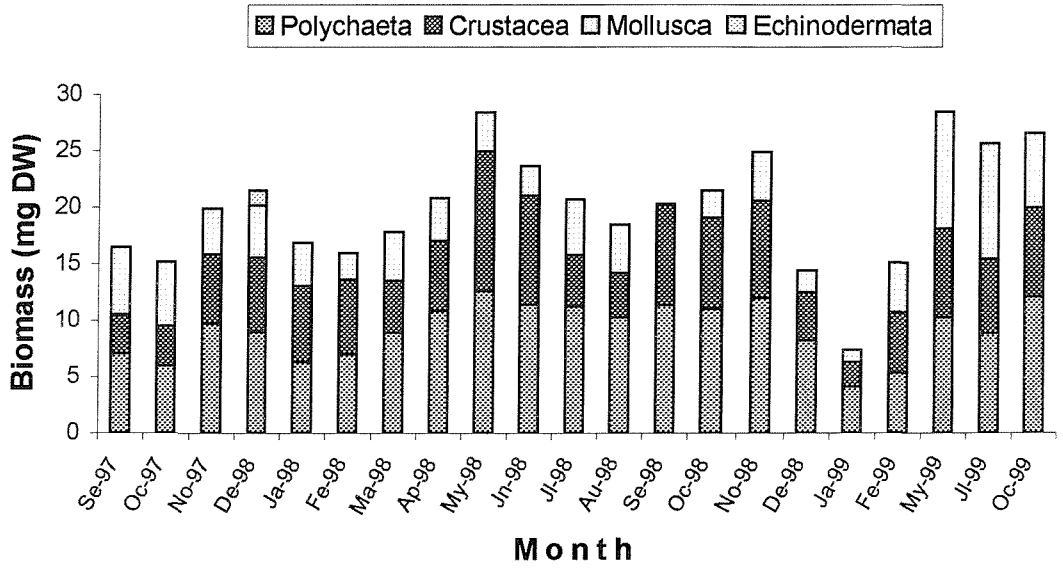

Fig.6.4. Macrozoobenthos biomass per core collected from the sparse seagrass bed of Ryde Beach (n = 5; core area = 28.27 cm^2).

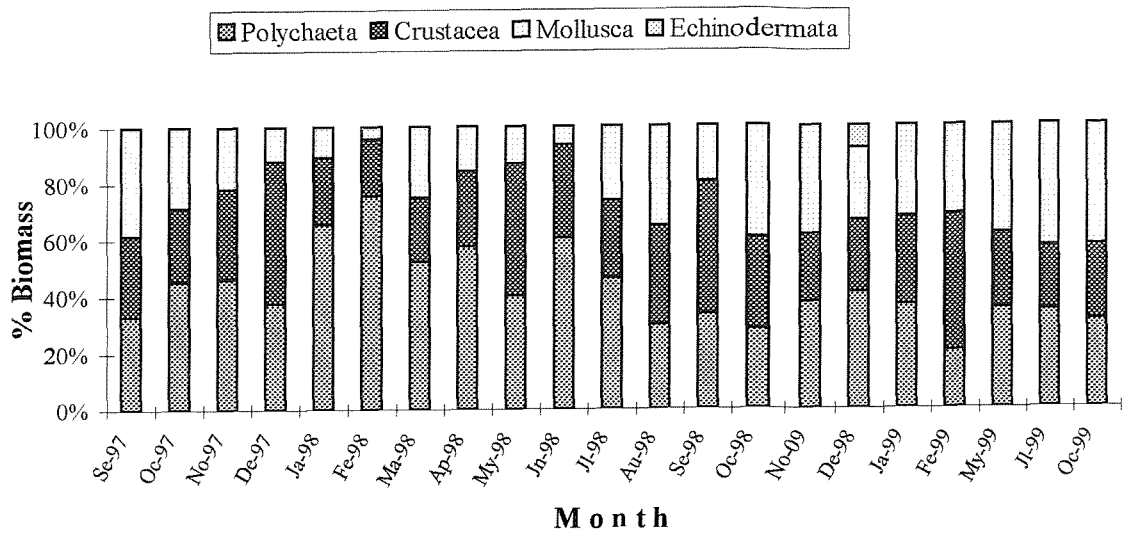

Fig.6.5. Mean percentage biomass of each macrozoobenthos group collected from the dense seagrass bed of Ryde Beach (n = 5).

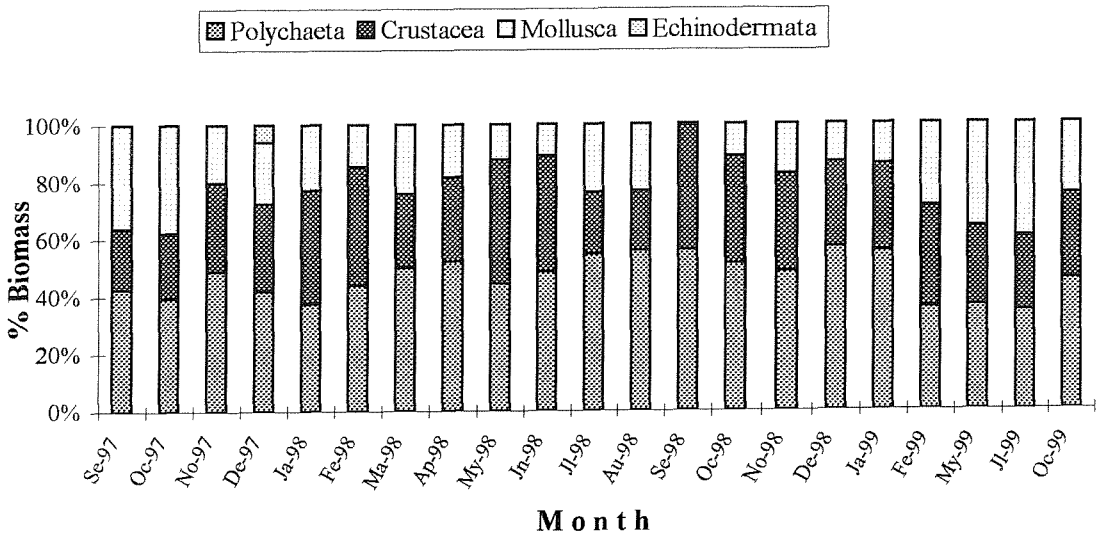

Fig.6.6. Mean Percentage biomass of each macrozoobenthos group collected from the sparse seagrass bed of Ryde Beach (n = 5).

6.2.5. Macrozoobenthos Diversity

Species diversity values, as measured by the Shannon-Wiener index, H, are given for both types of seagrass bed density in Figure 6.7. In general the index exhibited clear seasonal patterns but it did not vary greatly between the sites.

At the dense site, the average values of H index ranged between 1.7 (± 0.3) (January 1999) and 2.8 (± 0.2) (June 1998). The spring samples (April – June 1998 and May 1999) possessed the most diverse macrozoobenthic values as indicated by high values of H. The lowest diversities were found in all winter samples in the first year (December 1997 – February 1998) and from late autumn throughout the winter in the second year (November 1998 – February 1999).

At the sparse site the average values of the H index ranged between 1.9 (± 0.3) (December 1998) and 3.1 (± 0.2) (May 1999). As was shown at the dense site, it was apparent that the spring months also had the most diverse macrozoobenthic fauna as indicated by the high values of H, whereas the lowest diversity was found during the winter period. Although on several sampling occasions the sparse site had the higher values of the H index, statistically there was no difference in the species diversity when the two sites were compared (t-test; $P = 0.0457$).

There were seasonal and temporal patterns in the macrozoobenthos species richness (Figure 6.8.). The average values of species richness index, Margalef's d, of the dense site ranged between 2.6 (± 0.5) and 5.5 (± 0.2), whilst those of the sparse site ranged between 2.40 (± 0.56) and 3.89 (± 0.18). Samples collected in the winter months showed low values of d, indicating lower number of species. Amongst these samples, the lowest d values were recorded in January 1999 and December 1997 for the dense and sparse sites respectively. Spring and autumn periods showed the highest values for d index in which October 1999 and May 1999 samples had the highest d values for the dense and sparse site respectively. When the values of d from both sites were tested, they were very different significantly (t-test; $P < 0.001$). The sediments from the dense site always had the greater macrofaunal species richness.

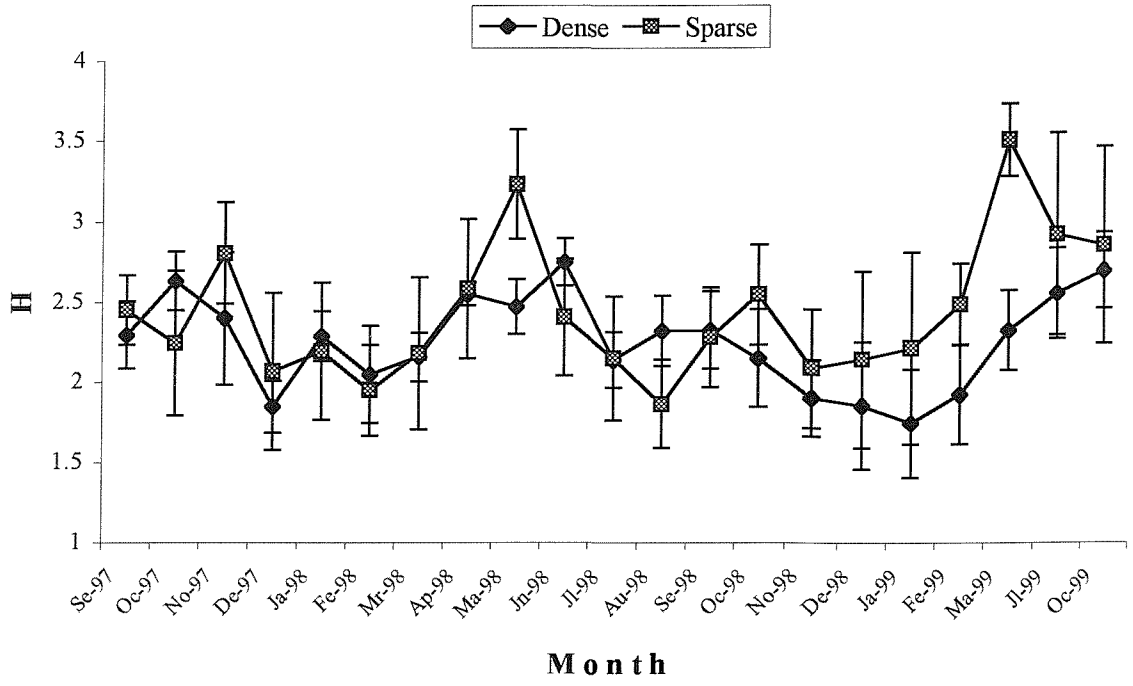

Fig.6.7. Mean species diversity (H, Shannon-Wiener) index per core for macrozoobenthos collected from the seagrass bed of Ryde Beach (n = 5; ± SD; core area = 28.27 cm^2).

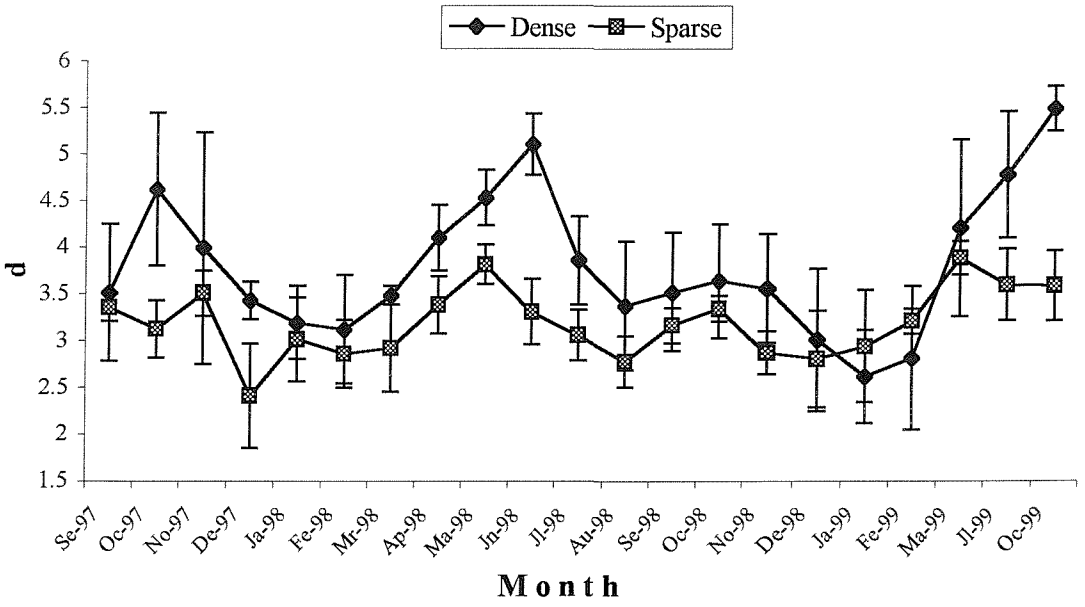

Fig.6.8. Mean species richness index (Margalef's d) per core for macrozoobenthos collected from the seagrass bed of Ryde Beach (n = 5; ± SD; core area = 28.27 cm^2).

The evenness of distribution of individuals between species was measured using Pielou's index, J. Equitability varied according to both season and the site (Figure 6.9.). In general, values for J were highest in the spring months with lower values in the winter months. Somewhat surprisingly, in the sparse site both the lowest and the highest values occurred in the winter. In the dense site, December 1997 samples had the lowest equitability value (J = 0.65 ± 0.06), whereas April 1998 had the highest value (J = 0.92 ± 0.02). For the sparse site, the lowest value was found for December 1997 (J = 0.66 ± 0.10), whilst the highest value occurred in January 1999 (J = 0.96 ± 0.03). Statistically, the evenness values between the dense and sparse sites were significantly different (t-test; $P < 0.001$). Except for August 1998, the samples of the sparse site were always more evenly distributed.

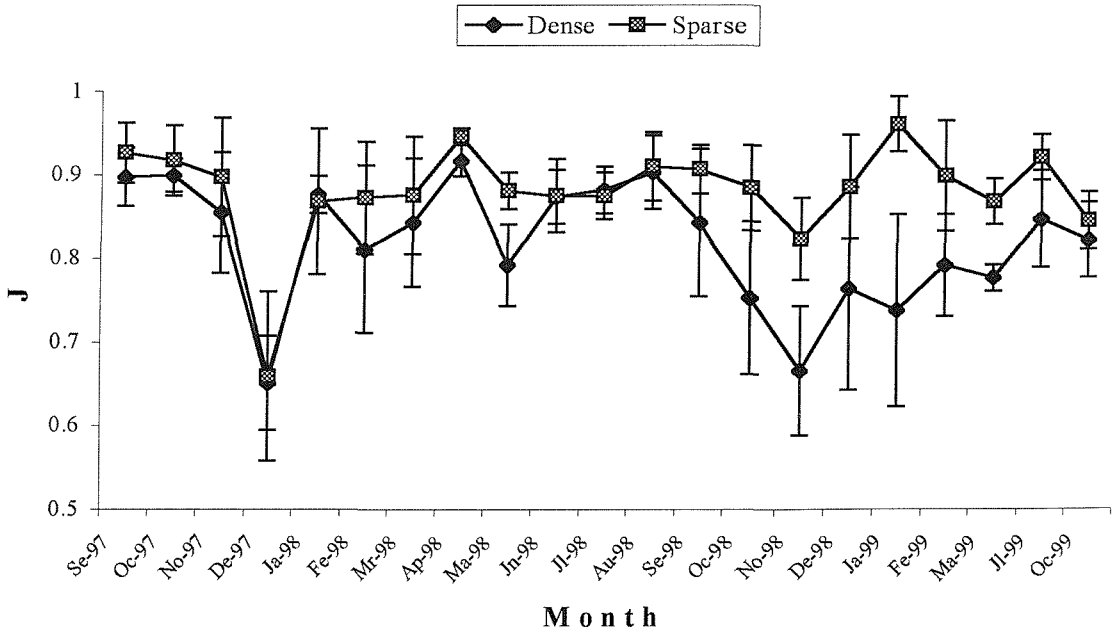

Fig. 6.9. Species evenness (Pielou) index of macrozoobenthos collected from the seagrass bed of Ryde Beach (n = 5; ± SD; core area = 28.27 cm^2).

The seasonal patterns for H (Figure 6.7.) and d (Figure 6.8.) were similar suggesting that changes in species diversity at both sites are largely influenced by changes in species richness rather than changes in evenness.

5.2.6. Macrozoobenthos Sample Similarity

Overall, monthly samples at the dense site were similar at 42 % or greater (Figure 6.10.). The maximum similarity between pairs of samples, 73 %, was shown between October 1999 and May 1999. Clustering of monthly samples was not well defined. Four clusters occurred at the 50 % similarity level. The majority of monthly samples were found in a single cluster (Cluster I) with the exceptions of March 1998 (Cluster II), December 1997 – February 1998 (Cluster III) and September 1997 (Cluster IV). The MDS analysis shows that these last three groups of samples were clearly separable from the others (Figure 6.11.).

In general, it was obvious that the autumn samples had the higher similarities with the spring samples rather than with the other seasons. These were shown by strong similarities in these pairings: May and October 1999, October 1997 and April 1998, and November 1997 with May - June 1998. It was also apparent that the winter samples tended to be clustered with each other compared with the other seasons.

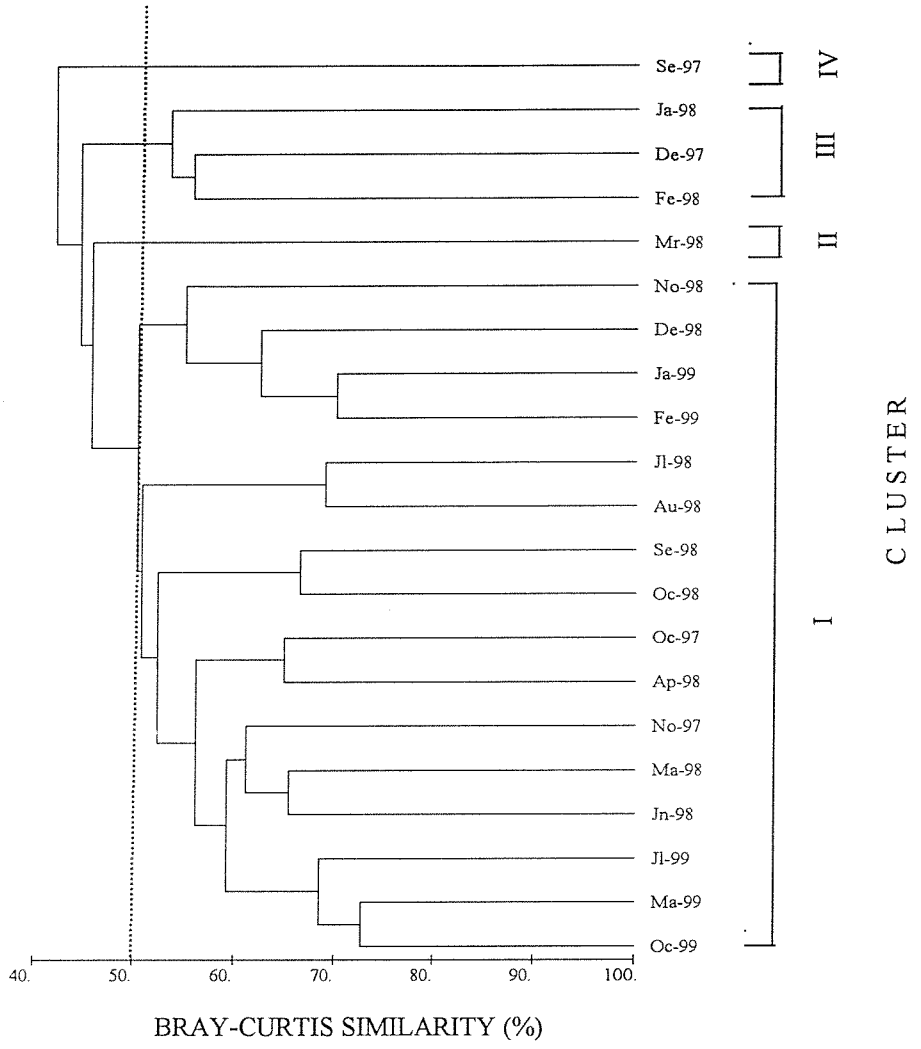

Fig. 6.10. Dendrogram of percentage fauna similarity among the macrozoobenthos samples at the dense site.

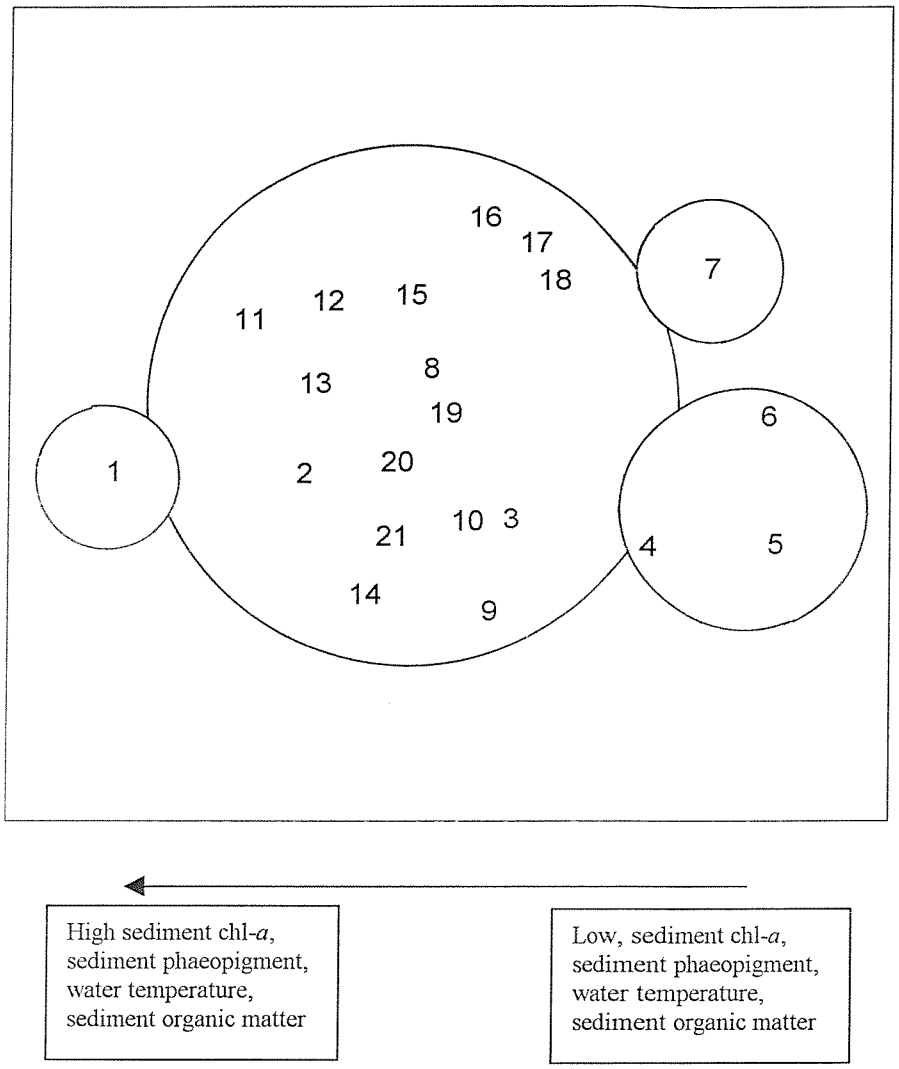

Fig. 6.11. MDS ordination plot of macrozoobenthos species taken from the dense site (stress = 0.22; 1 = September 1997, 2 = October 1997, 3 = November 1997, 4 = December 1997, 5 = January 1998, 6 = February 1998, 7 = March 1998, 8 = April 1998, 9 = May 1998, 10 = June 1998, 11 = July 1998, 12 = August 1998, 13 = September 1998, 14 = October 1998, 15 = November 1998, 16 = December 1998, 17 = January 1999, 18 = February 1999, 19 = May 1999, 20 = July 1999, 21 = October 1999).

Since clusters have been observed at the dense site, scaling based on the species abundance was carried out to follow which species causes the similarity and dissimilarity. In each month, the ten most abundant species were given score between 1 and 10. A ten score was given to the species with most abundant individually in the month, while the tenth ranked most abundant species was scored as 1. This used a shared ranks system, meaning it was possible more than 2 species share similar score. Results for these scorings are presented in Table 6.5. The results from this table, together with the data of seagrass biology and chemistry, environment parameters of the site, as well as similarity and MDS analyses, are used to discuss the trends of macrozoobenthos similarity in the dense site.

With 50 % similarity level, Cluster I was the biggest group of samples because it contained 17 out of 21 samples at the dense site. The importance of 14 common species to the faunal abundance was responsible for the dissimilarity of this cluster with the others at the dense site. The following species were recorded with high abundance in either all or most of group of samples: Nematoda, *A. minuta, C. capitata, E. lumbricoides, E. hebes, M. fuliginosus, P. elegans, S. armiger, T. prolifera, C. arenarium, E. punctatus, U. poseidonis, L. savignyii* and *H. ulvae.* In the cluster, the highest similarity, 69 %, was found from the remaining three seasonal samples in 1999. Among these three samples, May and October 1999 samples had 73 % similarity, the highest overall at the dense site. July 1999 samples contained *Euclymene robusta, Sphaerosyllis bulbosa* and *Cerastoderma edule,* whereas *Gammarus zaddachi, Macoma balthica* and *Retusa obstusa* were not recorded in this month but were in May and October 1999 samples.

Table 6.4. Scoring of macrozoobenthos based on species abundance at the dense site. (See the text for the meaning of the numbers).

Species	**Cluster**																				
	I																**II**		**III**		**IV**
	No-98	De-98	Ja-99	Fe-99	Jl-98	Au-98	Se-98	Oc-98	Oc-97	Ap-98	Ma-98	Jn-98	No-97	Ma-99	Oc-99	Jl-99	Mr-98	De-97	Ja-98	Fe-98	Se-97
Nematoda	4		6	2		2	4	6	2	1	5	5		4	8	2	3	3	4	2	6
Amphitrite edwardsi									1												
Arenicola marina											1	4		1	3			2			4
Aricidea minuta	3	7	7	7	4	6	8	8			1	6	8	4	1	2		8	4	6	
Capitella capitata	8	9	9	9	9	10	7	9	9	9	2	8	5	8	8	7	9	7	7	10	10
Chaetozone setosa																				6	
Cirratulus filliformis				1											1						
Clymenura clypeata										1		1									
Eteone foliosa																					3
Euclymene lumbricoides	6						4	2		1			1	1	1	2			2		6
E. oerstedii								1	1	2	1	1			1			2		2	
E. robusta						1															
Exogene hebes	9	8	8	8		5	8	7		10	7	1	6	7		1	6	3	8	9	
E. verugera			3								4	2		1			4				
Heteromastus filiformis										1		8									
Malacoceros fuliginosus					6		1	2	2	3	1	1		1	2	4					
Notomastus latericeus																	1			5	
Phyllodoce mucosa	1					1	2	1	1	1			1		1		3	1	1		
Polydora ciliata															1						
P. giardi							9	4													
Pygospio elegans	7	7	6	6	10	8			7	7	2	2	4	9	10	10	5	4	3	4	6
Scolelepis foliosa								1													
S. squamata							4	1							1						
Scoloplos armiger		5		3	8	7			6	5	6	7	3	5	7	7	4	4		3	9
Sphaerosyllis bulbosa							1														
Spio filicornis	1									1					2		7				

Table 6.4. Continued.

Species	Cluster I																Cluster II		Cluster III			Cluster IV
	No-98	De-98	Ja-99	Fe-99	Jl-98	Au-98	Se-98	Oc-98	Oc-97	Ap-98	Ma-98	Jn-98	No-97	Ma-99	Oc-99	Jl-99	Mr-98	De-97	Ja-98	Fe-98	Se-97
Syllis gracilis									8					1	1				2		
Typosyllis prolifera	1						7		10		1		1	2	6	3		1			
Tubifex benedii	4								2	1	1										5
Ampithoe gammaroides											1	1	1								
A. rubricata									1		6	9	9					9	10	3	
Atylus swammerdami							1				1	4									
Cheirocratus intermedius																					1
Corophium arenarium	5					3	3	3	5				2	2	4	6		5			7
C. volutator									4				2								6
Ericthonius difformis											2	6	1		1	1		10	9	8	
E. fasciatus	2			3										1	1			6	6	1	
E. punctatus	10	10	10	10		2	10	10	1	4	10	10	10	10	9	9	10	3	5		
Gammarus finmarchinus											8	1					8				
G. zaddachi											9	1	2								
Jassa falcata											3	3				2					
Lillebjorgia pallida											2				1						
Melita palmata											1		1								
Urothoe brevicornis								5								1				8	
U. marina	1				2				2					1	1	4					5
U. poseidonis					7	9	6		1	8			1	1	2						8
Caprella erithizon																			1		
Cumopsis longipes															1						
Carcinus maenas											1	3									
Parathalestris harpacticoides								1	1	6	1										
Idotea granulosa											1					1			3		

Table 6.4. Continued.

Species	Cluster I																II	III			IV
	No-98	De-98	Ja-99	Fe-99	Jl-98	Au-98	Se-98	Oc-98	Oc-97	Ap-98	Ma-98	Jn-98	No-97	Ma-99	Oc-99	Jl-99	Mr-98	De-97	Ja-98	Fe-98	Se-97
Tanais dulongi										1											
Leptochelia savignyi			5	5	5	4	1	3		1				3	1	6	1				
Cerastoderma edule													1					1	1		
Hydrobia ulvae	1	2	2		5	7	5	3	4		1	1	7	6	3	8					10
Littorina saxatillis		2																			
Retusa obstusa					3																

The samples of Cluster II (March 1998) were less similar to the rest of the data because many common species, i.e. *A. minuta, M. fuliginosus, T. prolifera, C. arenarium, U. marina* and *U. poseidonis* were absent. There were two species, *Venerupis saxatilis* and *Glycera tridactyla,* recorded only in March 1998. Additionally, *Chaetozone setosa,* a species that rarely occurred during the study (only recorded in February 1998) was found in this month. In this month an outburst of *Enteromorpha* occurred particularly at the dense site (Chapter II). This ecological phenomenon might influence the faunal figures.

Cluster III, December 1997 – February 1998 samples, were similar at 55 % level. This group is distinguished from the others because of the absence or low abundance of 3 common species, i.e. *M. fuliginosus, P. harpacticoides* and *H. ulvae*, and the occurrence of *Caprella erithizon* and *Crepidula fornicata.* January 1998 samples were less similar to the other two because they were the only ones containing *Amphitritides edwardsi, A. gracilis, Euclymene robusta, Scolelepis squamata, Euphrosyne foliosa, C. erithizon* and *C. fornicata,* meanwhile *Eumida sanguinea, Spiophanes bombyx* and *H. ulvae* were identified in December 1997 and February 1998 but not in January 1998. Perhaps strong waves and currents that influenced the dynamics of seagrass population (Chapter IV) as well as sediment pigment production (Chapter V) have also affected the faunal structure in this cluster.

The high dissimilarity of Cluster IV (September 1997) with the rest of the data is because of the occurrences of *Eteona foliosa, Perinereis cultrifera* and *Cheirocratus intermedius*, and the absences of most commonly found species such as *E. hebes, T. prolifera, E. punctatus, G. finmarchinus* and *L. savignyii.* Although *H. ulvae* was a common component at the dense site, it was only in September 1997 this species ranked first in term of species abundance. The overgrowth of the epiphytes and filamentous algae on *Z. noltii* leaf surfaces and on the sediment could be an important environmental factor causes the difference in faunal structure in this month.

As for the sparse site, dendrogram of macrozoobenthos species similarity and MDS obtained from PRIMER analyses are presented in Figures 6.12 and 6.13 respectively. Similar to that of the dense site, each number in the MDS graph also resembles each field visit in the same month. All monthly samples were similar at 32 % or greater. The maximum similarity between pairs of samples, 77 %, was also shown between October 1999 and May 1999. The clustering was also observed among the species, although they were not well defined. At the 48 % similarity level, six clusters were apparent. Cluster I consisted of all second year winter samples (December 1998 – February 1999) and the last three seasonal samples (May 1999, July 1999 and October 1999). Cluster II, the largest, was composed of the samples of January – April 1998, November – December 1997, June 1998 and September – November 1998. May 1998 and October 1997 samples were separated as Cluster III and IV respectively. Cluster V consisted of July – August 1998 samples, and Cluster VI was formed by the September 1997 samples.

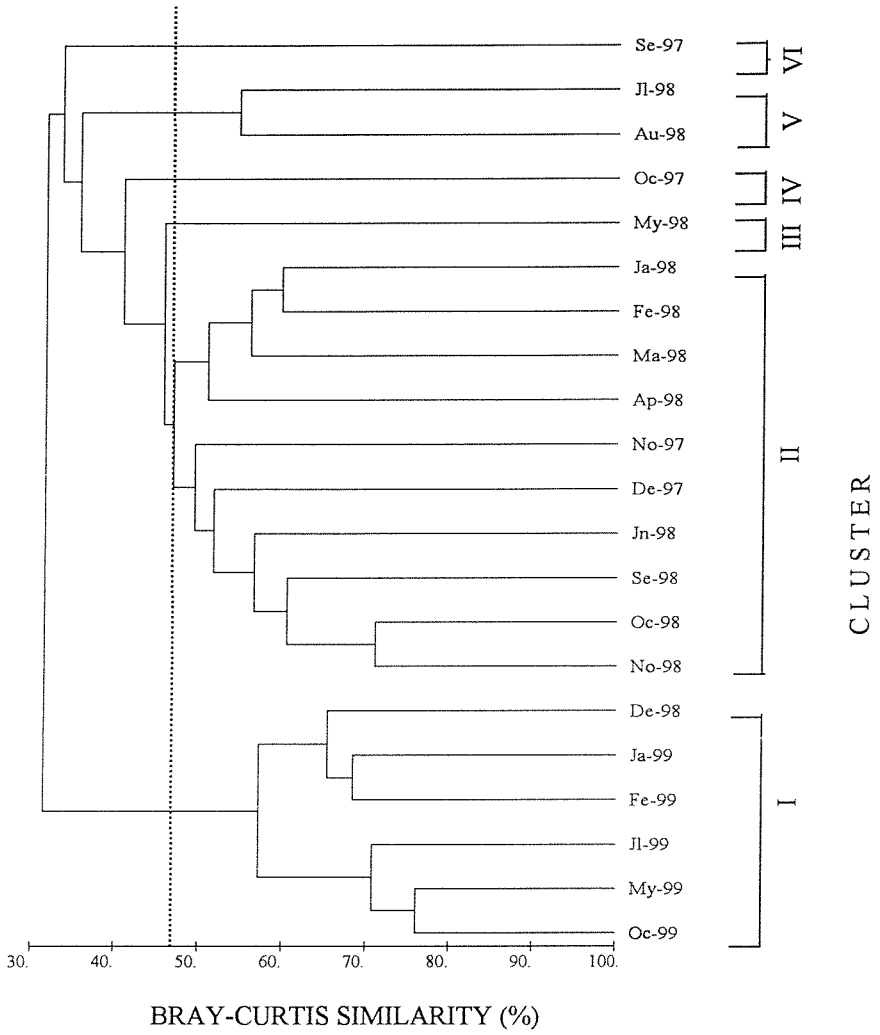

Fig. 6.12. Dendrogram of percentage fauna similarity among the macrozoobenthos samples at the sparse site.

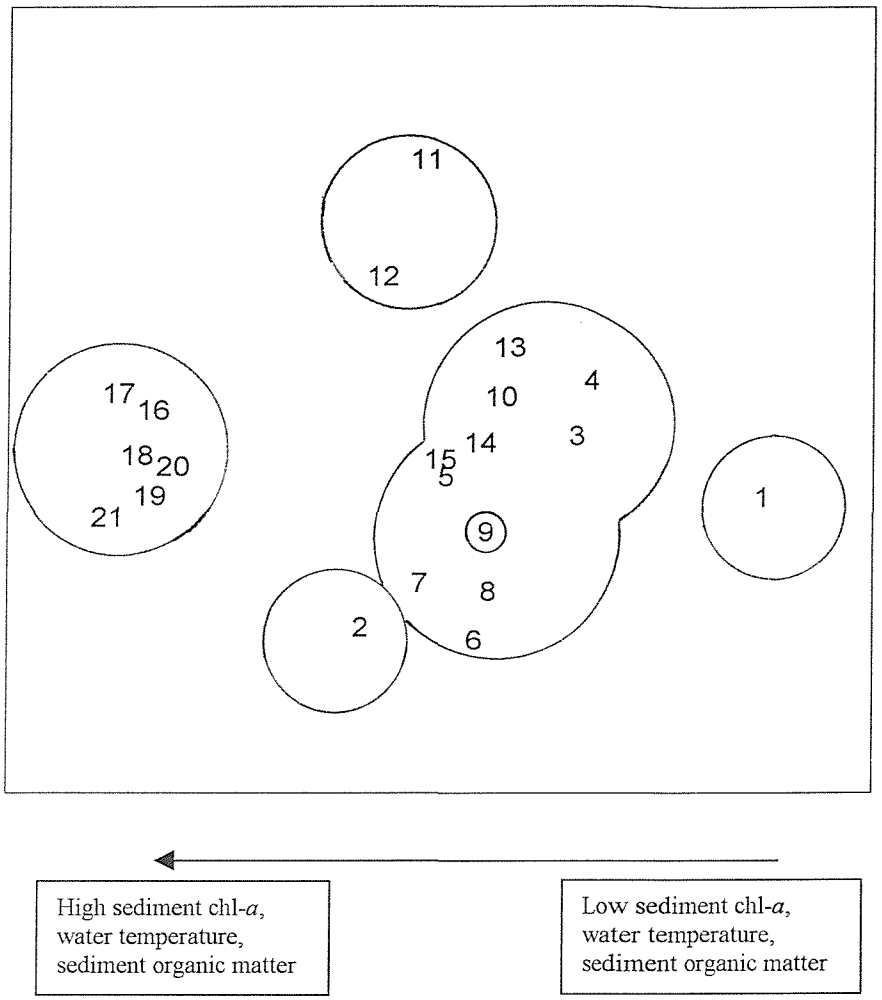

Fig. 6.13. MDS ordination plot (stress = 0.17) of macrozoobenthos species taken from the sparse site (stress = 0.17; 1 = September 1997, 2 = October 1997, 3 = November 1997, 4 = December 1997, 5 = January 1998, 6 = February 1998, 7 = March 1998, 8 = April 1998, 9 = May 1998, 10 = June 1998, 11 = July 1998, 12 = August 1998, 13 = September 1998, 14 = October 1998, 15 = November 1998, 16 = December 1998, 17 = January 1999, 18 = February 1999, 19 = May 1999, 20 = July 1999, 21 = October 1999).

In general, the samples had also higher species similarities with the others collected within the same season, though these trends were not as obvious as the ones seen at the dense site. As has been applied for the dense site, scaling based on the species abundance was also carried out to follow which species caused the similarity and dissimilarity at the sparse site. The results for these scaling are presented in Table 6.6. Combined with similarity and MDS analyses results as well as environmental parameters and variables measured, they were also used to explain the trends of macrozoobenthos similarity at the sparse site.

Cluster I samples were similar at the 58 % level. The similarity was caused by the high abundance of *P. elegans*, *S. bombyx*, *E. fasciatus*, *T. lilljeborgi*, *P. harpacticoides* and *Cylichnya cylindracea* and the absence or low abundance of common species as *S. armiger*, *T. prolifera*, *G. finmarchicus*, *U. poseidonis*, *L. savignyii* and *H. ulvae*. In detail, 2 subgroups of samples were shown in this cluster. The first consisted of December 1998 - February 1999 samples with 66 % of similarity. The absence of common species, i.e. *S. armiger*, *C. arenarium*, *U. poseidonis* and *H. ulvae*, caused these winter samples of the second year to differ from the others. The second was developed from the remaining three seasonal samples in 1999. As has been observed at the dense site, among these three also had the highest similarity, 71 %, compared to the others in the Cluster I as well as to the rest of the data. The occurrence of *C. clypeata*, *Pseudocuma* spp. and *Apseudes talpa*, that were not recorded or found only once in any other months, strongly linked these three samples.

Table 6.5. Scoring of macrozoobenthos based on species abundance at the sparse site.

Species	**Cluster**																							
	I										**II**										**III**	**IV**	**V**		**VI**
	De-98	Ja-99	Fe-99	My-99	Oc-99	Jl-99		Ja-98	Fe-98	Ma-98	Ap-98	Oc-98	No-98	Se-98	Jn-98	No-97	De-97		My-98	Oc-97	Jl-98	Au-98	Se-97
Nematoda		8	4							7					2				8	5			
Arenicola marina																4			5		5		5
Aricidea minuta	5	9	6	5								9	3	9	3	9	9		7		10	9	
Capitella capitata	9	9	8	8				10	9	7	10	8	8	8	6	8	5		2	10		10	9
Clymenura clypeata						5																	
Euclymene lumbricoides				1	1	6							3	4			4						8
E. oerstedii									3	7	4					3			4	3	3		
E. robusta																				3			
Exogene hebes	8		5	3		4		7	4	10	6	10	10	10	4	2	8		7			9	
E. verugera		7		1						7									9				
Heteromastus filiformis											8												
Malacoceros fuliginosus				1	1	6			5	8	9	5							2	2			5
Nicolea zostericola																					3		
Notomastus latericeus										7													
Orbinia sertulata																							3
Phyllodoce mucosa												5											
Polydora ciliata																					8	8	
Pygospio elegans	4	10	9	10	10	10		3	5	7	3	4	5	8	4	4	8		10				6
Scolelepis foliosa																							6
S. squamata		9	5			8															7	10	
Scoloplos armiger				6	9			9	10	8	9	7	4	5	7	5	3		6	2			10
Sphaerosyllis bulbosa																	6						
Spio filicornis											8	5											
Spiophanes bombyx				1	1	6																	
Syllis gracilis		9		2	4	4			10		2									5			
Typosyllis prolifera								8	3			6	6	6						7	8		
Tubifex benedii																							6
Ampithoe rubricata		7						2	5	7						7			8	4			
Atylus swammerdami				3															9				
Bathyporeia guilliamsoniana									3														

Table 6.5. Continued.

Species	Cluster I						Cluster II										Cluster III	Cluster IV	Cluster V		Cluster VI
	De-98	Ja-99	Fe-99	My-99	Oc-99	Jl-99	Ja-98	Fe-98	Ma-98	Ap-98	Oc-98	No-98	Se-98	Jn-98	No-97	De-97	My-98	Oc-97	Jl-98	Au-98	Se-97
Corophium arenarium															3	3					5
C. volutator															3	3					
Ericthonius fasciatus	10	9	10	9													2				
E. punctatus							5		10		9	9		9	10	10	1	8		7	
Gammarus finmarchicus								8			1	2				3	10				
G. zaddachi									6					6	3		4				
Jassa falcata																	5				
Melita palmata															3		1				
Pinnotheres pisum			5	3		7															
Urothoe brevicornis		7				4					7	2									
U. marina							7					3				3					
U. poseidonis										2			7	5		5			9	8	
Caprella linearis				1	2																
Cumopsis longipes								6													
Iphinoe serrata				2	2																
I. trispinosa				4	9		6						5								
Pseudocuma longicornis				3	6																
Carcinus maenas													5	4	3						
Pagurus benhardus																7					
Palaemon adspersus										4	4						3				
Parathalestris harpacticoides																		2			
Idotea granulosa																					3
Apseudes latreilli				1	3																
Tanaissus lilljeborgi	7	8	8	8	7	5															
Leptochelia savignyii							4	7	9	7	8	3	6				2		5	8	
Cylichnya cylindracea	6	7	7	6	8	9															
Hydrobia ulvae					5					5	5	3	5	1	5			9			9

All samples in Cluster II were similar at the 48 % level. The occurrences of *C. capitata, E. hebes* and *S. armiger* in every month together with the high contribution of *E. punctatus, L. savignyii* and *H. ulvae* being responsible for this similarity. *C. maenas* was found only contributed highly to the macrozoobenthos abundance in this cluster. Additionally, *E. fasciatus* and *T. lilljeborgi* were not recorded as important components. There were two groups of samples found in Cluster II. The first consisted of January – April 1998 samples and was similar at 52 % level. In this group, *C. capitata, E. hebes, S. armiger* and *L. savignyii* all included as the most important components to species abundance. The second group was created from 6 sampling months, i.e. November and December 1997, June 1998 and September – November. The samples were similar at the 51 % level with high abundance of *A. minuta, C. capitata, E. hebes, P. elegans, S. armiger, T. prolifera, E. punctatus* and *H. ulvae* accounting for the similarity in the group.

Cluster III (May 1998) samples were similar at the 47 % species similarity level or greater. The species that most influence the difference in this month were *G. finmarchinus, Atylus swammerdami, Ampithoe rubricata, Exogene verugera* and *Jassa falcata* which were included in the top ten of most abundant species. In general, this cluster had the greatest number of species of high abundance. The high level of sediment chl-*a* in this month (Chapter V and Statistical Analyses in this chapter) might support a greater diversity of macrozoobenthos.

The October 1997 (Cluster IV) samples were 41 % similar to Cluster I, II and III samples. Six common species, i.e. *A. minuta, E. lumbricoides, P. elegans, C. arenarium, U. brevicornis and L. savignyii,* were not identified in this month. In addition, *Siriella jaltensis* was only sampled in October 1997. The epiphytes and filamentous algae were still growing rapidly in this month, and this may have contributed to the faunal structure in the cluster.

Cluster V, July – August 1998 samples, were similar at the 57 % level. An absence of *M. fuliginosus, S. gracillis* and *A. rubricata,* together with reduction in abundance of *H. ulvae* to the total abundance cause the separation of this cluster from the rest of samples. Water temperatures reached the warmest level in these

months (Chapter III) and indeed it had an influence on the faunal abundance (Statistical Analyses, this chapter).

It was found that Cluster VI (September 1997) samples were 34 % similar to the rest of macrozoobenthic samples at the sparse site. The organisms that most influence this being among the twenty most common species found, in which eight of them, i.e. Nematoda, *A. minuta, E. hebes, S. gracillis, A. rubricata, E. punctatus, U. brevicornis* and *L. savignyii* were not recorded in September 1997. One species, *Orbinia sertulata*, was found only in this month. As has been observed at the dense site, the robust occurrence of the epiphytes and filamentous algae can be an important environmental factor causes the difference in faunal structure in this cluster.

6.2.7. Statistical Analysis

The overall multiple linear regression of the dense site showed that macrozoobenthos abundance over time did not correlate with the sediment and environmental variables (chl-*a*, phaeopigment, organic matter, water temperature) and other macrozoobenthos variables (species number, biomass) ($F_{15,5} = 4.79$; $P = 0.0465$; Table 6.6.), species number ($F_{15,5} = 4.54$; $P = 0.0517$; Table 6.7.) and biomass ($F_{15,5} = 8.66$; $P = 0.0130$; Table 6.8.). However the stepwise regression showed there were five variables, i.e. macrozoobenthos biomass, sediment chl-*a*, sediment organic matter, macrozoobenthos species number and sediment phaeopigment, that correlated with the macrozoobenthos abundance ($F_{1,19} = 55.7$; $P < 0.0001$; Table 6.9.).

Table 6.6. ANOVA of multiple linear regression between macrozoobenthos abundance and other variables measured in the dense seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	15	15485.3	1032.4	4.79	0.0465
Residual	5	1078.6	215.7		
Total	20	16563.9	828.2		

Table 6.7. ANOVA of multiple linear regression between macrozoobenthos species number and other variables measured in the dense seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	15	375.0	25	4.54	0.0517
Residual	5	27.5	5.50		
Total	20	402.5	20.12		

Table 6.8. ANOVA of multiple linear regression between macrozoobenthos biomass and other variables measured in the dense seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	15	10.361	0.6907	8.66	0.0130
Residual	5	0.399	0.0798		
Total	20	10.760	0.5380		

Table 6.9. ANOVA of forward stepwise regression between macrozoobenthos abundance and other variables measured in the dense seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	12350.4	12350.4	55.7	< 0.0001
Residual	19	4213.5	221.8		

The next stepwise regression test gave the results that besides correlating with macrozoobenthos abundance, macrozoobenthos species number also correlated with five other variables, i.e. total sediment chl-*a*, faunal biomass, sediment organic matter, sediment phaeopigment and water temperature ($F_{1,19}$ = 47.2; $P < 0.0001$; Table 6.10.). The macrozoobenthos biomass showed correlation with faunal abundance and species number, as well as with four other variables, i.e. sediment chl-*a*, sediment phaeopigment, sediment organic matter and water temperature, correlated with species number ($F_{1,19} = 65.5$; $P < 0.0001$; Table 6.11.).

Table 6.10. ANOVA of forward stepwise regression between macrozoobenthos species number and other variables measured in the dense seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	287.0	287.03	47.2	< 0.0001
Residual	19	115.4	6.08		

Table 6.11. ANOVA of forward stepwise regression between macrozoobenthos biomass and other variables measured in the dense seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	8.340	8.3403	65.5	< 0.0001
Residual	19	2.420	0.1274		

Amongst the variables correlated with macrozoobenthos abundance, the strongest correlation were shown with animal biomass ($P < 0.0001$; F-value = 55.69), sediment chl-*a* ($P < 0.0001$; F-value = 42.15) and sediment phaeopigment ($P < 0.0001$; F-value = 26.32). These were then followed by correlation with fauna species number ($P < 0.0001$; F-value = 25.89) and sediment organic matter ($P = 0.0024$; F-value = 12.30). The strongest correlation with species number was sediment chl-*a* ($P < 0.0001$; F-value = 47.24), and then followed by with faunal biomass ($P < 0.0001$; F-value = 43.71), faunal abundance, sediment organic matter ($P < 0.0001$; F-value = 16.00), sediment phaeopigment ($P = 0.0057$; F-value = 10.62); and water temperature ($P = 0.010$; F-value = 8.98). Faunal biomass had the strongest correlation with sediment chl-*a*, ($P < 0.0001$; F-value = 65.49), followed by with faunal abundance, faunal species number, sediment organic matter ($P <$

0.0001; F-value = 19.91), sediment phaeopigment ($P = 0.001$; F-value = 14.55), and water temperature ($P = 0.011$; F-value = 8.40). The results of correlation tests amongst the variables in the dense site are summarized in Table 6.12.

Table 6.12. Summary of Pearson product moment correlation tests of the macrozoobenthos in the dense site.

Group of Test	*P*-Value	Correlation Coefficient
Zoob. Abundance v Zoob. Species Number	< 0.001	0.759
Zoob. Abundance v Zoob. Biomass	< 0.001	0.864
Zoob. Abundance v Total Sediment Chl-*a*	< 0.001	0.831
Zoob. Abundance v Sediment Organic Matter	< 0.001	0.762
Zoob. Abundance v Sediment Phaeopigment	0.024	0.627
Zoob. Species Number v Zoob. Biomass	< 0.001	0.835
Zoob. Species Number v Total Sediment Chl-*a*	< 0.001	0.844
Zoob. Species Number v Sediment Org. Matter	< 0.001	0.676
Zoob. Species Number v Sediment Phaeopigment	0.005	0.600
Zoob. Species Number v Water Temperature	0.010	0.567
Zoob. Biomass v Total Sediment Chl-*a*	< 0.001	0.88
Zoob. Biomass v Sediment Organic Matter	< 0.001	0.715
Zoob. Biomass v Sediment Phaeopigment	0.001	0.659
Zoob. Biomass v Water Temperature	0.011	0.554

At the sparse site, the overall multiple linear regression tests also showed that variables were not significantly correlated with faunal abundance ($F_{15,5} = 7.15$; $P = 0.0198$; Table 6.13.), species number ($F_{15,5} = 9.29$; $P = 0.0111$; Table 6.14.) and biomass ($F_{15,5} = 29.0$; $P = 0.0008$; Table 6.15.). However, similar results for those of the dense site were shown when stepwise regression was applied for observing the correlation between faunal abundance and the other variables. There were five variables, i.e. faunal species number, faunal biomass, sediment chl-*a*, sediment phaeopigment and sediment organic matter, that significantly correlated with the faunal abundance ($F_{1,19} = 95.0$; $P < 0.0001$; Table 6.16.).

All six variables which correlated with faunal species number in the dense site, i.e. faunal abundance, faunal biomass, total sediment chl-*a*, sediment organic matter, sediment phaeopigment and water temperature, also correlated with faunal species number of the sparse site ($F_{1,19} = 95.0$; $P < 0.0001$; Table 6.17.). For the faunal biomass, the same variables correlated at both the dense and at sparse sites ($F_{1,19} = 59.6$; $P < 0.0001$; Table 6.18.).

Table 6.13. ANOVA of multiple linear regression between macrozoobenthos abundance and other variables measured in the sparse seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	15	5504.2	366.9	7.15	0.0198
Residual	5	256.5	51.3		
Total	20	5760.0	288.0		

Table 6.14. ANOVA of multiple linear regression between macrozoobenthos species number and other variables measured in the sparse seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	15	260.61	17.37	9.29	0.0111
Residual	5	9.35	1.87		
Total	20	269.69	13.50		

Table 6.15. ANOVA of multiple linear regression between macrozoobenthos biomass and other variables measured in the sparse seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	15	4.7393	0.3160	29.0	0.0008
Residual	5	0.0545	0.0109		
Total	20	4.7938	0.2397		

Table 6.16. ANOVA of forward stepwise regression between macrozoobenthos abundance and other variables measured in the sparse seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	4800.1	4800.1	95.0	< 0.0001
Residual	19	960.5	50.6		

Table 6.17. ANOVA of forward stepwise regression between macrozoobenthos species number and other variables measured in the sparse seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	224.9	224.95	95.0	< 0.0001
Residual	19	45.0	2.37		

Table 6.18. ANOVA of forward stepwise regression between macrozoobenthos biomass and other variables measured in the sparse seagrass bed.

Source of Variance	DF	SS	MS	F	*P*
Regression	1	3.636	3.6355	59.6	< 0.0001
Residual	19	1.158	0.0610		

Of the variables correlated with macrozoobenthos abundance at the sparse site, the first three strongest correlations were shown with faunal biomass ($P < 0.0001$; F-value = 55.69), sediment chl-*a* ($P < 0.0001$; F-value = 42.15) and sediment phaeopigment ($P < 0.0001$; F-value = 26.32), followed by correlation with faunal species number ($P < 0.0001$; F-value = 25.89) and sediment organic matter ($P = 0.0024$; F-value = 12.30). The strongest influence for the species number was related to sediment chl-*a* ($P < 0.0001$; F-value = 47.24), followed by faunal biomass ($P < 0.0001$; F-value = 43.71), faunal abundance, sediment organic matter ($P < 0.0001$; F-value = 16.00), sediment phaeopigment ($P = 0.0057$; F-value = 10.62); and water temperature ($P = 0.010$; F-value = 8.98). Faunal biomass had the strongest correlation with sediment chl-*a*, ($P < 0.0001$; F-value = 65.49), followed by faunal abundance, faunal species number, sediment organic matter ($P < 0.0001$; F-value = 19.91), sediment phaeopigment ($P = 0.001$; F-value = 14.55),

and water temperature ($P = 0.011$; F-value = 8.40). Table 6.19. summarizes results of correlation tests amongst the variables in the sparse site.

Table 6.19. Summary of Pearson product moment correlation tests of macrozoobenthos in the sparse site.

Group of Test	*P*-Value	Correlation Coefficient
Zoob. Abundance v Zoob. Species Number	< 0.001	0.913
Zoob. Abundance v Zoob. Biomass	< 0.001	0.834
Zoob. Abundance v Total Sediment Chl-*a*	< 0.001	0.769
Zoob. Abundance v Sediment Organic Matter	0.002	0.62
Zoob. Abundance v Sediment Phaeopigment	0.009	0.556
Zoob. Species Number v Zoob. Biomass	< 0.001	0.85
Zoob. Species Number v Total Sediment Chl-*a*	< 0.001	0.693
Zoob. Species Number v Sediment Org. Matter	0.0483	0.436
Zoob. Species Number v Sediment Phaeopigment	0.0211	0.501
Zoob. Species Number v Water Temperature	0.0238	0.491
Zoob. Biomass v Total Sediment Chl-*a*	< 0.001	0.871
Zoob. Biomass v Sediment Organic Matter	0.0015	0.649
Zoob. Biomass v Sediment Phaeopigment	0.0018	0.638
Zoob. Biomass v Water Temperature	0.0032	0.613

Following tests were applied to analyse the environmental factors cause the dynamics of macrozoobenthos abundance. The tests resulted that fauna abundance at both sites had a positive correlation with the sediment organic matter (Figure 6.14.) and water temperature (Figure 6.15.). These results confirmed former statistical analyses as presented in the Tables 6.6. – 6.19.

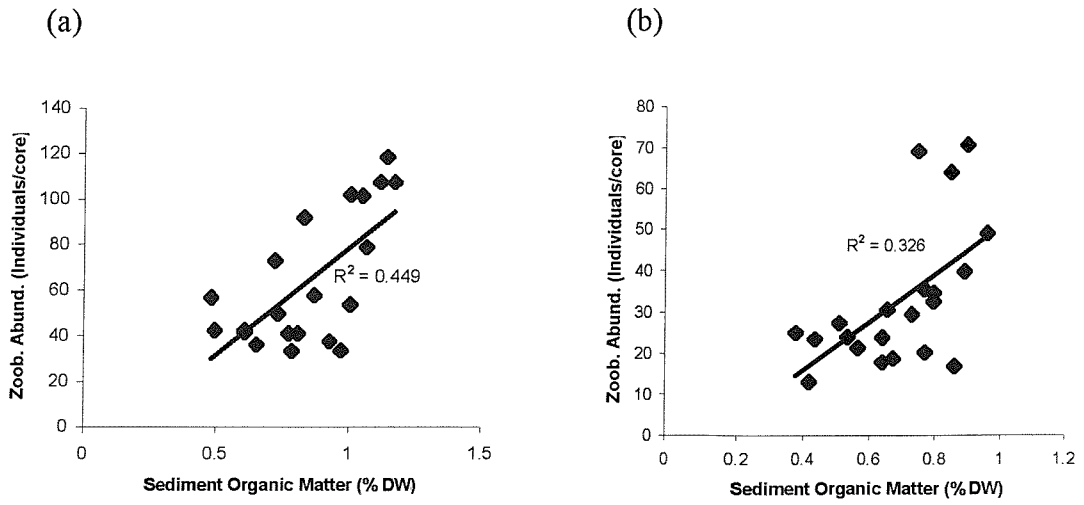

Figure 6.14. Correlation tests between macrozoobenthos abundance and sediment organic matter. (a = dense site, b = sparse site).

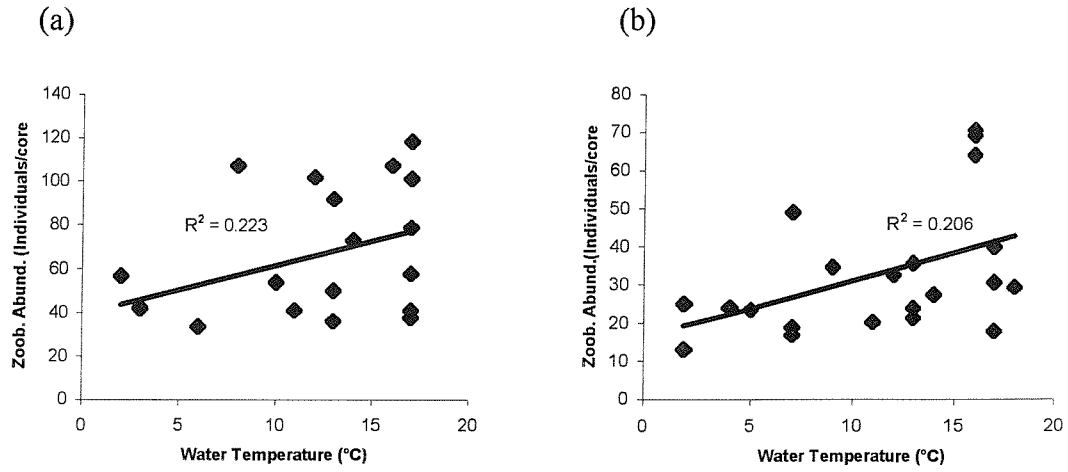

Figure 6.15. Correlation tests between macrozoobenthos abundance and water temperature. (a = dense site, b = sparse site).

Because the sediment analyses concluded that *Z. noltii* detritus made an overall minor contribution to sediment pigment concentration (Chapter V), tests were carried out to determine the degree of correlation between macrozoobenthos abundance and sediment chl-*a* and seagrass-associated pigments (chl-*b* and lutein/zeaxanthin). The tests showed that at both sites faunal abundance strongly correlated with chl-*a* ($R^2 = 0.249$ at the dense site and $R^2 = 0.322$ at the sparse site, Figure 6.16.) but not with chl-*b* ($R^2 = 0.009$ at the dense site and $R^2 = 0.033$ at the sparse site, Figure 6.17.) and lutein/zeaxanthin ($R^2 = 0.0026$ at the dense site and $R^2 = 0.0004$ at the sparse site, Figure 6.18.).

Since the bed sediment samples contained phaeopigment (Chapter V) and phaeopigment has been known to be an important indicator of benthic fauna activities, this study also tested the correlation between macrozoobenthos abundance and sediment phaeopigment. The results showed that the total phaeopigment positively correlated with fauna abundance at both sites ($R^2 = 0.277$ at the dense site and $R^2 = 0.216$ at the sparse site, Figure 6.19.). These results were in correspondent with the tests presented in Tables 6.12. and 6.19.

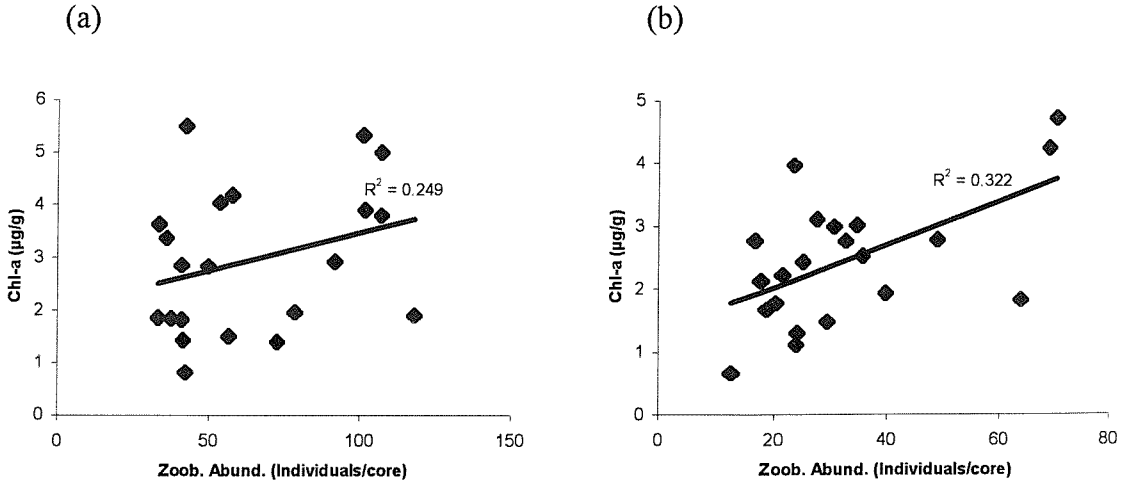

Figure 6.16. Correlation tests between macrozoobenthos abundance and sediment chl-*a*. (a = dense site, b = sparse site).

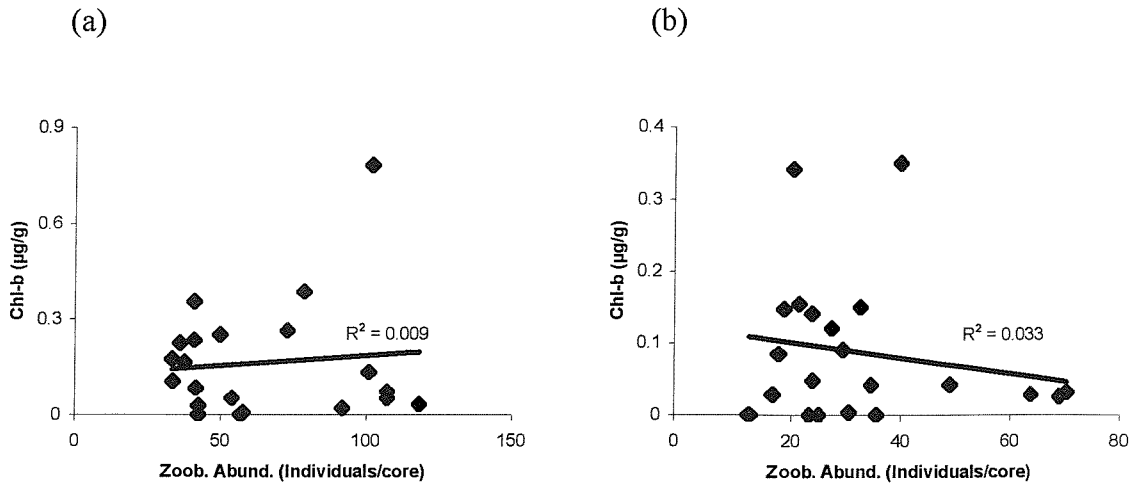

Figure 6.17. Correlation tests between macrozoobenthos abundance and sediment chl-*b*. (a = dense site, b = sparse site).

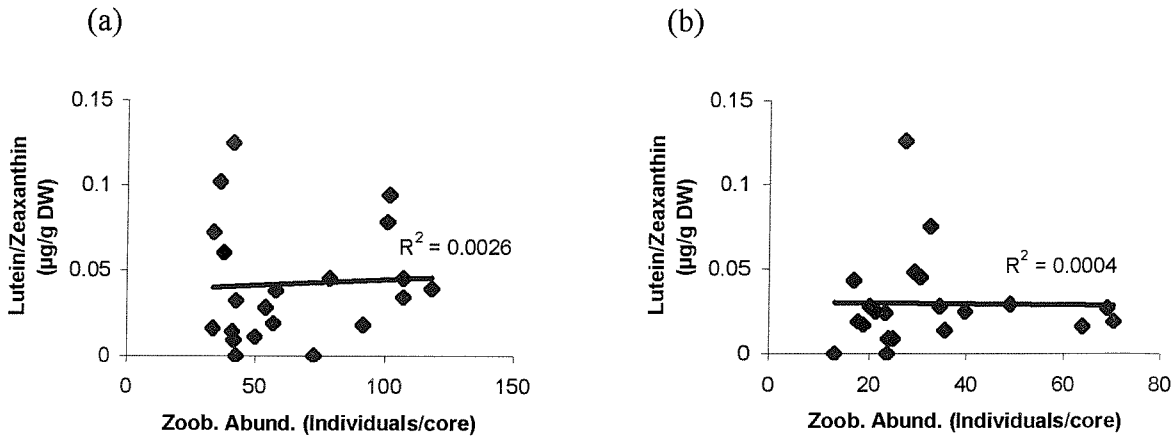

Figure 6.18. Correlation tests between macrozoobenthos abundance and sediment lutein/zeaxanthin. (a = dense site, b = sparse site).

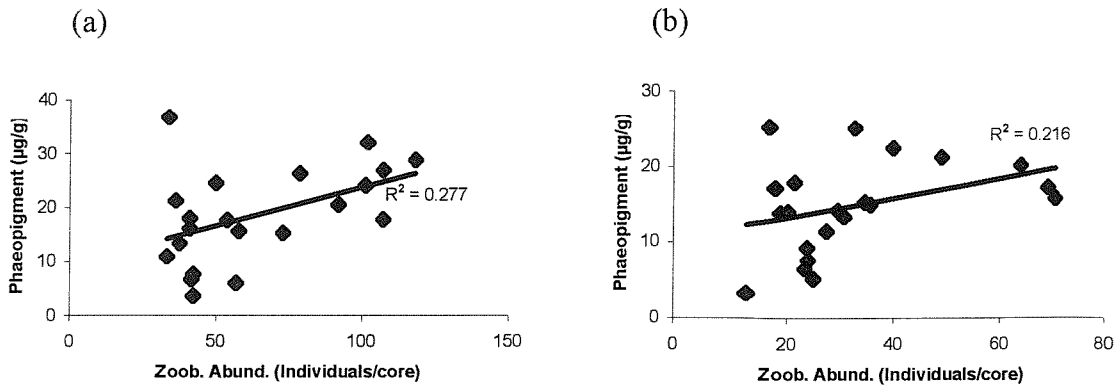

Figure 6.19. Correlation tests between macrozoobenthos abundance and sediment total phaeopigment. (a = dense site, b = sparse site).

Interestingly, the faunal abundance did not follow the patterns of seagrass density ($R^2 = 0.081$ at the dense site and $R^2 = 0.016$ at the sparse site, Figure 6.20.) and seagrass biomass ($R^2 = 0.018$ at the dense site and $R^2 = 0.033$ at the sparse site, Figure 6.21.). These results confirmed that seagrass detritus was not a major factor in supporting the dynamics of macrozoobenthos at the site. The influence of seagrass condition was also indicated by the results of the test between macrozoobenthos abundance and all chemical constituents. Phenolic ($R^2 = 0.024$ at the dense site and $R^2 = 0.010$ at the sparse site, Figure 6.22.), carbohydrate ($R^2 = 0.081$ at the dense site and $R^2 = 0.048$ at the sparse site, Figure 6.23.) and protein ($R^2 = 0.066$ at the dense site and $R^2 = 0.001$ at the sparse site, Figure 6.24.) did not correlate with the fauna abundance.

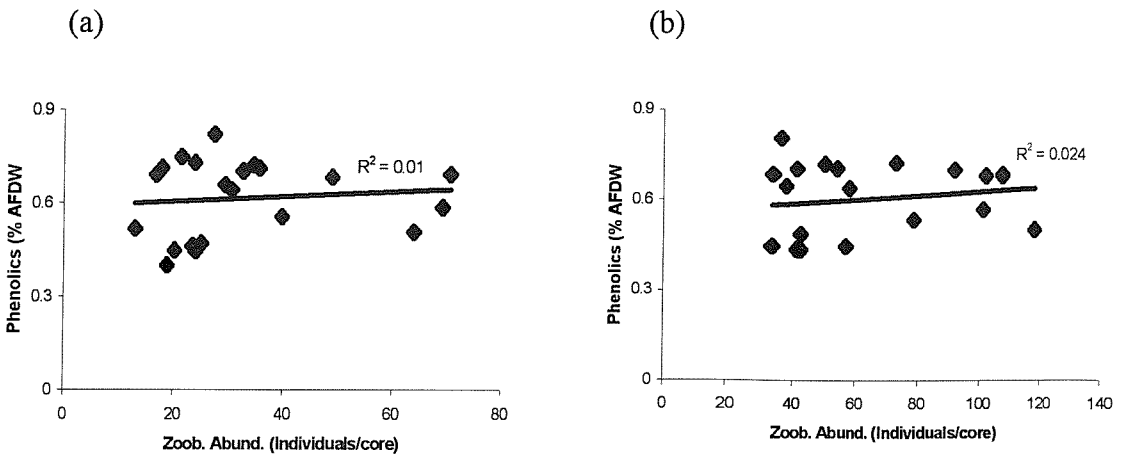

Figure 6.20. Correlation tests between macrozoobenthos abundance and seagrass shoot density. (a = dense site, b = sparse site).

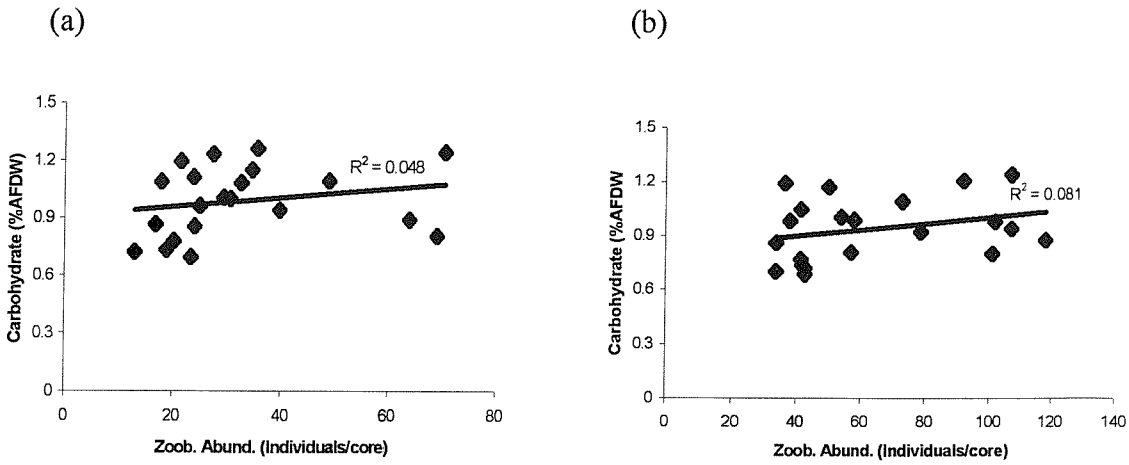

Figure 6.21. Correlation tests between macrozoobenthos abundance and seagrass shoot biomass. (a = dense site, b = sparse site).

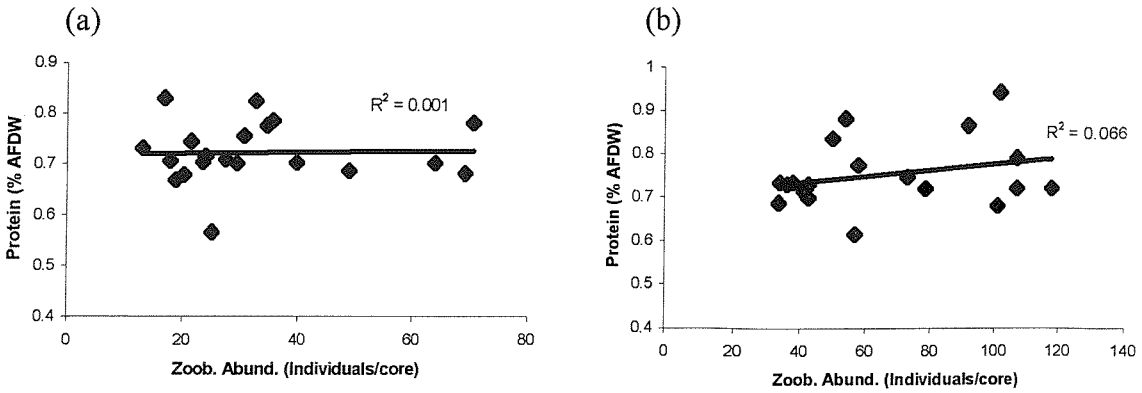

Figure 6.22. Correlation tests between macrozoobenthos abundance and seagrass total phenolics. (a = dense site, b = sparse site).

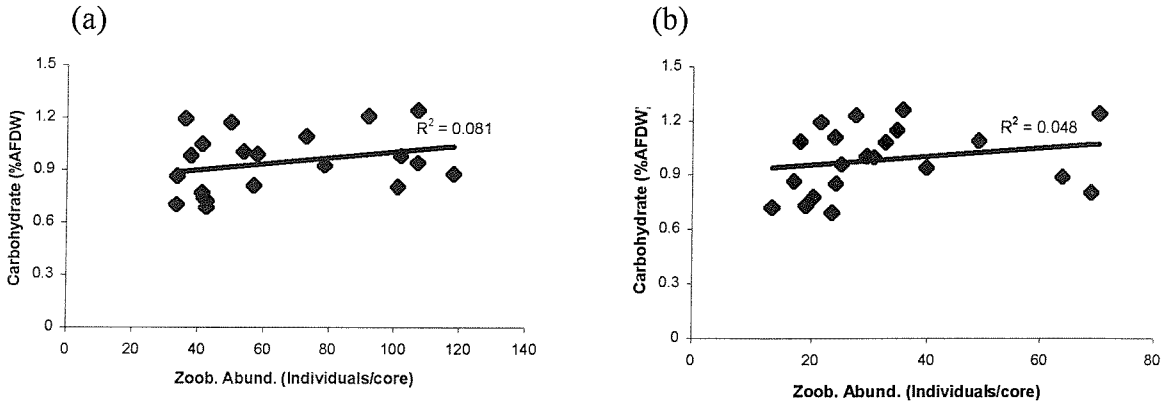

Figure 6.23. Correlation tests between macrozoobenthos abundance and seagrass total carbohydrate. (a = dense site, b = sparse site).

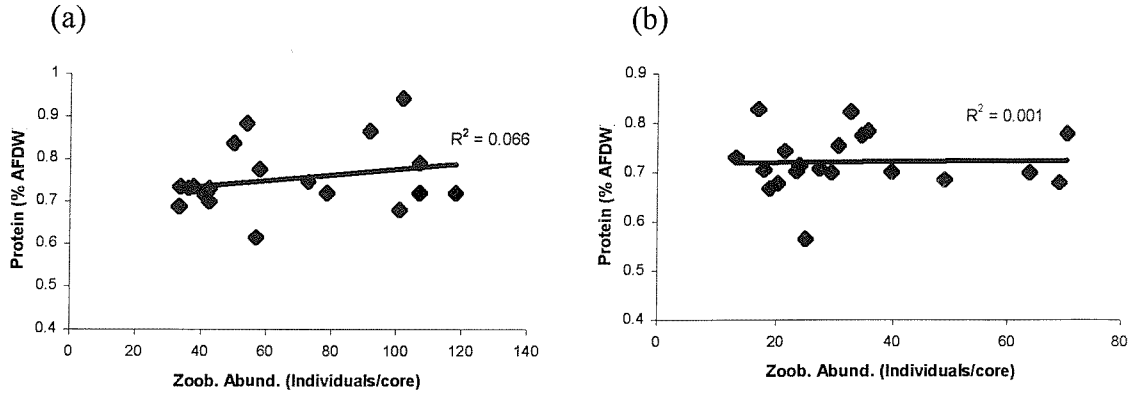

Figure 6.24. Correlation tests between macrozoobenthos abundance and seagrass total protein. (a = dense site, b = sparse site).

6.3. Discussion

In terms of species composition, the seagrass bed ecosystem of Ryde Beach was dominated by the polychaete worms which contributed 42.48 % and 40.43 % of the total number of species in the dense and sparse site respectively (Table 6.1.). Many studies on macrobenthic fauna associated with seagrass beds have reported similar patterns. From a former study conducted at the same site, it was reported that 46.6 % of the macrobenthic community was made up of polychaete species (Withers, 1979), whereas research from the western side of the English Channel recorded polychaetes contributed 43.2 % to the overall taxa (Webster *et al.*, 1998). Seagrass beds in eastern Mediterranean were found to contain 70.4 % of polychaetes (Çinar *et al.*, 1998). A study from Spanish water also confirmed the polychaetes as dominant intertidal macrozoobenthos figures seagrass meadows of *Z. noltii* (Junoy and Viéitez, 1992).

The next important group found from the present study were the amphipods that accounted for 29 species or 25.67 % and 19 species or 20.22 % at the dense and sparse site respectively. The occurrences of amphipods in relatively high numbers have been reported in other studies of Solent intertidal ecosystems (Withers, 1979; Bamber, 1993) as well as from other sites in Britain (13 species, Webster *et al.*, 1998).

Although the molluscs composed the third most dominant group, they only consisted of 19 species of which the gastropods contributed the highest percentage of the overall faunal taxa (10.62 % for the dense site and 12.77 % for the sparse site respectively). These findings were not surprising, since previous macrofaunal benthic studies in the Solent have given similar results. A study by Withers (1979) recorded only 4 species of the molluscs from the Ryde seagrass bed. The study conducted on patches of seagrass in Stanswood Bay, an adjacent area north-west of Ryde, also encountered 4 species of molluscs out of 54 macrofaunal species collected (Bamber, 1993). Amongst the collected molluscs, the present study identified the existence of 3 species from the genus of *Venerupis, i.e. V. aurea, V. pullastra* and *V. saxatilis*. Although these clams were not listed from the previous

study (Withers, 1979), the population of particular macrozoobenthic species are and have been variable in the long term. Indeed, a report on the macrozoobenthos study of the Solent recorded that two members of the genus of *Venerupis* reappeared in Langstone Harbour after being absent since 1962/1963 (Thorp, 1980).

Within the crustacea, the tanaids ranked second at the dense site and third at the sparse site. One study in the North American seagrass bed found significant numbers of tanaids from 3 species (Sheridan, 1997). Although the biological and ecological knowledge of this group is relatively poorly known (Lewis, 1998), they occur over a wide range of depths in the marine ecosystems and are usually benthic in habit (Holdich and Jones, 1983). Thus, it was not surprising that the *Z. noltii* beds of Ryde Beach supported this group of macrofauna. The most dominant tanaid was *L. savignyi*. This member of the Paratanaidae family was sampled in 14 and 16 field visits throughout the study at the dense and sparse site respectively. The species is cosmopolitan of the north Atlantic regions as well as in tropical seas (Holdich and Jones, 1983; Hayward and Ryland, 1990a), therefore its occurrences in the Solent coastal waters is to be expected. Holdich and Jones (1983) reported the species as occurring commonly in the shallow sublittoral, living intertidally in delicate self-structured tubes amongst roots and marine vegetation.

Isopods and cumaceans were also found frequently in the studied seagrass bed. Some species of these crustaceans are indeed typical of seagrass bed faunas. The isopods recorded from the present study mainly belonged to the Idoteid family. Species from the Idoteids are known to be common residents of macrophyte vegetation such as *Zostera* (Naylor, 1972; Hayward and Ryland, 1990a), because they are able to digest the fresh leaves as well as resulting detritus materials of the seagrass (Mazzella *et al.*, 1992). As for the cumaceans, they are known often to use the seagrass bed ecosystems for their spawning and as a nursery ground (Jones, 1976; Hayward and Ryland, 1990a). Furthermore, Alfonso *et al.* (1998) has observed the occurrences of cumaceans in the vegetated marine ecosystems of the Algeciras Bay, Strait of Gibraltar.

The current study identified only one species of echinoderm, i.e. *Amphipholis squamata*. The low diversity of molluscs and echinoderms is a common puzzling feature of not only the shores at Ryde Beach, but also of the other intertidal exposures alongside the Solent (Withers, 1979). The studies conducted by Oyenekan (1981) and Al-Suwailem (1991) for example, both also found evidence for very low species number for the echinoderms from Southampton Water and Gilkicker lagoon respectively. The report of a five-year monitoring programme of Southampton Water by Houston *et al.* (1983) recorded no echinoderms in the 104-macrozoobenthic taxa identified.

As perhaps expected, the dense seagrass bed at Ryde had higher values for species number of macrozoobenthos than the sparse bed. These findings also apply to a seagrass bed ecosystem in south-western England (Webster *et al.*, 1998) and for an eastern Australian bed (Edgar *et al.*, 1994). The first of these studies found averages of 17 species and 10 species in the high density and the low density *Z. marina* beds respectively. The second study reported 300 species and 265 species from the higher and lower seagrass densities respectively. The higher values in species number and total abundance of individuals observed in the present study are may be related to the differences in the chl-*a* concentrations in the sediment. Indeed, the statistical tests showed that there was a strong correlation between these two variables at both the dense site ($P < 0.0001$, correlation coefficient = 0.844, Table 6.12.; Figure 6.16.) and the sparse site ($P < 0.0001$, correlation coefficient = 0.693, Table 6.19.; Figure 6.16). Higher pigment concentration in the sediment is likely to promote higher productivity in the system, thus increasing the availability of food for the benthic fauna. As has been proposed before (Chapter V), the higher detrital pigment concentrations at the dense area are believed to be a result of the higher density of the *Z. noltii* shoots.

The other factor likely to influence the higher number of macrozoobenthic species at the dense site is the creation of additional habitats. More shoots in a defined area may create a wider area of niches, capable of supporting a larger number of species. At the dense site, protected living spaces for macrofauna are

created in the areas between leaves, around shoot bases and in or around the rhizome mats (Heck and Westone, 1977; Phillips and Meñez, 1998). Although the tests did not show correlation between macrozoobenthos species number and shoot density (Figure 6.20.) or shoot biomass (Figure 6.21.), however the significant difference in shoot number between the dense and sparse sites has supported the suggestion that the dense site has provided more niches.

This study found clear seasonal patterns in animal abundance as well as species number. Both of them declined drastically in the winter, followed by a rapid increase during the warmer months. It has been proposed that increasing temperature have supported blooms of microphytobenthos and facilitated the high sediment chl-*a* values (Chapter IV). Thus, the abundance of macrozoobenthos in the study site became more pronounced. Indeed, there is a strong correlation between the sediment chl-*a* concentrations and the animal abundance at the dense site ($P < 0.0001$, coefficient correlation = 0.831, Table 6.12.; Figure 6.16.) as well as at the sparse site ($P < 0.0001$, coefficient correlation = 0.769, Table 6.19.; Figure 6.16.). The relationships between sediment chl-*a* contents and the macrozoobenthos dynamics have been studied elsewhere. The results from the current study correspond with those from other areas in Europe, such as the Wadden Sea (see Beukema and Cadeé, 1997) and the north-western Mediterranean (see Gremare *et al.*, 1997). These authors concluded that the macrofaunal benthic population increased rapidly following chl-*a* blooms in the sediment.

Changes in the macrozoobenthos abundance at the study site have been observed to follow the peak of sediment pigment production, as indicated by sediment chl-*a* observed (Chapter V, also Figure 6.16. this Chapter). This is in accordance with findings from previous studies (Beukema and Cadeé, 1997; Gremare *et al.*, 1997). In general these studies postulated that enhanced levels of primary production and algae concentrations caused the increase in macrozoobenthos abundance and biomass. In this study, the macrozoobenthos

abundance, species number and biomass were clearly correlated with the fluctuation in the sediment chl-*a* contents (see Tables 6.12. and 6.19.).

The annual variations in animal abundance and species composition are common in the literature. These large changes may be ascribable to the normal periodicity in reproduction, recruitment and mortality (Kennish, 1996). Indeed, most of the animals in soft-bottom communities are small, cryptic, frequently with short life-cycles and high intra-annual density variations which drastically affects the potential for recolonization on a predictable seasonal basis (Hall *et al.*, 1992). Moreover, as for the seagrass bed community the changes of macrozoobenthic figures may also be attributable to the abiotic physical regimes of the ecosystem (Isakson and Pihl, 1992; de Jonge and de Jonge, 1992). Though there were no detailed observations conducted, both reproduction and recruitment seemed to occur predominantly in the spring and autumn months at this site. This was supported by the presence of juveniles and mature individuals during these periods.

The macrobenthic fauna at the two sites showed large variations in numerical densities. Indeed, in many cases the numerical densities of intertidal macrozoobenthos species varies from year to year. These variations are caused by variation in recruitment success, predation and especially winter mortality. Winter temperatures do have a synchronising effect on the population fluctuations of certain intertidal species. The synchronising effect of the severe winter in 1997/1998 and 1998/1999 in this study (as has been reported from another intertidal ecosystem by Essink and Beukema, 1986) is clearly visible. Seasonality patterns were noted as well for the density and biomass of macrozoobenthos from the Spanish Mediterranean (Sárda *et al.*, 1995). Although the seasonal pattern of abundance was quite different when both sites of seagrass bed in the present study are compared, a similar seasonal pattern of biomass was observed. Biomass values at the dense and sparse sites peaked in spring and autumn, and were at a minimum throughout the winter. The deviation from these monthly averages were much more important for the Ryde seagrass bed ecosystem where extreme temperatures recorded during the field visits, were up to 19 °C in August and down to 3 °C in

January (Figure 3.1., Chapter III). Indeed, the results of the correlation tests (Tables 6.12. and 6.19., Figure 6.15.) also supported the influence of water temperature on the dynamics of macrozoobenthic species number and biomass at both sites.

In general, the number of individuals per unit area as well as species number in this study were higher than that of the results reported from other studies on seagrass bed ecosystems along the British English Channel coasts. Previous work done at Ryde Beach had documented 57 species (Withers, 1979), but did not present the individual number per square metre. The investigation in the Yealm Estuary, south-western England, identified 83 species with the densities ranging from 1,911 to 12,229 individual m^2 (Webster *et al.*, 1998). These lower values perhaps reflect the smaller number of samples taken. Indeed, the *Zostera* bed in both of the above studies was visited only once compared to twenty one times over more than 2 years in the current study. Thus there is a very big possibility that both studies missed some of the more seasonal species. The other reason is likely due to the differences in shoot density. As was explained at the start of this section, shoot density did correlate with faunal abundance. The *Z. noltii* bed of Ryde Beach has a higher shoot density (averaged of 276 – 952 shoot m^2) compared than that of the Yealm Estuary (12 – 144 shoot m^2). Again, lower shoot density may generate less detritus available for the macrozoobenthic consumption.

Of the similarity analyses, it was observed that overall macrozoobenthos species showed similarities at 44 % level for the dense site (Figure 6.10.) and 32 % level for the sparse site (Figure 6.12.). A number of environmental factors might contribute to sample similarities. As has been observed in the species number and abundance, it was proposed that faunal recruitment, hydrodynamics in the seagrass bed and sediment bed properties perhaps influence the clustering.

Recruitment periodicity of the macrozoobenthos was seen as well in this study. Indeed, although this study was able to record the most common species

(Tables 6.3. – 6.4.) not all these species were sampled on every field visits (Appendices 3 – 6).

Strong waves and currents that affected the dynamics of seagrass population (Chapter IV) were likely responsible for the faunal structure in the winter. To some extent, water temperature also influenced the macrozoobenthos species structure (Figure 6.16 and Tables 6.12 and 6.19.). This was indicated by samples taken during the warmer months tended to group in the same cluster.

From the sediment data, it was observed that macrozoobenthos clustering was strongly correlated with both sediment organic matter and sediment chl-*a* (Figures 6.15 and 6.16.). Combined with high seasonality of water temperature, these two environmental parameters supported higher diversities of macrozoobenthos. Although clusters were not well defined (Figures 6.10 – 6.13.), in many cases samples collected in the summer grouped in the same cluster or if they were part of the big cluster, they were closer to each other than other season samples. The importance of this combination of three environmental parameters (sediment organic content, sediment chl-*a* and water temperature) to the animal abundance was obviously shown by May 1998 samples that developed as Cluster III at the sparse site.

Perhaps the bloom of other marine plants at the site can be accounted as other environmental phenomenon related to the fauna similarity. This study saw an outburst of green algae, *Enteromorpha intestinalis*, particularly at the dense site in March 1998. This could be an important factor infiuencing the structure of faunal groupings. The overgrowth of the epiphytes and filamentous algae on *Z. noltii* leaf surfaces and on the sediment might explain the difference in faunal structure in the first two months of the study. Indeed samples of September 1997 at both sites and October 1997 at the sparse site clustered separately (Figures 6.10 and 6.12.). Although *H. ulvae* was a common component at the dense site, it was only in September 1997 this species ranked first in term of species abundant. At the sparse site *H. ulvae* ranked second most abundance species in September and October

1997. The epiphytes and filamentous algae may have contributed to the high abundance of this snail, since it can feed as a herbivore.

In general, samples at the dense site had higher similarity values compared than that of the sparse site (Figures 6.10 and 6.12.). A relatively more stable environment, with more niches and higher pigment production may have enabled the dense site to maintain the species stability throughout the period. Regardless of site, similarity and MDS analyses revealed that groupings commonly occurred between samples taken in the similar month(s) and or season. In addition, samples from spring tended to be closer to those of the autumn samples, perhaps reflecting environmental condition.

Many species are stable components of the macrozoobenthos of the Ryde Beach seagrass bed, as shown by *C. capitata*, *P. elegans* and *H. ulvae*. This study and other on the North Atlantic coasts suggest that this phenomenon results from constant recruitment throughout the year (Sárda *et al.*, 1995). Another factor is suggested reflects the behaviour of these animals. *C. capitata,* for example, it is a opportunistic species and able to survive in wide range of environments (Hayward and Rayland, 1990a). Another study on the dynamics of *P. elegans* on the French side of the English Channel reported that this spionid worm is well distributed and exist all year around (Morgan, 1999). As a herbivorous species, *H. ulvae* is a common feature of the vegetated nearshore environments (Hayward and Ryland, 1990b).

The present study observed a clear seasonal pattern of macrozoobenthic biomass. Overall the biomass values peaked in the spring months. Annual biomass values ranged from 1.69 –10.81 g dry wt.m^{-2}. Environmental factors, such as sediment characteristics and wave action, influence the functioning of the less vegetated site, thus resulting in the lower density, species number and biomass values of macrozoobenthos observed. Coastal sediments with a higher content of mud fraction tend to have higher values of macrozoobenthic biomass (Edgar, 1994; Edgar *et al.*, 1994; Beukema and Cadeé, 1997). This applies to the findings of this study also. The dense site had a higher content of silt in the sediment. Muddy

sediments in general posses a higher organic content, hence the available food for deposit feeding macrozoobenthos is higher. The next characteristic of the sediment important in defining the biomass of the associated fauna is the organic content. Organic matters along with bacteria in the sediments are both often associated with particle surfaces. Since the surface area of fine particles is greater per unit volume than that of coarse sediments, it follows the available organic resources (organic matters and bacteria) are likely to be greater in fine rather than coarse sediments (Lockwood *et al.*, 1996). From the data of sediment characteristics (Figures 3.2. – 3.4., Chapter III), it was clear that the dense site sediments possessed the higher values of both the silt fraction and organic content compared to those of the sparse site. In fact, the sediment organic matter did clearly correlate with not only the macrozoobenthic biomass, but also with macrozoobenthic abundance and species number (Tables 6.12. and 6.19., Figure 6.14.).

An interesting result showed the abundance of macrozoobenthos did not correlate with the seagrass chemical constituents measured, i.e. phenolics, carbohydrate and protein (Figures 6.22. – 6.24.). This is not surprising since the previous discussion concluded that most of the *Z. noltii* production was not retained within the system (Chapter IV). Therefore the fauna variations was unlikely to be greatly influenced by the nutrition status of seagrass.

Faunal abundance neither correlated with chl-*b* (Figure 6.18.) nor lutein/zeaxanthin (Figure 6.19.). This finding indicates the low importance of seagrass detritus to the seagrass bed fauna and underpins, once again, the important contribution of sediment chl-*a,* together with sediment organic matter, water temperature and hydrodynamics characteristics, to the faunal dynamics at the site.

Chapter VII:
General Discussion and Conclusion

7.1. General Discussion

This study observed spatial and temporal variations in the dynamics of a *Z. noltii* population from the seagrass bed of Ryde Beach. Many variables of seagrass dynamics differed significantly between the dense and sparse beds and with season (Chapter IV). The physical disturbance at the site caused temporal decrease of shoot density in the winter. Indeed, during the winter periods, the seagrass population not only suffered from the cold temperature but also from sediment movement caused by strong waves and currents combined with the strong wind. The cold temperatures may have stopped or decreased the addition of new shoots; whilst the winter storms not only reduced survival, but also uprooted them from the seagrass bed. Effects of water dynamics and environmental conditions, particularly low temperatures, have been reported as important in preventing the establishment and maintenance of intertidal *Zostera* spp. community (de Jonge and de Jonge, 1992; van Katwijk and Hermus, 2000).

It is suggested that the herbivory from the macrozoobenthos, as well as higher animal groups, such as the waterfowl, have also affected the dynamics of the *Z. noltii* population at the study site. Seasonal grazing of the dark-bellied brent goose (*Branta bernicla bernicla*) to the study site, as reported also by Tubbs and Tubbs (1982, 1983) and Aspinal and Tasleer (1992), was shown to cause a decrease in the number of seagrass shoots in the winter. Valentine and Heck (1999) have recently presented the results of a study describing a significant reduction of *Zostera* population caused by herbivory. *Z. noltii* and *Z. marina* in the Solent were listed among the seven seagrass species from nine seagrass bed

ecosystems worldwide that are persistently grazed by migratory waterfowl. The other study using field experiments with net enclosures, estimated that migratory waterfowl removed and grazed 34 g DW m^{-2} of above-ground and 28 g DW m^{-2} of below-ground phytomass during the autumn (Nacken and Reise, 2000). The annual migration route of the geese that feed on *Z. noltii* in the Solent has been described by Ganter (2000). By the end of summer, they migrate from their breeding areas in the Taymyr peninsula in central Siberia to the White Sea and spend between 1 and 2 weeks there feeding on *Z. marina*. In the autumn (September - early December) they move to the Wadden Sea along the seagrass beds of Denmark, Germany and The Netherlands and graze on *Z. noltii*. When the seagrass supply is depleted they move on to southern England and northern France, where they spend the winter. In English and French estuaries they feed on *Zostera* while it is available, then switch to feeding on green algae, to saltmarsh feeding or upland feeding.

The higher numbers of Z. *noltii* shoots on Ryde Beach in the warmer months might be ascribed to the natural recruitment of the seagrass population. This study found evidence that the shoots were almost exclusively added through asexual rhizomal reproduction. The new shoots appeared from the rhizomal systems rather than from seed germination. However, since in particular months there were flowering shoots and some of these produced seeds, then some new shoots might have been recruited through germination of such seeds. The warmer water temperatures (Figure 3.1.) together with increased light intensity and penetration during the daytime, particularly during the spring and summer seasons have also been suggested as contributors to the maintenance of high numbers of seagrass shoots. Again, Valentine and Heck (1999) found that although the seagrass populations suffer consider biomass depletion following high grazing pressures, they persist with sufficient reserves to recover rapidly in the next growing period. This is because the stored reserves and sites of nutrient uptake for many seagrasses are located below-ground in the rhizomal system that is not accessible to most grazers. Additionally, the exudates and waste products from macrozoobenthos (see Mazella *et al.*, 1992) would also help to maintain the Z.

noltii population, since they act to recycle nutrients in the bed sediment. Figure 7.1. presents a model that describes the dynamics of *Z. noltii* population in this study.

This study found that *Z. noltii* contributed little overall pigment production to the seagrass bed sediment. The sediment analyses showed that pigment standing stock was mainly derived from microphytobenthos detritus, particularly from diatoms (Chapter V). As has been mentioned, correlation between chl-*a* and fucoxanthin indicated the importance of diatoms to the sediment pigment dynamics (Figure 5.17.). Also, the much lower concentrations of seagrass associated pigments, i.e. chl-*b*, lutein/zeaxanthin and *ß*-carotene, compared than that of fucoxanthin, an important diatom signature, support this assumption. Organic input to intertidal sediments dominated by autochthonously produced detritus from dynamic communities of benthic microphytes is very common (Jacobs and Noten, 1980; Wright and Jeffrey, 1987; Kristensen and Hansen, 1995 and papers therein). Additional indication for the importance of diatoms to the sediment pigment dynamics was that fucoxanthin and *ß*-carotene were always detected from the sediments throughout the study, whereas chl-*b* and lutein/zeaxanthin were often absent. Fucoxanthin is clearly contributed by the diatoms. As for the presence of *ß*-carotene, it could have been derived from benthic macrophytes (*Z. noltii* and algae) as well as diatoms in the bed. *ß*-carotene is not an exclusive seagrass signature, as it can be found in every type of marine vegetation (Jeffrey *et al.*, 1999; Lucas, 2000-personal communication), therefore the occurrence of this pigment in the sediment in every month was understandable.

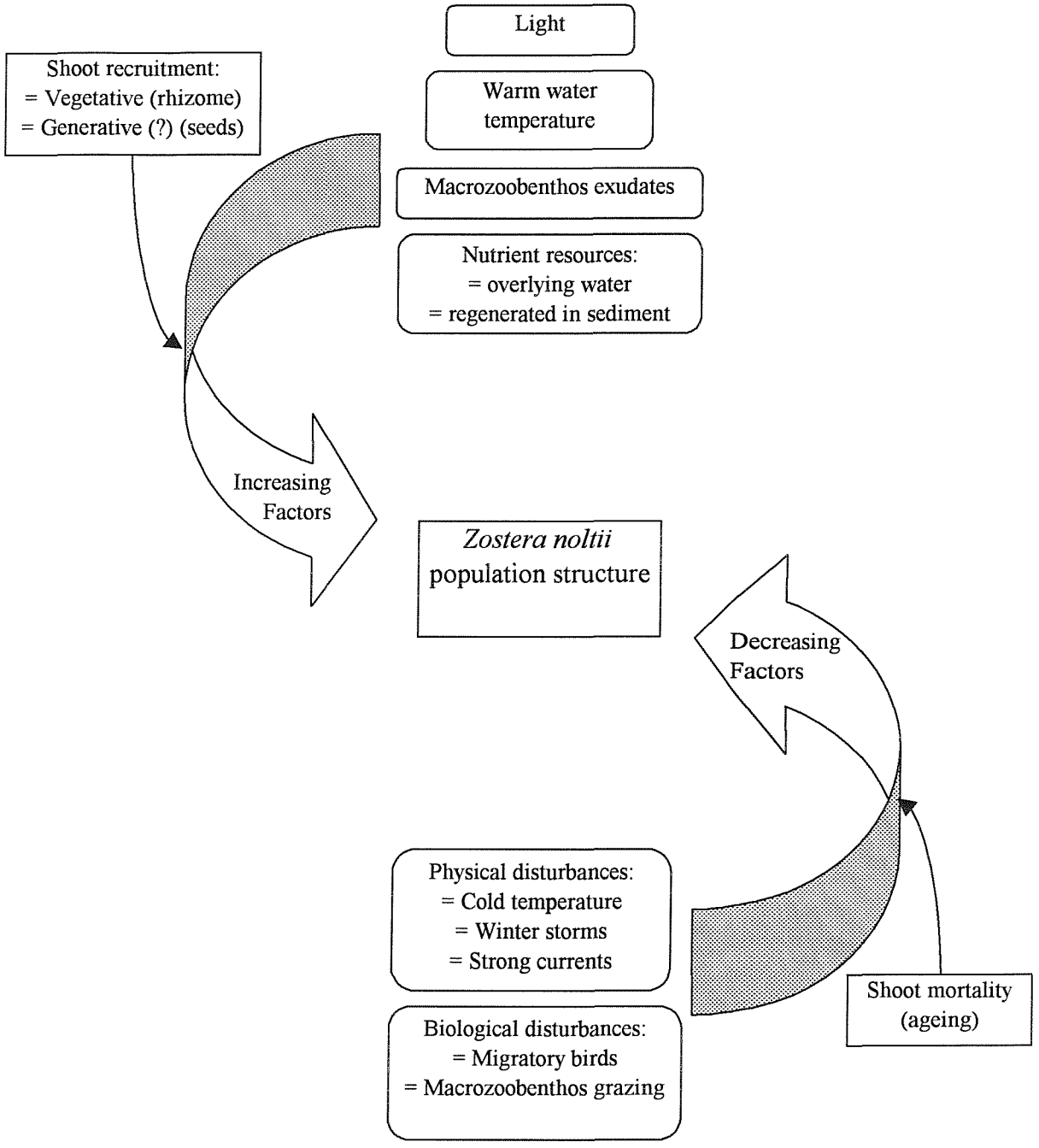

Fig. 7.1. Suggested model for *Z. noltii* dynamics at Ryde Beach seagrass bed.

Somewhat surprisingly, this study revealed that a very small amount of *Z. noltii* production was retained within the seagrass bed ecosystem. Statistical analyses showed that the dynamics of both chl-*b* and lutein/zeaxanthin in the sediment did not correlate with *Z. noltii* biomass (Figures 5.18. – 5.19 of Chapter V). Few factors have been established in this study to follow the fate of seagrass fresh-broken leaves as well as its detritus; these include physical and biological causes. Physically, winter storms (Suchanek *et al.*, 1985), tides and waves (Lamontagne *et al.*, 1986; de Jonge and de Jonge, 1992) have been mentioned as the main factors in transporting the *Z. noltii* detritus away from the site (Chapters IV and V and the beginning paragraphs of this Chapter). These phenomena would have minimised the chance of chl-*b* and lutein/zeaxanthin derived from *Z. noltii* detritus accumulating in the sediment.

The sediment type of the site has also showed the dynamics of physical factors within the seagrass bed in this study. Indeed, at both sites the sediments fell into the category of sandy sediment in which fine sand composed the highest percentage of sediment fractions (Chapter III). The chance of *Z. noltii* detritus to be retained within the sediment would have become reduced with such type of sediment.

Direct consumption by the herbivores was the prominent biological factor for the dispersal of *Z. noltii* materials from the site. Grazing by brent geese from the end of autumn to early spring, as has been mentioned previously (Chapter IV and Figure 7.1.), would have removed seagrass materials thus rendering them unavailable for deposition to the sediment. Because of this consumption, there was a reduction in the incorporation of seagrass detritus in the sediment; thus lowering the concentrations of seagrass associated pigments in the sediment. Nienhaus and Groenendijk (1986) found grazing pathway as the main factor for seagrass disappearance from a Dutch meadow, whereas Barnes and Hughes (1988) reported only 5 % of seagrass materials available for *in situ* consumers of a Caribbean seagrass meadow.

For the faunistic study, the present research identified many species of macrozoobenthos that were not reported from previous faunistic studies of the Isle of Wight such as that by Withers (1979) and of the Solent Waters in general (Bamber, 1993; Al-Suwailem, 1991). There has been a reappearance of some species as reported by Thorp (1980). Part of this increase must reflect the intensive sampling nature of the current study. A second reason may be that the water quality parameters of the site may have changed in the last decade or two. The seagrass bed then has either been successfully recolonized or it has been attracting new species of macrobenthic fauna. Indeed, more macrobenthic fauna species were recorded in this study compared with that found in the previous study (Withers, 1979) perhaps indicates improved quality of the bed. In addition, the regularity of the herbivorous migratory seabirds visiting the seagrass bed supports the view that the study site seagrass bed may be considered as a healthy ecosystem. The conditions at the site are such that *Z. nolti* stands can grow and are consequently able to house a great number of macrozoobenthic species whilst withstanding grazing pressure.

The existence of *Z. noltii* vegetation at the site has confirmed the hypothesis that a great diversity of macrozoobenthic population did live within the seagrass bed ecosystem. From a trophic viewpoint, the class Polychaeta dominated the macrozoobenthos assemblages in both species richness and abundance. Members of this group found in this study included surface-subsurface deposit feeders as well as the carnivores (Day 1967a, 1967b; George and Hartmann-Schroder, 1985; Hayward and Ryland, 1990a; Hartmann-Schroder, 1996).

Some direct consumers of seagrass added the trophic hierarchy to the species richness of the bed, although their numbers in some months were low. The herbivorous isopod *Idotea*, decapod *Carcinus* and gastropod *Hydrobia* fall in this category, since they are known to digest the fresh leaves of seagrass or algae (Naylor, 1972; Hayward and Ryland, 1990a; Hayward and Ryland, 1990b, Valentine and Heck, 1999). The polychaete *N. diversicolor* is also known to be a direct consumer of *Z. noltii* (Hughes *et al.*, 2000). Hydrobiid snails were sampled

in most field visits, whilst both *Idotea* and *Carcinus* were identified on many occasions. Members of Hydrobiidae are often found as an important component in temperate *Zostera* spp. meadows (Asmus and Asmus, 1985; Borum, 1987; Phillipart, 1994a, 1994b; Hyward and Ryland 1990b). They feed not only on microphytobenthos, bacteria and detritus on the bed, but also graze on periphyton present on seagrass leaves (Borum, 1987; Phillipart, 1995). The latter activity promotes the seagrass growth and development, since the snails suppress the periphyton biomass that reduces seagrass photosynthesis by shading. This study recorded a genus of molluscs, i.e. gastropod *Rissoa*, that is known to be grazer (Hayward and Ryland 1990b; George *et al.*, 1995). The occurrence of herbivorous macrozoobenthos in the seagrass beds is in fact very common. Indeed, in spite of the modest percentages of production consumed, highly productive seagrass species normally support high levels of herbivores production (Cebrián *et al.*, 2000).

The other strata of macrobenthic fauna found came from the animals that feed on the seagrass detritus. Amongst this group are some polychaetes, rissoid molluscs and amphipod crustaceans (Mazella *et al.*, 1992). *C. capitata*, one of the most dominant species at the site, and *N. diversicolor* are known to be detritivores, as well as carnivores (Hayward and Ryland, 1990a). It is also suggested that the mosaic of *Z. noltii* shoots can act as a sediment trap and detritus catchment, offering favourable food conditions for the detritivorous animals (as has been applied to the small amphipods, see Baden, 1990). The members of the cumaceans, are suggested as consumers of seagrass detrital products as well. This is because these animals are known to feed on microorganisms and organic materials derived from the bottom deposits in their environment (Jones, 1976).

This study did identify the macrozoobenthos from the highest trophic level. Many polychaetes from the families of Capitellidae, Cirratulidae, Maldanidae, Glyceridae, Nereidae, Phyllodocidae, Spionidae, Syllidae and Terebellidae found in this study are classified as carnivorous, predating the other macrozoobenthos species or the young and smaller individuals within their own species (Hayward

and Ryland, 1990a). The higher crustaceans, *C. crangon* and *P. bernhardus*, which are neither herbivorous nor detritivorous, were also sampled in several field visits. The occurrences of these carnivorous animals, in fact, are not surprising, since they may have visited the seagrass bed for predatory purposes. A commonly recorded prey species consumed by *C. crangon* includes *C. volutator* and *Nereis* spp. (Raffaeli *et al.*, 1989; Isakson and Pihl, 1992 and the papers therein). *Corophium* and *Nereis* species were also occasionally abundant at the site. Indeed, several authors (Heck and Thoman, 1984; Summerson and Peterson, 1984; Mazella *et al.*, 1989; Ševčić, 1991; Isakson and Pihl, 1992; Corbisier, 1994; Perkins-Visser *et al.*, 1996; Valentine and Heck, 1999) have explained visits to the seagrass beds by the predators as a common phenomenon.

In terms of quantitative composition, the benthic macrofaunal assemblages of the Ryde seagrass bed have similarities with comparably located faunas in European waters (Junoy and Viéitez, 1992; Boström and Bonsdorff, 1997; Çinar *et al.*, 1998; Webster *et al.*, 1998) and elsewhere in the world (Edgar *et al.*, 1994; Sheridan, 1997). The polychaetes were also dominant in their samples. However, regional comparison shows that the *Zostera* bed in this study contained a greater number of individuals as well as species of macrozoobenthos than many similar habitats in other European waters (Table 7.1.). This is understandable, since the studied seagrass bed had the denser population of seagrass. The other reason is, as part of the central region of the English Channel, Ryde Beach is located inside the transition zone between the Lusitanian (warm temperate) and Boreal (cold temperate) marine biological provinces (Irving, 1996; Dahl, 1998). Therefore it can be argued that this bed has the potential for higher species richness than the other temperate regions, since the residents from both regions may be represented here. Further comparison showed the sites with the lowest number of macrozoobenthos abundance as presented in Table 7.1, the *Zostera* bed of Gülbahçe Bay, Aegean Sea, also contained lowest number of species (108 taxa, Çinar *et al.*, 1998) compared with those recorded in this study (124 species). These lower values are perhaps related to the oligotrophy that is a characteristic of the Mediterranean Sea

(Margalef, 1985), which is even more pronounced in its Eastern Basin (Karakassis and Eleftheriou, 1997; Panayotidis *et al.*, 1999).

Table 7.1. Regional comparison of macrozoobenthos abundance and shoot density found in studies of fauna associated with *Zostera* communities.

Location	Animal Abundance (individuals·m^{-2})	Shoot Density (shoots·m^{-2})	Reference
Roscoff, English Channel	1,094 - 27,350	500 – 800	Jacobs, 1980
Yealm Estuary, English Channel	1,911 - 12,229	12 – 144	Webster *et al.*, 1998
Aland Archipelago, Baltic Sea	24,994 - 52,682	50 – 500	Boström and Bonsdorff, 1997
Eo Estuary, Atlantic Ocean	13,850 - 17,835	100 – 253	Currás *et al.*, 1993
Aegean Sea, East Mediterranean	754 – 982	nd	Çinar *et al.*, 1998
Chesapeake Bay, Atlantic Ocean	1,486 - 2,693	335	Mattila *et al.*, 1999
Isle of Wight, English Channel	7,215 – 416,637	276 – 1020	This study

nd: no data available

Seasonal patterns of macrozoobenthos were found in the present study (Chapter VI). Annual fluctuations are common recorded for dynamics the benthic macrofauna (George *et al.*, 1995). The variations in macrozoobenthos abundance, species number and biomass not only occurr for the seagrass bed-associated fauna (Junoy and Viéitez, 1992; Currás *et al.*, 1993; Nelson and Virnstein, 1995) but also for the macrobenthic fauna associated with the macroalgae (Boaden *et al.*, 1995; Albrecht, 1998) as well as the macrozoobenthos of shallow coastal waters (Sardá

et al., 1995; Osowiecki and Warzocha, 1996; Haque *et al.*, 1997; Karakassis and Eleftheriou, 1997; Laine *et al.*, 1997; Kucheruk *et al.*, 1998). In general perspective, the variations in abundance and species composition in marine communities are thought to be a consequence of factors influencing recruitment and mortality such as food availability, refuge and predation (Heck and Orth, 1980; Heck and Thoman, 1984; Thatje and Gerdes, 1997). These factors seemed to apply to the seagrass bed ecosystem of Ryde Beach as well. In detail, there seems to be few environmental factors being considered as governing the temporal variations of the macrobenthic fauna at the site. Indeed faunal abundance correlated positively with sediment organic matter, sediment chl-*a* and water temperature (Figures 6.14., 6.15. and 6.16. respectively). Low values of faunal abundance in the winter months have been suggested as resulting from low sediment bed pigment production along with the severe weather conditions (Chapter VI). The macrozoobenthos during this period have to endure not only food limitation, as indicated by low pigment concentrations, but also lower temperatures, strong wave and current action. The latter may cause a higher removal of the macrozoobenthos as well as the sediment with its detritus and microphytobenthos contents from the ecosystem. Meanwhile the high values in the spring are thought to correlate with the high pigment production following the bloom of the microphytobenthos, the arrival of macrozoobenthos offspring, and the stability of the weather conditions. The important signs of population recruitment in the spring were indicated by many of the crustaceans (mainly the amphipods and decapods) and the polychaetes (especially *P. elegans*, *A. minuta* and *S. armiger*), which were found bearing brood sacs.

The increasing temperature regime and the diminishing water dynamics also support the macrozoobenthic increase in the spring. The high values in the autumn may be attributed to population increase over the summer resulting from high sediment pigment contents, the more persistence of *Z. noltii* shoot number and the stability of water dynamics. Additionally, the denser seagrass shoots with the maximum heights in the autumn have been presumed to provide more habitats for

the animals. In the summer, values for the macrozoobenthic abundance and species number were also relatively high but generally lower than that found in most of spring and autumn months. These shifts can be caused by the amount of food and the high temperature. The warmer summer climate would also increase the growth of microphytobenthos but the blooms of primary producers in the sediment are over. In addition, the warmer temperatures during the summer would also increase the metabolic rates of the macrozoobenthic species; thereby increasing their demands for energy resources, i.e. food.

Interestingly, the high macrozoobenthos abundance and biomass values were recorded at the beginning of the winters, i.e. both December 1998 and 1999. These peaks were not surprising, since the sediments of the bed still contained relatively high values in phaeophorbide and phaeophytin (Figures 6.8 and 6.9.), important indicators of macrozoobenthos grazing activities (Mantoura and Llewellyn, 1983; Bianchi *et al.*, 1993). It can also be argued that few macrozoobenthos may have reached maturity following their energy storage throughout the warmer months. Hence, it is assumed that though their individual numbers were not too high, many of them were at the maximum size and contributed a significant proportion to the total biomass.

Spatial comparison showed that the denser bed had significantly higher values of the species number, abundance, biomass and species richness of the macrobenthic fauna compared to that of the sparse site. These findings were in agreement with the studies reported from Yealm estuary, south-west England (Webster *et al.*, 1998), Eo estuary, north-west Spain (Currás *et al.*, 1993), as well as other seagrass meadows world-wide (Isakson and Pihl, 1992; Edgar *et al.*, 1994). Higher levels in the shoot density, pigment values, silt and organic contents of the sediments are likely to have contributed to these high values.

It has been observed the sediment pigment standing stock of the seagrass bed, as shown by the chl-*a* contents, correlated with the variations in the macrozoobenthos figures at the site. Indeed, the relationships between chl-*a* concentrations and the macrozoobenthos dynamics have been studied to some

extent. Also, the results from the present study corresponded with those from other areas of the seagrass beds, such as the Wadden Sea (Beukema and Cadeé, 1997) and the northwestern Mediterranean (Gremaré *et al.*, 1997), as well as the shallow coastal waters of the eastern Mediterranean (Karakassis and Eleftheriou, 1997). Those authors concluded that the macrozoobenthos diversity and biomass increased rapidly following the chl-*a* blooms.

The present study has identified the different responses of the macrozoobenthos species number, species richness, species abundance and biomass between two densities of the *Z. noltii* population. This is interesting, because a great distance did not separate the two sites and they had almost identical seasonal ranges in the water salinity as well as temperature. The sediment granulometry of both sites was also very similar (Chapter III). In marine environments, as has been mentioned in Chapter I, changes in macrovegetation may also be accompanied by structural changes in associated animal communities (Isakson and Pihl, 1992 and the papers therein). Within a single seagrass bed ecosystem, faunal species diversity (Webster *et al.*, 1998) and biomass (Zieman and Wetzel, 1980) can be significantly different between areas exhibiting relatively small changes in shoot density.

Although the yearly variations in many aspects have been observed, the various degrees of macrozoobenthos species similarity were found at the site. Amongst the groups of samples, most of them were similar at 50 % level or higher, even in many cases they were similar at higher than 70 % level (Figures 6.9. and 6.11.), indicating a stable *Z. noltii* community at the site. The similar sediment type throughout the year (Chapter III) at the site perhaps influences this species homogeneity. The role of sediment type as an environmental factor determining macrozoobenthic community structure has been emphasized in many works (Karakassis and Eleftheriou, 1997; Seiderer and Newell, 1999).

Further macrozoobenthos species similarity analyses revealed that clusters were not well defined at either site. The fact that two sites were at the same shore level might contribute to this condition. Indeed, shore level/depth has been identified as the most important factor in controlling macrozoobenthos community

structure in the marine environment (Basford *et al.*, 1989; Karakassis and Eleftheriou, 1997). Comparison between two sites showed that there was greater variation at the sparse site, reflecting the stability of the seagrass community was higher at the dense site.

In general, the groups of macrozoobenthos species tended to be similar within the same month and or season. It has also been suggested that clusters of macrozoobenthos species were likely to depend on faunal recruitment and a number of environmental factors such sediment chl-*a*, sediment organic matter, sediment phaeopigment, water temperature and the occurrence of epiphytes and algae (Chapter V). Because fauna recruitment affected the dynamics of fauna abundance and species number, it is arguable that recruitment of particular species influenced the similarity between the months at the same site. In fact, it was apparent that the similarity was often caused by the high abundance as well as the absence of particular species (Tables 6.4. and 6.5.). Since recruitment has been established in causing the similarity, it is suggested that different timing of reproduction periods might cause the variation. Following the reproduction, macrozoobenthos abundance increases. The contribution of animal abundance to the species similarity between sampling periods has been reported in other studies (Gambi *et al.*, 1995; Çinar *et al.*, 1998; Webster *et al.*, 1998). The contribution of sediment chl-*a*, sediment organic matter and water temperature to the species similarity was understandable and has been mentioned heavily in Chapter VI and this chapter. This study synthesised that warm water temperature promotes the growth of microphytobenthos, as the main source of chl-*a* at the site, and this growth enriches organic materials to the sediment.

This study found that the occurrence of seagrass population at the site did not influence macrozoobenthos similarity between sampling months. This conclusion was supported by the analyses in which fauna abundance did not correlate with seagrass shoot density and shoot biomass (Figures 6.20. and 6.21.) as well as with all three seagrass chemical constituents (Figures 6.22 – 6.24.). This may explain the importance of microphytobenthos together with other

environmental parameters (sediment organic matter, water temperature) to the faunal figures. Moreover, the fact that chl-*b* and lutein/zeaxanthin did not correlate with the faunal abundance (Figures 6.17 and 6.18.) also highlighted the less prominent influence of seagrass population to the faunal community structure.

Since fauna abundance did not follow the values of seagrass carbohydrate (Figure 6.23.) or seagrass-associated pigments (Figures 6.17. and 6.18.), it is surmised that the carbon budget for macrozoobenthos in particular and the site in general, was mainly provided by the processes within the sediment. The dynamics of microphytobenthos and sediment organics could be important factors in providing the energy to the system, because both positively correlated with faunal abundance (Tables 6.12. and 6.19. and Figures 6.14. and 6.16.). This process is arguable because the site did contain higher number of detritrivorous animals, which are more dependent on sediment organics, compared with the herbivorous, which are more dependent on seagrass (Chapter VI). The low influence of seagrass material on animal abundance is also shown by the weak correlation between seagrass phenolics and faunal abundance (Figure 6.22. and Tables 6.12. and 6.19.). This is interesting, because phenolics are known to be poisonous to most benthic animals (Zapata and MacMilan, 1979; Mazella *et al.*, 1992) and this study recorded seasonal variation of this compound. However, phenolics concentrations did not affect the fauna figures at the site. Since this discussion observed the dependance of macrozoobenthos to the sediment properties was more obvious than that of the seagrass parameters, and the fact that water dynamics moved out a great proportion of seagrass materials, thus the less effect of phenolics to the fauna figures was understandable.

Apart from the sediment microphytobenthos and sediment organic matter, sources of energy in the seagrass bed system of Ryde may be contributed from the materials transported to the system through the water column. Carbon sources within the seagrass bed may originate from microorganisms (bacteria, protozoa), sediment meiofauna and respiration of the system itself.

It was not surprising that salinity did not influence the dynamics of the seagrass biology and chemistry (Tables 4.10 and 4.18.) and sediment pigment production (Tables 5.12. and 5.19.) or the macrozoobenthos (Tables 6.12. and 6.19.) at Ryde seagrass bed. Although it is an important environmental factor in seagrass bed ecosystems (Davison and Hughes, 1998), unlike water temperature and sediment organic content, salinity was relatively stable at the site (Figure 3.1.). This low variation presumably did not impose significantly on the system.

Finally, the factors that influence the dynamics of the macrozoobenthos of the seagrass bed ecosystem of Ryde Beach are presented in Figure 7.2. It is believed there are many other ecological variables from either the seagrass bed or the adjacent ecosystems that might have correlated with the benthic fauna figures in the site. However the variables included in the model were seen to be important.

To sum up, this study observed many factors that interact among each other within the Ryde Beach seagrass bed ecosystem. This study surmised that although the bed supports a considerable number of macrozoobenthos from different tropic levels, the *Z. noltii* population provides a small input to the energy budget of the macrozoobenthos. The energy source for the fauna benthic is mainly contributed by microphytobenthos and sediment organic matter. However, the occurrence of *Z. noltii* shoots enriches the availability of the organic matter in the sediment that later promotes the growth of microphytobenthos. The fact that detritivorous and carnivorous macrozoobenthos outnumbered the herbivores (Chapters VI and VII and Figure 7.3.) also indicates that the process within the sediment had more contribution to the faunal dynamics.

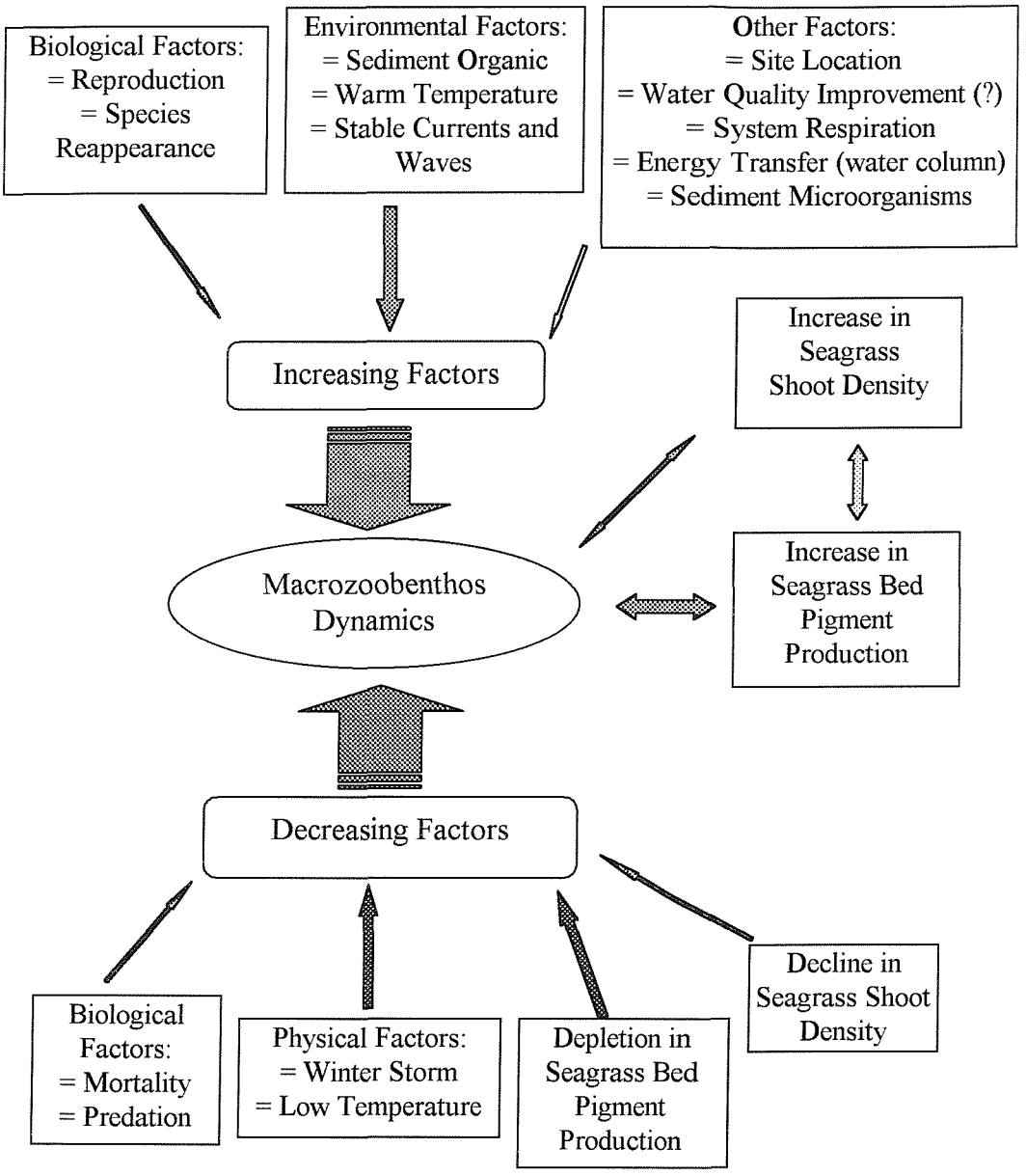

Fig. 7.2. A model proposed for the factors that influence the dynamics of the macrozoobenthos of Ryde Beach seagrass bed. (wider arrows indicate greater influence to the macrozoobenthos dynamics; double arrows indicate a two-way influence).

7.2. Conclusion

In conclusion, the features of Ryde Beach seagrass bed are:

1. The site is dominated by *Z. noltii*, in leaf throughout the year, and its population varies according to the season and bed density. Stable environmental conditions and rhizomal reproduction are seen to be the factors influencing the high shoot densities, shoot biomass, shoot leaf number and shoot height during the spring, summer and autumn seasons. The low values of these variables in the winter are likely ascribed to strong waves and currents, cold temperature and waterfowl herbivory.

2. Variations in both carbohydrate and phenolic contents are correlated with the seagrass life cycle; whilst the protein content remained constant throughout the year.

3. Pigment standing stock within the seagrass bed, as indicated by chl-*a* concentrations, fluctuates according to the season as well as seagrass density.

4. Microphytobenthos, mostly diatoms, contributed the main features of sediment pigment production. To a lesser extent, seagrass detritus also contributes to the pigment production of the bed.

5. The dynamics of the macrozoobenthos correlate with the season, seagrass density, sediment pigment production and sediment organic matter. The results indicate small importance of *Z. noltii* in supporting the food webs of the seagrass bed although all trophic levels of fauna feeding habits exist in the bed.

6. The polychaete worms, followed by amphipod crustaceans and gastropod molluscs dominate the figures of macrozoobenthos species number and abundance. In some months either the crustaceans or the molluscs achieved high abundance and biomass. Species abundance was responsible to the species similarity among the sampling periods.

7. The *Z. noltii* bed supports a great diversity of macrozoobenthos. The presence of seagrass may have indirectly enhanced the benthic production by contributing to the detritivorous food web through the input of decaying plant

materials. The dynamics of macrozoobenthos may be partly dependent on seagrass detritus that becomes incorporated within the sediments.

8. A simple model of the food web at the seagrass bed of the site is described in Figure 7.3.

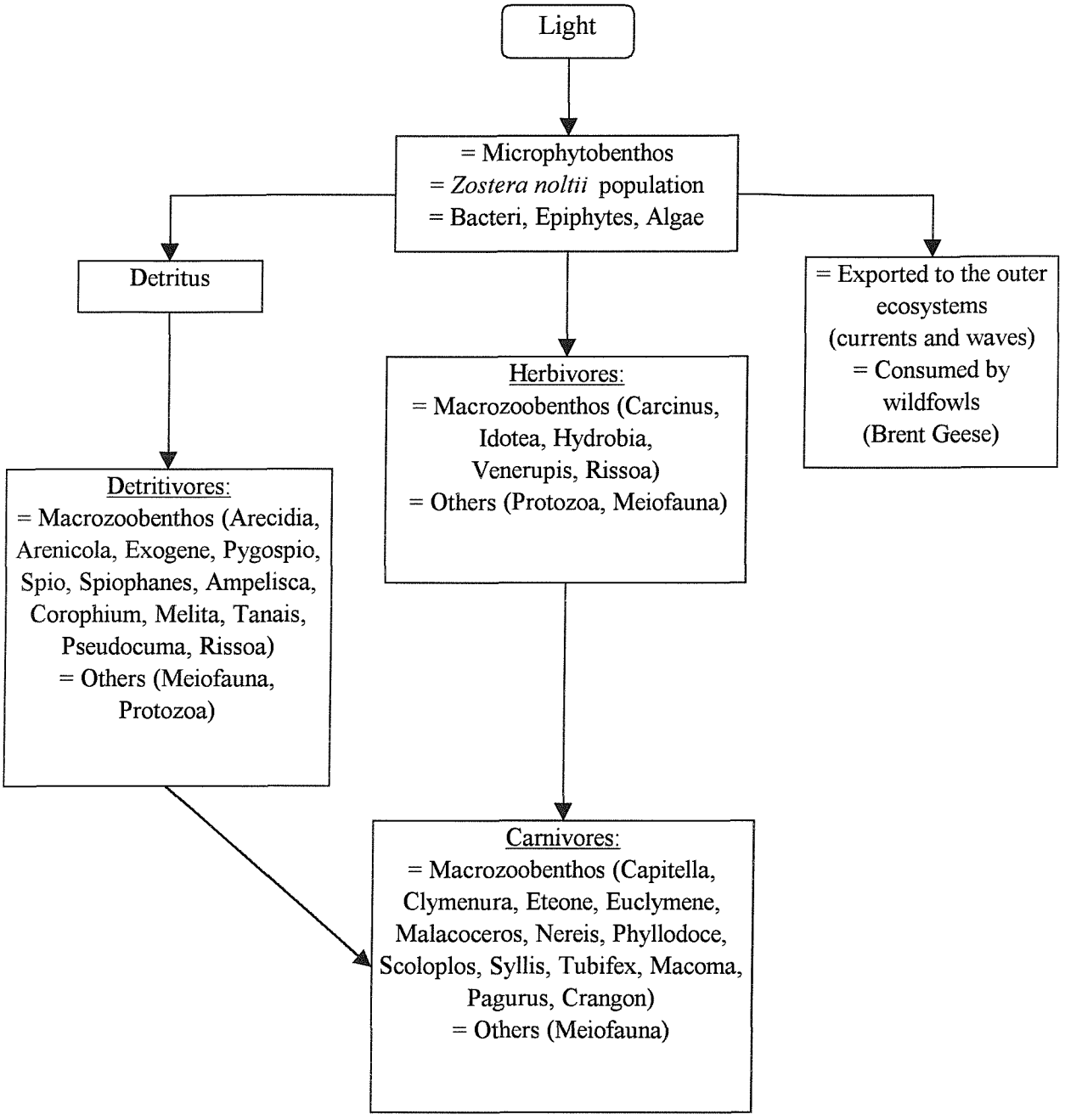

Fig. 7.3. The suggested food web complexities of *Z. noltii* bed of Ryde Beach.

7.3. Future Considerations

Future investigations might examine the seagrass materials produced within the systems and which are consumed by the macrozoobenthos and the higher levels of herbivores, waterfowl in particular. The future studies may use the stable isotope, gut content analyses or reconstructive sampling as have been applied in many areas of the Mediterranean Sea, the Indian and the Pacific Oceans (Valentine and Heck, 1999). Since few species of macrozoobenthos were dominant during the sampling periods, more observations are required to monitor the shift in animal populations. Further studies may also address other aspects of *Z. noltii* biology that have not been observed in this study, such as below-ground production, leaf area index and bed coverage.

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Appendix 1. Selected examples of reading area of each pigment from sediment analysed through HPLC method.

Sample	VA	SW	Pigment Area								
	(ml)	(g)	Chl-*a*	Chl-*b*	Chl-*c1+c2*	Fuco.	19 Hex.	Zea./Lut.	β-car	Diad	Diat
D1 Oct97	5	0.8193	49316	8057	5508	27124	7304	0	1775	2641	0
D2 Oct97	5	0.8907	99680	2321	17306	68445	10291	2210	3813	7447	0
S1 Oct97	5	0.829	52336	4557	7135	26955	6476	2672	2957	3228	0
S2 Oct97	5	0.6529	60908	6047	7021	37727	8668	2949	4000	3511	0
D4 Jan98	5	0.6696	68226	0	10359	48597	5633	2356	4719	6701	4085
D5 Jan98	5	0.6543	56694	0	8787	39944	4242	2293	3521	5304	3705
S1 Jan98	5	0.6354	62627	0	0	41594	8520	1807	3529	6449	4041
S2 Jan98	5	0.6226	58251	0	6967	49734	4643	0	3227	8115	6074
D1 May98	5	0.6044	40302	3393	4937	35371	10922	3482	4934	4242	0
D2 May98	5	0.6467	34689	0	7912	34257	8648	1610	3804	5968	4394
S1 May98	5	0.6434	45118	0	9843	36874	4069	4611	4340	3256	0
S2 May98	5	0.5698	33224	0	8362	26444	6534	0	3430	2762	0
D1 Aug98	5	0.6422	84487	9012	5255	31458	6065	18685	14739	4818	3829
D2 Aug98	5	0.7038	67406	7193	4295	28557	7163	15393	9075	3180	2166
S1 Aug98	5	0.7405	48880	2062	7921	37956	4688	2222	6133	3359	4335
S2 Aug98	5	0.7409	48272	0	8394	43248	4101	2555	5795	4416	0
D1 Nov98	5	0.6958	126761	56209	13669	86637	66166	19695	39300	5351	0
D2 Nov98	5	0.7733	89762	8806	11940	66290	24192	7769	11243	6060	5937
S1 Nov98	5	0.7012	108023	10883	11810	49080	6672	18666	10440	4801	0
S2 Nov98	5	0.7173	59250	3635	7279	31068	5640	6593	7768	3444	0
D1 Feb99	5	0.562	75163	0	2281	55462	0	1350	5091	6733	3178
D2 Feb99	5	0.571	127116	3022	9496	98646	0	6078	10172	13573	5185
S1 Feb99	5	0.5	108194	0	8317	89968	0	2226	8235	14789	5686
S2 Feb99	5	0.512	91256	0	10310	75423	0	1862	5946	11644	4566
D1 May99	5	0.516	69732	1963	4034	63284	4002	1919	6130	8690	0
D2 May99	5	0.512	174089	12433	3155	12273	7893	20205	22088	17063	8336
S1 May99	5	0.525	67041	777	0	63744	4255	1451	5685	9807	5608
S2 May99	5	0.505	84836	1277	3004	69342	0	2602	6947	11031	6901
D1 Jul99	5	0.555	93619	565	4271	75688	5188	3654	8445	12754	2910
D2 Jul99	5	0.513	86969	697	6275	66032	4062	2876	8040	10256	3952
S2 Jul99	5	0.519	75998	633	0	57094	2676	5275	9609	9762	3183
S2 Jul99	5	0.532	69450	414	0	52760	3605	4978	8911	9141	4248
D1 Oct99	5	0.501	75707	0	2623	63932	6923	730	5575	8978	3490
D2 Oct99	5	0.503	102329	2463	3934	81024	7702	4620	9029	12236	4599
S1 Oct99	5	0.508	76515	0	1770	62845	8507	1344	5823	10253	5100
S2 Oct99	5	0.54	80593	0	5317	67608	4870	1933	6996	11833	6612

VA=volume of acetone; SW=sediment weight; Chl-*a*=Chlorophyll-*a*; Chl-*b*=Chlorophyll-*b*; Chl-*c1+c2*=Chlorophyll *c1+c2*; Fuco=Fucoxanthin; 19 Hex.=19-Hexanoyloxyfucoxanthin; Zea./Lut.= Zeaxanthin/ Lutein co-elute; β-car= β-carotene; Diad.=Diadinoxanthin; Diat.= Diatoxanthin; D samples indicate sediments collected from the dense site; S samples indicate sediments collected from the sparse site.

Appendix 2. Selected examples of sediment pigment concentration. (Resulted from the calculation using reading area in Appendix 1 and formula given in Chapter II Section 2.6.3.).

Sample	Pigment Concentration								
	Chl-*a*	Chl-*b*	Chl-*c1+c2*	Fuco.	19 Hex.	Zea./Lut.	β-car	Diad	Diat
D1 Oct97	1.713	0.289	0.054	0.323	0.869	0.000	0.025	0.019	0.000
D2 Oct97	3.185	0.077	0.157	0.749	1.126	0.017	0.049	0.049	0.000
S1 Oct97	1.797	0.161	0.070	0.317	0.762	0.022	0.040	0.023	0.000
S2 Oct97	2.655	0.272	0.087	0.563	1.294	0.031	0.069	0.032	0.000
D4 Jan98	2.900	0.000	0.125	0.707	0.820	0.024	0.080	0.059	0.057
D5 Jan98	2.466	0.000	0.108	0.595	0.632	0.024	0.061	0.048	0.053
S1 Jan98	2.805	0.000	0.000	0.638	1.307	0.020	0.063	0.060	0.060
S2 Jan98	2.663	0.000	0.090	0.779	0.727	0.000	0.059	0.077	0.092
D1 May98	1.898	0.165	0.066	0.570	1.762	0.040	0.093	0.041	0.000
D2 May98	1.526	0.000	0.099	0.516	1.304	0.017	0.067	0.054	0.064
S1 May98	1.996	0.000	0.124	0.559	0.617	0.050	0.076	0.030	0.000
S2 May98	1.659	0.000	0.119	0.452	1.118	0.000	0.068	0.029	0.000
D1 Aug98	3.744	0.412	0.066	0.477	0.921	0.202	0.260	0.044	0.056
D2 Aug98	2.726	0.300	0.049	0.396	0.992	0.152	0.146	0.027	0.029
S1 Aug98	1.878	0.082	0.086	0.500	0.617	0.021	0.094	0.027	0.055
S2 Aug98	1.854	0.000	0.092	0.569	0.540	0.024	0.089	0.035	0.000
D1 Nov98	5.184	2.372	0.159	1.214	9.271	0.197	0.640	0.045	0.000
D2 Nov98	3.303	0.334	0.125	0.836	3.050	0.070	0.165	0.046	0.072
S1 Nov98	4.384	0.456	0.136	0.682	0.928	0.185	0.169	0.040	0.000
S2 Nov98	2.351	0.149	0.082	0.422	0.767	0.064	0.123	0.028	0.000
D1 Feb99	3.806	0.000	0.033	0.962	0.000	0.017	0.103	0.071	0.053
D2 Feb99	6.335	0.155	0.134	1.684	0.000	0.074	0.202	0.140	0.085
S1 Feb99	6.158	0.000	0.134	1.754	0.000	0.031	0.187	0.174	0.107
S2 Feb99	5.072	0.000	0.163	1.436	0.000	0.025	0.132	0.134	0.084
D1 May99	3.846	0.112	0.063	1.196	0.756	0.026	0.135	0.099	0.000
D2 May99	9.676	0.713	0.050	0.234	1.503	0.274	0.489	0.196	0.153
S1 May99	3.634	0.043	0.000	1.184	0.790	0.019	0.123	0.110	0.100
S2 May99	4.781	0.074	0.048	1.338	0.000	0.036	0.156	0.129	0.128
D1 Jul99	4.800	0.030	0.062	1.329	0.911	0.046	0.173	0.135	0.049
D2 Jul99	4.824	0.040	0.099	1.255	0.772	0.039	0.178	0.118	0.072
S2 Jul99	4.167	0.036	0.000	1.072	0.503	0.071	0.210	0.111	0.058
S2 Jul99	3.715	0.023	0.000	0.967	0.661	0.065	0.190	0.101	0.075
D1 Oct99	4.300	0.000	0.042	1.244	1.347	0.010	0.126	0.106	0.065
D2 Oct99	5.789	0.144	0.063	1.570	1.493	0.064	0.204	0.143	0.086
S1 Oct99	4.286	0.000	0.028	1.206	1.633	0.018	0.130	0.119	0.094
S2 Oct99	4.247	0.000	0.080	1.220	0.879	0.025	0.147	0.129	0.115

Chl-*a*=Chlorophyll-*a*; Chl-*b*=Chlorophyll-*b*; Chl-*c1+c2*= Chlorophyll *c1+c2*; Fuco=Fucoxanthin; 19 Hex.=19-Hexanoyloxyfucoxanthin; Zea./Lut.=Zeaxanthin/ Lutein co-elute; β-car= β-carotene; Diad.=Diadinoxanthin; Diat.= Diatoxanthin; D samples indicate sediments collected from the dense site; S samples indicate sediments collected from the sparse site.

Appendix 3. Macrozoobenthos species recorded at the dense site of Ryde Beach seagrass bed (x = species recorded; - = species not recorded).

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
NEMATODA																					
Nematoda	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
ANNELIDA																					
Polychaeta																					
Amphitrite edwardsi	-	x	-	-	x	-	-	x	-	x	-	x	-	x	-	-	-	-	-	-	x
Amphitritides gracilis	x	-	x	x	x	-	-	-	-	x	-	x	-	-	-	-	-	-	x	x	-
Arenicola marina	x	x	-	x	-	-	-	-	x	x	x	-	-	-	-	-	-	-	x	x	x
Aricedia minuta	x	x	x	x	x	x	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Capitella capitata	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Chaetozone setosa	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirratulus filliformis	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	x	x	x	x
Cirriformia tentaculata	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
Clymenura clypeata	x	x	-	-	-	-	-	x	x	x	-	x	-	x	-	x	-	-	x	x	x
Eteone foliosa	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
E. longa	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
E. picta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Euclymene lumbricoides	x	x	x	x	x	x	-	x	x	x	x	-	x	x	x	x	-	x	x	x	x
E. oerstedii	-	x	x	x	x	x	x	x	x	x	-	-	-	x	-	x	-	x	x	x	x
E. robusta	-	-	-	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-	x	-
Eulalia aurea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Eumida sanguinea	-	-	-	x	-	x	x	-	-	x	-	-	-	-	-	-	-	-	-	-	-
Euphrosyne foliosa	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Exogene hebes	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
E. verugera	-	-	x	-	-	-	x	-	x	x	-	x	-	-	x	-	x	x	x	-	-
Glycera tridactyla	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heteromastus filiformis	-	-	x	x	-	-	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-
Lanice conchilega	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laonice cirrata	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Malacoceros fuliginosus	x	x	x	-	x	x	-	x	x	x	x	-	x	x	-	x	x	x	x	x	x
Nepthys caeca	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	x	-	x
Nereis diversicolor	x	x	x	-	-	-	x	x	-	-	-	-	x	-	x	-	-	x	-	x	x
Nicolea zostericola	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nicomache lumbricalis	x	x	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-

Appendix 3. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Polychaeta (continued)																					
Notomastus latericeus	x	-	-	-	-	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Perinereis cultrifera	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phyllodoce longipes	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. mucosa	x	x	x	x	x	x	x	x	x	-	x	x	x	x	x	-	x	x	x	x	x
Pista cristata	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
Polydora ciliata	-	x	-	-	-	-	-	-	-	x	-	-	-	-	x	-	-	-	x	-	x
P. giardi	-	x	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-
Pygospio elegans	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Sabellidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Scolelepis foliosa	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
S. squamata	-	x	x	-	x	-	x	-	x	x	-	-	x	x	-	-	-	-	-	-	x
Scoloplos armiger	x	x	x	x	-	x	x	x	x	x	x	x	-	-	x	x	x	x	x	x	x
Sphaerosyllis bulbosa	-	-	x	x	-	-	x	-	x	-	-	-	x	x	-	-	-	-	-	x	-
Spio filicornis	-	x	-	x	-	-	x	x	-	-	-	-	-	-	x	-	-	-	x	-	x
Spiophanes bombyx	-	-	-	x	-	x	-	-	x	-	-	-	-	-	-	-	-	-		-	x
Syllis gracilis	-	x	x	-	x	-	-	x	-	x	-	-	x	-	-	x	x	x	x	x	x
Terebellidae sp.	x	-	-	-	x	-	-	-	-	x	-	-	-	x	x	-	-	-	-	-	-
Typosyllis prolifera	-	x	x	x	-	-	-	-	x	x	x	x	x	x	x	x	-	-	x	x	x
Oligochaeta																					
Tubifex benedii	x	x	x	-	-	x	x	x	x	x	-	x	-	x	x	x	-	-	x	-	-
ARTHROPODA																					
Amphipoda																					
Ampelisca brevicornis	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Ampithoe gammaroides	-	x	x	x	-	x	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-
A. rubricata	-	x	x	x	x	x	-	x	x	x	-	x	-	-	-	-	-	-	-	-	-
Atylus swammerdami	-	-	x	x	-	-	-	x	x	-	-	-	x	-	-	-	x	-	x	x	x
Bathyporeia guilliamsonia	-	x	x	-	-	-	-	x	-	x	-	-	x	-	x	-	-	-	x	-	-
Chaetogammarus marinus	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cheirocratus intermedius	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. sundevallii	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corophium arenarium	x	x	x	x	-	-	-	x	-	x	x	x	x	x	x	x	-	-	x	x	x
C. crassicorne	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 3. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Amphipoda (continued)																					
C. volutator	x	x	x	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	x	x	x
Erichthonius difformis	-	-	x	x	x	x	-	-	x	x	-	-	-	-	-	-	-	-	x	x	x
E. fasciatus	-	x	-	x	x	x	-	-	x	-	-	-	-	-	x	-	-	x	x	-	x
E. punctatus	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Gammarus finmarchinus	-	-	x	-	-	-	x	x	x	x	-	-	x	x	x	x	x	x	x	x	x
G. zaddachi	-	-	x	-	x	-	x	-	x	x	-	x	-	x	-	-	-	-	x	-	x
Hyale nillssoni	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-
Jassa falcata	x	x	x	-	-	-	x	-	x	x	-	-	-	x	x	-	-	-	x	x	x
J. pusilla	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-
Lillebjorgia pallida	-	-	-	-	-	-	-	-	x	-	-	-	x	-	-	-	-	-	-	-	x
Melita palmata	x	-	x	-	-	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-	x
M. obtusata	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microprotopus maculatus	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-
Orchestia gammerella	-	-	-	-	x	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x
Pinnotheres pisum	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-
Urothoe brevicornis	-	-	-	x	-	x	x	x	-	x	-	-	-	x	-	x	x	-	x	x	-
U. marina	x	x	-	-	-	-	-	x	-	x	x	-	-	-	x	x	-	x	x	x	x
U. poseidonis	x	x	x	-	-	-	-	x	-	x	x	x	x	x	-	-	-	-	x	x	x
Copepoda																					
Hersilioides latericeus	-	x	-	-	-	-	-	x	-	-	x	-	-	-	-	-	-	-	-	x	-
Caprellidae																					
Caprella erithizon	-	-	-	-	x	x	-	-	x	-	-	-	-	-	x	-	-	-	-	-	x
Cumacea																					
Cumopsis longipes	-	x	-	-	-	-	-	x	-	-	-	-	-	-	x	-	-	x	x	-	x
Iphinoe trispinosa	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	x
Decapoda																					
Carcinus maenas	-	-	-	-	-	-	-	-	x	x	-	x	x	x	x	-	-	-	-	x	x
Pagurus bernhardus	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-

Appendix 3. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Harpacticoida																					
Parathalestris harpacticoi	-	x	-	-	-	-	x	x	x	-	x	x	x	x	-	-	-	-	x	x	-
Isopoda																					
Idotea granulosa	-	-	-	-	x	x	x	-	x	x	-	-	-	x	-	-	-	-	x	x	x
I. neglecta	-	-	x	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	x	-
Palaemonidae																					
Palaemon longirostris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x
Tannaidacae																					
Apseudes talpa	-	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tanais dulongi	-	x	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-
Tanaissus lilljeborgi	-	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptochelia savignyi	-	x	-	-	-	x	x	x	x	x	x	x	x	x	-	-	x	x	x	x	x
MOLLUSCA																					
Bivalvia																					
Cerastoderma edule	-	-	x	x	x	-	-	-	-	-	-	-	x	-	-	x	x	x	-	x	-
Macoma balthica	x	-	-	-	-	-	-	x	-	-	-	-	-	-	x	x	-	-	x	-	x
Venerupis aurea	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
V. pullastra	-	-	-	x	x	-	-	-	-	x	x	x	-	-	-	-	-	-	-	-	-
V. saxatilis	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gastropoda																					
Buccinum undatum	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crepidula fornicata	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cylichnya cyllindrica	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Hydrobia neglecta	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	x
H. ulvae	x	x	x	x	-	-	-	x	x	x	x	x	x	x	x	x	x	-	x	x	x
Littorina littorea	-	-	-	-	-	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-	-
L. neglecta	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x	-	x	-	-	-
L. saxatillis	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-
Lornacea lucinalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-

Appendix 3. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Gastropoda (continued)																					
Mytilus edulis	x	x	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	x
Parvicardium exiguum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
Retusa obstusa	-	-	-	-	-	-	-	-	x	-	x	x	x	x	x	x	x	-	x	-	x
Rissoa parva	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	x	x
R. sarsi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Tornus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	x	-	-
ECHINODERMATA																					
Ophiuroida																					
Amphipholis squamata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-

Appendix 4. Macrozoobenthos species recorded at the sparse site of Ryde Beach seagrass bed (x = species recorded; - = species not recorded).

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
NEMATODA																					
Nematoda	-	x	-	x	x	-	x	x	x	x	x	x	-	-	x	x	x	x	x	x	x
ANNELIDA																					
Polychaeta																					
Amphitrite edwardsi	x	-	-	-	-	-	-	x	x	-	x	x	x	x	-	x	-	-	-	-	-
Arenicola marina	x	-	x	-	x	-	-	-	x	-	x	-	x	x	-	x	x	-	x	x	x
Aricidia minuta	-	-	x	x	x	x	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x
Capitella capitata	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Chaetozone setosa	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirratulus filliformis	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	x
Cirriformia tentaculata	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clymenura clypeata	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x	x	x
Eteone foliosa	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E. longa	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
E. picta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x
Euclymene lumbricoides	x	-	-	x	x	-	x	-	x	x	-	x	x	x	x	x	-	x	x	x	x
E. oerstedii	x	x	x	-	-	x	x	x	x	-	x	-	-	-	x	x	-	-	x	x	x
E. robusta	x	x	-	x	-	-	-	-	x	-	-	-	-	-	x	-	-	-	-	-	-
Eumida sanguinea	-	-	-	-	x	-	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-
Exogene hebes	-	x	x	x	x	x	x	x	x	x	-	x	x	x	x	x	-	x	x	x	x
E. verugera	-	-	x	-	-	-	x	-	x	x	-	-	-	-	-	x	x	x	x		
Glycera tridactyla	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heteromastus filiformis	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-
Laonice cirrata	-	x	-	-	-	-	-	x	-	-	x	-	-	-	-	-	-	-	-	-	-
Malacoceros fuliginosus	x	x	-	x	-	x	x	x	x	x	-	-	-	x	x	-	x	x	x	x	x
Nereis diversicolor	-	-	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	x	x	x	-
Nicolea zostericola	-	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	-	-
Nicomache lumbricalis	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notomastus latericeus	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Orbinia sertulata	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phyllodoce mucosa	-	-	-	x	x	x	x	-	-	-	x	x	-	x	x	-	-	-	-	-	-
Polydora ciliata	-	x	-	-	-	x	-	-	x	-	x	x	-	-	-	-	-	-	-	-	-

Appendix 4. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Polychaeta (continued)																					
Pygospio elegans	x	-	x	x	x	x	x	x	x	x	-	-	x	x	x	x	x	x	x	x	x
Scolelepis foliosa	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S. squamata	-	-	x	x	x	-	-	-	-	-	x	x	-	-	-	x	x	x	-	x	-
Scoloplos armiger	x	x	x	x	x	x	x	x	x	x	-	-	x	x	x	-	-	-	x	-	x
Sphaerosyllis bulbosa	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Spio filicornis	-	-	-	-	-	x	-	x	x	-	-	-	-	x	-	-	-	-	-	-	-
Spiophanes bombyx	-	-	-	-	-	-	x	-	x	-	-	-	-	-	-	x	-	x	x	x	x
Syllis gracilis	-	x	x	-	x	x	x	x	-	-	-	-	-	x	x	x	x	x	x	x	x
Typosyllis prolifera	x	x	x	x	x	x	-	-	x	x	x	x	x	x	x	x	x	x	-	x	x
Oligochaeta																					
Tubifex benedii	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ARTHROPODA																					
Amphipoda																					
Ampelisca brevicornis	-	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-	x	-	-	-
Ampithoe rubricata	-	x	x	-	x	x	x	-	x	-	-	-	-	-	-	-	x	x	x	-	x
Apherusa jurinei	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-
Atylus swammerdami	-	-	x	-	-	-	-	-	x	x	-	x	-	-	-	-	-	-	x	-	x
Bathyporeia guilliamsonia	-	-	-	-	-	x	-	x	x	-	-	-	x	x	-	-	-	-	-	-	-
Corophium arenarium	x	-	x	x	-	-	-	-	-	x	x	x	x	x	x	-	-	-	x	x	-
C. volutator	x	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	x
Erichthonius difformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	-	-
E. fasciatus	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	x	x	x	x	x	x
E. punctatus	-	x	x	x	x	-	x	x	x	x	x	x	-	x	x	x	x	-	x	x	x
Gammarus finmarchinus	-	-	-	x	x	x	x	x	x	-	-	-	-	x	x	x	-	-	x	-	-
G. zaddachi	x	-	x	x	x	-	x	-	x	x	-	-	-	-	-	-	-	-	-	-	-
Jassa falcata	-	-	x	-	-	x	-	-	x	-	-	-	-	x	-	-	-	-	-	x	-
Lillebjorgia pallida	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	x	-	-	-	-
Melita palmata	-	-	x	x	-	-	-	-	x	-	-	-	-	x	-	-	x	-	-	-	-
Orchestia gammarella	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pinnotheres pisum	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	x	x	x	x	x	x
Urothoe brevicornis	-	-	x	-	-	-	x	x	x	-	-	-	-	-	x	x	x	x	x	x	-

Appendix 4. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Amphipoda (continued)																					
U. marina	-	-	-	x	x	x	-	x	x	-	-	-	-	-	x	-	-	x	x	x	x
U. poseidonis	x	x	x	x	-	-	-	x	-	x	x	x	x	-	x	-	-	-	-	-	-
Caprellidae																					
Caprella linearis	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x
Cumacea																					
Cumopsis longipes	-	x	-	-	x	x	x	-	-	x	x	-	-	x	-	-	-	-	-	-	-
Iphinoe serrata	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x	x	-	x
I. trispinosa	-	x	x	-	x	x	-	-	-	-	-	-	x	-	x	-	-	-	x	-	x
Pseudocuma longicornis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	x
P. similis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
Decapoda																					
Carcinus maenas	-	-	x	-	-	-	-	-	x	x	x	-	x	-	-	-	-	-	-	-	-
Crangon crangon	-	-	-	-	-	-	-	-	-	x	-	-	x	x	-	-	-	-	-	-	-
Pagurus bernhardus	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Harpacticoida																					
Parathalestris harpacticoi	x	x	-	x	x	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x
Mysidacea																					
Siriella jaltensis	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Palaemonidae																					
Palaemon adspersus	-	-	x	x	-	-	-	x	x	x	-	-	-	x	x	-	-	-	-	-	-
P. longirostris	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda																					
Cirolana cranchii	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-
Idotea granulosa	x	-	x	x	x	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x
I. neglecta	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 4. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Tannaidacae																					
Aspeudes latreilii	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
Tanais dulongi	-	x	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Tanaissus lilljeborgi	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	x	x	x	x	x	x
Leptochelia savignyi	-	-	-	-	x	x	x	x	x	-	x	x	x	x	x	x	-	x	-	-	-
MOLLUSCA																					
Bivalvia																					
Cerastoderma edule	x	x	-	-	-	-	-	-	-	-	-	x	x	-	-	-	x	x	x	-	-
Macoma balthica	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Gastropoda																					
Buccinum undatum	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cylichna cylindricea	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
Hydrobia ulvae	x	x	x	-	x	-	-	x	-	x	x	-	x	x	x	-	-	-	x	x	x
Lacuna vincta	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Littorina littorea	-	-	-	x	-	-	-	-	-	x	-	-	-	x	x	-	-	-	-	-	x
L. neglecta	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	x	-
L. saxatillis	-	-	x	x	-	-	-	-	-	-	-	-	-	x	-	-	-	x	x	-	-
Lornacea lucinalis	-	-	-	-	-	-	-	-	-	-	-	x	-	-	x	-	-	x	-	-	-
Retusa obstusa	-	-	-	-	-	-	-	-	-	x	-	x	-	x	-	x	-	-	x	x	x
Rissoa parva	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	x	-	x
ECHINODERMATA																					
Ophiuroida																					
Amphipholis squamata	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 5. Average abundance of macrozoobenthos species (individuals per core) recorded at the dense site of Ryde Beach seagrass bed.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
NEMATODA																					
Nematoda	1.6	1.4	0.2	1.4	2.2	1.0	1.0	1.0	4.0	2.8	0.6	1.6	2.4	4.2	2.2	0.2	1.8	1.0	3.6	1.0	6.8
ANNELIDA																					
Polychaeta																					
Amphitrite edwardsi	0.0	1.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.2	0.0	0.2	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.2
Amphitritides gracilis	0.2	0.0	0.2	0.4	0.4	0.0	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0
Arenicola marina	0.8	0.2	0.0	1.2	0.0	0.0	0.0	0.0	1.6	2.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.6	2.8
Aricedia minuta	0.2	0.4	3.8	9.2	2.2	2.4	0.0	0.2	0.8	3.2	1.6	2.4	6.0	9.6	2.0	1.8	2.0	4.0	3.6	1.0	0.8
Capitella capitata	5.6	4.4	2.6	8.0	7.8	7.0	3.6	4.8	3.0	4.8	5.2	7.8	5.2	10.0	10.8	5.4	5.8	4.8	6.8	3.4	6.8
Chaetozone setosa	0.0	0.0	0.0	0.0	0.0	1.8	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cirratulus filliformis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.4	0.2	0.8
Cirriformia tentaculata	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Clymenura clypeata	0.4	0.2	0.0	0.0	0.0	0.0	0.0	1.0	0.4	1.6	0.0	0.2	0.0	0.2	0.0	0.2	0.0	0.0	0.4	0.2	0.6
Eteone foliosa	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
E. longa	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
E. picta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0
Euclymene lumbricoides	1.6	0.6	1.0	0.6	1.2	0.2	0.0	1.2	0.2	0.4	0.6	0.0	2.4	1.4	2.8	0.4	0.0	0.6	1.0	1.0	1.6
E. oerstedii	0.0	0.8	0.4	1.2	0.0	1.0	0.6	1.4	1.0	1.2	0.0	0.0	0.0	1.0	0.0	0.2	0.0	0.2	0.4	0.2	1.0
E. robusta	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Eulalia aurea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Eumida sanguinea	0.0	0.0	0.0	0.2	0.0	0.2	0.6	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphrosyne foliosa	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Exogene hebes	0.0	0.4	3.0	1.4	8.0	6.2	1.6	5.4	5.8	1.6	0.6	2.2	6.0	7.6	12.8	3.2	5.6	4.4	5.0	0.8	0.6
E. verugera	0.0	0.0	0.2	0.0	0.0	0.0	1.2	0.0	3.4	2.2	0.0	0.2	0.0	0.0	0.4	0.0	0.6	0.4	0.8	0.0	0.0
Glycera tridactyla	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heteromastus filiformis	0.0	0.0	0.4	0.2	0.0	0.0	0.8	0.2	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lanice conchilega	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laonice cirrata	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Malacoceros fuliginosus	0.2	1.6	0.4	0.0	0.2	0.6	0.0	1.6	1.8	1.2	3.0	0.0	1.2	1.4	0.0	0.2	0.2	0.2	1.4	1.8	2.4
Nepthys caeca	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.6
Nereis diversicolor	0.2	0.2	0.2	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.0	0.4	0.0	0.4	1.2
Nicolea zostericola	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Polychaeta (continued)																					
Nicomache lumbricalis	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notomastus latericeus	0.2	0.0	0.0	0.0	0.0	1.6	1.8	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Perinereis cultrifera	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phyllodoce longipes	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
P. mucosa	0.4	0.8	1.4	1.0	1.0	0.2	1.0	0.8	0.6	0.0	0.2	0.8	1.4	1.0	1.4	0.0	0.4	0.2	0.2	0.2	0.8
Pista cristata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polydora ciliata	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	1.0
P. giardi	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.2	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pygospio elegans	1.6	3.6	2.2	1.6	1.6	1.4	1.4	3.2	2.6	2.0	8.0	5.0	0.4	0.4	4.6	1.8	1.8	3.0	16.6	11.6	22.6
Sabellidae sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Scolelepis foliosa	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. squamata	0.0	0.2	0.4	0.0	0.4	0.0	0.4	0.0	0.6	0.2	0.0	0.0	2.4	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8
Scoloplos armiger	3.4	3.2	1.8	1.6	0.0	1.2	1.2	2.2	4.2	4.4	4.2	3.0	0.0	0.0	0.6	0.8	0.6	1.2	4.2	3.4	5.0
Sphaerosyllis bulbosa	0.0	0.0	0.2	0.2	0.0	0.0	0.2	0.0	0.4	0.0	0.0	0.0	0.8	0.6	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Spio filicornis	0.0	0.2	0.0	0.4	0.0	0.0	2.2	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.6	0.0	0.2
Spiophanes bombyx	0.0	0.0	0.0	0.2	0.0	0.6	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Syllis gracilis	0.0	3.8	0.6	0.0	1.2	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.2	0.0	0.0	0.2	0.2	0.2	1.2	2.0	2.4
Terebellidae sp.	0.2	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Typosyllis prolifera	0.0	8.4	1.4	1.0	0.0	0.0	0.0	0.0	0.8	0.6	0.2	0.6	4.0	0.6	0.8	0.4	0.0	0.0	2.0	1.4	4.6
Oligochaeta																					
Tubifex benedii	1.2	1.6	0.2	0.0	0.0	0.2	0.2	0.8	1.2	0.4	0.0	0.4	0.0	0.6	2.2	0.2	0.0	0.0	0.2	0.0	0.0
ARTHROPODA																					
Amphipoda																					
Ampelisca brevicornis	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6
Ampithoe gammaroides	0.0	0.4	0.8	0.4	0.0	0.2	0.0	0.0	1.2	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
A. rubricata	0.0	0.8	7.4	16.2	8.8	1.2	0.0	0.2	4.2	5.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Atylus swammerdami	0.0	0.0	0.4	0.4	0.0	0.0	0.0	0.8	2.6	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.4	0.0	0.2	0.2	0.4
Bathyporeia guilliamsonia	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.2	0.0	0.6	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0
Chaetogammarus marinus	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cheirocratus intermedius	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. sundevallii	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Amphipoda (continued)																					
Corophium arenarium	2.2	2.8	1.4	2.4	0.0	0.0	0.0	0.2	0.0	0.4	0.2	1.8	2.0	1.6	2.4	0.2	0.0	0.0	2.4	2.2	3.2
C. crassicorne	0.2	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. volutator	1.6	2.0	1.6	0.0	0.0	0.0	0.0	0.2	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.6	0.4
Erichthonius difformis	0.0	0.0	1.0	50.0	8.4	5.2	0.0	0.0	3.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.8	1.8
E. fasciatus	0.0	0.2	0.0	3.8	3.8	0.8	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	1.2	1.0	0.0	0.8
E. punctatus	0.0	1.0	8.2	1.4	3.4	0.6	11.2	2.0	40.0	15.8	0.2	1.6	19.6	34.8	49.0	15.2	18.8	15.6	32.4	7.4	15.6
Gammarus finmarchinus	0.0	0.0	0.6	0.0	0.0	0.0	2.4	0.4	8.2	1.4	0.0	0.0	0.2	1.6	0.8	0.8	0.6	1.6	3.0	0.6	4.4
G. zaddachi	0.0	0.0	1.6	0.0	0.4	0.0	0.2	0.0	12.0	1.8	0.0	0.6	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.6
Hyale nillssoni	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jassa falcata	0.4	0.4	0.4	0.0	0.0	0.0	0.2	0.0	3.2	2.4	0.0	0.0	0.0	0.6	0.2	0.0	0.0	0.0	0.2	1.0	0.6
J. pusilla	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lillebjorgia pallida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2
Melita palmata	0.4	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.2
M. obtusata	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microprotopus maculatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orchestia gammerella	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Pinnotheres pisum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Urothoe brevicornis	0.0	0.0	0.0	0.4	0.0	6.0	0.6	0.6	0.0	0.2	0.0	0.0	0.0	3.6	0.0	0.2	0.2	0.0	0.4	0.8	0.0
U. marina	1.2	0.8	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.6	1.0	0.0	0.0	0.0	0.8	0.2	0.0	0.2	0.8	2.0	0.8
U. poseidonis	2.8	1.4	1.2	0.0	0.0	0.0	0.0	3.6	0.0	0.6	3.6	5.2	5.0	0.2	0.0	0.0	0.0	0.0	0.8	0.4	1.4
Copepoda																					
Hersilioides latericeus	0.0	0.2	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Caprellidae																					
Caprella erithizon	0.0	0.0	0.0	0.0	0.8	0.4	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2
Cumacea																					
Cumopsis longipes	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.2	0.2	0.0	0.8
Iphinoe trispinosa	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2
Decapoda																					
Carcinus maenas	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	2.4	0.0	0.4	0.4	0.4	0.2	0.0	0.0	0.0	0.0	0.6	0.6
Pagurus bernhardus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Harpacticoida																					
Parathalestris harpacticoi	0.0	0.8	0.0	0.0	0.0	0.0	0.2	2.6	1.2	0.0	0.2	0.2	0.2	1.0	0.0	0.0	0.0	0.0	0.2	0.4	0.0
Isopoda																					
Idotea granulosa	0.0	0.0	0.0	0.0	1.6	0.2	0.2	0.0	0.8	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.8	0.4
I. neglecta	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Palaemonidae																					
Palaemon longirostris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2
Tannaidacae																					
Apseudes talpa	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tanais dulongi	0.0	0.6	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Tanaissus lilljeborgi	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leptochelia savignyi	0.0	0.4	0.0	0.0	0.0	0.4	0.8	1.0	0.2	0.4	1.8	2.0	0.8	1.4	0.0	0.0	1.0	2.0	3.2	2.2	1.0
MOLLUSCA																					
Bivalvia																					
Cerastoderma edule	0.0	0.0	0.0	0.8	0.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.2	0.2	0.0	0.2	0.0
Macoma balthica	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.2	0.0	0.4
Venerupis aurea	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
V. pullastra	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.2	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
V. saxatilis	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda																					
Buccinum undatum	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crepidula fornicata	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cylichnya cyllindrica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hydrobia neglecta	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
H. ulvae	5.6	2.6	3.6	0.6	0.0	0.0	0.0	0.2	1.2	1.2	3.0	3.0	3.0	1.4	1.4	0.6	0.8	0.0	4.4	6.0	2.8
Littorina littorea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
L. neglecta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0
L. saxatillis	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.6	0.0	0.0	0.0	0.0	0.0
Lornacea lucinalis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 5. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Gastropoda (continued)																					
Mytilus edulis	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Parvicardium exiguum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Retusa obstusa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	1.2	0.4	0.4	0.2	0.2	0.2	0.2	0.0	0.2	0.0	0.2
Rissoa parva	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.4	0.4	0.4
R. sarsi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2
Tornus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0
ECHINODERMATA																					
Ophiuroida																					
Amphipholis squamata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0

Appendix 6. Average abundance of macrozoobenthos species (individuals per core) recorded at the sparse site of Ryde Beach seagrass bed.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
NEMATODA																					
Nematoda	0.0	1.4	0.0	0.2	0.2	0.0	0.6	0.2	2.8	1.6	0.2	0.6	0.0	0.0	0.4	0.2	0.8	0.6	0.8	0.4	1.2
ANNELIDA																					
Polychaeta																					
Amphitrite edwardsi	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	0.2	0.2	0.2	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Arenicola marina	1.0	0.0	1.0	0.0	0.4	0.0	0.0	0.0	1.4	0.0	2.0	0.0	0.2	0.2	0.0	0.2	0.2	0.0	0.6	0.2	0.8
Aricidia minuta	0.0	0.0	4.2	3.2	0.2	0.2	0.0	0.0	2.2	2.2	6.8	1.2	3.0	2.8	1.0	1.0	1.0	1.8	2.6	0.6	0.2
Capitella capitata	3.6	3.8	3.2	1.2	6.6	3.4	0.6	2.2	0.8	4.8	0.0	3.0	2.0	2.4	3.6	2.8	1.0	2.4	5.8	2.0	0.8
Chaetozone setosa	0.0	0.0	0.0	0.2	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cirratulus filliformis	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4
Cirriformia tentaculata	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clymenura clypeata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.0	0.6
Eteone foliosa	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
E. longa	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
E. picta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2
Euclymene lumbricoides	1.8	0.0	0.0	1.0	0.4	0.0	0.2	0.0	0.2	0.6	0.0	0.2	0.6	0.4	1.0	0.2	0.0	0.2	1.2	1.4	1.6
E. oerstedii	0.4	0.8	1.0	0.0	0.0	0.6	1.0	0.8	1.2	0.0	0.8	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.4	0.4	0.2
E. robusta	0.4	0.8	0.0	0.2	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Eumida sanguinea	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.2	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Exogene hebes	0.0	0.4	0.8	2.6	1.6	0.8	3.0	1.2	2.2	2.4	0.0	1.2	5.0	7.2	9.8	1.8	0.0	1.0	1.8	0.8	0.2
E. verugera	0.0	0.0	0.2	0.0	0.0	0.0	0.6	0.0	3.2	2.0	0.0	0.0	0.0	0.0	0.0	0.2	0.6	0.2	1.2	0.0	0.0
Glycera tridactyla	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Heteromastus filiformis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Laonice cirrata	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Malacoceros fuliginosus	1.4	0.6	0.0	0.2	0.0	1.0	1.4	1.8	0.8	1.2	0.0	0.0	0.0	0.8	0.2	0.0	0.2	0.2	1.2	1.2	1.6
Nereis diversicolor	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.2	0.0
Nicolea zostericola	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nicomache lumbricalis	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notomastus latericeus	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orbinia sertulata	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Phyllodoce mucosa	0.0	0.0	0.0	0.2	0.6	0.4	0.4	0.0	0.0	0.0	0.2	0.4	0.0	0.8	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Polydora ciliata	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	4.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 6. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Polychaeta (continued)																					
Pygospio elegans	1.6	0.0	1.0	2.6	0.6	0.8	1.0	0.6	4.2	2.4	0.0	0.0	1.0	2.2	1.2	0.0	0.0	0.0	2.8	0.0	3.6
Scolelepis foliosa	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
S. squamata	0.0	0.0	0.2	0.2	0.4	0.0	0.0	0.0	0.0	0.0	4.0	3.0	0.0	0.0	0.0	0.6	1.0	1.0	0.0	2.0	0.0
Scoloplos armiger	4.2	0.6	1.8	0.6	3.2	3.6	1.4	1.8	1.8	6.2	0.0	0.0	1.0	2.2	1.2	0.0	0.0	0.0	2.8	0.0	3.6
Sphaerosyllis bulbosa	0.0	0.0	0.0	1.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Spio filicornis	0.0	0.0	0.0	0.0	0.0	0.4	0.0	2.0	0.4	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spiophanes bombyx	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.4	1.2	1.4	1.4
Syllis gracilis	0.0	1.2	0.4	0.0	0.2	3.6	0.2	0.8	0.0	0.0	0.0	0.0	0.0	0.6	0.2	0.2	1.0	0.4	1.4	0.8	2.4
Typosyllis prolifera	0.4	1.8	0.4	0.4	2.2	0.6	0.0	0.0	0.2	0.4	1.0	0.4	1.0	0.4	1.2	1.6	0.2	0.2	0.0	0.2	0.2
Oligochaeta																					
Tubifex benedii	1.4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ARTHROPODA																					
Amphipoda																					
Ampelisca brevicornis	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Ampithoe rubricata	0.0	0.8	2.4	0.0	0.6	1.0	0.6	0.0	6.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.2	0.4	0.0	0.6
Apherusa jurinei	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Atylus swammerdami	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	8.8	0.6	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.2
Bathyporeia guilliamsonia	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.2	0.4	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corophium arenarium	1.0	0.0	0.8	0.6	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.2	0.4	0.4	0.2	0.0	0.0	0.0	0.2	0.2	0.0
C. volutator	0.4	0.0	0.8	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.6
Erichthonius difformis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.6	0.0	0.0
E. fasciatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	3.0	1.0	4.4	8.6	0.4	0.6
E. punctatus	0.0	2.8	7.0	26.4	1.2	0.0	3.0	0.4	1.4	6.4	0.4	1.8	0.0	5.6	5.2	0.4	0.2	0.0	0.4	0.2	0.4
Gammarus finmarchinus	0.0	0.0	0.0	0.6	0.4	2.2	0.2	0.2	12.0	0.0	0.0	0.0	0.0	0.8	0.8	0.2	0.0	0.0	0.2	0.0	0.0
G. zaddachi	0.2	0.0	0.8	0.4	0.2	0.0	0.4	0.0	2.4	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jassa falcata	0.0	0.0	0.4	0.0	0.0	0.2	0.0	0.0	3.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Lillebjorgia pallida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Melita palmata	0.0	0.0	0.8	0.2	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Orchestia gammarella	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pinnotheres pisum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.6	0.2	1.0	1.8	1.4	0.2

Appendix 6. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Amphipoda (continued)																					
Urothoe brevicornis	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.2	0.2	0.0	0.0	0.0	0.0	2.2	0.8	0.4	0.6	0.2	0.4	0.8	0.0
U. marina	0.0	0.0	0.0	0.6	1.6	0.4	0.0	0.4	0.6	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.2	0.8	0.6	0.8
U. poseidonis	0.4	0.2	0.4	1.2	0.0	0.0	0.0	0.8	0.0	2.0	1.2	2.0	2.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Caprellidae																					
Caprella linearis	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	1.8
Cumacea																					
Cumopsis longipes	0.0	0.2	0.0	0.0	0.4	1.8	0.2	0.0	0.0	0.2	0.4	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Iphinoe serrata	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2	1.4	0.0	1.8
I. trispinosa	0.0	0.2	0.4	0.0	1.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.2	0.0	0.0	0.0	2.2	0.0	6.0
Pseudocuma longicornis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	3.6
P. similis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.6	0.8
Decapoda																					
Carcinus maenas	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.2	1.6	0.2	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crangon crangon	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pagurus bernhardus	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Harpacticoida																					
Parathalestris harpacticoi	0.2	0.6	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.4	0.2	0.2
Mysidacea																					
Siriella jaltensis	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Palaemonidae																					
Palaemon adspersus	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.8	1.0	0.2	0.0	0.0	0.0	0.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0
P. longirostris	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isopoda																					
Cirolana cranchii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Idotea granulosa	0.6	0.0	0.4	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.4	0.2	0.2
I. neglecta	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 6. Continued.

Species	Se-97	Oc-97	No-97	De-97	Ja-98	Fe-98	Ma-98	Ap-98	My-98	Jn-98	Jl-98	Au-98	Se-98	Oc-98	No-98	De-98	Ja-99	Fe-99	My-99	Jl-99	Oc-99
Tannaidacae																					
Aspeudes latreilii	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.2	2.2
Tanais dulongi	0.0	0.4	0.6	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tanaissus lilljeborgi	0.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.8	2.4	7.2	1.0	3.8
Leptochelia savignyi	0.0	0.0	0.0	0.0	1.0	2.0	2.2	1.4	0.8	0.0	2.0	1.0	1.6	2.4	1.0	0.2	0.0	0.2	0.0	0.0	0.0
MOLLUSCA																					
Bivalvia																					
Cerastoderma edule	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.2	0.2	0.2	0.0	0.0
Macoma balthica	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda																					
Buccinum undatum	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cylichna cylindricea	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.6	2.0	2.8	2.6	5.0
Hydrobia ulvae	3.6	3.4	2.2	0.0	0.2	0.0	0.0	1.0	0.0	1.0	0.4	0.0	1.2	0.8	1.0	0.0	0.0	0.0	0.6	0.4	2.8
Lacuna vincta	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Littorina littorea	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.4
L. neglecta	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.6	0.0
L. saxatillis	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.2	0.0	0.0
Lornacea lucinalis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.0
Retusa obstusa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.6	0.0	0.2	0.0	0.2	0.0	0.0	0.4	0.2	1.2
Rissoa parva	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.6	0.0	1.4
ECHINODERMATA																					
Ophiuroida																					
Amphipholis squamata	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0