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Role of *Posidonia oceanica* bed structure in determining the diversity of associated macroinvertebrate assemblages

By

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Role of *Posidonia oceanica* bed structure in determining the diversity of associated macroinvertebrate assemblages

JOSEPH ANTHONY BORG

Abstract

Seagrass beds are highly productive shallow-water marine ecosystems and serve as a habitat for numerous invertebrates and fishes, some of which constitute important fisheries species. Seagrass beds play an important role in physical coastal dynamics, since they stabilise soft bottoms, while their leaf canopy attenuates strong wave action and currents, thereby, reducing coastal erosion. However, seagrass habitats are undergoing a decline worldwide, hence, there is an urgent need for data on the influence of bed fragmentation and changes in plant architecture on the diversity of associated biota. In the Mediterranean Sea, the endemic seagrass *Posidonia oceanica* forms extensive beds that have a high structural complexity and support a high biodiversity, making them one of the most important marine habitat types in the region. The present study investigated the influence of *P. oceanica* bed structure (seagrass bed morphology and within-bed architecture) on the diversity of associated macrofauna. Pilot surveys were made to map the occurrence and spatial distribution of different types of *P. oceanica* beds present off the northeastern coast of the Maltese Islands, to enable selection of four appropriate study locations. A quantitative sampler, which samples the total macroinvertebrate assemblages of *P. oceanica* beds, was designed and tested to determine the appropriate area and number of sampling units required to achieve given levels of accuracy and precision. Using data gathered from the pilot survey, studies were made to examine for differences in *P. oceanica* plant architecture, and in the species richness and abundance of motile macroinvertebrates between continuous (non-fragmented) and reticulate (fragmented) beds of the seagrass, across three different spatial levels: (a) large (several km), (b) medium (*circa* 100 m) and small (tens of metres). A separate study examined differences in the species richness and abundance of associated motile macroinvertebrates between living matte (bearing living shoots) and dead matte (without living shoots) of *P. oceanica.* Results of univariate and multivariate analyses indicated that there was no consistent pattern of significant differences in plant architecture, and in the species richness and abundance of associated motile macroinvertebrates between the two *P. oceanica* bed types. Significant differences in macroinvertebrate species richness and abundance were detected between *P. oceanica* beds at the large spatial level that were significantly related to seagrass epiphytes and mean sediment grain size. Significant differences in macroinvertebrate species richness and abundance were detected between *P. oceanica* beds at the medium spatial level that were significantly related to shoot biomass. Significant differences in the assemblage composition of macroinvertebrates associated with *P. oceanica* beds were detected by multivariate analysis at the large and small spatial levels, with the best explanation for the multivariate assemblage structure being a combination of environmental variables that included epiphytes and sediment grain size. The results of the study comparing the motile macroinvertebrates of living and dead matte showed that dead matte supported significantly higher species richness and abundance of associated motile macroinvertebrates, and had a significantly different macroinvertebrate assemblage structure, compared to living matte. Furthermore, a greater number of species occurred exclusively in dead matte than in living matte. It was concluded that natural fragmentation of continuous to reticulate *P. oceanica* beds does not lead to changes in plant architectural differences, or to a reduction in diversity of associated macroinvertebrates, nor does complete loss of the foliar canopy necessarily lead to a reduced diversity of macrofauna. Local factors, including nutrient levels in the water column (which enhanced epiphytic growth on the seagrass), sediment grain size and the hydrodynamic regime, were more important in influencing the diversity of macrofauna associated with *P. oceanica* beds, than bed type, leading to significant spatial variation in the associated macroinvertebrate assemblages. The study concluded that the relative importance of different factors in influencing the diversity of macroinvertebrates associated with *P. oceanica* beds varied, depending on scale. The results are discussed in the light of the available published data on fragmentation of seagrass habitat and on current Euro-Mediterranean proposals for the conservation of different bed types of *P. oceanica.* Attempts to classify different bed types of *P. oceanica* in categories according to value should be based on adequate ecological data. Different bed types of *P. oceanica* all form part of a dynamic heterogeneous landscape where transformation from one bed type to another may occur, but which does not necessarily lead to loss of biodiversity. Hence, equal effort should be directed at conserving and managing different bed types of *P. oceanica*.

To my family

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Signed ....

Date ....26th March 2004....

CHAPTER 1

GENERAL INTRODUCTION

1.1 IMPORTANCE OF STUDYING SEAGRASS BED STRUCTURE

Biological diversity (or 'biodiversity'), the variety among living organisms, can be viewed at various levels: genetic, species, phyletic, functional, assemblage, habitat and ecosystem (Gray, 1997). Natural and human processes act at all these levels, causing alteration of biodiversity (Huston, 1994). Biodiversity provides essential resources for farming, biotechnology, recreation, fuels and raw materials for industry. Furthermore, biodiversity provides essential services for recycling waste, controlling the global nutrient and chemical cycles, and buffering against climate change. Alteration that leads to loss of biodiversity is of major concern, as evidenced by the huge scientific research effort and attention of international policymakers to the concept (e.g. the 1992 United Nations Convention on Biological Diversity). Rapid growth of the human population in recent years, accompanied by increased industrialisation, land use and exploitation of natural resources, and associated indirect anthropogenic effects (e.g. pollution and global warming), have led to alteration and/or loss of habitat, the most serious threat to biodiversity, since this leads to loss, and possibly extinction, of species (Wilcox & Murphy, 1985). Efforts to counteract habitat loss are hindered by the dearth of knowledge of the relative ecological value of different habitats, natural factors controlling their physical and biotic characteristics, the biology of the species inhabiting them, and effects of alteration by anthropogenic activities. Since the survival of a species depends on the properties of the surface or medium on/in which it lives, one of the most important attributes of a habitat that influences its biological diversity is its 'structure'; its physical arrangement in the environment (McCoy & Bell, 1991). Habitat structure varies greatly between different habitats and also between habitats of the same type located in different environmental regimes (e.g. Wiens, 1989). Habitat structure can be quantified in different ways in order to examine the relationships between the physical and environmental characteristics of a habitat and its associated biodiversity (Bell et al., 1991).

Coastal areas support a greater variety of marine habitats than the open ocean (Gray, 1997). Many coastal habitats, for example, coral reefs, mangrove forests and seagrass beds, support biotic assemblages with a very high biodiversity (Costanza et al., 1997), which provide important resources and services for the human population, including fisheries, aquaculture, biotechnology, recreation and fuels. However, being located closest to human settlement, coastal areas are bearing the brunt of anthropogenic disturbance and degradation, and loss of marine coastal habitats is occurring at an alarming rate. For example, Wilkinson et al. (1993) claimed that more than half of the coral reefs of southeast Asia, which constitute a third of the world's coral reef habitat, have already been destroyed, or are on the verge of destruction. Hammond (1992) claimed that 40 – 70% of Africa's mangrove forests have been lost, while in the Philippines and Equador over 70% of this habitat type has been destroyed to make way for shrimp farms (Honculada Primavera, 1991). Degradation and decimation of seagrass habitats is equally alarming and a global decline is evident (Short & Wyllie Echeverria, 1996; Ruckelshaus & Hays, 1998; Green & Short, 2003), with global loss estimated at 16% (Short & Wyllie Echeverria, 2000). As a result, marine biodiversity is a priority for conservation and management (Ehrlich & Ehrlich, 1992; Perrings et al., 1992; O'Neill, 1997).

Seagrasses form beds that consist of one or more phanerogam species and constitute habitats that have a high ecological value. They are highly productive and serve as refugia against predation and as a nursery for many motile macroinvertebrates and fishes (see reviews by den Hartog, 1967; Kikuchi & Peres, 1977; Kikuchi, 1980; Philips & McRoy, 1980; Hemminga & Duarte, 2000). Several seagrass-associated macrofauna, for example, large decapods and fishes, constitute important fishery species (see review by Jackson et al., 2001). Seagrass beds also have an important influence on the physical environment, since their leaf canopy traps suspended matter (Ward et al., 1984) and acts as a buffer against strong water movement (Fonseca et al., 1982; Fonseca & Kenworthy, 1987; Fonseca & Cahalan, 1992), while their root-rhizome layer consolidates soft sediments (Strawn, 1961; den Hartog & Phillips, 2001), thereby reducing coastal erosion. Because of their high productivity and important interaction with the physical environment, seagrass beds are considered to be important shallow-water ecosystems, with very high ecological and economic values (Costanza et al., 1997). Consequently, many countries have adopted conservation measures to protect seagrass habitats against degradation and loss (Green & Short, 2003), while in other areas, seagrass beds are the focus of special conservation and management programmes (e.g. Pulich et al., 1997). However, effective conservation is hindered by lack of data on the relationships between seagrass bed structural attributes, such as bed type and within-bed plant architecture, and the diversity of associated biotic assemblages. As a result, conservation biologists and coastal managers are unable to: (i) determine whether alteration of seagrass bed structure (i.e. fragmentation) will affect the associated biodiversity; (ii) justify the application of different (or similar) conservation measures for different bed types (e.g. fragmented vs non-fragmented); (iii) quantify loss of biodiversity when seagrass beds are fragmented or lost completely; and (iv) quantify and/or predict gain of biodiversity during attempts to restore seagrass habitat. Clearly, it is important that a detailed understanding of seagrass bed structure and its relationship with the associated biodiversity is obtained.

1.2 SEAGRASS BIOLOGY

1.2.1 Seagrass diversity

Seagrasses are angiosperms that occur in shallow, coastal areas worldwide, including estuaries and brackish waters, but are generally absent from freshwater environments (den Hartog, 1967; 1979), although some species are capable of tolerating fresh or hypersaline waters (Hemminga & Duarte, 2000; Short et al., 2001). Palaeontological evidence suggests that seagrasses colonised the marine environment, probably the Tethys Sea, during the Cretaceous (Brazier, 1975; Mazzella et al., 1986; Phillips & Menez, 1988). Three genera of living seagrasses, *Halophila*, *Zostera* and *Posidonia* comprise around 55% of seagrass species and appear to have evolved from lineages that appeared relatively early in time (den Hartog, 1970). Traditional views on the origin of seagrasses have maintained an evolutionary descent from coastal plants, rather than hydrophytes, and the possession of lignified stems by most seagrass taxa supports this theory (Larkum & den Hartog, 1989). However, the holders of such views also suggest that the more recently evolved seagrass species, such as those belonging to the genus *Enhalus,* have evolved from a freshwater ancestor (Larkum & den Hartog, 1989). Evidence from genetic studies (e.g. Les et al., 1997) indicates a polyphyletic origin of seagrasses from three major ancestral groups: (i) a freshwater plant for the Hydrochartaceae, (ii) a saltmarsh or aquatic ancestor for the Zosteraceae, and (iii) an ancestor of *Ruppia* for the remaining families. Whatever the evolutionary lineage, seagrasses have acquired three key adaptations to enable them to colonise the marine environment successfully: (i) leaves that are morphologically adapted to a high-energy environment, (ii) hydrophyllous pollination, (iii) extensive lacunar systems to allow transport of oxygen to belowground structures buried in anoxic sediment, and (iv) the plants acquire bicarbonate ions from the water rather than carbon dioxide for their carbon requirements (Hemminga & Duarte, 2000). All seagrasses have a relatively similar gross morphology, characterised by the presence of linear or strap-like leaves (den Hartog, 1967). Different seagrasses, however, exhibit a broad structural anatomy (den Hartog, 1970). The considerable plasticity of seagrass morphology has led to the use of different characters for taxonomic purposes, resulting in disagreement on the exact number of living species (Hemminga & Duarte, 2000). However, most authors agree that there are around 60 species of seagrasses, grouped into 13 genera and 5 families (den Hartog, 1970;

Short et al., 2001). The family Posidoniaceae Lotsy comprises a single genus *Posidonia* König, with nine species: *P. sinuousa* Cambridge & Kuo, *P. angustifolia* Cambridge & Kuo, *P. australis* Hook, *P oceanica* (Linnaeus) Delile, *P. oestenfeldii* den Hartog, *P denhartogii* Kuo & Cambridge, *P. robertsoniae* Kuo & Cambridge, *P. kirkmanii* Kuo & Cambridge, and *P. coriacea* Cambridge & Kuo (Kuo & den Hartog, 2001). Of these, eight species occur in Australia and one (*P. oceanica*) occurs in the Mediterranean Sea.

1.2.2 Seagrass distribution

The global distribution of seagrasses has been described by several workers (see den Hartog, 1970, Phillips & Menez, 1988; Green & Short, 2003), however, distribution data are lacking for the southeast Pacific, South America, West Africa and Antartica (Short et al., 2001), and for deeper waters worldwide (e.g. Lee Long et al., 1996). Thus, estimates of gobal seagrass cover have been made indirectly and are only approximate (e.g. 0.6×10^6 km^2 = 0.15% of the global ocean; Charpy-Roubaud & Sournia, 1990). In general, seagrasses have a wide geographical distribution, extending from above the Arctic Circle southward to the southern hemisphere (Short et al., 2001). Hemminga & Duarte (2000) discriminated between nine different biogeographical seagrass floras, however, separation between them was not distinct, since several seagrasses occur in more than one biogeographical group. The presence of congeneric species in different floras may have resulted from fragmentation of a much wider distribution through rearrangement of continental land masses, followed by extinction of some taxa (Larkum & den Hartog, 1989). Seagrasses occur in a broad variety of ecosystems, ranging from estuaries to the open sea (den Hartog & Phillips, 2001), from the intertidal to water depths of around 50 m (den Hartog & Phillips, 2001). Most species grow on soft sediment substrata but some (e.g. *Phyllospadix*) grow on rocky substrata (Hemminga & Duarte, 2000). Overall, the primary factors influencing the distribution of seagrasses appear to be nutrient and light availability

(Dennison, 1987; Short, 1987), however, the quality and type of substratum are also important determinants (Marbà & Duarte, 2001). For example, soft sediments with high organic content may have high concentrations of phytotoxic compounds (e.g. sulphide), which inhibit seagrass growth (Hemminga, 1998).

Posidonia oceanica (Linnaeus) Delile is endemic to the Mediterranean Sea, where it is the dominant seagrass throughout both west and east basins. Of the five seagrass species known from the Mediterranean Sea [*P. oceanica* (L.) Delile, *Cymodocea nodosa* (Ucria) Ascherson, *Zostera marina* Linnaeus, *Zostera noltii* Hornemann and *Halophila stipulacea* Forsskal], *P. oceanica* forms the most extensive beds (estimated total coverage of 2.5 – 5.5 million hectares; Buia et al., 2000) and is common at depths ranging between 1 and 40m (den Hartog, 1970), where it may comprise the dominant habitat type (Boudouresque et al., 1975). *P. oceanica* thrives best on sandy bottoms in clean waters, but also occurs frequently on rocky substrata (Pessani et al., 1984; Augier, 1986; Chimenz et al., 1989) where it can form continuous meadows. *P. oceanica* does not occur in estuaries (Procaccini et al., 2003), but has been reported from hypersaline (42-46‰) environments (e.g. Perez-Ruzafa et al., 1989). *P. oceanica* may occur at depths that are unusual for other seagrasses (> 40m), for example in Levant Island (France) (Augier & Boudouresque, 1979), in Sulana Bay (Corsica) (Boudouresque et al., 1990a), and in Malta (Borg & Schembri, 1995a). The spatial extent of *P. oceanica* beds has been mapped in several parts of the Mediterranean, mainly using side-scan sonar (e.g. Rey & Diaz del Rio, 1989; Piazzi et al., 2000) or aerial photography (e.g. Augier & Boudouresque, 1976; Ramos Esplá, 1984; Boudouresque et al., 1985b) in combination with diving techniques to enable ground-truthing of data collected remotely. Studies of the spatial distribution of *P. oceanica* beds have also been made to monitor temporal changes in coverage of the seagrass. In surveys of the last type, the periphery of the seagrass beds has been marked by permanent means (for example small moorings) and progression/regression of the bed boundary measured with time (Augier, 1986; Boudouresque et al., 1990b). Other workers have monitored changes in *P. oceanica* coverage and within-bed structure with time by deploying permanent quadrats (e.g. Boudouresque et al., 1981). The results obtained from such monitoring indicate a general trend of decrease in shoot density and coverage during the past few decades (Procaccini et al., 2003).

1.2.3 Reproduction in seagrasses

Seagrasses reproduce using sexual and asexual mechanisms, however, there are large differences in the reproductive strategy used by different (and sometimes the same) seagrass species in different regions. For example, on exposed sandy bottoms in the Baltic Sea, *Z. marina* propagates mainly by vegetative propagation, whereas in sheltered areas it reproduces sexually (e.g. Baden & Bostrom, 2001). *P. oceanica* is a monoecious species, with both male and female flowers occurring in the same inflorescence (den Hartog, 1970; Procaccini et al., 2003). Dispersal of *P. oceanica* occurs mainly by: (i) dispersal of cuttings that are separated from the parent bed by strong wave action and transported to a new site where they become established; (ii) production of new shoots by asexual reproduction, leading to lateral growth of the parent bed; and (iii) sexual reproduction, which involves the production of flowers followed by fruiting, with seeds germinating if conditions are favourable. Of these three methods of dispersal, the first two are by far the commonest. Sexual reproduction occurs sporadically (den Hartog, 1970; Pergent et al., 1989; Procaccini et al., 2003) as can be seen from the irregular records of flowering (e.g. Pergent, 1985; Acunto et al., 1996). The predominantly asexual reproductive strategy of this seagrass has resulted in populations having very low genetic variability (Procaccini et al., 1996; Procaccini & Mazzella, 1998).

1.2.4 Growth of seagrasses

Seagrasses possess a root-rhizome system that enables some species to live in nutrient-poor waters by exploiting the higher concentration of nutrients present in sediments (Hemminga, 1998). The growth rate of seagrass leaves varies with species and environmental conditions, particularly the availability of light and water temperature (e.g. Ibarra-Obando et al., 1997), but is typically around 5 mm per day (den Hartog & Phillips, 2001). Thus, the dynamics underlying seagrass growth and productivity are driven primarily by light, temperature and availability of nutrients (Sand-Jensen, 1975; Dennison, 1987; Short, 1987; Hemminga et al., 1991). Recent experiments have demonstrated that seagrasses can translocate nutrients, in particular inorganic carbon and nitrogen, between adjacent ramets of the same clone, hence, enabling physiological integration within the same plant, which can be exploited for clonal growth and expansion (Marbà et al., 2002).

P. oceanica is a very slow-growing species of seagrass (Duarte, 1991); around 10 leaves are produced annually per shoot (Ott, 1980). Besides light, temperature and nutrient availability (Alcoverro et al., 1997a), another factor influencing growth of this seagrass is the sediment redox potential (Alcoverro et al., 1995). To exploit the low nutrient concentration of the Mediterranean's oligotrophic waters, *P. oceanica* can acquire nutrients (e.g. phosphorous) from the water column through its leaves and from sediment pore water through its root-rhizome system (Alcoverro et al., 1997b). *P. oceanica* can thrive in waters with nutrient concentrations low enough to limit other seagrasses, such as *C. nodosa* (Perez et al., 1991; 1994). Moreover, depending on the season, *P. oceanica* is capable of reutilising internal nutrients (namely nitrogen and phosphorous) by reclamation from the root-rhizome system and from the older leaves, before the latter are detached from the shoot (Alcoverro et al., 2000). Nutrient uptake from the external medium occurs during winter, such that their concentration in tissue exceeds that of carbon. Conversely, nutrient reclamation from internal pools occurs during spring and autumn, when the external nutrient concentrations are low and internal carbon balance high (Alcoverro et al., 2000).

The growth pattern exhibited by *P. oceanica* is remarkably different from that of other seagrasses: (i) its leaves have strong seasonal growth, with rates being highest in spring and lowest in late summer (Wittman & Ott, 1982; Alcoverro et al., 1995), and high longevity (mean leaf lifespan of 150 - 300 days; Romero, 1989a), which exceeds that recorded for most other seagrass species (Duarte, 1991); (ii) there is a time delay in leaf production of around one month between shallow (circa 5 m), intermediate (circa 15 m) and deep (circa 30 m) beds (Mazzella & Ott, 1984; Mazzella et al., 1989); (iii) the plant accumulates unusually high carbohydrate reserves (Pirc, 1989), which can be mobilised to balance out the asynchrony between carbon fixation and use (Alcoverro et al., 2001), therefore enhancing its survival (Genot et al., 1994); (iv) the plant accumulates an unusually high belowground biomass (Ott, 1980); and (v) rates of elongation of *P. oceanica* rhizomes can vary in response to different sedimentation regimes, hence counteracting burial by sediment (Boudouresque et al., 1984). The genus *Posidonia* has the lowest rhizome elongation rates among the seagrasses (Hillman et al., 1989). Two types of rhizomes are recognised: (i) orthotropic, which grow vertically and (ii) plagiotropic, which grow horizontally. The plant usually has 4 to 8 strap-like leaves per shoot (Boudouresque & Meinesz, 1982), which can exceed a metre in length (Drew & Jupp, 1976). Leaf phenology is influenced strongly by season, but changes in shoot density are negligible over an annual period (Buia et al., 2000), although interannual variations do occur (Buia & Mazella, 2000). As in most seagrasses, leaf fall occurs in autumn (Mazzella & Ott, 1984), by which time the leaves are laden heavily with epiphytes, which aid detachment from the rhizomes by strong currents and wave action. The slow decomposition/fragmentation of *P. oceanica* leaves and transport to adjacent habitats constitutes a highly important source of detritus, which is thought to influence secondary production in other shallow-water ecosystems (Bellan-Santini & Picard, 1984). Leaves washed ashore form dense banks, known as 'banquettes', which serve as a habitat for a characteristic assemblage of invertebrates (Procaccini et al., 2003) and protect beaches against erosion (Boudouresque & Meinesz, 1982).

1.3 SEAGRASS BED STRUCTURE

While most seagrass beds tend to be monospecific, beds that consist of several seagrass species occur in many places (Duarte, 2000). Such beds are considered to have a relatively simple assemblage composition composed of a small number of species (maximum of around 12; den Hartog, 1967; Kirkman, 1985), of which only one or two comprise the bulk of the seagrass biomass (Terrados et al., 1998). In some geographical areas, particularly in tropical and sub-tropical regions, there is a vertical 'zonation' pattern of occurrence of seagrasses, the structure and sequence of which depends on the growth strategy and specific ecological requirements of the individual species (den Hartog, 1967). In many places, zonation and succession of seagrasses is influenced greatly by natural environmental processes including the ecophysiological requirements of the individual species, interspecific competition, and/or human disturbance (den Hartog, 1967). For example, in the Mediterranean Sea, *C. nodosa* often precedes *P. oceanica* in the succession sequence and may recolonise the area again when beds of the latter undergo degradation (Moliner & Picard, 1951; Aleem, 1955).

In general, seagrass coverage varies greatly over both large and small spatial scales such that patterns of occurrence of natural beds range from small patches to large continuous beds (Robbins & Bell, 1994; Fonseca & Bell, 1998). Seagrass patches have sizes ranging from less than 1 m^2 to tens of square metres (Fonseca et al., 1983; Irlandi, 1997; Reusch, 1998; Frost et al., 1999; Bowden et al., 2001), while continuous beds cover extensive areas of several square kilometres (e.g. Worcester, 1995). Seagrass beds may also occur interspersed with a different habitat type, for example, bare sand, to form reticulate beds (also referred known as 'semi-continuous' beds, 'interconnected patches' or beds with 'blow-outs') (Kirkman & Kuo, 1990; Fonseca & Bell, 1998; Hovel & Lipcius, 2001; 2002), which may have a coverage that varies between several square metres and hundreds of square metres, or greater. Such bed patterns, or landscapes (Robbins & Bell, 1994), are thought to result from the seagrass growth response to the physical setting of the particular locality where the seagrass occurs (Patriquin, 1975; Fonseca et al., 1983; Fonseca & Kenworthy, 1987; Kirkman & Kuo, 1990; Fonseca & Bell, 1998). Within-bed characteristics of seagrass beds are also influenced by local factors, since plant architecture (which comprises the plant morphological characteristics, i.e. number of leaves, leaf length, leaf width, shoot density, epiphytic load etc.) varies (Robbins & Bell, 1994) depending on the current regime (Fonseca et al., 1983), wave exposure (Fonseca & Bell, 1998), the physico-chemical properties of the substratum (Terrados et al., 1998), and the temperature (Koch, 2001) and physico-chemical properties of the water column (e.g. Tomasko et al., 1996). Other probable controlling factors of bed structure include disturbance by storms (Patriquin, 1975; Kirkman, 1985), bioturbation (Suchanek, 1983; Valentine et al., 1994; Townsend & Fonseca, 1998) and grazing by megafauna (e.g. Preen, 1995). The way in which these factors influence patterns of seagrass bed structure is undoubtedly complex but they probably act by promoting or halting development at the bed boundaries, or by creating pockets (also known as 'blowouts'; Patriquin, 1975) within the seagrass beds that are devoid of plants (den Hartog, 1970; Kirkman, 1985). Disturbance from anthropogenic activities also affects seagrass bed morphology and plant architecture through direct physical damage (e.g. deployment of moorings or anchoring;

Hastings et al., 1995; Francour et al., 1999) and through indirect degradation, such as that resulting from alteration of water quality (e.g. Delgado et al., 1997; 1999; Pergent et al., 1999; Ruiz et al., 2001; Dimech et al., 2002) (see Section 1.7).

The first detailed descriptions of the morphology and growth dynamics of *P. oceanica* beds were by Moliner & Picard (1952), who maintained that *P. oceanica* beds constituted the climax community in a succession started in shallow waters by the smaller seagrass *C. nodosa*. The latter acts as a pioneer species, spreading over sandy substrata and enriching the sediment with organic matter. Detached *P. oceanica* plants take root and form circular patches within the *C. nodosa* meadows, eventually completely replacing the latter through lateral spreading (Moliner & Picard, 1952). *P. oceanica* is one of the largest marine angiosperms, with leaf lengths that may exceed a metre in length and a leaf width of around 1 cm (Drew & Jupp, 1976). The plant forms beds having a high shoot density (e.g. 1,200 shoots m^{-2} at a depth of 5 m) and a high biomass (e.g. 1617g dw m^{-2} at a depth of 5 m) (Mazzella et al., 1992) compared with other phanerogams (Pergent et al., 1994; Duarte & Chiscano, 1999). The characteristic growth pattern of *P. oceanica* leads to formation of beds that have an extensive root-rhizome network called 'matte' (Figure 1), which provides firm anchorage for new plants and can be thousands of years old (Mateo et al., 1997). The lignified *P. oceanica* rhizomes of this belowground structure may contribute to more than 50% of the total seagrass biomass (Mateo & Romero, 1997). Vertical growth of the rhizomes, coupled with accumulation of sediment in the matte interstices (Boudouresque et al., 1984), causes a slow upward lifting of this biogenic structure at the rate of around 1 cm/yr (Moliner & Picard, 1952; Boudouresque & Jeudy De Grissac, 1983). However, vertical growth of the matte varies interannually, depending on variations in sedimentological processes of the locality, such as rates of transport and deposition of soft sediment (Boudouresque et al., 1984). In some Mediterranean bays and inlets, for example, in France (Moliner & Picard, 1952; Augier & Boudouresque, 1970), Sicily (Calvo & Frada-Orestanio, 1984; Accardo-Palumbo et al., 1992), along the north African coast (Aleem, 1955) and in Malta (Borg & Schembri, 1995a), vertical growth of the *P. oceanica* matte close to the water's surface at mean sea level has led to the formation of 'reefs' which, in some cases, have closed off the inner parts of bays to form lagoons (den Hartog, 1970; Accardo-Palumbo et al., 1992). A number of different reef types have been described from France and Corsica (Boudouresque et al., 1985b, and references therein).

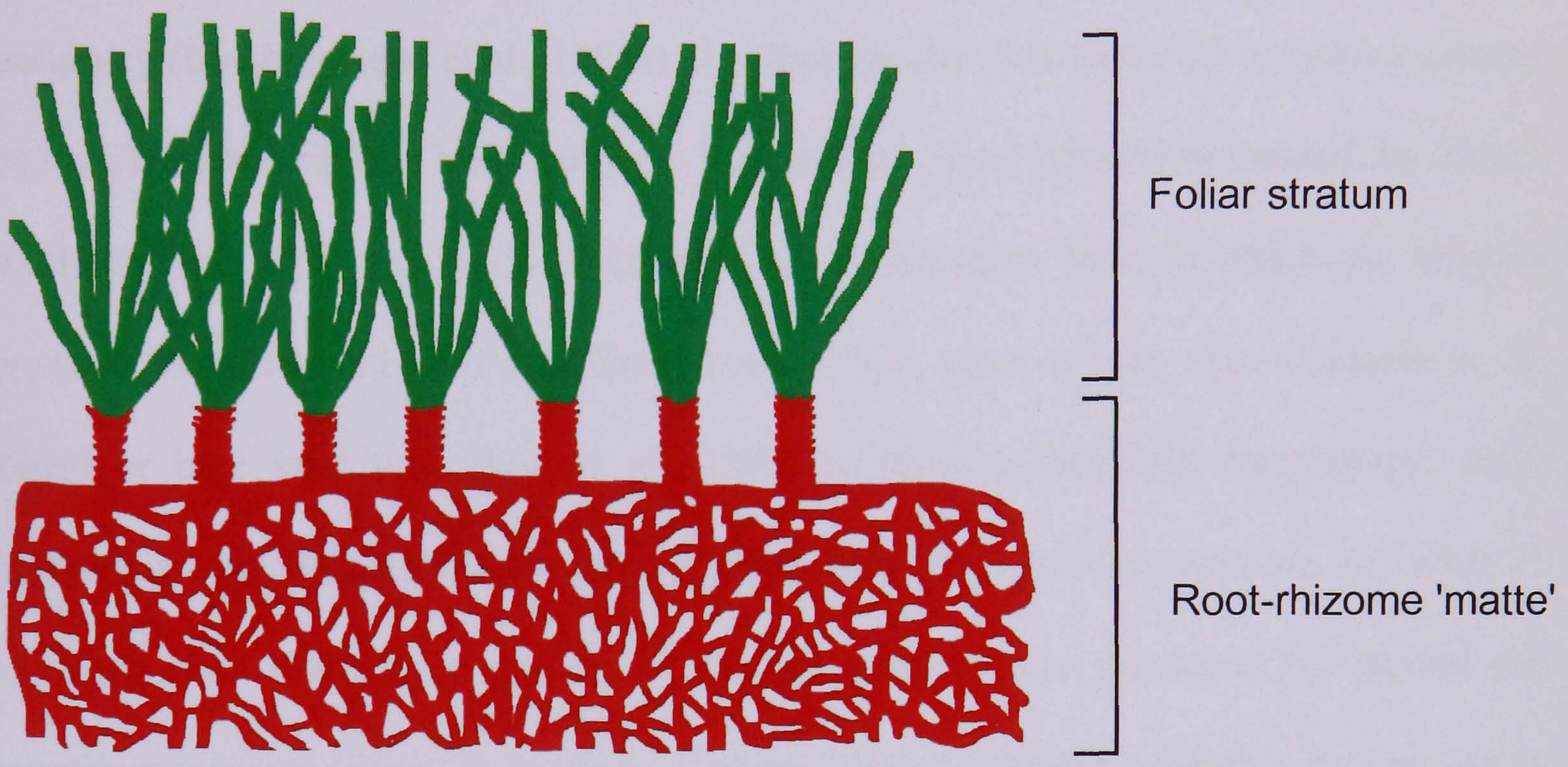

Figure 1. *Posidonia oceanica* bed structure.

Because of the peculiar growth pattern exhibited by *P. oceanica*, its high and dense foliar stratum, and the thick matte formed, beds of this seagrass have a high structural complexity (Buia et al., 2000). Furthermore, since both the leaf stratum and root-rhizome matte play important roles in the complex interactions with the substratum, this seagrass is known to have profound influences on the sediment texture and the hydrodynamic regime (Jeudy de Grissac, 1984; De Falco et al., 2000; Granata et al., 2001). *P. oceanica* bed morphology is plastic and numerous forms can be recognised, ranging from very small patches to large and extensive continuous beds, all of which can be found growing on soft and hard bottoms (Mazzella et al., 1986; Buia et al., 2000). The dynamics underlying the formation of different *P. oceanica* bed types (Buia et al., 2003) are complex, with different forms resulting mainly from the influence of different physical environmental factors, amongst which water movement and the sedimentary regime exert major influences (Colantoni et al., 1982; Blanc & Jeudy de Grissac, 1984; Jeudy de Grissac, 1984). *P. oceanica* forms patches that range in size between one and several square metres (Mazzella et al., 1986). An unusual *P. oceanica* patch type, known as 'colline', resembles a small hillock and results from a higher rate of growth of the matte at the centre than at the periphery (Boudouresque et al., 1985a). Another peculiar bed type of *P. oceanica* consists of long narrow strip-like beds that have been named 'tigre' (striped or banded) by French workers (Buia & et al., 2003). Discontinuous *P. oceanica* beds, in which the seagrass meadow is intermixed with a different bottom type, such as rock (e.g. Chimenz et al., 1989) or bare sand (e.g. Buia et al., 1989) to attain a reticulate morphology, occur commonly (e.g. Barberá Cebrian et al., 2002). According to some workers, reticulate *P. oceanica* beds result from erosion of the bed along certain directions by sagittal and longshore currents (Blanc & Jeudy de Grissac, 1984) to produce channels that are cut in the *P. oceanica* matte (known as 'intermatte' channels; Boudouresque & Meinesz, 1982; Pérès, 1982; Buia et al., 1989). Eventually, complete erosion of the matte exposes the underlying sandy bottom (Boudouresque & Meinesz, 1982). Continuous *P. oceanica* beds occupy the upper extreme end of the broad range of different bed morphologies, and comprise extensive and fairly homogeneous beds of the seagrass, which cover areas that can be tens of square kilometres (e.g. Colantoni et al., 1982). Differences in environmental factors, such as variation in the light, temperature and hydrodynamic regimes that occur with changes in water depth, cause large variations in the within-bed structure of *P. oceanica* beds (Panayotidis et al., 1981; Dalla Via et al., 1998; Zupo et al., 1997; Gobert et al., 2003). The general tendency is for within-bed structural attributes, such as shoot density, leaf biomass and mean leaf length, to decrease with increasing water depth (Gambi et al., 1992; Pirc, 1984). In extreme adverse conditions, for example, when the matte surface reaches a critical water depth such that it becomes exposed to erosion by wave action (Boudouresque & Meinesz, 1982; Blanc & Jeudy de Grissac, 1984; Meinesz et al., 1988), or in conditions of eutrophication or pollution (e.g. Ramos Éspla, 1984; Bourcier, 1989), complete death of the *P. oceanica* shoots occurs and the resulting bare root-rhizome matrix is known as 'dead matte' (Harmelin, 1964; Vaccarella et al., 1981; Abada Guerroui & Willsie, 1984; Bellan Santini et al., 1986; Somaschini et al., 1994).

1.4 FLORA AND FAUNA ASSOCIATED WITH SEAGRASS BEDS

Several authors (e.g. Kikuchi & Pérès, 1977; Kikuchi, 1980; Mazzella et al., 1986) divide the flora and fauna associated with seagrass beds into a number of categories: (i) the epiphytic flora and the micro- and meiofauna present on the shoots and rhizomes; (ii) the sessile macrofauna associated with the leaves and rhizomes; (iii) the mobile epifauna that creep or crawl on the leaves; (iv) the swimming fauna that rest on the leaves; (v) the highly mobile fauna that swim above and under the leaf canopy; (vi) the mobile epifauna associated with the root-rhizome surface; and (vii) the infauna.

Numerous phototrophic epiphytes, mainly consisting of cyanobacteria, diatoms and algae are associated with seagrass beds (Humm, 1964; Novak, 1984; Borowitzka et al., 1990; Moncreiff & Sullivan, 2001). The species richness of algal epiphytes can be very high, with recruitment being controlled largely by the growth pattern and age of the individual seagrass plants (Borowitzka et al., 1990; Trautman & Borowitzka, 1999). For example, Humm (1964) recorded 113 algal epiphytes from a *Thalassia testudinum* Banks & Soland ex Koenig bed in Florida, while Borowitzka et al. (1990) recorded 150 species from an

Amphibolis griffithii (Black) den Hartog bed in Western Australia. Algal epiphyte production in seagrasses has been reported to attain a biomass of up to 60% of the seagrass itself (e.g. Morgan & Kitting, 1984; Moncreiff & Sullivan, 2001); however, such high epiphytic biomass is usually the result of nutrient enrichment of the water column and/or low herbivory rates (den Hartog & Phillips, 2001). According to most workers, seagrass algal epiphytes are mostly facultative and are found growing on other macrophytes and on hard substrata; relatively few species are confined exclusively to seagrasses (den Hartog, 1967). Furthermore, while some algal epiphytes have a seasonal occurrence, others are present on the seagrass all year round (den Hartog, 1967). The species richness and abundance of epiphytes are strongly influenced by the leaf turnover rates of a particular seagrass species, which vary between 11-24 days in *Halophila ovalis* (R. Brown) Hook (den Hartog & Phillips, 2001) and 150-300 days in *P. oceanica* (Romero, 1989a).

The sessile epifauna of seagrass beds mainly comprises hydroids, bryozoans, sponges and ascidians (e.g. Pansini & Pronzato, 1985; Borowitzka & Lethbridge, 1989; Pessani et al., 1989; Trautman & Borowitzka, 1999). In comparison to the motile macrofauna associated with seagrass habitats, the sessile epifauna has distributional patterns (on the host plant), life cycles and growth characteristics intimately related to the growth characteristics of the seagrass (Trautman & Borowitzka, 1999). Furthermore, because space is a very limited resource, the sessile epifauna of seagrasses have adaptations that enable them to compete interspecifically. For example, different hydroids may have different orientation of growth such that some grow downward toward the younger parts of the seagrass leaves (Hughes et al., 1991b).

Of all the biotic components associated with seagrass beds, the motile macroinvertebrate fauna has probably received the greatest attention, with the majority of studies showing that, in terms of species richness and abundance, gastropods, polychaetes and crustaceans dominate (Brook, 1977; 1978; Heck, 1977; Young & Young, 1978; Greening & Livingston, 1982; Virnstein, 1987; Virnstein & Howard, 1987a; Pihl Baden, 1990; Ansari et al., 1991; Knowles & Bell, 1998). Abundance values of motile macroinvertebrates recorded in the literature vary greatly, depending on sampler mesh size. For example, the following maximum values of macroinvertebrate abundance have been recorded from *Z. marina* beds: 80,000 individuals m^{-2} (Pihl Baden, 1990; 0.2 mm mesh size), 25,000 individuals m^{-2} (Marsh, 1973; 0.5 mm mesh size), and 160 individuals m^{-2} (Pihl Baden & Pihl, 1984; 1 mm mesh size). Seagrass beds constitute important nursery habitats for several commercial species (e.g. blue crab *Callinectes sapidus* Rathbun; Heck & Thoman, 1981; Orth & van Montfrans, 1987; 1990). While many motile invertebrates are permanent residents of seagrass beds and complete their reproductive cycles in the seagrass habitat, others are temporary inhabitants and visit at some time during the day to feed or during a specific part of the year to reproduce (e.g. prawns; Howard, 1984; Bauer, 1985; Gray 1991a; 1991b). Some of the associated macroinvertebrates have specialised niches; for example, some isopods and polychaetes are capable of mining the tissue of seagrasses belonging to the genus *Posidonia* (e.g. Brearly & Walker, 1995). Herbivores constitute an important component of seagrass-associated macrofauna, with the majority of species feeding on epiphytes or on the detritus (e.g. Nelson, 1997). However, direct consumption by grazers can exert a profound influence on seagrass beds, for example, sea urchins may control seagrass density (Alcoverro & Mariani, 2002). The species richness and abundance of macroinvertebrate assemblages associated with seagrass beds has been shown to vary diurnally (Brook, 1977; Greening & Livingston, 1982; Bauer, 1985; Howard et al., 1989; Connolly & Butler, 1996), seasonally (e.g. Gray, 1991a; 1991b), and inter-annually (e.g. Virnstein, 1987). For example, Bauer (1985) noted that the abundance of caridean shrimps was higher at night and attributed this partly to nocturnal emergence of the animals from burrows in the sediment. Gray (1991a) suggested that the prawn *Macrobrachium intermedium* Stimpson migrates out from seagrass in winter to deeper waters. Temporal variation in the diversity of macroinvertebrates associated with seagrass beds may also result from changes in predation pressure (e.g. Nelson et al., 1982).

Several studies have considered the fish fauna associated with seagrass beds (see reviews by Pollard, 1984; Bell & Pollard, 1989; Jackson et al., 2001, and references therein). Fishes constitute a highly mobile biotic component of seagrass habitat; while some species are permanent inhabitants of seagrass beds (e.g. gobiids and other small fishes), others (e.g. sparids) are temporary visitors and use them as feeding grounds and/or nurseries (Weinstein & Heck, 1979; Burchmore et al., 1984; Middleton et al., 1984; Aliaume et al., 1993; Gray et al., 1996). Large variations in the species richness and abundance of seagrass-associated fishes have been noted to occur diurnally, however, seasonal variations are less pronounced (Weinstein & Heck, 1979; Orth & Heck, 1980).

The species composition and structure of the biotic assemblages associated with *P. oceanica* have received considerable attention since the pioneering works of Keneïs (1960), Ledoyer (1962) and Harmelin (1964). Around 800 species have been recorded from *P. oceanica* beds, of which some are exclusive to this habitat (e.g. the noble pen shell *Pinna nobilis* Linnaeus) and having become rare or endangered (Procaccini et al., 2003). Because of this high biodiversity, some authors (e.g. Boudouresque & Meinesz, 1983; Boudouresque et al., 1994) consider the *P. oceanica* community as the most diverse in the Mediterranean Sea.

The epiphytic flora associated with *P. oceanica* has been well studied (e.g. Cinelli et al., 1984; Casola et al., 1987; Buia et al., 1989) and the published results show a high species richness of algal epiphytes. For example, Battiato et al. (1982) recorded 81 leaf epiphytic algae from a *P. oceanica* meadow in the island of Ischia (Naples), of which *Fosiliella* sp. and *Myrionema orbiculare* Agardh had the highest abundance in terms of leaf coverage. Several algal epiphytes, including the red algae *Pneophyllum fragile* Kutzing and *Hydrolithon farinosum* (Lamoroux), and the brown algae *Giraudia sphacelarioides* Derbes & Solier and *M. orbiculare,* occur exclusively in *P. oceanica* beds (Procaccini et al., 2003). Leaf epiphytes also constitute a considerable proportion of the total primary production of *P. oceanica* beds (Battiato et al., 1982; Mazzella et al., 1992; Cinelli et al., 1984; Mazzella & Ott, 1984; Casola et al., 1987; Alcoverro et al., 1997a). The occurrence and species composition of leaf epiphytic assemblages of *P. oceanica* tends to be strongly dependent on the life cycle of the epiphytes, the growth characteristics of the seagrass leaves, and on physical factors such as water movement, temperature and availability of light (Cinelli et al., 1984; Mazzella & Ott, 1984; Mazzella et al., 1989; Alcoverro et al., 1997a). For example, in their study of a *P. oceanica* meadow that extended between depths of 1 m and 32 m, Mazzella & Ott (1984) noted a discontinuity in epiphyte biomass at a depth of 15 m, which coincided with sharp changes in leaf architectural characteristics of the seagrass and hydrodynamic features characteristic of a high-energy environment. Battiato et al. (1982) found that the most abundant leaf algal epiphytes were red algae (61 species), followed by brown algae (15 species) and green algae (5 species), and concluded that the species composition and abundance of the leaf algal epiphyte community was influenced by the *P. oce*anica meadow structure and by water movement. Three zones have been identified on the *P. oceanica* leaves that appear to be colonised predominantly by different epiphytes: (i) the basal parts, which are colonised by pioneer species, namely bacteria and diatoms; (ii) the ageing portion, which is encrusted with soft and calcareous encrusting algae; and (iii) the tips, which support a layer of upright algae (namely red and brown algae) growing on the encrusting epiphytes (Casola et al., 1987; Mazzella & Russo, 1989). In general, the epiphytic assemblages of *P. oceanica* have been found to be more diverse in shallow beds than in deeper ones (Mazzella et al., 1989). The *P. oceanica* matte surface frequently supports a more sciaphilic algal assemblage, dominated mainly by *Peyssonnelia squamaria* (Gmelin) Decaisne and *Flabellia petiolata* (Turra) Nizamuddin (e.g. Moliner & Picard, 1959-1960; Kerneïs, 1960).

The heterotrophic sessile epipytes of *P. oceanica* comprise mainly bryozoans (e.g. Fresi et al., 1982, Balduzzi et al., 1983; Castritsi-Catharios & Ganias, 1989), hydroids (e.g. Boero, 1981a; 1981b) and sponges (Pansini & Pronzato, 1985), the latter occurring mainly on the rhizomes and matte surface. Some of the hydroids (e.g. *Aglaophenia harpago* Schenck and *Sertularia perpusilla* Stechow) and bryozoans (e.g. *Electra Posidoniae* Gantier) occur exclusively in *P. oceanica* beds (Mazzella et al., 1986; Procaccini et al., 2003), while other sessile epiphytes have very specific growth and reproductive strategies closely tied and adapted to the life cycle of the seagrass. For example, the hydroid *S. perpusilla* has a very peculiar growth strategy and is able to survive on the seagrass shoots beyond the life of the individual leaves by means of asexual reproduction and colonisation of young leaves by stolonisation (Hughes et al., 1991a; Rossi et al., 1997). The species richness of these sessile macroinvertebrates can be high for *P. oceanica* beds, but not as high as for the motile macrofauna. For example, Pessani et al. (1989) recorded a total of 68 species of sessile epifauna from *P. oceanica* beds off the Ligurian coast, of which 12 species were hydrozoans and 32 bryozoans; Boero et al. (1985) recorded a total of 25 hydroids from a single meadow in Ischia (Naples, Italy); Castritsi-Catharios & Ganias (1989) recorded 49 species of bryozoans from *P. oceanica* beds in the Gulf of Patras (Greece); and Pansini & Pronzato (1985) recorded 75 species of Porifera from Italian *P. oceanica* beds located in two different locations.

The motile macroinvertebrates associated with *P. oceanica* beds comprise mainly crustaceans, molluscs, polychaetes and echinoderms (Mazzella et al., 1989; 1992). The majority of investigations on the motile macroinvertebrates of *P. oceanica* beds have considered either the leaf stratum (Mazzella et al., 1989; Gambi et al., 1989b; 1992; Scipione et al., 1996; Sánchez Jerez et al., 1999a; Barberá Cebrián, 2002) or the root-rhizome layer (e.g. Bourcier & Willsie, 1986; Willsie, 1986; Somaschini et al., 1994; García Raso et al, 1996); few have considered the whole motile macrofauna of both subhabitats (e.g. Templado, 1984; Bianchi et al., 1889; Chimenz et al., 1989). Where both leaf stratum and root-rhizome layer have been studied, the investigations generally deal with a single taxon, for example, polychaetes (Gambi et al., 1995), molluscs (Russo et al., 1983; 1985) and decapods (García Raso, 1990). Several studies are available for specific groups of macroinvertebrates associated with the leaf stratum, including molluscs (Russo et al. 1983-84; 1984a; 1984b), polychaetes (Colognola et al., 1984; Gambi et al., 1989b), mysids (Barberá Cebrián et al., 2002) and amphipods (Scipione & Fresi, 1984; Scipione, 1999). In the foliar stratum, the highest abundance values are contributed by the Mollusca and Amphipoda, while the polychaetes of this subhabitat have a low abundance but high species richness (Mazzella et al., 1989; Gambi et al., 1989b). Relatively few studies have centered on the macroinvertebrates of the root-rhizome stratum and most of these deal with the polychaetes (Harmelin, 1964; San Martin & Vieitez, 1984; Bourcier & Willsie, 1986; Willsie, 1986; Somaschini et al., 1994; Gambi et al., 1995; García Raso et al, 1996). Polychaetes are more abundant in the root-rhizome layer than in the leaf canopy, with syllids being dominant in both subhabitats (San Martin & Vieitez, 1984; Colognola et al., 1984; Gambi et al., 1989b; Gambi et al., 1995). Despite the high species richness of polychaete assemblages recorded from single studies of the *P. oceanica* matte, for example, 100 - 218 species (Harmelin, 1964; San Martin & Vieitez, 1984; Somaschini et al., 1994), the majority of the recorded species also occur in other habitats and none occurs exclusively in the root-rhizome matte (Chimenz et al., 1989; Gambi et al., 1995; Procaccini et al., 2003). The *P. oceanica* matte also constitutes an important habitat for a large variety of decapods, such that for this group of macrofauna, this subhabitat may be more important than the leaf canopy (García Raso, 1990; García Raso et al, 1996). The published data indicate that the root-rhizome layer of *P. oceanica* beds supports a higher species richness of associated macroinvertebrates (Chimenz et al., 1989; Templado, 1984; Gambi et al., 1995; Borg & Schembri, 2000), which for some groups (e.g. polychaetes; Somaschini et al., 1994) may be higher than that recorded from other habitats. A recent review has pointed out that this compartment lacks detailed study (Buia et al., 2000).

Several workers have found a diurnal variation in the species richness and abundance of motile macroinvertebrates associated with *P. oceanica,* which was attributed to diurnal differences in the vertical migration pattern between the root-rhizome layer and the leaf canopy (e.g. Sánchez Jerez et al., 1999b). The species composition of assemblages of some other abundant macroinvertebrate groups associated with *P. oceanica* beds, for example, the mysids, has received relatively little attention (but see Maj & Taramelli, 1989; Barberá Cebrián et al., 2002). This is due partly to the lack of taxonomic expertise and dearth of Mediterranean identification keys for such groups.

As with most seagrass beds, *P. oceanica* meadows are recognised as important spawning, nursery and feeding grounds for numerous fishes, including scorpaenids, serranids, sparids and labrids (Bell & Harmelin-Vivien, 1982; Harmelin-Vivien, 1982; Harmelin-Vivien, 1984), many of which are of considerable economic importance (Procaccini et al., 2003). The species richness of fishes recorded from *P. oceanica* beds off the southern coast of France varied in the range of 41 – 58, however there was diurnal variation in both species richness and abundance, with a tendency for higher values at night (Harmelin-Vivien, 1984).

1.5 PRODUCTIVITY AND TROPHIC DYNAMICS OF SEAGRASS BEDS

The primary productivity of seagrasses may be very high, with an estimated average net production of circa 1012g dw m^2 $year^{-1}$ (Duarte & Chiscano, 1999), which is comparable to that of terrestrial plants (e.g. Hillman et al., 1989). Seagrasses serve as important feeding grounds for herbivores that consume the living seagrass leaves and the seagrass epiphytes (e.g. Moncreiff & Sullivan, 2001) or feed on the detritus (Klumpp et al., 1989). Several birds, marine mammals and reptiles consume the living leaves of seagrass (see review by Thayer et al., 1984). Generally, it is accepted that because of the high content of refractory substances in seagrass tissue (namely structural carbohydrates, lignin and cellulose, which make it not easily digestible), few macroinvertebrates feed directly on seagrasses (Thayer et al., 1984; den Hartog & Phillips, 2001) and most of the primary production of seagrasses is either stored in the root-rhizome compartment or is exported to adjacent marine ecosystems via the detrital pathway (e.g. Thresher et al., 1992). However, a recent review by Valentine & Heck (1999) challenged this paradigm and proposed that direct herbivory on seagrasses may have been underestimated. In any case, the high content of refractory substances in seagrass tissue and the unusual C:N:P ratios (Enriquez et al., 1993) slow down the rate of decomposition of detached shoots and leaves, and conversion to detritus (Thayer et al., 1977; Bourguès et al., 1996). For example, *Z. marina* beds located in an estuary in North Carolina (USA) had an estimated rate of detrital export that ranged between 4.9 – 6.0 g dw mo^{-1} m^{-2} for sheltered embayment-type beds and 1.0 – 13.0 g dw mo^{-1} m^{-2} for exposed beds (Bach et al., 1986). The difference in rates of export was attributed to entrapment of detrital material by the embayment type beds (Bach et al., 1986). The role of seagrass beds as producers or sinks of detritus is dictated by the hydrodynamic regime of a particular locality; they serve as a source of detritus when located in areas characterised by high current velocities and as a sink when located in areas characterised by low current velocities (Fonseca et al., 1983). Release of inorganic nutrients (e.g. nitrogen and phosphorous) through decomposition of seagrass tissue occurs at a faster rate than that of macroalgae and, therefore, seagrasses appear to play a significant role in the recycling of inorganic nutrients (Bourguès et al., 1996). Hence, export of seagrass litter to nearby or distant ecosystems, including those located at great depths (e.g. Wolf, 1976), may represent an important supply of detritus and nutrients (Duarte & Cebrian, 1996), and constitutes one of the two major trophic pathways; the other pathway is that based on grazing (Klumpp et al., 1989). Studies have suggested that the nutritional value of detritus consumed by macrofauna actually lies in the micro- and meiofauna associated with it (Fenchel, 1977; Coull, 1990), while epiphytes may also be important contributors to secondary production, possibly more than the detritus (Kitting, 1984; Johnson & Johnstone, 1995; Moncreiff & Sullivan, 2001).

Crustaceans, nemerteans, sipunculids and ophiuroids mainly constitute the detritivorous guild in seagrass beds, while polychaetes and bivalves are the main suspension feeders (e.g. Greenway, 1995). A significant proportion of the total associated macrofauna, mainly comprising the amphipods and the gastropods, constitutes a herbivorous guild that grazes on seagrass algal epiphytes (e.g. Lewis & Hollingworth, 1982; Greenway, 1995). Recent studies have indicated that some herbivores contribute to productivity via complex mechanisms. For example, suspension-feeding bivalves may increase seagrass bed productivity by consuming epiphyte propagules, thereby, controlling excessive proliferation of epiphytes, which may have an adverse impact on seagrass (Reusch et al., 1994; Reusch & Williams, 1998; Peterson & Heck, 2001a; 2001b).

The total secondary production of seagrass beds can be very high. For example, total macroinvertebrate secondary production for a mixed *Z. marina* and *Ruppia maritima*

Linnaeus bed has been estimated at around 200 g dw m^2 yr^{-1} (Fredette & Diaz, 1990). Pihl (1986) recorded a total annual value of 6 g dw m^2 yr^{-1} for macroinvertebrate secondary production in a Swedish *Z. marina* bed. In addition to macroinvertebrate carnivores, the presence of a diverse and abundant class of opportunistic omnivores in seagrass beds contributes to complex inter-specific relationships and trophic processes, and adds to the overall complexity of these ecosystems (e.g. Nelson, 1981). Because of their important contribution to energy transfer to higher trophic levels, mainly fishes (e.g. Brook, 1977; Young & Young, 1978; Stoner, 1980; Burchmore et al., 1984; Leber, 1985; Greening, 1995), the macroinvertebrate fauna of seagrass beds constitute a highly important component and studies of this group form an important basis for understanding their ecological role in seagrass habitat and in ecosystem function. Overall, therefore, the contribution of seagrass beds to coastal productivity is considerable, and in some regions, may account for a major proportion of the total primary production.

Several studies have measured the production of *P. oceanica* beds. For example, measurements of the total production of *P. oceanica* made off the Medes Islands (Spain) ranged from 925 g dw m^{-2} yr^{-1} at a depth of 5 m to 490 g dw m^{-2} yr^{-1} at a depth of 12 m (Romero, 1989b). These estimates are in close agreement with values recorded from other studies (e.g. Plante-Cuny & Libes, 1984) and with the more recently estimated net primary production of 130-1284 g dw m^{-2} yr^{-1} for the Mediterranean (Pergent-Martini et al., 1984). However, the influence of water depth on the primary production of individual shoots of *P. oceanica* is not as large as one would expect since: (i) the amount of photosynthetically active radiation (PAR) available throughout the depth range occupied by the seagrass is usually well within the levels at which photosynthesis saturation occurs, and (ii) shoot density values of *P. oceanica* beds decrease with depth, thereby counteracting conditions of reduced light imposed by self-shading by leaves (Hemminga & Duarte, 2000). For example, Romero (1989b) did not find significant differences in production of individual shoots of *P. oceanica* with depth. This author estimated the following mean values of production of individual shoots of the seagrass: 2.53 g dw m^{-2} yr^{-1}, 2.14 g dw m^{-2} yr^{-1}, 2.04 g dw m^{-2} yr^{-1} and 1.34 g dw m^{-2} yr^{-1}, at the respective depths of 5 m, 6.5 m, 8.7 m and 13 m Romero (1989b). As a result, differences in productivity with depth are mainly due to reduced rates of primary production of *P. oceanica* per unit area, resulting from changes in shoot density values (Romero, 1989b). Consequently, as the water depth increases, values of leaf standing crop decrease (Drew & Jupp, 1976; Bay, 1984; Buia et al., 1992).

A particular characteristic of *P. oceanica* is the distinct partitioning of primary production into shoot and root-rhizome compartments, with leaf production accounting for more than 90% (Wittman, 1984), even though the root-rhizome compartment contributes up to 50% of the total biomass (Mateo & Romero, 1997). Overall, *P. oceanica* production is very high (Ott, 1980) and values exceed those of other seagrasses, including the Australian *Posidonia* species (Mazzella & Zupo, 1995).

Several works have addressed the trophic role of *P. oceanica* and those of the biota associated with beds of this seagrass (e.g. Vizzini et al., 2002). *P. oceanica* beds support meiofaunal production of the order of 7.5 – 13.2 g C m^{-2} yr^{-1}, which is one of the highest recorded worldwide (Danovaro et al., 2002). However, the production efficiency of this seagrass is lower (3 – 5%) than that of other seagrasses such as *C. nodosa* or *Z. noltii* (Danovaro et al., 2002). There are relatively few direct grazers of *P. oceanica* (Mazzella et al., 1992); these comprise mainly the fishes *Sarpa salpa* Linnaeus (Velimirov, 1984), echinoderms (Zupo & Fresi, 1984), some polychaetes and isopods (Guidetti et al., 1997), some palaemonid shrimps (Vizzini et al., 2002), and the decapod *Galathea squamifera* Leach (Chessa et al., 1989). Therefore, the seagrass itself contributes very little to direct consumption by herbivores (circa 2% of *P. oceanica* leaf production is consumed by herbivores; Cebrian et al., 1996). This is probably due to the poor nutritional value and high lignocellulose content of *P. oceanica* (Ott & Maurer, 1977), hence, most of the seagrass tissue enters the detrital food chain (Velmirov et al., 1981; Wittman et al., 1981), thereby constituting an important pathway in *P. oceanica* trophic dynamics (Mateo & Romero, 1997; Vizzini et al., 2002). There are, however, numerous herbivorous species that graze the epiphytes growing on *P. oceanica,* including taxa that form part of the meiofauna (e.g. nematodes; Novak, 1984), gastropods (Mazzella & Russo, 1989; Takada et al., 1999) and amphipods (Scipione & Fresi, 1984; Scipione, 1989; Scipione & Mazzella; 1992). Such grazers constitute an important trophic guild through which epiphytic matter enters the trophic system of the *P. oceanica* habitat (Vizzini et al., 2002). The grazer guild appears to be considerably complex, with niche separation occurring between closely-related species within the same macrofaunal group. For example, Mazzella & Russo (1989) noted that the two trochid gastropods *Gibbula ardens* (Von Salis) and *Gibbula umbilicaris* (Linnaeus) feed on different *P. oceanica* leaf algal epiphytes: *G. ardens* feeds on the bacteria and diatoms present on the newer basal parts of the seagrass leaves, while *G. umbilicaris* feeds on the erect macroalgae present on the older parts of the leaves. Overall, the motile macroinvertebrates of *P. oceanica* beds constitute the main diet of fishes (Khoury, 1984), including several species that are commercially important (Harmelin-Vivien, 1982).

The fish fauna of *P. oceanica* beds feed primarily on crustaceans, while polychaetes and molluscs also contribute to their diet (Bell & Harmelin-Vivien, 1983). The total prevalence of carnivorous fishes in *P. oceanica* beds contrasts with the common occurrence of herbivorous and detritivorous fishes in seagrass beds outside the Mediterranean (Bell & Harmelin-Vivien, 1983).

Given that *P. oceanica* beds constitute a major component of the Mediterranean infralittoral zone, the study of the ecology of the associated motile macroinvertebrates constitutes the basis for an understanding of the contribution of seagrass habitat to coastal productivity and biodiversity in the region.

1.6 INFLUENCE OF SEAGRASS BED STRUCTURE ON ASSOCIATED MACROFAUNA

In the course of the extensive research on the ecology of seagrass beds and their associated fauna, a number of studies concluded that seagrass beds supported higher species richness and abundance of fauna than other habitat types such as bare sand (e.g. Lewis, 1984; Orth et al., 1984; Pihl, 1986; Connolly, 1997), however, there are doubts as to the validity of generalising this concept to fish fauna (Jackson et al., 2001 and references therein). Since the early 1980s, the structural organisation (sometimes referred to as ‘complexity’) of seagrass beds (at different spatial scales) was proposed as the main factor responsible for the observed high diversity of associated fauna (Phillips & McRoy, 1980; Orth et al., 1984; Virnstein, 1987 and reviews therein), as has been surmised for other marine habitats (Huston, 1994). Considerable work has addressed this hypothesis and numerous studies have been undertaken in attempts to confirm its validity, and to identify the specific attribute that influenced most the diversity of the macrofauna associated with seagrass beds (see reviews by Heck & Orth, 1980a; Orth et al., 1984; Virnstein, 1987). According to the paradigm that has developed (e.g. Leber, 1985; Summerson & Peterson, 1984), seagrass structural complexity enhances macrofaunal abundance by providing refugia from predation, increased habitat space and/or increased food availability (Young & Young, 1978; Nelson, 1979; Heck & Orth, 1980a; Orth et al., 1984; Virnstein et al., 1984, Mattila, 1995; Ray & Stoner, 1995 and reviews therein). Accordingly, total plant biomass and/or plant surface area have been used as measures of seagrass structural complexity and, therefore, as predictors of macrofaunal abundance (Lewis, 1984; Heck & Wetstone, 1977; Heck & Orth, 1980b; Stoner, 1980; Gore et al., 1981; Ansari et al., 1991). However, despite the great effort, there has been a lack of concordance in the conclusions reached by the different workers. For example, Young & Young (1982) did not find a relationship between seagrass biomass and macroinvertebrate diversity, nor were the number of species recorded from the seagrass habitat significantly higher than those from bare sand. Brook (1978) investigated the abundance of macrofauna associated with *T. testudinum* at different locations, and concluded that the positive correlation between seagrass biomass and faunal abundance does not always hold true. Bell & Westoby (1986a, b) showed that correlations between seagrass bed density and the associated macrofaunal species richness and abundance were not consistent when beds located at different sites were compared. Young & Young (1978) noted that the abundance of macrofauna associated with seagrass did not decrease following clipping and removal of the leaf layer. Connolly (1995) showed that removal of the leaf canopy of a seagrass bed had a weak effect on the macrofaunal abundance associated with the seagrass. Gray (1991b) found that the abundance and demographic patterns of the prawn *M. intermedium* were similar between two seagrasses (*Zostera capricorni* Ascherson and *P. australis*) that had broadly different bed architectural characteristics, hence different structural complexity. Virnstein & Howard (1987a, b) showed that classical seagrass bed structural descriptors, such as plant biomass and surface area, were poor predictors of macrofaunal abundances, and that additional processes such as plant-animal interactions and active habitat selection may also be playing an important role in determining the diversity of associated macrofauna. In particular, there was lack of agreement between two paradigms concerning bed structure: one proposed that prey abundance increased with increasing structural complexity, because predation success decreases concordantly (e.g. Nelson, 1979; Heck & Orth, 1980a; Stoner, 1982), while the other proposed that prey abundance increased with increasing structural complexity because of preferential habitat selection by the prey itself (Bell & Westoby, 1986b,c). The lack of disagreement led to enthusiastic debates and spawned subsequent investigations in attempts to uncover the specific factor/s that was mainly responsible for the high biodiversity found in seagrass beds (e.g. review by Virnstein, 1987). There are several reasons for the lack of concordance between the conclusions reached by different workers, including the following:

(i) Seagrass beds constitute highly complex systems (den Hartog, 1979; Livingston, 1984; Knowles & Bell, 1998), whose structure and function are influenced by a large number of inter-related environmental factors that go beyond structural attributes of the beds (Heck & Orth, 1980a; Orth et al., 1984; Leber, 1985; Knowles & Bell, 1998). It is, therefore, very difficult to single out a 'main' factor or milieu responsible for the high species richness and abundance of associated fauna (Bell et al., 1985).

(ii) Lack of understanding of the basic ecological processes underlying seagrass systems (for example, the spatial and temporal dynamics of seagrass coverage and other seagrass habitat attributes, and the trophic dynamics of associated fauna) has hindered the unravelling of the potentially complex role of seagrass bed structure in determining the species richness and abundance of associated species.

(iii) Use of selected taxa (for example, decapods and fishes; e.g. Nelson, 1979; Coen et al., 1981; Gore et al., 1981; Stoner, 1982; Leber, 1985) in attempts to identify the main factors responsible for the high biodiversity supported by seagrass beds, has often led to generalisations and extrapolations from the single taxon level to the much more complex community levels, despite the caution advocated by some workers (e.g. Young & Young, 1978) against this approach.

(iv) Use of cages (e.g. Young & Young, 1978; Mattila, 1995) and tethering techniques (e.g. Heck & Thoman, 1981) in predator-exclusion experiments introduce confounding effects (e.g. cages trap pelagic larvae and create an environment of decreased water flow in their vicinity), which make interpretation of results very difficult (Virnstein, 1987). As a result, the majority of studies of this type have not shown convincingly that exclusion of predators from seagrass habitats results in an increase in species richness of prey macrofauna.

(v) Attributes of seagrass beds, such as the physical structure of the habitat and the abundance of associated plant and animal assemblages, vary greatly between beds formed by different seagrass species (e.g. Young, 1981; Lewis, 1984; Virnstein & Howard, 1987a; 1987b; Hovel & Lipcius, 2002) and between beds of the same species at different localities that have broadly different environmental characteristics (e.g. Sogard et al., 1987). Observations made for a particular seagrass bed cannot readily, therefore, be generalised and extrapolated to other beds or bed types.

(vi) Despite the large number of available studies on the ecology of the macrofauna associated with seagrasses, few studies have adopted designs that included adequate spatial replication. As a result, relationships between high macrofaunal abundance and seagrass architectural attributes (e.g., leaf density, see Bell & Westoby, 1986a) are not likely to be consistent over larger spatial scales (Brook, 1978; Virnstein et al., 1984; Bell & Westoby, 1987). Harlin et al. (1996) emphasised that quantitative investigations of macrophyte habitats and associated invertebrates should adopt designs that incorporate a number of study sites, while Tanaka & Leite (2003) stated that descriptions of phytal communites should include several spatial scales.

(vii) There has been a general lack of standardisation of sampling techniques and, at times, use of inadequate or inefficient sampling methods (see Virnstein, 1987; Borg et al., 2002), despite the caution indicated by some workers (e.g. Lewis & Stoner, 1981). As a result, it is frequently difficult to compare and assess the results obtained by different studies aimed at investigating the same ecological aspect.

(viii) Most studies emphasising the high diversity of macrofauna associated with seagrass beds have done so by comparison with adjacent unvegetated habitats (Lewis, 1984; Orth et al., 1984; Pihl, 1986; Heck et al., 1989; Böstrom & Bonsdorff, 1997; Connolly, 1997; Gray et al., 1996; 1998). However, comparisons with other vegetated habitats are rare and the available data indicate that the macrofaunal diversity of seagrass beds is not particularly high when compared with other macrophyte habitats (e.g. Sogard & Able, 1991; Sheridan, 1997).

More recently, Attrill et al. (2000) suggested that the general inference of using seagrass biomass as a measure of bed structural complexity (e.g. Heck & Orth 1980b; Stoner, 1980; Gore et al., 1981; Ansari et al., 1991) is incorrect, since biomass is effectively a measure of plant surface area, but not necessarily of architectural complexity. For example, shoots belonging to two different species of seagrass may have similar biomass values, but their architectural characteristics (e.g. number of leaves) may differ. Thus, the species richness and abundance of macroinvertebrates associated with seagrass beds may follow a simple space-occupancy model, described by the classical 'species-area relationship' (e.g. McGuiness, 1984), in which an increase in habitable area (e.g. leaf surface) leads to an increase in species diversity, hence implying a sampling artifact in many of the results presented to date (Attrill et al., 2000). Furthermore, there has been a general lack of consideration of adequate scales in studies of relationships between seagrass bed structural complexity and the diversity of associated macrofaunal assemblages (Robbins & Bell, 1994; Attrill et al., 2000; Bartholomew et al., 2000). For example, the perception of a dense seagrass bed differs between an amphipod and a large crab (the 'perception windows' of Attrill et al., 2000). There is increasing evidence that the importance of factors such as the presence and amount of seagrass epiphytes, and grazing, in determining the species richness and abundance of seagrass-associated macrofauna, may have been underestimated (e.g. Harlin, 1980; van Montfrans et al., 1984; McGlathery, 1995; Jernakoff et al., 1996; Bologna & Heck, 1999; Heck et al., 2000; Schanz et al., 2000). Sessile organisms associated with seagrass, such as mussels and algal epiphytes also contribute to the habitat of a seagrass bed and, therefore, may themselves (rather than the seagrass plants *per se*) be the more important factor in determining the diversity of certain macroinvertebrate groups. For example, Greening & Livingston (1982), Leber (1985) and Hall & Bell (1988) found that seagrass algal epiphytes provide a refuge to small macroinvertebrates (amphipods and copepods) against predation. Most studies have been centered on the foliar canopy, however, the role of the root-rhizome compartment in influencing the diversity of associated macrofauna has drawn less attention, despite the importance of this compartment in enhancing macroinvertebrate species richness and abundance (e.g. by serving as a refuge against predation; Orth, 1977; Reise, 1977). Therefore, it appears that the most frequently posed questions (i.e. Why do seagrass beds support a high biodiversity and which attributes of the seagrass bed influence the diversity of associated plant and animal assemblages the most?) have not been adequately answered through the research carried out so far.

Of the five seagrass species that occur in the Mediterranean Sea, the endemic *P. oceanica* (L.) Delile forms the most extensive beds down to depths of around 45 m, which constitute an important, but vulnerable, shallow-water ecosystem (Buia et al., 2000; Procaccini et al., 2003, and references therein). Besides plant and animal interactions, *P. oceanica* has important interactions with the physical environment. In turn, these may have indirect influence on the associated biotic assemblages. The thick leaf canopy acts as a buffer against strong wave action and water movement (Gambi et al., 1989a), thereby, reducing hydrodynamic erosive forces acting on the seabed and the shore. In addition, the leaves trap suspended sediment (Gacia & Duarte, 2001), while the *P. oceanica* matte stabilises soft bottoms by reducing transport of mobile sediments and the banquettes on beaches help protect the underlying mobile sediments against loss by erosion (Boudouresque & Meinesz, 1982; 1984; Mazella et al., 1986).

Although the available literature on the biology of *P. oceanica*, and on the ecology of flora and fauna associated with beds of this seagrass, is very extensive, most of the ecological studies carried out to date are mainly descriptive and have focused on analyses of environmental gradients and seasonal trends (see review by Buia et al., 2000). For example, studies of the macrofaunal assemblages associated with *P. oceanica* deal mainly with the influence of depth and the concomitant changes in seagrass bed structure on the assemblage structure of motile macrofauna (Mazzella et al., 1989; Gambi et al., 1989b; Gambi et al., 1992; Borg & Schembri, 2000). However, since depth also influences plant architecture (Bay, 1978; Mazzella & Ott, 1984; Mazzella et al., 1989; Borg & Schembri, 2000), such studies have not concluded whether the observed differences in the associated macroinvertebrate assemblages with changes in water depth were due to environmental changes (e.g. water movement, sediment characteristics, light and temperature) along the bathymetric gradient, or due to changes in bed architecture of the *P. oceanica* beds that occur with changes in bathymetry. Furthermore, most of the available experimental studies lack spatial replication and many have serious shortcomings of inappropriate experimental designs and/or sampling techniques (see reviews in Underwood, 1997 and Borg et al., 2002). Therefore, studies of the role of *P. oceanica* meadow structural complexity in determining the diversity of associated macrofaunal assemblages are lacking. This lack of data has hindered efforts to assess loss of biodiversity, if any, that may occur when the bed structure of this seagrass is altered, for example, as happens when natural and anthropogenic factors act to fragment continuous beds into non-continuous ones, and change the bed's architectural attributes. Very few data are available on the influence of overall change in bed structure (i.e. fragmentation) of *P. oceanica* and within-bed changes in plant architecture on the associated macrofauna. A study by Barberá Cebrián et al. (2002) on the mysid assemblages inhabiting the foliar canopy of naturally fragmented beds of *P. oceanica* concluded that fragmented seagrass beds supported a higher species richness and abundance of mysids than homogeneous beds. However, Barberá Cebrián et al.'s (2002) study area had a mixture of two fragmented seagrass bed types (*P. oceanica* and *C. nodosa*), each of which was also interspersed with bare sand, hence, their study design lacked direct comparison between continuous and fragmented beds of the same seagrass. Overall, studies designed specifically to address the influence of fragmentation and changes in plant architecture of *P. oceanica* beds on the associated macrofauna are unavailable.

Several investigations have addressed the macrofaunal assemblages associated with dead *P. oceanica* matte (Harmelin, 1964; De Metrio et al., 1978; 1980; Vaccarella et al., 1981; Willsie, 1983; Abada Guerroui & Willsie, 1984; Bellan Santini et al., 1986; Somaschini et al., 1994). Most of these studies noted that dead *P. oceanica* matte appeared to support a high diversity of associated macrofauna. This was attributed to the presence of numerous small cavities and hollow interstices, which provide microhabitats for cryptic macroinvertebrates (e.g. Vaccarella et al., 1981; Somaschini et al., 1994), and the abundance of organic matter originating from the decaying roots and rhizomes, which provided a rich food supply (e.g. Harmelin, 1964). However, these results have remained largely ignored and, except for Somaschini et al.'s (1994) study (which only considered the polychaete fauna), no further recent work on the diversity of macrofauna associated with dead *P. oceanica* matte has been undertaken. In the meantime, dead *P. oceanica* matte has been generally viewed as a degraded habitat with low ecological value (Notiziario S.I.B.M., 2003).

1.7 ECONOMICAL IMPORTANCE AND CONSERVATION OF SEAGRASS BEDS

Clearly, the published data highlight the functional role of seagrass beds as an important link between terrestrial and marine ecosystems (e.g. Holligan & De Boois, 1993). Also, seagrass beds are highly productive habitats (Zieman & Wetzel, 1980; Hillman et al., 1989) that serve as nursery areas and feeding grounds for a large number of invertebrate and vertebrate species (Heck & Orth, 1980a; Jacobs et al., 1981; Orth et al., 1984; Virnstein et al., 1987; Bell & Pollard, 1989, Howard et al., 1989; Edgar, 1990). Seagrass beds also act as traps and stabilisers of sediments, and as natural buffers against strong water movement and wave action, thereby reducing coastal erosion (Orth, 1977; Ward et al., 1984; Fonseca & Fisher, 1986).

Traditional uses of seagrasses by human populations in various parts of the globe (Wyllie Echeverria & Cox, 2000) date back hundreds, and possibly thousands of years (see review by Hemminga & Duarte, 2000). Up to the early 20th century, leaves of *Zostera* & *Heterozostera* spp. were widely used in Australia for house insulation and as a soil improver, while up to the late 1990s beach-cast leaves of *Posidonia* spp. were used for the latter purpose (Kirkman & Kendrick, 1997). However, the high ecological and economic importance of seagrass beds was only realised around the late nineteenth century (Phillips & Menez, 1988). The work of Petersen & Boysen-Jensen (1911), and the occurrence of the seagrass 'wasting disease' in the 1930s (Stauffer, 1937; Rasmussen, 1977; den Hartog, 1987), highlighted the loss of biodiversity following decimation of seagrass beds and stimulated increased interest in seagrass ecology worldwide. Following these works, extensive research on the ecology of seagrass beds has firmly established their high ecological and economic value.

The economic value of seagrasses is linked to their various important ecological characteristics and uses to humans, namely: (i) dynamic role in physical coastal processes, (ii) role as a habitat for a large number of species that have either a direct economic importance to fisheries, or that serve as food for economically important species, and (iii) role in biogeochemical cycles.

The role of the canopy of seagrass beds as a buffer against strong wave action and water movement (Fonseca et al., 1982; Fonseca et al., 1983; Fonseca & Fisher, 1986; Gambi et al., 1989a; Fonseca & Cahalan, 1992), and of the role of the root-rhizome matrix in consolidating and stabilizing soft bottoms (e.g. Strawn, 1961; Gacia & Duarte, 2001), is widely acknowledged. Through these roles, seagrass beds help protect shores against coastal erosion, and reduce resuspension and shifting of mobile sediments from one place to another (Terrados & Duarte, 2000; Gacia & Duarte, 2001), thereby contributing directly against economic losses; for example, those incurred by the tourism industry when large amounts of soft sediments are lost from popular sandy beaches by erosion, resulting in reduction of their size and thus utilisation. The economic importance of seagrass beds to the fisheries industry is documented widely and supported by published data (see Jackson et al., 2001). Seagrass beds serve as nurseries and feeding grounds for decapods (for example blue crab *C. sapidus*; Orth & van Montfrans, 1987, and the prawn *M. intermedium*; Gray, 1991a; 1991b) and fishes (e.g. Burchmore et al., 1984; Jackson et al., 2001) that constitute important food items for human consumption. The role of seagrass beds in contributing to marine chemical and biogeochemical cycles has probably been underemphasized. Seagrasses act as modulators in the recycling of carbon, oxygen and nitrogen in the water column and sediments, hence contributing to the biogeochemical linkage between the water column and the seabed (Hemminga & Duarte, 2000), and maintenance of the balance between nutrient input and utilisation in littoral environments (Buzzelli & Meyers, 1998). The high rates of seagrass oxygen production (e.g. around 4-20 litres oxygen m^{-2} day^{-1} are produced by *P. oceanica*; Bay, 1978) may help counteract anoxic conditions in low-energy coastal areas subjected to eutrophic conditions. Parallel with increased concern with the onset of global warming, there has been increased awareness of the role of seagrass ecosystems as carbon sinks; circa 15% of the total carbon storage in all marine ecosystems is contributed by seagasses (Duarte & Cebrian, 1996; Mateo et al., 1997). Hence, seagrasses help counteract anthropogenic production of carbon gases (Hemminga & Duarte, 2000).

Being frequently located in shallow waters close to the shore, seagrass beds are highly susceptible to disturbance from both natural events and anthropogenic activities (Short & Wyllie Echeverria, 1996; Green & Short, 2003), however, the degree to which a seagrass bed is adversely impacted varies between different seagrasses. For example, Livingstone (1984) noted that seagrass beds in the Gulf of Mexico were easily disturbed, but were more resilient than beds of different seagrasses that may be more resistant to disturbance.

Natural factors, in particular the hydrodynamic regime (Fonseca & Bell, 1998), together with other physical processes such as sporadic floods, which lead to deposition of large amounts of silt (e.g. Hanekom & Baird, 1988), may fragment seagrass beds, hence altering their morphology and plant architectural characteristics (den Hartog & Phillips, 2001). However, despite the documented alteration of seagrass habitat resulting from natural disturbance events, data on the effects of fragmentation on the macrofauna associated with seagrass beds and the resulting potential loss of biodiversity are scarce.

The worldwide intensification of coastal development and other anthropogenic activities in recent decades is believed to have led to the decline of seagrasses in many countries (Thayer et al., 1975; Cambridge & McComb, 1984; Larkum et al., 1989). Recently, there has also been an increase in awareness of the potential loss of seagrass habitat resulting from global warming; the predicted adverse impacts include altered growth rates and physiological function resulting from increased water temperature, and large changes in the distributional patterns of seagrasses resulting from increased water depths, changes in tidal variation and increased frequency of storms (Short & Neckles, 1999). Adverse anthropogenic factors include increased turbidity of the water column and nutrient loading of coastal waters (e.g. Orth & Moore, 1983a). Reduced transparency of the water column due to an increase in phytoplankton populations resulting from excessive nutrient input, or an increase in the amount of suspended matter, or a combination of both, lead to a reduction in the amount of light reaching the seagrass, with consequent reduced photosynthetic rates and subsequent reduced growth or even death of the plants (Hemminga, 1998). In particular, eutrophication resulting from nutrient inputs into the marine environment is thought to be a major cause of regression of seagrass beds (Orth & Moore, 1983a; Cambridge & McComb, 1984; Larkum & West, 1990; Duarte, 1995; Kirkman, 1996; Short & Burdick, 1996). Eutrophication leads to an increase in the amount of epiphytes growing on the seagrass leaves, reducing further the light reaching the plant photosynthetic tissue (Silberstein et al., 1986, Buzzelli & Meyers, 1998), leading to impaired growth and possibly death (den Hartog, 1994; Hemminga, 1998; den Hartog & Phillips, 2001).

Such adverse impacts are envisaged to result in degradation of seagrass beds, involving gradual death of plants in parts of the bed (Nienhius, 1983; Walker & McComb, 1992; den Hartog & Phillips, 2001), leading to fragmentation of the habitat (i.e. continuous beds → semi-continuous/reticulate beds → patches). Other adverse impacts include pollution from oil spills (e.g. den Hartog & Jacobs, 1980), industry (e.g. Pihl Baden, 1990) and offshore drilling for oil and gas (Weber et al., 1992), fertilizer used in agriculture (e.g. ammonium, see Van Katwijik et al., 1997), disposal of sewage (e.g. Neverauskas, 1987), and other forms of pollution resulting from land reclamation and changes in land use (e.g. Thayer et al., 1975; Kemp et al., 1983). Workers have shown that degradation of seagrass habitat resulting from pollution has led to a decline of commercially important fisheries stocks, for example, in Japan (Kikuchi, 1974) and Spain (Perez-Ruzafa et al., 1991), but their studies are not supported by data showing whether the decrease in fisheries stock was directly due to alteration of seagrass habitat structure or to other effects of pollution.

The adverse impacts of physical damage to seagrass habitat resulting from anthropogenic activities such as trawling (e.g. Sánchez Lizaso et al., 1990; Sánchez Jerez & Ramos Esplá, 1996; Martín et al., 1997; Sánchez Jerez et al., 2000) and anchoring and/or deployment of moorings (e.g. Hastings et al., 1995; Francour et al., 1999) are well documented. In particular, the adverse impact of boat moorings on seagrass habitat has been well described. For example, initial deployment of boat moorings in Australia was found to decimate seagrass in the vicinity, leading to a bare sandy patch, which extends in size with time. Sandy patches may eventually coalesce, leading to increased fragmentation of the seagrass habitat and loss of seagrass area, such that loss of nearly 20% of the original beds occurred over the span of 50 years (Hastings et al., 1995). However, quantitative data showing whether fragmentation of seagrass beds resulting from direct physical damage due to such activities leads to loss of biodiversity are lacking (Sánchez Jerez & Ramos Esplá, 1996; Martín et al., 1997; Sánchez Jerez et al., 2000).

Once the source of disturbance is removed, the time taken for recovery of a seagrass bed depends on various factors, including the seagrass species and the degree of damage suffered. Slow-growing seagrasses, such as *P. oceanica* (Duarte, 1991), take longer to recover than fast-growing species such as *Z. marina*. In any case, recovery of the seagrass is generally slow (Kirkman & Kuo, 1990) and may require human intervention for effective regeneration within a reasonably short time-span (Fonseca et al., 1988; West et al., 1990). Furthermore, if conditions remain unfavourable for seagrass growth (i.e. adverse conditions persist), efforts to rehabilitate seagrass beds will be hindered or indeed rendered impossible (Tamaki et al., 2002). Given such slow recovery (if any), rather than allowing uncontrolled fragmentation followed by attempted recovery/restoration, it makes more sense to gain an understanding of the influence of seagrass bed structure on the associated biodiversity, so that the conservation value of seagrass habitat is established and fragmentation mitigation efforts established.

On a regional scale, the ecological and economic importance of *P. oceanica* beds has been recognised widely, and many countries have adopted conservation measures and legislation to protect this habitat (Procaccini et al., 2003). Furthermore, *P. oceanica* habitats are listed in the EC Habitats Directive 92/43/EEC as priority habitats whose protection requires special areas of conservation to be designated (EEC, 1992). Mediterranean coastal populations have exploited *P. oceanica* for some traditional uses, including use of leaves as packing material in mattresses, cushions, pillows and sound proofing panels, as an agricultural fertiliser and as a constituent of fodder in animal husbandry (Mazzella et al., 1986; Chemello & Toccacelli, 1990). The beneficial interactions between *P. oceanica* beds and the environment, namely attenuation of wave action and currents (e.g. Gambi et al. 1989a) and stabilization of soft sediment bottoms (Jeudy de Grissac, 1984; Gacia & Duarte, 2001), contribute significantly to protection against coastal erosion (Boudouresque & Meinesz, 1982; Jeudy de Grissac, 1984; Boudouresque et al., 1994) and have very important economic implications, especially given the high importance of the Mediterreanean's shore and coastal areas to the region's tourism industry. The direct ecological and economic importance of *P. oceanica* beds is also highlighted by their contribution to fisheries, since the habitat supports numerous fishes (e.g. sparids, serranids, labrids and scorpaenids) and invertebrates (e.g. the urchin *Paracentrotus lividus* Lamarck) which have high commercial demand (Procaccini et al., 2003). Several authors also view *P. oceanica* as a very useful indicator of water quality (e.g. Augier et al., 1984; Pergent et al., 1995; Pergent et al., 1999). The ability of this seagrass to form large reservoirs of carbon (Mateo et al., 1997) and phosphorous (Delgado & Vidal, 1989) in its rhizomes, and its capacity to mobilise them to the rest of the plant under certain circumstances, has important implications for cycling of these elements in the Mediterranean Sea (Hemminga & Duarte, 2000).

P. oceanica is a relatively hardy seagrass but disturbance from adverse natural and anthropogenic factors has led to regression and damage to beds of this seagrass in many parts of the Mediterranean (Procaccini et al., 2003). Natural disturbance processes include strong wave action and currents, which cause direct physical damage to *P. oceanica* beds, and heavy rainfall, which increases the turbidity of coastal waters through runoff carrying suspended material into the sea.

Numerous anthropogenic activities impact *P. oceanica* beds adversely, leading to a decline of the seagrass (Boudouresque et al., 1975; Pérès, 1984; Boudouresque et al., 1985b;

Bourcier, 1989; Boudouresque et al., 1994; Marbà et al., 1996; Pergent-Martini & Pasqualini, 2000). As with seagrass beds worldwide, the most widespread adverse anthropogenic impacts on *P. oceanica* beds are those arising from nutrient enrichment of coastal waters and the addition of suspended matter in the water column. Increased nutrient concentrations in the water column enhance the growth of epiphytes on the seagrass leaf surfaces (Pergent et al., 1999; Ruiz et al., 2001; Dimech et al., 2002) and may also lead to phytoplankton blooms, both of which reduce the amount of light reaching the seagrass, with consequent reductions in plant growth rates or possibly even death of the plants (Boudouresque et al., 1994). The presence of suspended sediments in the water column, such a those originating from dredging works and artificial beach replenishment projects (Astier, 1984), also lead to turbid conditions which reduce the amount of photosynthetically active radiation (PAR) reaching *P. oceanica*, with resulting adverse impacts leading to regression and loss of seagrass habitat (Boudouresque et al., 1994). For example, Astier (1984) recorded that the lower distribution limit of *P. oceanica* beds migrated upwards from 28 m to 15 m, following the construction of jetties and the creation of artificial sandy beaches in Toulon (France). Other forms of coastal development (Meinesz et al., 1982; Blanc & Jeudy de Grissac, 1989; Ruiz et al., 1993) and pollution resulting from harbour activities, discharge of sewage (Balduzzi et al., 1984; Ramos Esplá, 1984; Accardo-Palumbo et al., 1995; Pergent-Martini & Pasqualini, 2000), fish farming activities (Delgado et al., 1997; 1999; Pergent et al., 1999; Ruiz et al., 2001; Dimech et al., 2002) and oil spills (Sandulli et al., 1992) have contributed to degradation of *P. oceanica* in many parts of the Mediterranean.

Despite the widespread degradation and regression of *P. oceanica* beds resulting from eutrophication and other forms of pollution, data on alteration of bed architecture resulting from these factors are restricted mainly to studies of the impact of offshore fish farms on nearby beds of the seagrass. For example, Delgado et al. (1999), Pergent et al. (1999), Ruiz et al. (2001) and Dimech et al. (2002) recorded reductions in leaf length, shoot biomass and shoot density of *P. oceanica* located in the vicinity of fish farms in their respective study areas, which implies that excessive nutrient loading in the vicinity of seagrass beds results in gross alteration of their bed architecture. Dimech et al. (2002) noted changes in the diversity of seagrass macrofauna with increasing distance from the fish cages, but it was not clear whether this was due mainly to the nutrient gradient or to changes in seagrass bed architecture, since the two effects could not be separated in the study design.

Adverse impacts involving direct physical damage to *P. oceanica* beds include boat anchoring (Francour et al., 1999) and trawling (Ardizzone & Pelusi, 1984; Sanchez Lizaso et al., 1990; Martín et al., 1997; Ramos Esplá et al., 1997). Studies carried out to assess the impact of trawling on *P. oceanica* beds and their associated biota in the western Mediterranean have detected some differences in the assemblage composition and structure of macroinvertebrates (Sánchez Jerez et al., 1996) and fishes (Sánchez Jerez et al., 2000) between trawled and untrawled areas. According to these authors, both seagrass coverage and shoot density were significantly different between pristine *P. oceanica* beds and ones degraded by trawling (e.g. Sánchez Jerez et al., 2000), but other plant architectural attributes, namely shoot biomass, foliar area and epiphyte biomass, were not significantly different. Martín et al. (1997) estimated that a medium-sized trawler may root out between 99,200 and 363,300 *P. oceanica* shoots per hour, depending on the state of degradation of the meadow (i.e. whether the meadow is pristine or has already undergone physical alteration by previous trawling activities).

Changes in the species composition and structure of assemblages associated with *P. oceanica* beds resulting from coastal development and harbour activities have been recorded by some workers. For example, Accardo Palumbo et al. (1995) noted an increase in the abundance and number of detritivorous gastropods in *P. oceanica* beds exposed to disturbance from coastal development activities, namely harbour construction works, which were attributed to changes in the sedimentary and hydrodynamic regimes of the area. Azzolina & Hamelin (1989) noted that the abundance of the holothurian *Holothuria polii* Delle Chiaje increased in beds of *P. oceanica* degraded by pollution, while that of *Holothuria tubulosa* Gmelin, which is more characteristic of pristine beds, decreased. However, these works lack quantitative data on seagrass bed structural attributes between healthy and degraded seagrass beds in their study area.

The recent introduction of exotic species into the Mediterranean, for example, the alga *Caulerpa taxifolia* (Vahl) Agardh (Meinesz & Hesse, 1991), poses new threats to *P. oceanica* beds, since these may be able to displace the seagrass (Ribera et al., 1996). Cecherelli et al. (2000) concluded that the alien alga *Caulerpa racemosa* (Forsskal) Agardh had a higher potential to invade heterogeneous *P. oceanica* beds that were interspersed with bare sand (reticulate beds), than continuous beds of the same seagrass, thereby highlighting the higher vulnerability of fragmented *P. oceanica* beds to alien macrophytes.

Although there are several published studies dealing with the adverse impacts on *P. oceanica*, fewer works have addressed its recovery following disturbance. These limited studies indicate that *P. oceanica* has a low resilience and requires several years to recover following an adverse impact (e.g. Meinesz & Lefevre, 1984; Delgado et al., 1999, Pergent-Martini & Pasqualini, 2000). As in other species of the same genus (Gordon et al., 1994), recovery of abundance after mortality is poor in *P. oceanica*. This probably results from the large belowground biomass and low rhizome growth rate, such that recolonisation in areas where the seagrass has died requires vegetative propagation from other beds, or germination of plants from seeds transported to the site (Ruiz et al., 2001). It is also thought that because asexual reproduction constitutes the main mode of spread of *P. oceanica*, the limited genetic flow may also contribute to its decline, especially in places where conditions are unfavourable (Procaccini et al., 1996).

Attempts to restore *P. oceanica* beds have focused on vegetative transplantation techniques (e.g. Meinesz et al., 1992; Molenaar & Meinesz, 1992; Molenaar et al., 1993; Molenaar & Meinesz 1995) and, to a lesser extent, on planting of seeds and seedlings (e.g. Meinesz et al., 1993; Balestri et al., 1998). The success rates for the former techniques have been rather low, probably as a result of the lack of knowledge on the environmental factors which influence survival of transplanted shoots (e.g. sediment stability, Molenaar & Meinesz, 1995). On the other hand, very encouraging results have been obtained from studies on techniques of planting of seeds and seedlings where the type of substratum is an important determinant for their survival (Balestri et al., 1998).

There is a dearth of information on basic ecological characteristics of different bed types of *P. oceanica*, such as data on whether plant architectural characteristics and the species richness and abundance of associated macrofauna differ between fragmented and non-fragmented beds, and between living and dead matte of the seagrass. Several published studies are available showing changes in macrofaunal assemblages with variation of *P. oceanica* bed structure, as a function of changing depth, or with degradation resulting from anthropogenic activities. However, such studies do not present data on changes in plant architectural attributes and in the diversity of associated fauna that may possibly accompany fragmentation of the seagrass beds. Such data will enable ecologists to establish whether fragmentation of *P. oceanica* beds, or complete loss of the foliar canopy, will result in loss of biodiversity, and will therefore help in the formulation/revision of recommendations for the conservation and management of different beds types of the seagrass.

1.8 STUDY AIMS

The general study aim was to compare plant architectural features and the diversity of macrofauna assemblages between different *P. oceanica* seagrass bed types. The results of such a study will increase our understanding of the influence of bed structure on the species richness and abundance of seagrass-associated flora and fauna, which will help assess the relative ecological value of different seagrass bed types and predict loss of biodiversity and habitat that may result from alteration of this system (e.g. alteration of plant architecture and bed fragmentation) resulting from natural or anthropogenic disturbance. In turn, such information will help in the formulation of appropriate conservation and management strategies for seagrass habitats. However, collection of useful data on which to base sound conclusions depends a great deal on the appropriateness of the study design.

The specific study aims were:

(i) Identify the main different bed forms of *P. oceanica* in the Maltese islands to enable selection of a bed type that represents a fragmented seagrass habitat, for comparison of plant architectural characteristics and associated macroinvertebrate diversity with those of non-fragmented beds. An important requirement was that the fragmented *P. oceanica* bed types selected for the present study had widespread occurrence, enabling the planning of an appropriate experimental design, based on the inclusion of a number of spatial levels and adequate spatial replication (Chapter 2).

(ii) Design a suitable sampler that enabled appropriate and efficient collection of the motile macroinvertebrates associated with *P. oceanica* beds, given that the sampling techniques employed in other studies either had practical problems of use in the field, or are considered inefficient in collecting the total macroinvertebrate assemblage associated with *P. oceanica* beds (Chapter 2).

(iii) Determine whether two different bed types of *P. oceanica*, continuous and reticulate (= naturally fragmented) beds, sampled at a number of spatial scales, had different plant architectural characteristics, given the apparent importance of seagrass bed structure in influencing the diversity of associated macrofauna. To address this aspect of study, the null hypothesis tested was that within-bed architecture did not differ between adjacent reticulate and continuous beds, over spatial scales varying from kilometres to metres. Establishing whether different bed types of *P. oceanica* have different plant architectural characteristics (and the spatial scales at which such differences may occur) will enable assessment of the degree of within-bed structural change that may take place when beds of this seagrass undergo fragmentation as a result of natural or anthropogenic disturbance (Chapter 3).

(iv) Determine whether continuous and reticulate (= naturally fragmented) beds of *P. oceanica,* sampled at a number of spatial scales, support motile macroinvertebrate assemblages with different species richness, abundance, and composition. To address this aspect of study, the null hypothesis tested was that seagrass plant architectural characteristics did not have a significant influence on the species richness, abundance and composition of motile macroinvertebrate assemblages associated with *P. oceanica* beds, over spatial scales varying from kilometres to metres. Establishing whether fragmentation of seagrass beds results in a lower diversity of associated macrofauna is important, in view of the widely held paradigm that habitat fragmentation results in loss of biodiversity (Chapter 4).

(v) Determine whether the diversity of associated motile macroinvertebrate assemblages, sampled at a number of spatial scales, differed between *P. oceanica* living matte (supporting living shoots of the seagrass) and dead matte (not supporting living shoots of the seagrass). To address this study aspect, the null hypothesis tested was that the species richness, abundance and composition of motile macroinvertebrate assemblages did not differ between living and dead *P. oceanica* matte. Establishing the effects of loss of the foliar layer of *P. oceanica* beds on the associated macrofaunal assemblages is important, given that dead matte often remains following severe anthropogenic disturbance and adverse natural environmental processes (Chapter 5).

(vi) Assess, through integrating the results and interpretations made in the various stages of the proposed study with a comparison of the current knowledge of the influence of seagrass bed structure on the associated macrofauna and current conservation guidelines, the implications of the study's findings for conservation and management of *P. oceanica* beds in the Maltese islands and the rest of the Mediterranean. Establishing conservation proposals and recommendations for further research will help Mediterranean conservation biologists and environmental managers to update current conservation guidelines, propose new conservation measures and identify related issues that require further investigation for *P. oceanica* habitat (Chapter 6).

CHAPTER 2

SELECTION OF STUDY SITES, EXPERIMENTAL DESIGN, AND CHOICE OF GEAR AND TECHNIQUE FOR SAMPLING *POSIDONIA OCEANICA* BEDS

Part of this chapter has been included in the following publication:

Borg J. A., Attrill M. J., Rowden A. A., Schembri P. J. & Jones M. B., 2002. A quantitative technique for sampling motile macroinvertebrates in beds of the seagrass *Posidonia oceanica* (L.) Delile. *Scientia Marina* 66 (1): 53-58.

2.1 INTRODUCTION

2.1.1 Study design

The importance of adopting a well thought-out design for ecological studies has been emphasised often (e.g. Green, 1979; Hairston, 1989; Kingsford & Battershill, 1998). In most ecological surveys, the specific subject of study is conceived usually after an observation raises a specific question, for which an explanation is desired. In such a case, the most widely adopted procedure is for the investigator to formulate a hypothesis and, subsequently, to test it by designing an appropriate experiment. Such an approach has arisen with time from scientific philosophy (Ford, 2000). The outcome, validity and overall success of an ecological experiment depend, ultimately, on the appropriateness and robustness of the underlying design (Underwood, 1997). Assessment of the practical feasibility and successful implementation of a particular sampling design requires adequate prior knowledge of the environment/habitat/organism under study. In addition, to ensure collection of a robust data set, the worker needs to acquire information on the minimal sample size that should be collected, the number of replicates required and the optimal design of the sample collecting device (Andrew & Mapstone, 1987). Although information on prior knowledge and sampling effectiveness may be obtained from previous studies carried out by other workers, such sources are hardly ever likely to be a reliable substitute for a pilot study made by the workers themselves (Downing & Anderson, 1985). A pilot study has the added advantage of helping the investigator become familiar with the study area and its environmental characteristics. Pilot studies, therefore, constitute an important preliminary part of any detailed ecological study (Green, 1979).

The present study aimed to identify the main different forms of *Posidonia oceanica* Linnaeu*s* (Delile) beds in the Maltese islands, to enable selection of bed types that represent naturally fragmented and non-fragmented seagrass habitats, for comparison of plant architectural characteristics and associated macroinvertebrate diversity. An important requirement was that the bed types selected for the present study had widespread occurrence, enabling the implementation of an appropriate experimental design, based on the inclusion of a number of spatial levels and adequate spatial replication. Furthermore, the study aimed to design a suitable sampler that enabled appropriate and efficient collection of the motile macroinvertebrates of *P. oceanica*, given that the sampling techniques employed in other studies either had practical problems of use in the field, or are considered inefficient in collecting the total macroinvertebrate assemblage associated with *P. oceanica* beds (Borg et al., 2002).

2.1.2 Selecting an appropriate sampling design

Compared to manipulative experiments, where the experimenter imposes some external factor/s on the experimental units, mensurative experiments usually only require collection of data in space and/or in time (Hurlbert, 1984). If some statistical tests are applied to test for the significance of difference between different treatments, then the experiment is classified as 'comparative mensurative' (Hurlbert, 1984). The inclusion of spatial replication (i.e. replication applied at different spatial scales) in sampling programmes designed for mensurative benthic studies has been increasingly evident in recent years (e.g. Morrisey et al., 1992, James & Fairweather, 1996; Kendall & Widdicombe, 1999; Cole et al., 2001). The issue of scale is central to the design of ecological studies, since environments are seldom homogeneous, and because factors and processes that influence the biology of species and the structure of biotic assemblages are scale dependent (Wiens et al., 1986; Wiens, 1989; Levin, 1992). As a result, the scale of sampling has an important influence in determining the outcome of an ecological experiment and the validity of the results obtained (e.g. Thrush, 1991). Studies of seagrass habitats are no exception; no single scale should be considered sufficient for investigating them (Robbins & Bell, 1994; Virnstein, 1995). The appropriate choice of scale, and number of scales, underlying the experimental design must be a trade-off between an ability to observe landscape processes without losing information on the finer scale, and an ability to detect fine-scale information, without being hindered by unrelated environmental 'noise' (Andrew & Mapstone, 1987; Dutilleul, 1993). Choice of the appropriate scale depends also on the region where the study is held (Virnstein, 1995). For the purpose of the present study, three spatial scales were selected to test the proposed hypotheses: (i) 'large' (kilometres), (ii) 'medium' (few hundreds of metres) and 'small' (tens of metres). Comparison of the different *P. oceanica* bed types over the large spatial scale required identification of a number of study 'locations' within a suitably large stretch of coast. Within one of the locations, selection of a number of 'sites' would enable comparison at the medium scale, while selection of a number of 'plots' within one of the sites would enable comparison at the small spatial scale. Establishing four sampling stations at each spatial scale enables sound spatial replication without imposing excessive demands on sampling and effort and analyses that would render the study programme unpractical. In this way, the basic experimental design would incorporate adequate spatial replication between different *P. oceanica* bed types, across a number of spatial scales (Robbins & Bell, 1994; Virnstein, 1995).

Data collected using such an experimental design, involving a hierarchy of spatial scales, have been analysed frequently using univariate statistical tests, such as Analysis of Variance (ANOVA), which estimates variance components at each hierarchical level (for the proposed study, the different spatial scales). The most frequently advocated strategy is to have a fully balanced nested (FBN) design (Morrisey et al., 1992; Underwood, 1997)

(Figure 2). However, FBN designs are not without problems. For example, since allocation is hierarchical, there is more information available on the lower nested factors than on the higher ones, resulting in unequal allocation of degrees of freedom between the lower and higher levels (Pettitt & McBratney, 1993; Khattree et al., 1997). Furthermore, FBN designs require huge sampling and processing efforts, such that they may not be cost effective or even affordable (Khattree et al., 1997). For example, a FBN design that involves three levels, two sampling compartments on the first level, four on the second and eight on the third, will require sampling from a total of 8 stations. If three replicates are taken from each station, the total number of required sampling units is 24. If such a design were to be applied to the present study plan, that is, four locations (large scale) having four sites (medium scale) nested in each, and with four plots (small scale) nested in each site, and if say four sample units are collected per station from each of two different seagrass bed types, the whole sampling programme will involve collection of a total of 512 (4 x 4 x 4 x 4 x 2) samples! Such a large number of samples would require an exceedingly long period of time to collect and process, which by far exceeds what is usually practically possible. Sampling effort in a FBN design may be reduced by limiting the number of sampling compartments at the upper scale, e.g. by reducing the number of proposed locations for the present study to 2, but this is not recommended since it aggravates the problem of having

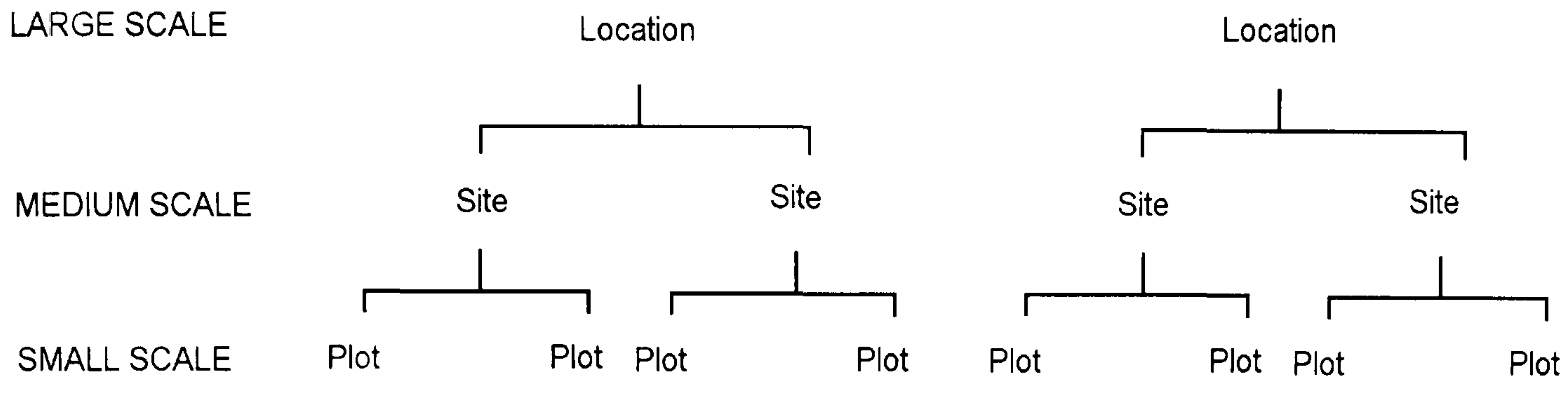

Figure 2. Fully balanced nested design with three spatial levels and eight sampling compartments.

an unequal distribution of degrees of freedom. On the other hand, reducing the number of sampling compartments at each level, say to 2, would reduce the robustness of the design in detecting spatial variation, since only a small number of localities are sampled at each spatial scale.

An alternative design proposed by some statisticians (e.g. Pettitt & McBratney, 1993) is 'staggered nesting' (Figure 3). Staggered nested (SN) designs reduce sampling effort but retain the same number of sampling compartments at each level (Pettitt & McBratney, 1993; Khattree et al., 1997). For example, a SN design that involves three levels (two sampling compartments on the first level, three on the second and four on the third) will require sampling from a total of 4 stations (half the number that would be required for an equivalent FBN design). If three replicates are taken from each station, the total number of samples required is 16. SN designs have the added advantage that they do not produce negative estimates of the variance components, which could pose problems in fully nested designs (Khattree et al., 1997). Furthermore, SN designs allow for an equal number of degrees of freedom at each level (except the highest, which has one less than the lower one), ensuring that no level is estimated more efficiently than another (Khattree et al., 1997). However, a major problem with SN designs is that they cannot be used in experiments that involve mixed (both random and fixed) factors, since estimation of the

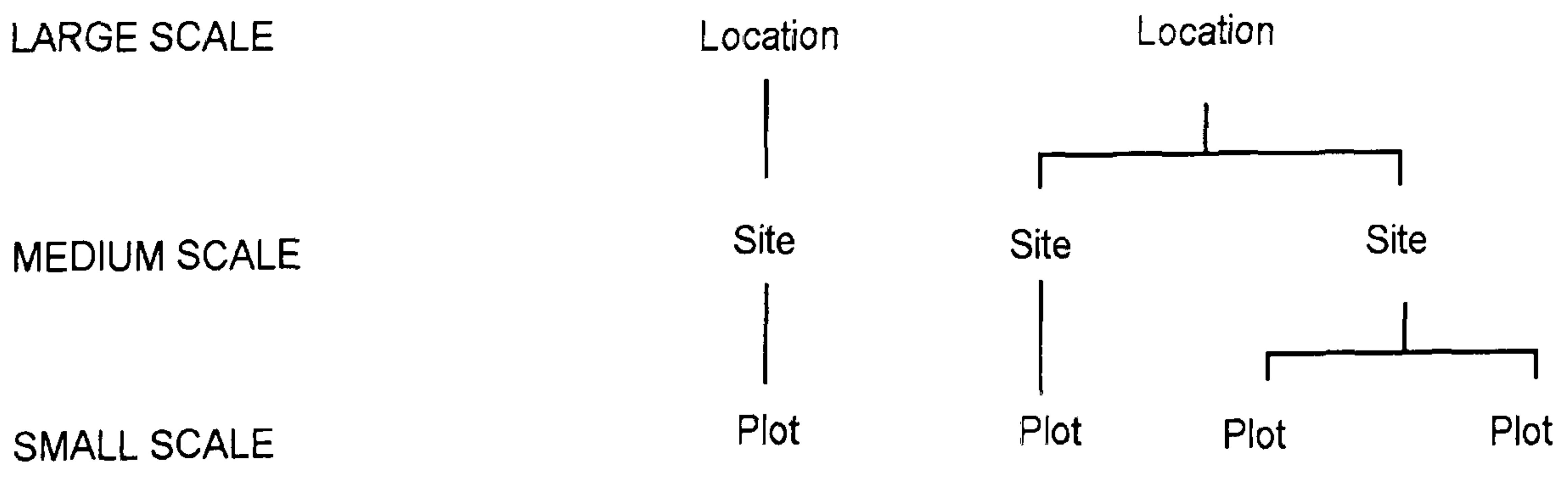

Figure 3. Staggered nested design with three spatial levels and four sampling compartments.

variance components is not commensurable and, therefore, illogical where interactions occur (Underwood & Petraitis, 1993), although some workers (e.g. Burdik & Graybill, 1992) have shown that calculations of this type can be made. Another disadvantage is that SN designs have been used rarely in ecological studies and their applicability to research in ecology is still at an 'experimental stage' (Cole et al., 2001), so much so that the availability of statistical programs based on this method is very restricted (Cole, 2001).

Given the problems of fully balanced nested and staggered designs, it is thought appropriate to employ a design in which adequate spatial replication is not compromised and the required total number of samples collected is not exceedingly large to pose problems of excessive cost and effort. To meet these requirements, the proposed study design consisted of three different spatial scales (small, medium and large) across which to test differences in *P. oceanica* bed structure and the diversity of associated macroinvertebrates (Figure 4). Using this design, which in principle is based on staggered nesting, sampling stations were planned at each of four localities within each of the three different spatial scales: small, medium and large. Differences in bed structure, and in the diversity of associated macroinvertebrates between bed types, can be tested at each of

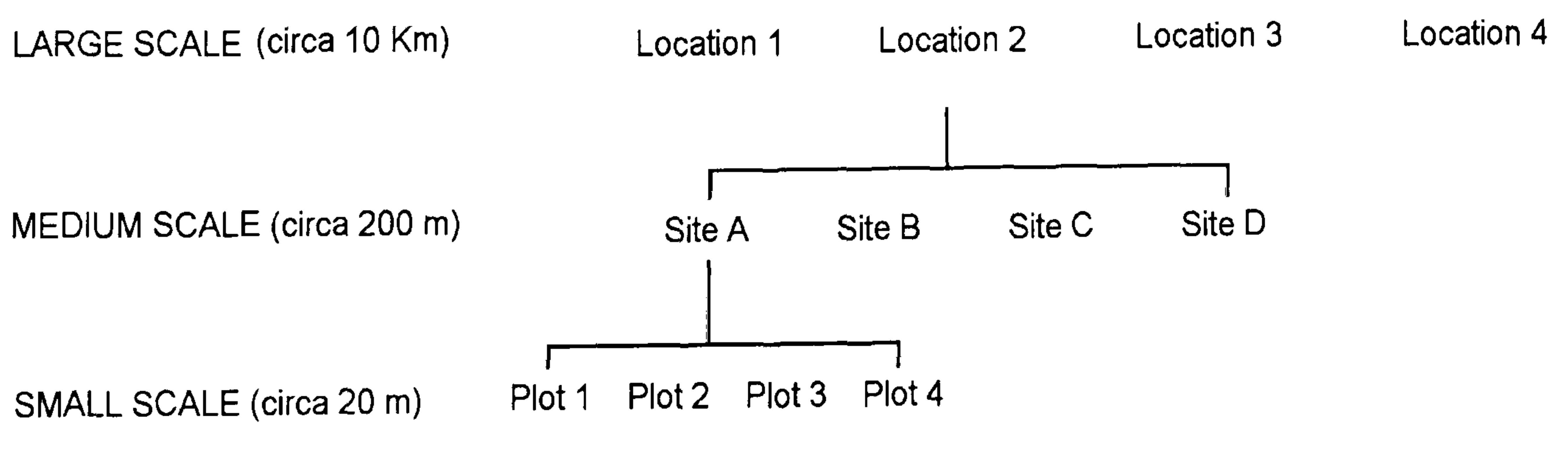

Figure 4. The experimental design proposed for the present study. There are three spatial levels, with a total of ten sampling compartments.

the three different spatial scales using a 2-factor ANOVA, in which bed type is a fixed factor and sampling locality is random. In addition, this design enabled the use of multivariate analyses to test for differences in the composition of macroinvertebrate assemblages between the different bed types. Multivariate techniques are used in the analysis of ecological data to reduce the apparent dimension of large data sets, by making the classification of samples more visual. Using this technique, samples are classified into groups, depending on the similarity between the species composition and abundance recorded from the various samples.

2.1.3 Selecting bed types and appropriate study sites

Acquiring complete information on the environmental characteristics of a study location, prior to commencement of the actual investigation is crucial, since establishment of the study design and successful implementation of the sampling programme are dependant entirely on detailed knowledge of the environmental characteristics of the proposed study area (Green, 1979; Andrew & Mapstone, 1987). In particular, the first step in ecological studies on seagrass beds is the collection of baseline data on the occurrence, condition and spatial extent of the habitat (Kirkman, 1996). Therefore, to meet the main aim of the present study, that is, to examine the influence of *P. oceanica* bed structure on the diversity of associated macroinvertebrate assemblages, it was essential to gather information on the distribution of *P. oceanica* beds around the coast of the Maltese Islands and, subsequently, select those bed types and localities that would support the testing of the central hypothesis of the proposed study: that is, identify locations and sites where such bed types are located in broadly similar environmental conditions (e.g. similar depth, exposure and water quality) and distributed throughout the Maltese Islands. Adherence to the latter two criteria would allow a degree of control over confounding factors (Green, 1979; Underwood, 1997) and enable an adequate, spatially-replicated sampling programme, given the importance of including adequate spatial replication in ecological experiments (Andrew & Mapstone, 1987; Thrush, 1991; Underwood, 1997). Adequate spatial replication ensures the detection of natural variation, where present, and also ascertains that sampling is not pseudoreplicated (Hurlbert, 1984).

The Maltese Islands consist of a small archipelago, aligned northwest-southeast, located at the centre of the Mediterranean Sea, between latitudes 35.48° and 36.05° North and between longitudes 14.11° and 14.35° East (Figure 5). Being located at the centre of the Mediterranean Sea, the Maltese Islands have biogeographical features that are characteristic of both west and east Mediterranean basins. As in most other Mediterranean coastal areas, the most extensive marine coastal benthic habitat types present in the shallow Maltese coastal waters to a depth of around 40 m are those of photophilic algae, beds of the seagrass *P. oceanica* and bare sand (Borg et al., 1997). Detailed maps of the distribution of marine benthic assemblages are lacking for the Maltese Islands, however the precise spatial distribution of *P. oceanica* beds in some Maltese coastal areas is known from surveys commissioned by local environmental agencies[1], from undergraduate and postgraduate projects undertaken at the University of Malta, and from works forming part of baseline surveys and assessments of environmental impacts prepared by local private agencies (e.g. Borg et al., 1997). Where data are lacking, maps showing the spatial distribution of shallow-water marine benthic habitats, including seagrass beds, can be produced from aerial photographs taken during local remote surveys commissioned by the Maltese Government. Aerial photographs are a very useful source of data since they can provide detailed information on the occurrence and distribution of seagrasses (Meinesz et al., 1982; Orth & Moore, 1983b; Kirkman, 1996; Short & Coles, 2001).

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[1] The main local Governmental organisation responsible for issuing requests for baseline surveys, environment impact assessment/statement studies and other environmental surveys is the Environment Protection Directorate (EPD) of the Malta Environment and Planning Authority (MEPA).

The geology of the Maltese Islands is characterised by marine sedimentary rocks, mainly limestones, which were deposited during the Oligo-Miocene (Pedley et al., 1976; 1978). The two main islands, Malta and Gozo, are both tilted to the northeast, such that their southwestern coast is characterised mainly by high cliffs, while their northeastern coast is characterised mainly by gently sloping shores. Tectonism, coupled with changes in sea level, have led to submergence of coastal valleys to produce 'drowned valleys' whose existence is indicated by the many headlands, creeks and bays, in particular those found along the low-lying northeastern coast (Paskoff & Sanlaville, 1978; Ellenberg, 1983).

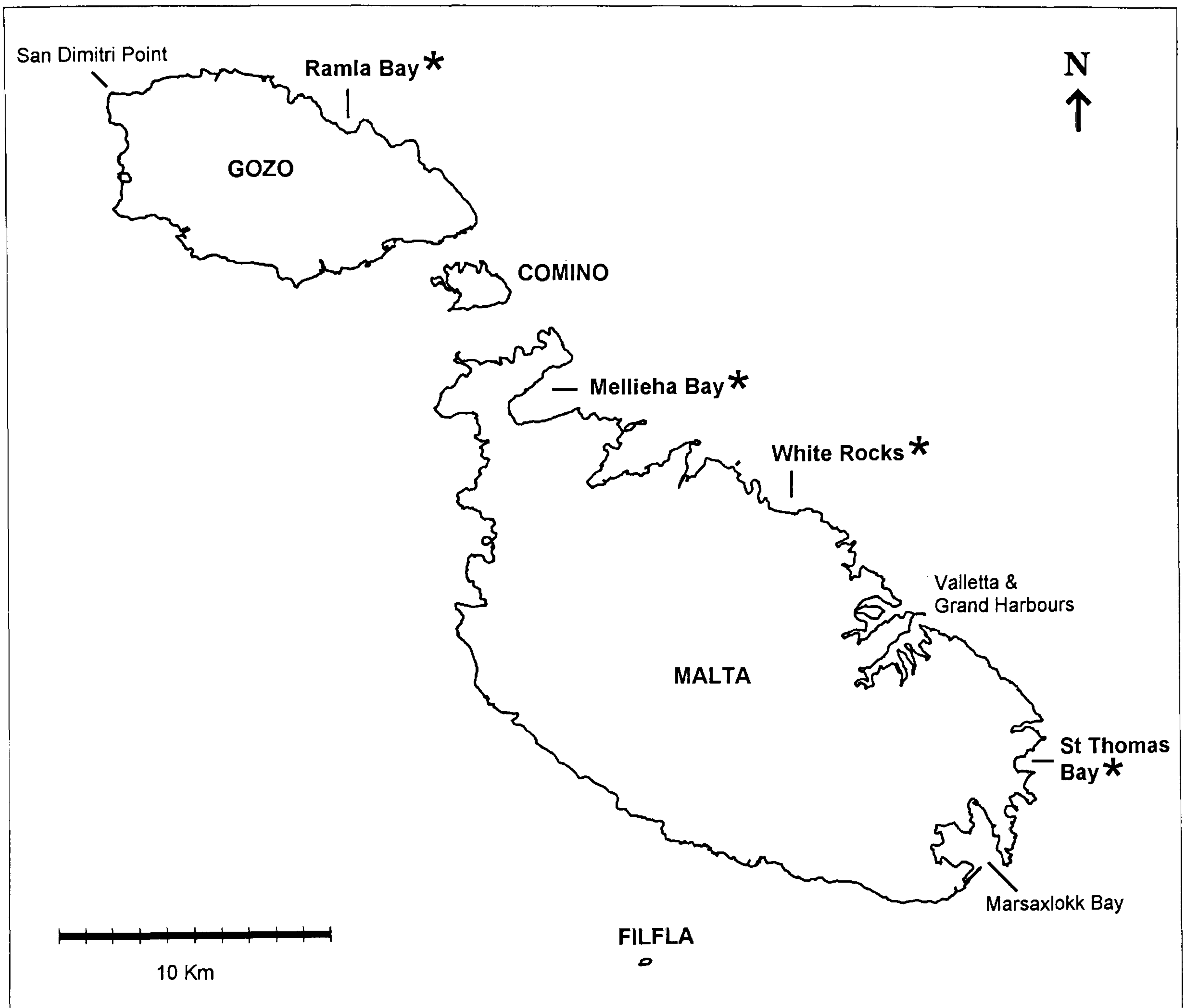


Figure 5. The Maltese Islands showing the study inlets (*) on the northeastern coast.

Off the southwestern coast, the predominant typical geomorphology consists of steep sloping escarpments (known locally as 'rdum'), which support boulder fields at their base and extend downwards atop cliffs that lead to the sea. The vertically-faced cliffs found in these parts of the Maltese islands extend down to mean sea level and beyond, such that the seabed located a few tens of metres away from the cliff bases may lie at a depth of 30 m or more. As a result, the coastal area is characterised by extensive assemblages of photophilic algae that cover the vertical submarine cliff faces, drop-offs and large boulders littering the seabed close to the cliff bases. Bare sand is usually present close to the cliff bases, at depths of 30 – 60 m, where narrow bands of 'maerl' (accumulations of living and dead unattached non-geniculate carcareous rhodophytes that form a distinct habitat; BIOMAERL team, 2003) often occur. However, because sandy bottoms in shallow waters are uncommon in these coastal areas, seagrass beds are rarely encountered and, where present, are confined to around five small bays and inlets.

Off the northeastern coast of the islands, along rocky headlands and off rocky shores, the seabed is characterised by a gently sloping bottom, which extends underwater to a depth of around 3 - 5 m and supports a narrow band (mean width circa 15 m) of photophilic algal habitat. Further offshore (circa 10 – 20 m horizontal distance from the shore), at depths of 4 – 6 m, the bottom is characterised by a heterogeneous mixture of different habitat types: bare sand, patches of photophilic algae on bedrock and boulders, and small patches of seagrasses (*P. oceanica* and *Cymodocea nodosa* (Ucria) Ascherson). At greater depths (6 - 45 m), the predominant habitat types are those of *P. oceanica* beds and bare sand. At depths exceeding 45 m, which corresponds to the 'lower infralittoral/upper circalittoral transition zone', the characteristic habitat types are bare sand and maerl beds (Borg et al., 1998; Schembri, 1998).

Physical oceanographical data for the Maltese Islands are generally lacking. During summer, a strong thermocline is present to a depth of 30 m, with a temperature difference between surface and bottom, which may exceed 10°C (Havard, 1978; 1979; Drago, 1997). During winter, the water mass is well mixed by storms to depths of more than 50 m (Havard, 1978; 1997). In bays and inlets, the water column is more homogeneous and may have temperatures in excess of 27°C due to intense surface heating and water stratification, while retention time is relatively long (Drago, 1997). As for most of the Mediterranean, the seas around the archipelago are microtidal (maximum tidal range = 0.20 m), with fluctuations in mean water level of less than 0.5 m and mainly arising from differences in atmospheric pressure. However, Drago (1995) noted that diurnal variations in sea levels may also be related to coastally-trapped (topographic) waves on the continental shelf between Malta and Sicily. Two main opposite flowing currents occur close to the Maltese islands in the Strait of Sicily; one consisting of surface water (Modified Atlantic Water) flowing east from the Atlantic, and the other consisting of an underlying denser layer flowing west from the Levantine Basin (Drago et al., 2003). A transitional layer occurs between these two water masses, coinciding with a permanent thermocline and halocline, where mixing of the Levantine and Atlantic waters occurs (Drago; 1997; Drago et al., 2003).

The Maltese Islands present an obstacle to the general surface water exchange between the western and eastern basins of the Mediterranean. As a result, the Atlantic flow separates west of Malta and results in a surface current, which flows predominantly in a southeast direction in the Malta Channel (Havard, 1978; 1979; 1980; Drago et al., 2003). This predominant southeast current flow is reinforced by waves generated by the prevailing northwesterly winds (Havard, 1980; Drago et al., 2003). Coastal current measurements made off the northeastern coast of Malta have detected a general southeast current having a mean value of around 0.1 - 0.2ms^{-1} which, however, may exceed 3 ms^{-1} in gale conditions, and has a strong diurnal variation (Havard, 1978; 1979). Coastal currents off the northeast coast also have a strong longshore component, with a mean transport to the southeast (Havard, 1980). The coastal current regime is affected also by a strong seiche that pervades the whole coastal region round the Maltese Islands and which causes water body movements with very short time periods of the order of 20 min (Drago, 1999). Consequently, the hydrodynamic regime around the Maltese Islands is considerably complex. The complex coastal current regime is probably responsible in some way for the observed natural occurrence of different bed types (e.g. patchy, reticulate, continuous, etc; Fonseca & Bell, 1998; Fonseca et al., 2002) and distribution of *P. oceanica* beds (Borg & Schembri, 1995a).

The Maltese Islands have a combined surface area of around 315 km^2 and a total shoreline length of circa 271 km (Mallia et al., 2002). The climate is typically Mediterranean, with hot dry summers and mild wet winters. Annual rainfall is within the range 500 – 599 mm, with most (circa 85%) occurring from October to March. Although the islands have several small water courses and streams, there are no permanent rivers or estuaries, and the main supply of fresh water to the marine environment consists of sporadic runoff following rainfall, mainly during autumn and winter. Mean monthly temperatures range from 12.3°C to 26.3°C, with the coldest months being January, and February, and the hottest being July and August. The mean annual sea surface temperature is 19.7°C, with the highest value (circa 27°C) being recorded in August and the lowest (circa 14°C) during January to March (Chetcuti et al., 1992).

Given the absence of rivers and the sporadic runoff following rainfall, coastal turbidity following precipitation probably does not have a major influence on the distribution of *P.*

oceanica beds around the Maltese Islands. Consequently, input of allocthonous material and nutrients into the Maltese marine environment is relatively low. Hence, eutrophication and turbidity resulting from terrestrial runoff are not expected to have major influences on *P. oceanica* bed form (via fragmentation). On the other hand, fragmentation of *P. oceanica* beds resulting from anthropogenic disturbance has almost certainly taken place in some areas, particularly in bays and inlets where extensive coastal development to accommodate hotels has taken place, and in the vicinity of Valletta and the Grand Harbours (Figure 5), which support intense shipping, yachting, ship repair and other port-related activities, and where Malta's largest sewage outfall is located (see Borg & Schembri, 1995a).

At the end of September 2003, the Maltese population was 398,985 (Malta National Statistics Office), making Malta the most densely populated country in Europe. Because of this high population density, and Malta's popularity with tourists, the coastal environment is also under intense pressure from other forms of human disturbance, including water sports and other leisure activities, fishing, fish farming and disposal of effluents from desalination plants and from power station cooling systems (Mallia et al., 2002). Disturbance from such anthropogenic activities is therefore likely to have an impact on *P. oceanica* in some coastal areas by causing bed fragmentation and by altering the plant architectural features of beds of the seagrass.

By acquiring data on the occurrence and spatial extent of *P. oceanica* from locally-available survey reports and aerial photographs, Borg & Schembri (1995a) established a coarse, large-scale map of the spatial distribution of this seagrass in the Maltese Islands (Figure 6). The most extensive *P. oceanica* beds occurred off the northeastern coast, whereas off the southwestern coast, *P. oceanica* was much less abundant and beds of this seagrass were present mainly in a small number of shallow embayments and inlets (Borg &

Schembri, 1995a). Benthic mapping surveys carried out locally (Borg et al., 1997) indicated that, where present, the pattern of occurrence of different bed types of *P. oceanica* beds around the Maltese Islands was similar to that recorded from other parts of the Mediterranean (e.g. Colantoni et al., 1982; Mazzella et al., 1986; Meinesz et al., 1988; Mazzella et al., 1992). Furthermore, while several different bed types of *P. oceanica* occurred locally (e.g. reefs, patches, and reticulate and continuous beds), only two were found adjacent to each other, at a similar depth and in broadly similar environmental conditions. These were: continuous beds and reticulate beds (Figure 7). The continuous type comprised extensive and relatively homogeneous beds (Figure 8a), while the reticulate type comprised beds that may also be extensive, but in which the seagrass was

Figure 6. Map showing the distribution of *P. oceanica* habitat (green shading) in the Maltese Islands. Adapted from Borg & Schembri (1995a). Also shown are the four sites, which were selected for subsequent study.

interspersed with another different habitat, such as bare sand (Figure 8b) or photophilic algae on rock (Colantoni et al., 1982; Buia et al., 2000). The occurrence of adjacent zones of different seagrass bed types of *P. oceanica* in the Maltese Islands results, probably, from a gradient of environmental conditions. For example, in a recent study, Manzanera & Romero (2000) reported differences in the structure of *P. oceanica* beds exposed to different degrees of environmental disturbance. Throughout the Mediterranean, *P. oceanica* frequently forms continuous and reticulate beds (e.g. Boudouresque & Meinesz, 1982; Colantoni et al., 1982; Buia et al., 2000; Barberá Cebrián et al., 2002), therefore, the present study focused on a comparison of these two bed types. Although desirable, the inclusion of patchy beds in the comparison was not possible, since these occurred at

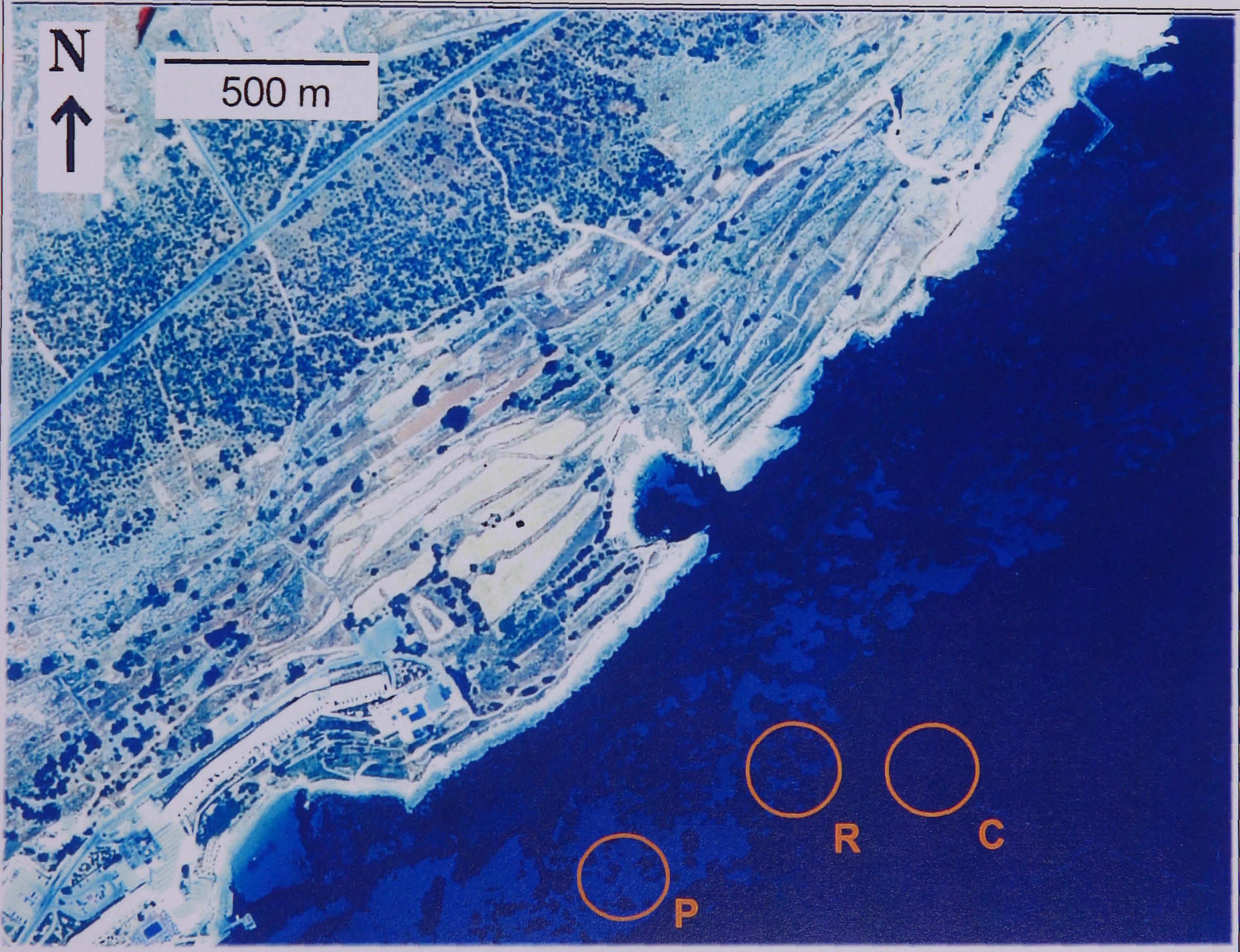


Figure 7. Aerial photograph showing the distribution of *P. oceanica* beds (dark blue) in the 4 – 13 m depth range, in a part of Mellieha Bay. Adjacent reticulate (R) and continuous (C) beds of the seagrass, are indicated by the orange circles. Patches of *P. oceanica* present on rock amongst photophilic algal assemblages (PA) are not distinguishable. However, some patches of *P. oceanica* on sand are visible in places (P).

depths of 4 – 6 m that were largely different from those at which the reticulate and continuous beds occurred; it has been well established that *P. oceanica* architectural characteristics may vary greatly with changes in depth (e.g. Gobert et al., 2003).

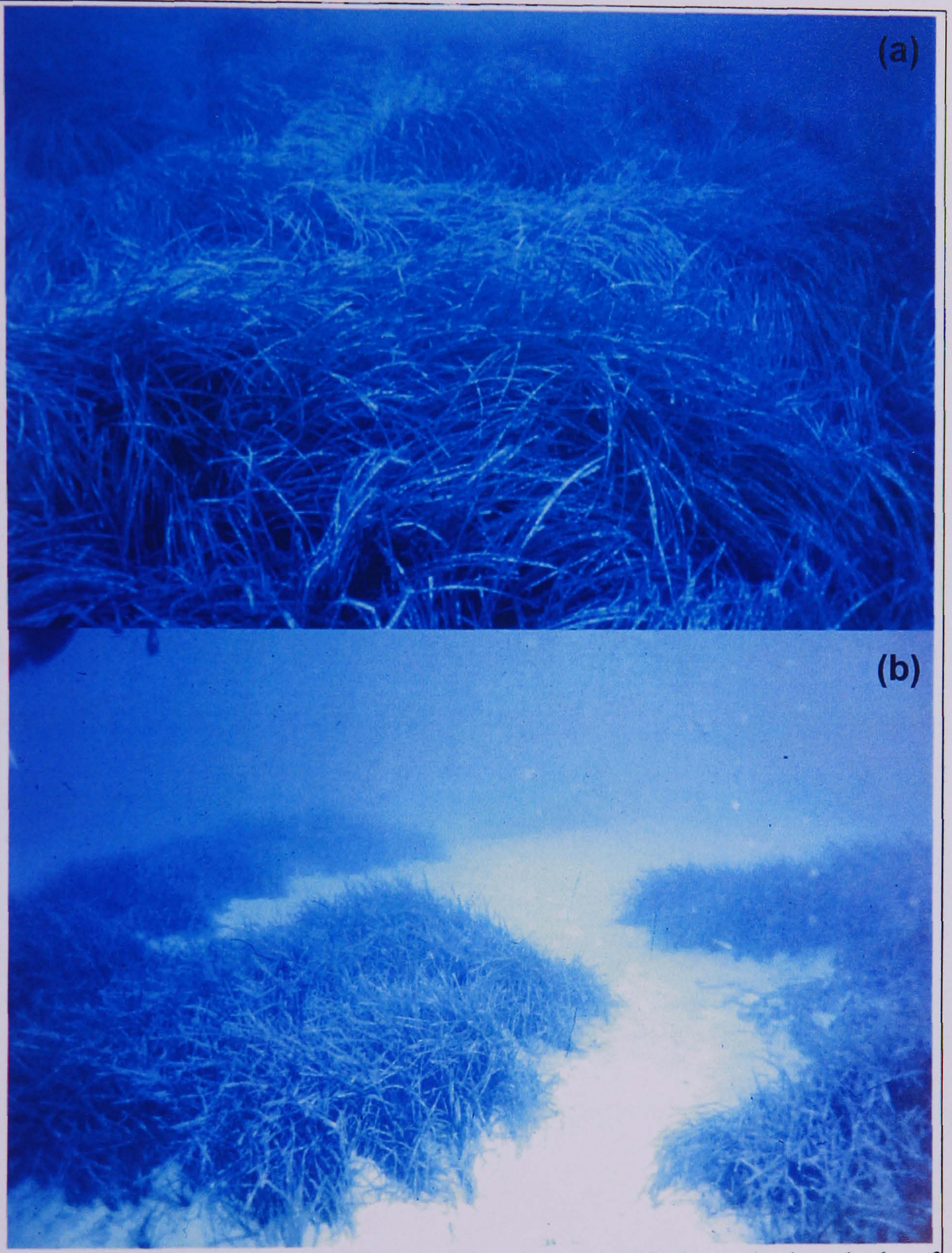


Figure 8. Photographs showing: (a) continuous and (b) reticulate beds of *Posidonia oceanica* at a depth of 11 m in Mellieha Bay, Malta.

Based on the above assessment of the study area, potential study sites for the present study were examined at four locations on the northeastern coastal area of the Maltese Islands for potential use in the proposed experimental design (Section 2.1.2). The four potential study locations were Ramla Bay, Mellieha Bay, White Rocks and St Thomas Bay (Figure 5).

Selection was based on the presence of extensive reticulate and continuous *P. oceanica* beds (Borg & Schembri, 1995a), their relatively undisturbed characteristics (as compared to other local coastal areas exposed to disturbance and pollution), and because they are separated from each other by a similar distance (circa 10 km), which made them suitable for the large-scale comparison.

The successful implementation of an appropriate sampling programme ultimately depends on identification of locations having sufficiently large and representative areas of the habitat under study. Therefore, for the present study, it was necessary to map the spatial distribution of the two different bed types of *P. oceanica* (continuous and reticulate beds) to identify suitable areas where they were present with sufficient coverage and in broadly similar environmental conditions, hence avoiding any confounding effects. Knowing the location and spatial extent of the two different bed types also enabled the allocation of sampling stations at each of four localities within each of the three different spatial scales: small, medium and large.

2.1.4 Selecting an appropriate sampling device/technique

Increased interest in seagrass research over the last three decades has resulted in the development and use of a wide array of remote and *in-situ* sampling devices and techniques, including dredges, trawls, push nets, hand nets, drop nets, drop traps, corers, suction samplers and box samplers (see Heck and Wilson, 1990; Rozas & Minello, 1997). The area or volume sampled by these different techniques varies greatly, and such lack of use of standardized methods has hindered comparison of the results obtained from different studies (Virnstein, 1987; Attrill *et al.*, 2000). Furthermore, the choice of sampler and sampling procedure has often lacked critical appraisal, despite the importance of these aspects in the design of ecological studies (Andrew & Mapstone, 1987). The need to assess the appropriateness of sampling methodology and design is even more evident in the Mediterranean, where the majority of seagrass ecological research has centered on meadows of *P. oceanica* (L.) Delile (see review by Buia et al., 2000). The robust physical nature of *P. oceanica* (Section 1.3) makes sampling difficult (Ott, 1990) and has contributed to the lack of effort towards improving techniques for sampling the associated macro-invertebrate assemblages from both leaf and root-rhizome strata of this seagrass. In the Maltese Islands, sampling of *P. oceanica* is even more difficult since this seagrass is known to have some of the highest values of shoot density in the Mediterranean (Borg & Schembri, 1995b; Micallef, 1996). Most studies of the ecology of macroinvertebrates associated with *P. oceanica* meadows have employed hand-held nets and/or suction samplers, or removal of the entire plant to collection bags by hand (Buia et al., 2003). However, these techniques have severe limitations and are open to the following criticisms.

The hand-held net technique (e.g. Ledoyer, 1962; Mazzella *et al.*, 1989) is semi-quantitative and collects mainly the macroinvertebrates inhabiting the foliar stratum (Gambi *et al.*, 1992). Suction samplers have also been commonly employed, sometimes in combination with the hand-held net technique (e.g. Gambi *et al.*, 1995). Although suction sampling gives reproducible, quantitative results (e.g. Brook, 1978), the device is usually bulky, and difficult to transport and operate underwater. Furthermore, its efficiency in capturing species inhabiting the deeper layers of the *P. oceanica* matte is also questionable, and the fauna collected usually suffers extensive damage from the pronounced turbulence generated in the airlift and collection bag, making later identification difficult or even impossible. Manual removal of portions of the *P. oceanica* matte together with attached living shoots, has been adopted by some workers (e.g. Garcia-Raso, 1990; Somaschini et al., 1994) but the more mobile component of the macrofauna may be lost during sampling.

Sampling techniques that utilise 'enclosure devices' (such as corers) provide the most reliable and reproducible quantitative data on motile macrofauna associated with submerged aquatic vegetation, due to their high catch efficiency (Rozas & Minello, 1997) and have been used successfully in quantitative studies of seagrass-associated macroinvertebrates (e.g. Stoner, 1980; Lewis & Stoner, 1981). However, with few exceptions (e.g. Vaccarella et al., 1981; Willsie, 1983), the use of corers and other enclosure devices to sample macrofauna associated with *P. oceanica* has been avoided, with the result that the potential of these techniques for studying Mediterranean seagrass ecosystems has remained largely ignored. Thus, the study aimed to design a suitable sampler that enabled appropriate and efficient collection of the motile macroinvertebrates associated with *P. oceanica* beds. A corer that samples quantitatively the total macroinvertebrate community associated with *P. oceanica* meadows, was designed and tested in the field. Tests were also carried out to establish an appropriate sample unit size and to determine the number of replicates required to achieve two pre-determined levels of precision, given the importance of these aspects in ecological experimental design (Lewis & Stoner, 1981; Andrew & Mapstone, 1987).

2.2 MATERIALS AND METHODS

2.2.1 Seagrass bed survey

Data on the spatial distribution of *P. oceanica* at each of the four study locations were obtained from colour aerial photographs (scale 1:10,000) taken in May 1998 by Datatrak Ltd (Malta) (Appendix A). The aerial photographs were scanned at a resolution of 300 dpi and the area occupied by *P. oceanica* beds, and other habitat types, delineated by eye using PC imaging software (Corel Draw). Differences in colour and shade of different habitats makes them easily identifiable from aerial photographs (Kirkman, 1996), especially given the clear transparent coastal waters of the Maltese Islands, and since local seagrasses (namely *P. oceanica* and *Cymodocea nodosa*) mainly occur in monospecific beds. Ground truthing of these data was carried out using SCUBA diving, according to standard methods (e.g. Orth & Moore, 1983b; Kirkman, 1996). Because of the large areas involved, only part (circa half) of the sea areas in Mellieha Bay and St Thomas Bay were surveyed. For this purpose, the northwestern sides of these two bays were chosen.

All fieldwork was carried out from January to July 1998. During fieldwork, shore-normal transect lines, graduated at 5 m intervals, were laid underwater by the divers. The divers swam along the transects and recorded the distance from the shore of the boundaries of *P. oceanica* beds and of the other main benthic habitats present, using waterproof slates and pencils. Adjacent transects were separated by a distance of circa 150 m, while the exact location of the transect starting points was predetermined following an examination of the aerial photographs, scale maps of Maltese coastal areas and Admiralty Charts showing the bathymetry of local sea areas.

Selection of the transect starting points was based on availability of access to the sea from the shore or by boat, and on the presence of topographic features, such as promontories and indentations of the shore, that could be readily identified on a map. The length of the transects varied between 200 m and 800 m, while the maximum depth reached during the surveys was 25 m. Because of the limitation of the maximum time spent underwater during any one SCUBA dive, transects longer than 300 m were subdivided into separate shorter ones that had a maximum length of 100 – 300 m and which were surveyed during separate dives, but which were all aligned along the same compass bearing (shore-normal). To survey transects located offshore at distances greater than 300 m, divers were transported to the transect starting points using a 4.5 m boat, which remained on site to accompany the divers and to collect them at the end of the dive. Position finding, to record the geographical location of the two extreme ends of the transects, was made from the boat using a portable Geographical Information System (GPS) set (Garmin 45, USA).

To map the distribution of the benthic habitats of the four study sites, electronic images of the aerial photographs (Appendix A) were georeferenced and orthorectified (Green et al., 2000; Lillesand & Kiefer, 2000) against accurate digital survey maps (Mapping Unit, Malta Environment and Planning Authority) using the GIS computer program Erdas Imagine 8.4 (Erdas Inc., USA). Following fieldwork, transect data were compared with the *P. oceanica* spatial distribution data acquired from the aerial photographs and, where necessary, adjustments made such that the spatial extent of the seagrass, as shown on the map, was a true representation of its coverage in the field. Using the same GIS computer program, the electronic images of the aerial photographs were used to obtain estimates of coverage for the two different seagrass bed types, at each of the four study sites. This was done by selecting randomly a standard length of shore (*circa* 600m), which included both reticulate and continuous seagrass beds, and extending the area out from the shore to the 13 m contour. The relative coverage of each bed type was then estimated using unsupervised classification techniques (Green et al., 2000; Lillesand & Kiefer, 2000).

To obtain an estimate of the exposure of at each of the four study sites, the Relative Exposure Index (REI) proposed by Keddy (1982) and adapted by Fonseca & Bell (1998), was used:

$$\mathrm{REI} = \sum_{i=1}^{8} (\mathrm{Vi} \times \mathrm{Pi} \times \mathrm{Fi})$$

where i = *i*th compass heading (1 to 8; i.e. N, NE, E, SE, S, SW, W & NW); V = mean monthly maximum wind speed in m s^{-1}; P = percent frequency which wind occurred in the *i*th direction, and F = effective fetch. Values of V were calculated using wind data records obtained from the local Meteorological Office (Malta International Airport) for the three years prior to the study (1997 – 1999), to obtain mean values over an appropriately long period (see Fonseca & Bell, 1998). Wind velocities that exceeded 95% of the recorded velocities (> 10 m s^{-1}; 'exceedance winds', Keddy, 1982) were removed from the data set, and the remaining values used to calculate V, which was therefore the grand mean (mean of monthly means of daily maximum wind speeds). Fetch was taken as the distance from the particular site under consideration (taken at the centre of the bay/inlet) to land along a given compass heading (Shore Protection Manual, 1977). Effective fetch was estimated by measuring fetch along 4 lines radiating out from either side of the *i*th compass heading with a spacing of 11.25°, and along the *i*th heading (n = 9), and then averaging the product of each of the 9 lines multiplied by cosine of the angle of departure from the *i*th heading (Shore Protection Manual, 1977).

2.2.2 Sampler selection

Sample size and replicate number is often a trade-off between precision and effort/cost expenditure. A good sampler must have an adequate construction and design for the required purpose, and be practical to deploy in the field. To meet these demands, a cylindrical corer was designed which had a simple yet sturdy construction and was light and easy to use in the field. Three different corer diameters were selected and the corresponding sample unit sizes assessed for relative accuracy, precision, and efficiency of sampling as defined by Andrew & Mapstone (1987). Choice of corer diameters was based on criteria given in Andrew & Mapstone (1987), that is, setting: (i) a lower sample unit size (0.05 m^2), which was at least an order of magnitude larger than the upper size limit

(40 mm) of the macroinvertebrates studied, and (ii) an upper sample unit size (0.16 m^2), which corresponded to the dimension limit that the operator could handle reasonably well. Furthermore, consideration was given to the practicality of use of the sampler in *P. oceanica* meadows, especially penetration of the dense matte. Therefore, three cylindrical corers, differing only in diameter (25, 35 and 45 cm) and height (40, 50 and 63 cm respectively) were constructed using galvanised sheet metal (0.55 mm thickness) (Figure 9). A band-saw blade (25 x 1 mm) was welded along one of the cylinder's open ends, whilst a reinforcing circular metal bar (20 x 5 mm) was welded at the other end. Two strong handles were riveted to the cylinders, one on each side. A 0.5 mm mesh collecting bag was attached to the top of each sampler and held in place by a length of twine inserted in the bag's seam (Figure 10).

Figure 9. The three cylindrical corers used in the pilot survey; left to right: 25 cm, 35 cm and 45 cm diameter. The ruler visible in the photograph is 30 cm long.

Figure 10. The 25 cm diameter corer with the 0.5 mm mesh collecting bag attached to the mouth. The ruler visible in the photograph is 30 cm long.

Fieldwork was carried out during September 1998 in a pre-designated area (50 x 100 m) of a continuous seagrass bed in Mellieha Bay (Figures 5 & 6). Sampling was carried out by SCUBA diving, during which six replicates were taken randomly using each of the three different corers. Adjacent samples were at least 10 m apart and collections were always made in the afternoon. During each collection, the sampler was placed over the *P.oceanica* and the serrated edge lowered quickly onto the bed. The sampler was held by the handles and driven slowly into the *P. oceanica* matte by a turn-cutting action until a vertical penetration of 10 cm was achieved. A 'Bushman garden knife' was used to make vertical incisions in the matte surrounding the sampler to produce a small 4-5 cm wide gap between the matte and the outer wall of the corer into which the diver's hand could be inserted. Incisions in the matte, angled under the corer, were also made to separate the matte core from the rest of the root-rhizome layer. Complete detachment of the sample was achieved by inserting the diver's hand down the sides of the corer and under the lower edge of the device. Once this was achieved, the sampler was removed from the bed, inverted quickly and the sample pushed into the collecting net. In this way, the core of excised *P. oceanica* matte served as a 'plunger', pushing down the whole sample into the net. The net was then removed from the corer and closed tight with the draw-string before sealing with a knot.

In the laboratory, each sample was washed in seawater, and the shoots and *P. oceanica* matte separated and examined carefully to remove the motile macroinvertebrates. The remaining sediment and washings were passed through a 0.5 mm sieve and the retained material sorted in trays under a x5 magnifying lens. Macroinvertebrates were fixed in 10% formaldehyde in seawater and transferred to 70% ethanol prior to identification. Where identification to species level was not possible, the putative species present were labelled using an alphabetical code (e.g. Syllidae sp. A etc.). Identification of polychaetes to species level presented special difficulties, given the incomplete knowledge on Mediterranean Polychaeta and the lack of good identification keys for this group in the region. Sessile macroinvertebrates (sponges, cnidarians and bryozoans) and small fishes were also collected but were not considered in the present study.

Throughout the different sampling stages, the time taken to achieve each of the following was recorded: (i) collection, (ii) washing and sieving, and (iii) sorting. Total time per replicate was taken as the sum of these components. The highest mean estimates obtained for standardised total abundance, and for the number of species recorded, were taken as the greatest estimates of accuracy (Andrew & Mapstone, 1987). This estimation of accuracy is based upon the assumption that what is not present cannot be counted and, therefore, overestimation is very unlikely (Caughley, 1977). Differences between mean values of total abundance and species richness (untransformed data, checked for homogeneity of variances) obtained for the three different core sizes were analysed using one-way ANOVA (at $\alpha = 0.05$). Precision was calculated from the ratio SE/x, where SE is the Standard Error and x is the Sample Mean (Pihl & Rosenberg, 1982; Morin, 1985). Precision increases as the value approaches 0 (for example, 0.1 is more precise than 0.2). The number of replicates (n) required to achieve two levels of precision (0.1 and 0.2) for both abundance and number of species was calculated for each of the three core sizes using $n = [sd/(px)]^2$, where sd is Standard Deviation and p is the pre-established precision (Andrew & Mapstone, 1987). Efficiency was estimated by multiplying 'n' by the mean total time taken to process samples collected by the respective corers (James & Fairweather, 1996). A one-way ANOSIM permutation analysis (number of permutations = 5000) was carried out on the species-abundance matrix (Clarke & Green, 1988), using the software package PRIMER (Clarke & Gorley, 2001), to test for differences in assemblage composition within and between groups of replicate samples collected by each of the three corer sizes. SIMPER analysis (Clarke, 1993) was also carried out using the PRIMER software package to identify the species contributing to the observed similarity within, and dissimilarity between, groups of replicate samples.

2.3 RESULTS

2.3.1 Seagrass bed survey

Overall, there was very good agreement between the distribution of *P. oceanica* determined from the aerial photographs and data collected from the ground-truthing surveys. Scale maps showing the distribution of *P. oceanica* beds at the four study sites are presented in Figures 11 – 14. At each site, the general pattern of *P. oceanica* distribution was as follows. In shallow waters (2 m – 4 m), *P. oceanica* occurred as small patches on a rocky substratum; patches varied greatly in size but rarely exceeded 1 m x 1 m. In deeper waters (5 – 10 m), the patchy stands were often replaced by reticulate beds consisting of *P. oceanica* interspersed with bare sand. Further offshore (11 – 13 m), a transition from reticulate to continuous beds occurred, where both reticulate and continuous beds occurred on a thick matte growing on fine to medium sand. Continuous beds extended to depths of around 25 - 30 m and eventually formed reticulate or patchy beds in deeper (>25 m) water. Therefore, the sequence of occurrence of the different *P. oceanica* bed types, moving away from the shore, was: patchy – reticulate – continuous – reticulate – patchy (Figures 11 – 14). In Mellieha Bay, patches of dead *P. oceanica* matte interspersed amongst living matte were also encountered in various places during the survey, at depths ranging between 5 m and 13 m. These patches of dead matte varied in size from < 1 m^2 to around $100m^2$.

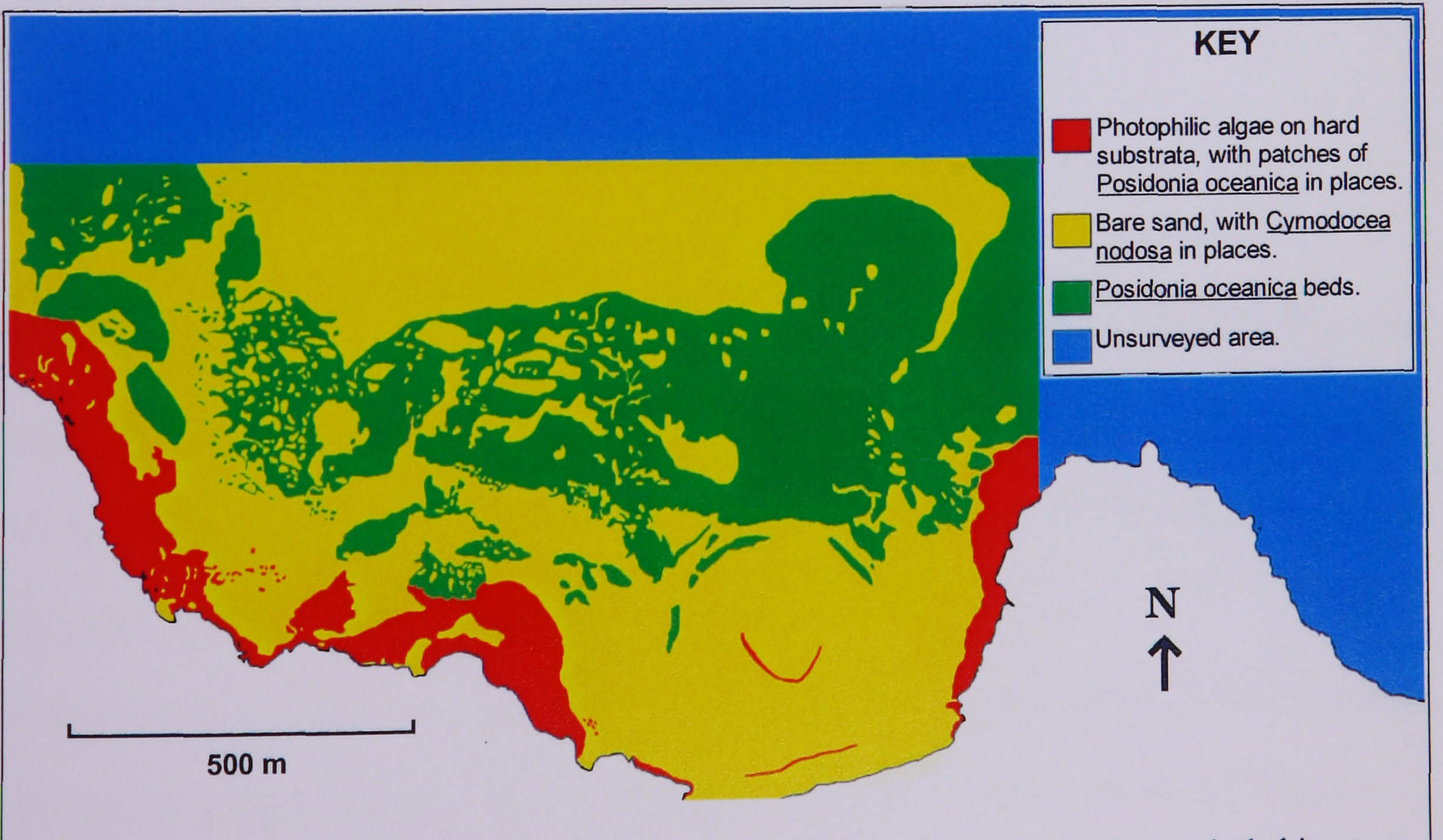


Figure 11. Map showing the distribution of *Posidonia oceanica* beds and other main habitat types in Ramla Bay.

The results of the GIS analyses to determine the area of seagrass cover are given in Table 1. The areas surveyed in Mellieha Bay, White Rocks and St Thomas Bay had very similar total seagrass coverage values (circa 30,000 m^2 – 39,000 m^2), while Ramla Bay had much less coverage (circa 9,600 m^2). Ratios of reticulate:continuous bed coverage recorded from each location varied considerably with an overall tendency for the ratio to decrease between sites in a southeast direction (0.9 – 0.3). Estimated values of Relative Exposure Index for the four study sites are given in Table 2. St Thomas Bay and Ramla Bay had the highest exposure, followed by White Rocks, while Mellieha Bay had the lowest exposure.

Table 1. Coverage (m^2) of the two different *Posidonia oceanica* bed types recorded from each of the four study sites.

Locality	Total area surveyed	Total seagrass coverage	Reticulate bed coverage (R)	Continuous bed coverage (C)	Coverage ratio R:C
Ramla Bay	437745	95930	44910	51020	0.9
Mellieha Bay	391966	306921	124939	181982	0.7
White Rocks	393987	365212	131438	233774	0.6
St Thomas Bay	394692	386172	87326	298846	0.3

2.3.2 Sampler selection

Field sampling with the 25 cm and 35 cm corers was carried out without difficulty, and intact samples of *P. oceanica* matte with attached shoots were obtained easily. Using the 45 cm corer, however, separation of an intact core was not achieved without difficulty and, on most occasions, portions of the sample dropped out of the corer and were lost. This loss of sample was reflected in the reduced mean total time taken for collection and processing of samples using the 45 cm diameter compared with the 35 cm diameter corer (Table 3).

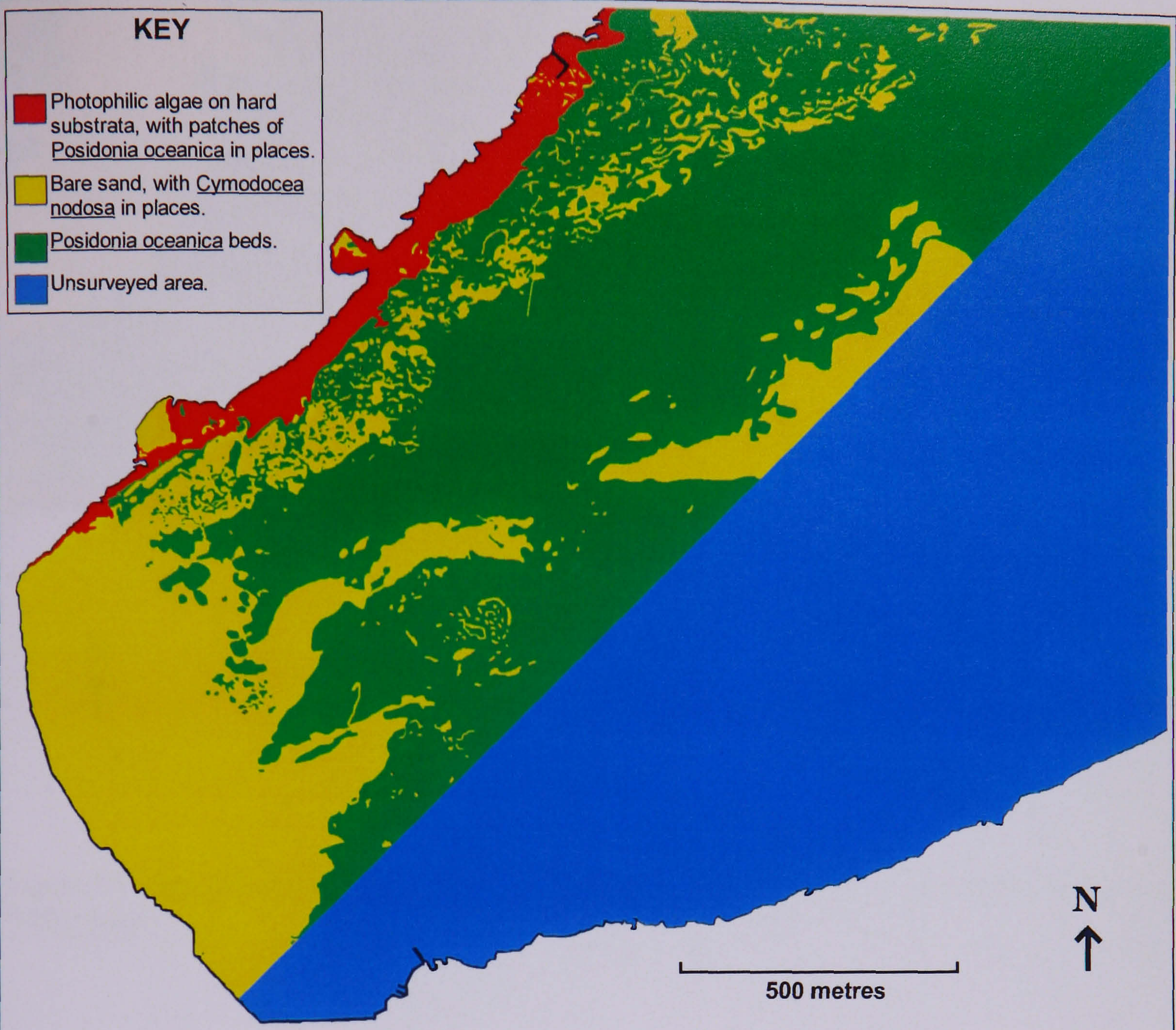


Figure 12. Map showing the distribution of *Posidonia oceanica* and other main habitat types in Mellieha Bay.

Table 2. Values of Relative Exposure Index (REI) estimated for each of the four study locations.

Locality	**REI value**
Ramla Bay	3.22 X 10^6
Mellieha Bay	1.66 X 10^6
White Rocks	2.46 X 10^6
St Thomas Bay	3.28 X 10^6

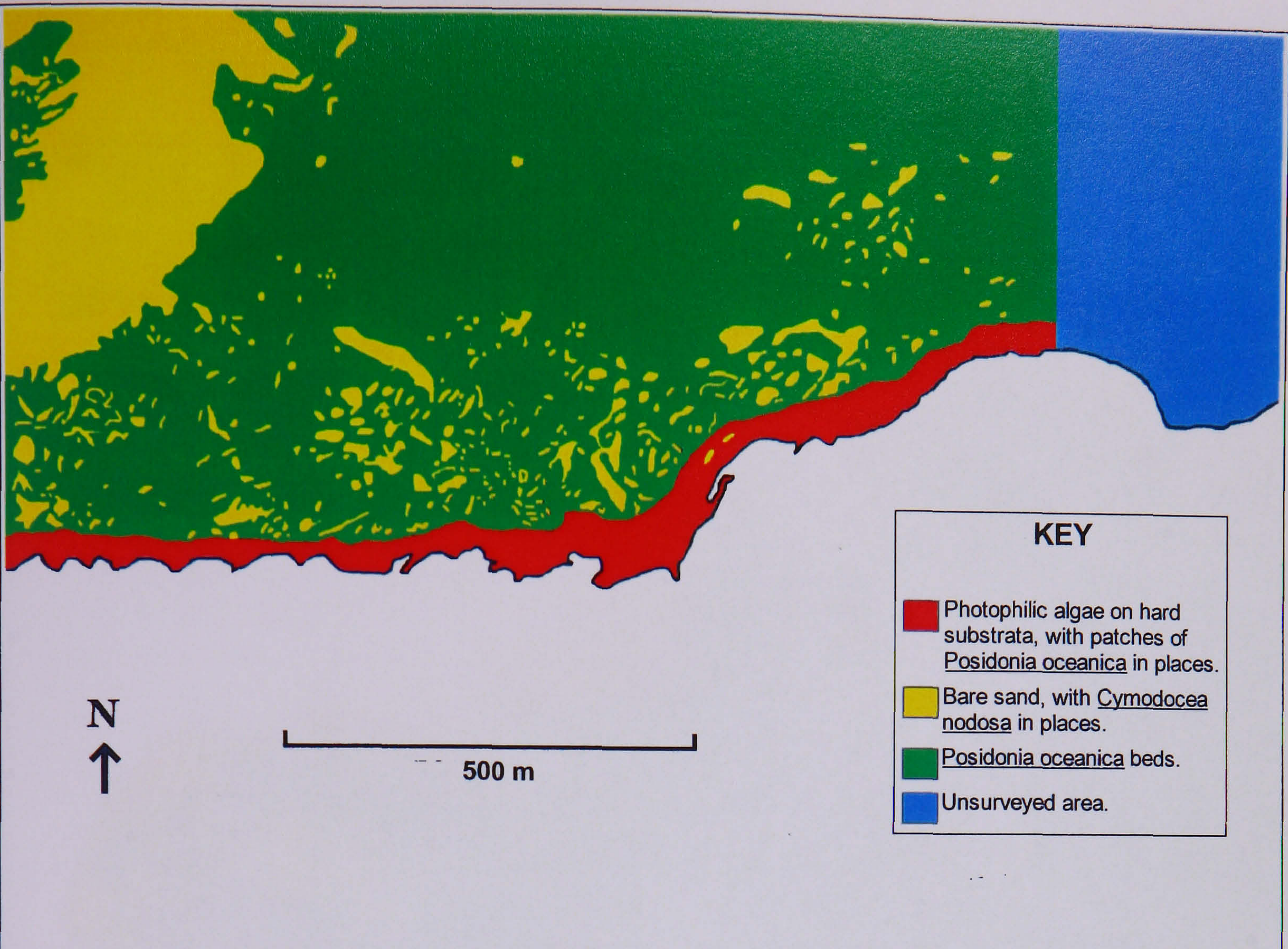


Figure 13. Map showing the distribution of *Posidonia oceanica* and other main habitat types at White Rocks.

Table 3. Mean time taken (±1SD) for collection, washing and sorting of samples collected using the three different samplers (diameter 25, 35 & 45 cm). n = 6 for each sampler.

Sampler	**Mean time (minutes)**			
	Collection	Washing	Sorting	Total
25 cm	10.2 ± (2.7)	48.8 ± (8.0)	213.2 ± (29.8)	272.2 ± (24.6)
35 cm	12.2 ± (2.3)	65.5 ± (21.3)	330.2 ± (68.4)	407.8 ± (61.6)
45 cm	19.3 ± (4.1)	81.0 ± (21.9)	240.0 ± (137.5)	340.3 ± (128.8)

A total of 1018 individual motile macroinvertebrates (2 nemerteans, 330 polychaetes, 439 crustaceans, 233 molluscs and 14 echinoderms) comprising 154 species were collected from the 18 samples (Appendix B). ANOVA indicated that there were significant differences in macroinvertebrate abundance between the 25 cm and the 35 cm diameter corers ($F = 10.9$, $p < 0.01$), and between the 25 cm and 45 cm diameter corers ($F = 14.16$, $p < 0.01$), but not between the 35 cm and 45 cm diameters corers. Significant differences

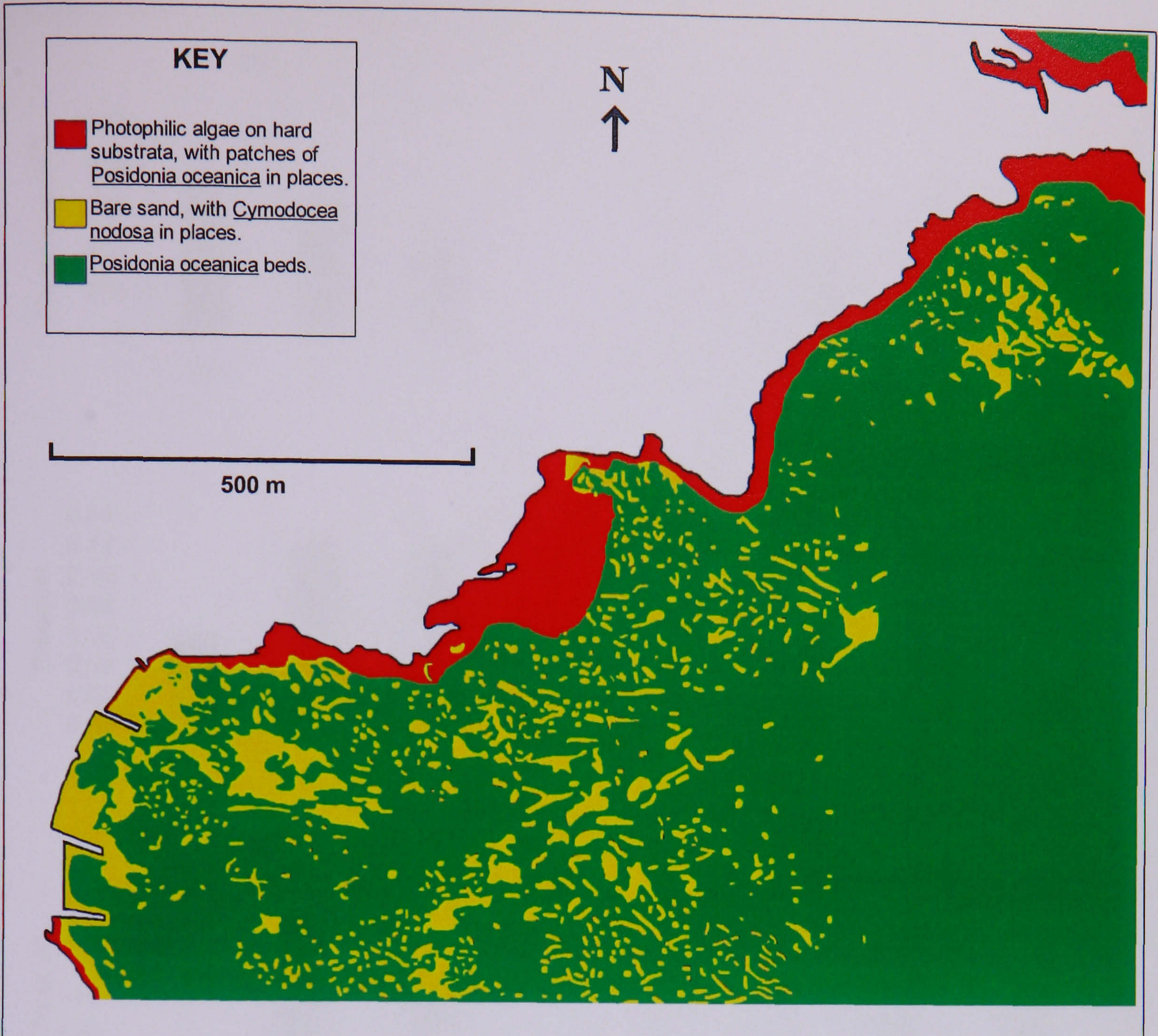


Figure 14. Map showing the distribution of *Posidonia oceanica* and other main habitat types in St Thomas Bay.

were detected also in the mean number of species recorded from groups of replicate samples between the 25 cm and 35 cm diameter corers cm ($F = 7.16$, $p < 0.05$), and between the 25 cm and 45 cm diameter corers cm ($F = 7.65$, $p < 0.05$), but not between the 35 cm and 45 cm diameter corers.

Comparison of the relative accuracy measurements showed that the estimate based on abundance was highest for the 25 cm diameter corer, whilst that based on number of species was highest for the 35 cm diameter corer (Figures 15a & 15b). The 25 cm diameter sampler gave the best estimates of precision (Figures 15c & 15d) and efficiency (Figures 15e & 15f) for both abundance and number of species. Table 4 shows the total number of replicates required for each core size to attain the two levels of precision (0.1 & 0.2).

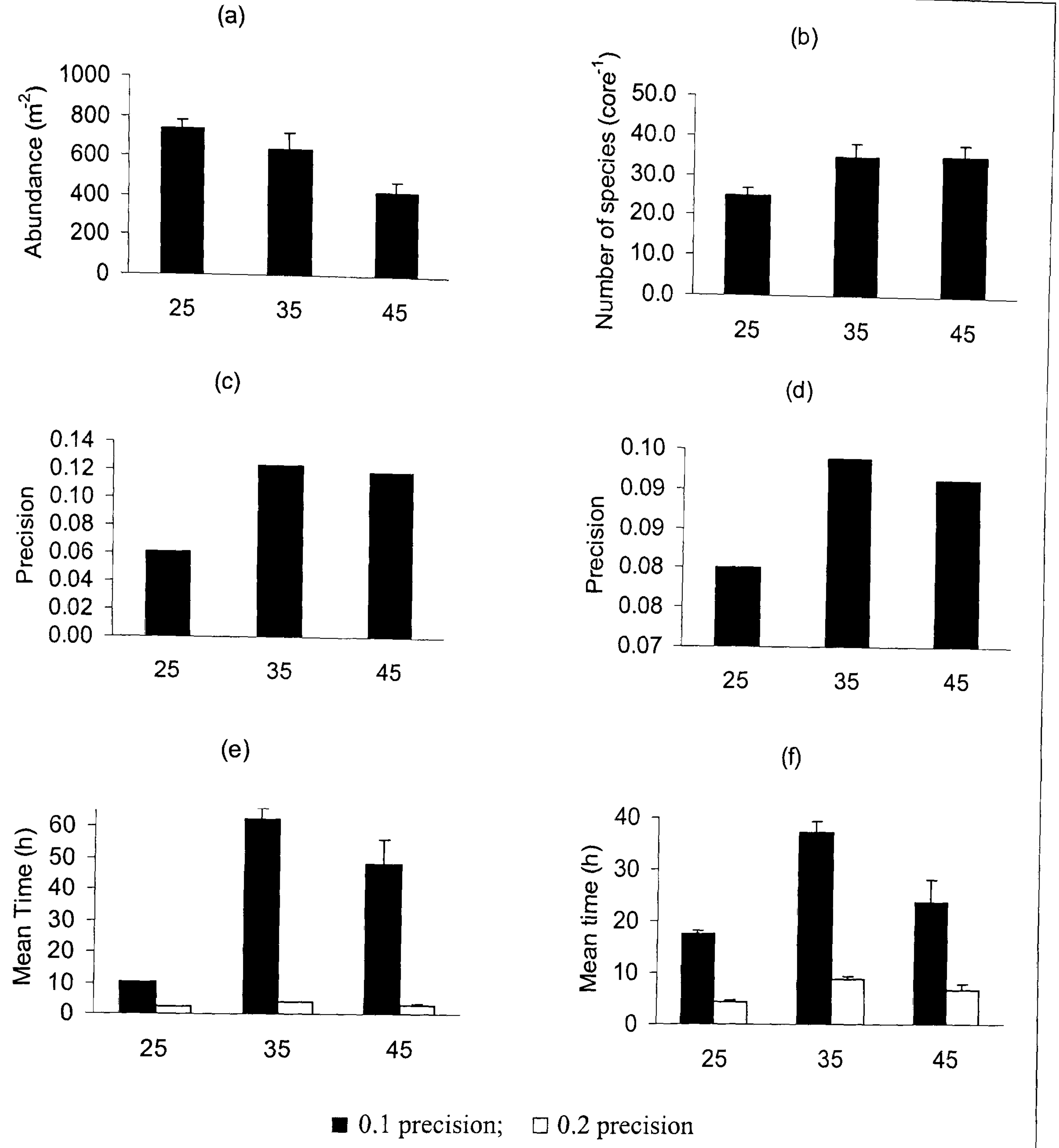


Figure 15. Estimates of accuracy (a & b), precision (c & d) and efficiency (e & f) for the three core sizes (25, 35 and 45 cm diameter; n = 6). a, c and e: estimates based on standardised abundance (per m^2); b, d and f: estimates based on number of species (per core). Error bars are +1SE.

ANOSIM indicated a significant difference ($R = 0.221$, $p < 0.06$) in the composition of the macroinvertebrate assemblages between groups of replicates collected by the 25 cm and the 45 cm diameter corers, but not between either the 25cm and 35 cm or 35cm and 45 cm diameter corers (Table 5).

Table 4. Estimated total number of replicates of each core size required for two pre-established levels of precision. Estimates are for total mean abundance and number of species.

Core size (cm)	Precision level	Number of replicates (abundance)	Number of replicates (species)
25	0.1	2.2	3.9
35	0.1	9.2	5.3
45	0.1	8.5	5.0
25	0.2	0.6	1.0
35	0.2	2.3	1.3
45	0.2	2.1	1.2

Table 5. Results of ANOSIM. S = 25 cm core replicates; M = 35 cm core replicates; L = 45 cm core replicates. ** = $p < 0.01$.

Groups	Statistic value	Possible permutations	Permutations used	Significant statistics	Significance level
S, M	0.081	462	462	119	25.8%
S, L	0.407	462	462	3	0.6% **
M, L	0.169	462	462	30	6.5%

SIMPER analysis revealed that the five species contributing most to the difference between the 25cm and 45 cm diameter core replicates were the amphipod *Lysianassa longicornis* Lucas (1.76%), the polychaete *Piromis eruca* (Claparède) (1.64%), the thalassinidean shrimp *Gourretia denticulata* (Lütze) (1.53%), the polychaete *Notomastus latericeus* M. Sars (1.52%) and the bivalve *Anadontia fragilis* (Philippi) (Table 6).

Table 6. Results of the SIMPER analysis for the five species having the highest dissimilarity values between the 25 cm and 45 cm core replicates. Average dissimilarity between the two groups of replicates = 62.19 %.

Species	Average abundance 45 cm core	Average abundance 25 cm core	% Contribution	% Cumulative
Lysianassa longicornis	4.50	1.08	1.76	1.76
Piromis eruca	1.00	1.17	1.64	3.40
Gourretia minor	0.17	1.08	1.53	4.93
Notomastus latericeus	1.17	1.92	1.52	6.45
Anadontia fragilis	0.33	0.92	1.52	7.97

2.4 DISCUSSION

Once an appropriate experimental design was selected from a review of the literature, the first aim of the present study was to identify and map the main different bed types of *P. oceanica* in the Maltese Islands at each of four proposed study locations. The second aim was to design and test a suitable sampler for appropriate and efficient collection of the motile macroinvertebrates of *P. oceanica.*

The survey results indicated that three main types (patchy, reticulate and continuous) of *P. oceanica* beds occurred at each of the four localities surveyed. While seagrass patches occurred mainly on bedrock in shallow waters (circa 4 m), the continuous and reticulate beds (with broadly similar shoot densities) occurred adjacent to each other, at similar depths, on fine to medium sand.

The occurrence of patches and beds of *P. oceanica* on rock has been reported from other parts of the Mediterranean (e.g. Mazzella et al., 1986), while reticulate beds growing on sandy bottoms have been described often by other Mediterranean workers as meadows with 'inter-matte' channels (e.g. Colantoni et al., 1982). The presence of adjacent reticulate (≅ fragmented) and continuous (≅ non-fragmented) beds of *P. oceanica* provided an opportunity to study and compare attributes of plant architecture diversity of associated fauna, between the two different bed types. That is, the results of the seagrass bed survey confirmed that the four proposed study locations were appropriate for the planned sampling programme, since each supported adjacent non-fragmented and fragmented beds, located at the same depth and in broadly similar environmental conditions. Furthermore, one of the locations (Mellieha Bay) was large enough to support the sampling programme dealing with the two lower spatial scales: (i) medium (hundreds of metres) and small (tens of metres).

GIS analyses indicated that the *P. oceanica* beds at the four localities surveyed had different reticulate/continuous (R:C) coverage ratios. This variation cannot be ascribed to any single environmental factor and results, probably, from differences in the degree of influence exerted by a complex set of environmental variables at the different localities, including variations of the hydrodynamic regime (Colantoni et al., 1982) and other factors such as the physico-chemical characteristics of the substratum and bottom geomorphology (Fonseca et al., 2002). Several studies have shown that seagrass beds tend to be more fragmented where water movement is strong, whereas, in more sheltered places, beds tend to have a more continuous morphology (Fonseca et al., 1983; Marbà & Duarte, 1995). The Maltese Islands are severely exposed to high winds. On average, only 7.7 days of the year are calm in the Maltese Islands; winds of between 1.8 and 39 kmh^{-1} occur during the rest of the year. The predominant winds are northwesterly, which, on average, blow during 19% of the year (Chetcuti et al., 1992). As a result, San Dimitri Point (Figure 5), which lies on the northwestern tip of the island of Gozo, is the most exposed point in the Maltese Islands, while the southeastern tip of Malta, Marsaxlokk Bay (Figure 5) is, on average, the most sheltered. Therefore, this exposure regime, coupled with the main currents flowing towards the southeast (Harvard, 1978; 1979; 1980; Drago, 1991), may partly explain the decrease in the R:C coverage ratio (hence decrease in reticulate bed coverage) in a southeasterly direction along the northeastern coast of the Maltese Islands. On the other hand, the estimated REI values indicate a similar exposure for Ramla Bay and St Thomas Bay, while Mellieha Bay had the lowest REI value. However, the hydrodynamic properties of a particular locality are not determined solely by wave exposure. The submarine geomorphology (e.g. Fonseca et al., 2002), currents (e.g. Havard, 1978; 1979) and other physical environmental factors (e.g. seiches; Drago, 1999) also contribute to the hydrodynamic properties of a particular locality. Both Mellieha Bay and St Thomas Bay have extensive shoal areas located outside the mouth of the bays, which are expected to dampen wave action and currents. For example, Drago (1997) described Mellieha Bay as a low-energy environment, resulting from the presence of the extensive shoal area outside the bay and complex hydrodynamic processes, which inhibit flushing. Therefore, it is envisaged that since the index used for calculating the exposure for Mellieha Bay and St Thomas Bay did not take the presence of shoals into consideration, the obtained values are probably overestimates.

Overall, the results of the seagrass survey pilot study confirmed that the proposed experimental design can be applied to the field. That is, comparisons at three spatial scales, of differences in plant architecture and in the diversity of associated motile macroinvertebrate assemblages between reticulate and continuous bed types can be carried out in an unconfounded manner by sampling different *P. oceanica* bed types where they are located adjacent to each other at a depth of 9-12 m.

The occurrence of dead *P. oceanica* matte, interspersed with live matte, is interesting since there are no nearby sources of pollution or other anthropogenic disturbances which may have led to death of the seagrass. It appears that death of the *P. oceanica* matte has resulted from natural environmental processes, possibly following physical damage to the shoots by strong wave action (Colantoni et al., 1982; Blanc & Jeudy de Grissac, 1984). Dead *P. oceanica* matte effectively represents the lower extreme along the seagrass bed fragmentation gradient, hence it would be interesting to study the assemblage structure and composition of macroinvertebrates associated with this habitat, and to compare these attributes with those of living matte. Thus, the presence of dead matte, as revealed by the seagrass survey, presents the useful possibility of comparing the macroinvertebrate assemblages associated with dead and living *P. oceanica* matte in Mellieha Bay.

The study designed to enable selection of an appropriate sampling device/technique demonstrated that a cylindrical enclosure sampler, not much different in design from a basic corer, is a useful and practical device for quantitative sampling of the macroinvertebrates associated with beds of the seagrass *P. oceanica.* Of the three samplers tested, the smallest (25 cm diameter) gave the highest precision and efficiency estimates for both abundance and number of species. In their comparative study of the relative efficiency of three core sizes (5.5, 7.6 and 10.5 cm diameters) in sampling the macrofauna of *Thalassia testudinum* Banks & Soland ex Koenig dominated seagrass meadows, Lewis & Stoner (1981) also concluded that a smaller corer collected significantly more macroinvertebrates than either of the two larger ones used in their study. The 25 cm diameter sampler used in the present study gave the highest accuracy estimate for abundance but not for number of species, suggesting that this sample unit size is suitable for comparative studies between different meadows/sites but not for surveys in which complete species richness and abundance estimates for a specific area are required. In the latter case, use of the 35 cm diameter corer may be more appropriate since it gave the highest accuracy estimate for number of species. The lower accuracy estimate for abundance obtained by the 35 cm diameter corer was somewhat unexpected since the predictions from classical species-area relationships are that the total number of species and individuals collected in a given sampling unit should increase as the size of the sampler is increased. However, loss of sample (namely of matte) during collection, albeit unnoticed in the field, may have contributed to the lower accuracy estimate for abundance obtained for the 35 cm diameter sampler. On the other hand, the smaller 25 cm diameter sampler enabled collection of a more 'intact' core, without loss of sample.

Serious difficulties were experienced using the largest corer (45 cm diameter). Besides being more cumbersome to use in the field than the smaller corers, there was often partial loss of the sample during collection. This is reflected clearly in the relative densities of deep-burrowing macrofauna such as the polychaetes *P. eruca* and *N. latericeus,* the thalassinidean shrimp *G. denticulata,* and the bivalve *A. fragilis*, which were the species contributing most (as revealed by the SIMPER analysis) to the differences between samples collected by the 25 and the 45 cm diameter samplers.

Overall, the sampler selection study indicated that, for comparative studies, the 25 cm diameter corer provided robust quantitative samples of the macroinvertebrates associated with both the foliar and root-rhizome strata of *P. oceanica* meadows. To achieve a precision level of 0.1 the survey showed that, using this core size, three replicates for abundance estimates and four replicates for species richness estimates were required. Based upon these conclusions, it is most prudent to use four replicates taken with the 25 cm diameter corer to estimate the species richness and abundance of macroinvertebrates associated with *P. oceanica* beds for the subsequent research programme.

Therefore, based on the results of the pilot studies, a scientifically-robust comparison of within-bed plant architectural characteristics, and motile macroinvertebrate diversity between continuous and reticulate *P. oceanica* beds, can be best achieved by collecting four replicate samples using a specifically-designed 25 cm diameter corer at each of three spatial scales within a staggered nested sampling design. This same sampling strategy is also useful to compare motile macroinvertebrate diversity between dead and living matte of *P. oceanica*. This approach was used in subsequent work (Chapters 3, 4 and 5).

CHAPTER 3

ARCHITECTURAL CHARACTERISTICS OF TWO BED TYPES OF THE SEAGRASS *POSIDONIA OCEANICA* OVER DIFFERENT SPATIAL SCALES

Part of this chapter has been included in the following:

(i) Poster entitled 'Structural Characteristics of two different bed types of *Posidonia oceanica* (L.) Delile', presented at the 5th International Seagrass Biology Workshop, 7th – 11th October 2002, Ensenada, Mexico.

(ii) Paper entitled 'Architectural characteristics of two bed types of the seagrass *Posidonia oceanica* over different spatial scales', accepted for publication in *Estuarine, Coastal and Shelf Science*.

3.1 INTRODUCTION

Seagrass beds are highly complex habitats, with a structure that varies with the constituent seagrass species, and the complex interactions between numerous biotic and abiotic factors (Heck & Orth, 1980; Attrill et al., 2000; Hemminga & Duarte, 2000 and references therein). Seagrass beds occur in a wide range of morphotypes, ranging from small patches to large reticulate stands and continuous beds (Virnstein, 1995; Fonseca & Bell, 1998). This spatial patterning enables the direct application of the principles underlying landscape ecology (formerly a concept applied exclusively to the terrestrial realm) to the marine environment (see Robbins & Bell, 1994). Recently, numerous seagrass studies have addressed important landscape ecological issues, such as the effect of patch size on the diversity of associated biotic assemblages (e.g. Bowden et al., 2001). Data generated by such studies provide an understanding of the fundamental processes underlying the dynamics of seagrass ecosystems, thereby, underpinning appropriate management and conservation strategies (Robbins & Bell, 1994; Fonseca et al., 2002; Hemminga & Duarte, 2000).

Seagrass beds are undergoing a worldwide decline as a result of both natural and anthropogenic disturbances (Short & Wyllie Echeverria, 1996). Adverse impacts can lead to fragmentation of this habitat, whereby, continuous seagrass beds are transformed to discontinuous ones through decimation of parts of the bed, resulting in a decrease in overall area coverage of the seagrass (Hemminga & Duarte, 2000). The consequences of seagrass habitat fragmentation may include changes in physical environmental characteristics (e.g. sediment grain size), and in the structure of associated flora and fauna (Marbá & Duarte, 1997; Frost et al., 1999; Bell et al., 2001). Furthermore, regression of seagrass is often a self-accelerating process (Duarte, 1995) such that recovery, if any, is often very slow (Hemminga & Duarte, 2000). Since effective management of seagrass habitats depends on knowledge of the processes that govern the spatial and temporal properties of seagrass beds (Fonseca et al., 2002), there is an urgent need to study the ecological consequences of the physical alteration of seagrass habitats (Virnstein, 1995). Given the lack of data on the consequences of fragmentation of seagrass habitat, a useful starting point is an examination of the role of variability in plant architectural characteristics of different natural bed types.

The architectural characteristics of seagrass beds are determined partly by the morphological features of the individual plants, such as the number of leaves, leaf length, leaf width and epiphytic load, and by the number of plants present per unit area (shoot density) within a seagrass bed (Kikuchi & Pérès, 1977). In turn, the morphological attributes of individual seagrass plants depend on the growth characteristics of the particular species (Hemminga & Duarte, 2000), while shoot density varies, depending on the plant's dispersal pattern and local environmental factors; namely, the amount of available light and the physico-chemical properties of the substratum and water column (e.g. Panayotidis et al., 1981; Gobert et al., 2003).

In the Mediterranean Sea, the endemic *Posidonia oceanica* (L) Delile is the most abundant seagrass species (Buia et al., 2000 and references therein). *P. oceanica* occurs at depths ranging from 1 m to 40 m (den Hartog, 1970) and forms some of the most productive seagrass beds worldwide (Pergent et al., 1994). Beds of this seagrass serve as feeding and nursery grounds for many species (Mazzella et al., 1992), including commercially important fishes (Bell & Harmelin-Vivien, 1982). Furthermore, *P. oceanica* beds constitute important marine autotrophic ecosystems, since they contribute a source of net oxygen release and act as a carbon sink (Romero et al., 1994; Mateo et al., 1997; Hemminga & Duarte, 2000). Because of these important features, *P. oceanica* beds are, arguably, the single-most important shallow-water marine habitat in the Mediterranean Sea. Consequently, *P. oceanica* beds are listed in Annex I of the EU's Habitats Directive (92/43/EEC) on the Conservation of Natural Habitats and of Wild Fauna and Flora, as a habitat whose presence requires the designation of Special Areas of Conservation, and are further designated as a priority habitat type (EEC, 1992). The need to implement such protection and conservation measures has become even more apparent following the conclusion that *P. oceanica* is experiencing a widespread regression in the Mediterranean (Perés, 1984; Marbá et al., 1996).

Besides being a large plant, with strap-like leaves around 1 cm wide and sometimes exceeding 1 m in length (Drew & Jupp, 1976), *P. oceanica* forms a dense root-rhizome mat, known as 'matte', that can sometimes develop to a thickness of several metres (see Romero et al., 1994). Similar to beds formed by other seagrasses, *P. oceanica* bed morphology is influenced by natural events and environmental processes such as storms, currents and sedimentation (Blanc & de Grissac, 1984; Marbá & Duarte, 1997), and by anthropogenic activities such as trawling (e.g. Sánchez Lizaso et al., 1990), coastal development and beach rehabilitation works (Ruiz et al., 1993), boat anchoring (e.g. Francour et al., 1999) and pollution (e.g. Bourcier, 1989). As a result, *P. oceanica* beds may be patchy (collection of isolated patches, each completely surrounded by a different habitat type), reticulate (non-continuous beds intermixed with a different habitat type, for example 'bare' sand) or continuous (Colantoni et al., 1982; Buia et al., 1989; 2000). The growth pattern of *P. oceanica* (Wittmann, 1984) can also lead to the formation of peculiar bed types such as 'collines' (seagrass patches resembling hillocks, with a thick matte at the centre but not at the periphery; Boudouresque et al., 1985) and extensive reef structures (Moliner & Picard, 1952; Augier & Boudouresque, 1970; Calvo & Orestano, 1984).

While some studies have addressed the spatial variation of *P. oceanica* bed structural characteristics (Manzanera & Romero, 2000; Gobert et al., 2003), data on differences in plant architecture with bed type are generally lacking. Although previous studies of the seagrass *Zostera marina* established differences in architecture between patchy and continuous beds (e.g. Irlandi, 1997), similar information for reticulate and continuous seagrass beds is almost entirely lacking (but see Hovel & Lipcius, 2001). *P. oceanica* is an ideal candidate for such studies since, unlike other seagrasses, it does not undergo large seasonal changes in spatial coverage or shoot density (Hovel & Lipcius, 2001). Therefore, the confounding effects introduced by temporal changes in seagrass structure are avoided in comparative studies of *P. oceanica* bed types.

Consideration of spatial variation in ecological studies is crucial, since environments are seldom homogeneous, and because factors and processes that influence the occurrence and distribution of species populations are scale dependent (Wiens et al., 1986; Wiens, 1989; Levin, 1992). Therefore, the inclusion of a number of appropriate scales in a sampling programme is highly advisable (Harlin et al., 1996; Tanaka & Leite, 2003), since this enables examination of the magnitude of variability in space of the attribute under study. On the other hand, the appropriate choice of scales in an experimental design must be a trade off between an ability to observe landscape processes without losing information on the finer scale, and an ability to detect fine-scale information, without being hindered by unrelated environmental 'noise' (Andrew & Mapstone, 1987). The appropriate choice of scales will depend also on logistic considerations, such as availability of funds and time to implement sampling, and on practical feasibility of sampling (Green, 1979, Underwood, 1997; Kingsford & Battershill, 1998).

For the purpose of the present study, three spatial scales were selected to test the proposed hypotheses: (i) 'large' (kilometres); (ii) 'medium' (few hundreds of metres); and 'small' (tens of metres). Comparison of the different *P. oceanica* bed types over the large spatial scale required identification of a number of study 'locations' within a suitably large stretch of coast. Within one of the locations, selection of a number of 'sites' would enable comparison at the medium scale, while selection of a number of 'plots' within one of the sites would enable comparison at the small spatial scale. Establishing four sampling stations at each spatial scale enables sound spatial replication without imposing excessive demands on sampling effort and analyses that would render the study programme unpractical. In this way, the basic experimental design would incorporate adequate spatial replication between different *P. oceanica* bed types, across a number of spatial scales (see Chapter 2).

Data on the architectural characteristics of different *P. oceanica* bed types collected over appropriate spatial scales will contribute to our understanding of how seagrass habitat fragmentation may affect the diversity of the associated biotic assemblages, given that macrofaunal assemblage composition has been shown to vary with seagrass bed architecture (e.g. Tolan et al., 1997; Webster et al., 1998). Thus, the aim of the present study was to examine the foliar architecture of two different bed types of *P. oceanica*, reticulate (≡ fragmented) and continuous (≡ non-fragmented), over a range of spatial scales; varying between several kilometres to a few tens of metres. The null hypothesis tested was that seagrass bed architecture did not differ between adjacent reticulate and continuous beds, over the range of spatial scales examined.

3.2 MATERIAL AND METHODS

3.2.1 Study sites and experimental design

The distribution of *P. oceanica* beds along the coastline of the Maltese Islands was established recently from mapping surveys using SCUBA diving and aerial photography (Borg et al., 1997). In some places, these beds extended to a depth of 43 m (Borg & Schembri, 1995a) and shoot densities were some of the highest recorded from the Mediterranean (Borg and Schembri, 1995b). Surveys indicated that dense, healthy *P. oceanica* beds were present along the northeastern coast of the Maltese Islands where four locations were selected for conducting the present study (see Chapter 2). The distribution of *P. oceanica* at these four locations [Ramla Bay (RB), Mellieha Bay (MB), White Rocks (WR) and St Thomas Bay (STB); see Figure 5] was characterised by a general pattern in which the seagrass occurred as small patches in shallow waters (2 – 4 m) and as reticulate and continuous beds in deeper waters (5 – 30 m) (Figures 7 & 8).

Within the 9 – 12 m depth range, all four locations had reticulate beds adjacent to continuous ones, which enabled comparison of the two bed types without introducing external influences (e.g. differences in bathymetry) that would confound the experimental design. The four locations, which were separated from each other by a distance of circa 12 km, were free from major pollutant discharges and riverine inputs, and have a similar underwater geology. However, the southern half of the Maltese Islands, where White Rocks and St Thomas Bay are located, is more densely populated and supports a higher industrial activity than the northern half, resulting in higher nutrient loading of coastal waters (Axiak et al., 2000). Furthermore, because of the small size and high exposure of the Maltese Islands (overall length just under 40 km, some differences in exposure between the different locations were present. The extreme northwestern parts of the islands are the most exposed due to the predominant northeasterly winds, while the main currents flow towards the southeast (Harvard, 1978; 1979; 1980) (see Chapter 2).

For the purpose of the present study, three spatial scales were selected to test the proposed hypotheses: (i) large (kilometres); (ii) medium (few hundreds of metres); and small (tens of metres) (Figure 16). Establishing four sampling stations at each spatial scale enables adequate replication between different *P. oceanica* bed types, across a number of spatial scales (Chapter 2).

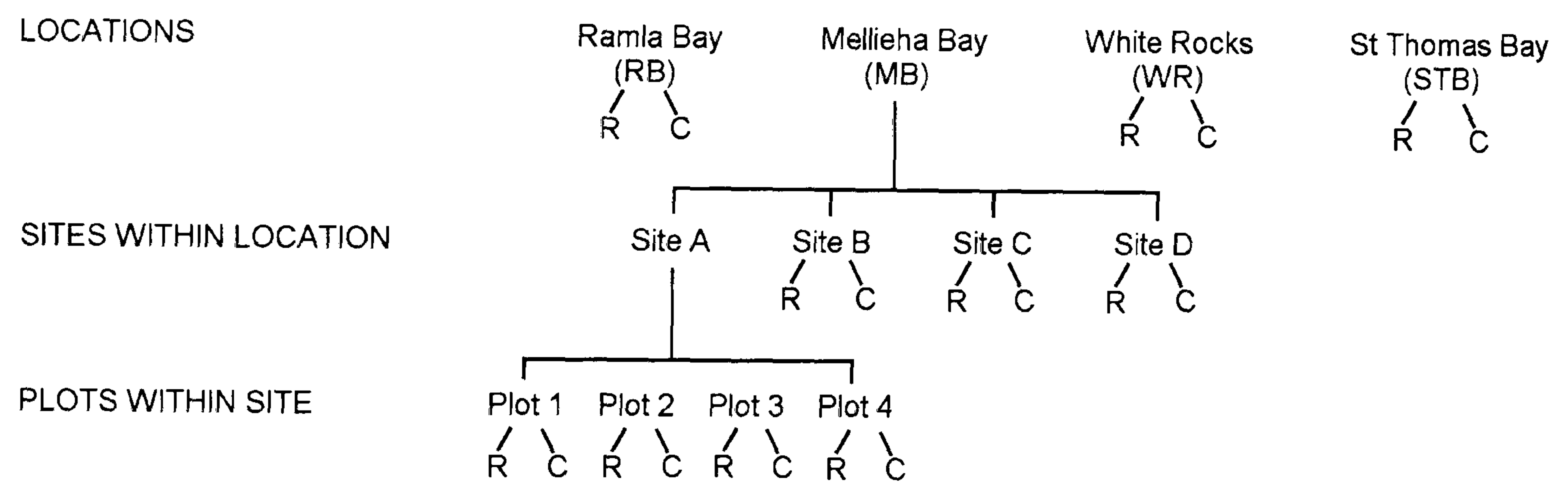


Figure 16. The experimental design. There are four plots (small scale) in adjacent continuous and reticulate *Posidonia oceanica* beds, all of which are nested within site A in Mellieha Bay. The four sites A – D (medium scale) are located within Mellieha Bay, one of the four locations (large scale).

To test for differences in the plant architecture of reticulate and continuous *P. oceanica* bed types over the large spatial scale, sampling stations were established within each of the two different bed types, at each of the four different locations (Figure 17). To test for differences in architectural characteristics of the two *P. oceanica* bed types over the medium spatial scale, four sites, separated from each other by a distance of circa 150 m were selected within one of the locations, Mellieha Bay (Figure 18a). Each site measured 50 m x 100 m and had continuous and reticulate bed types (Figure 18b). To test for differences over the small spatial scale, eight plots (four plots in the continuous and four in

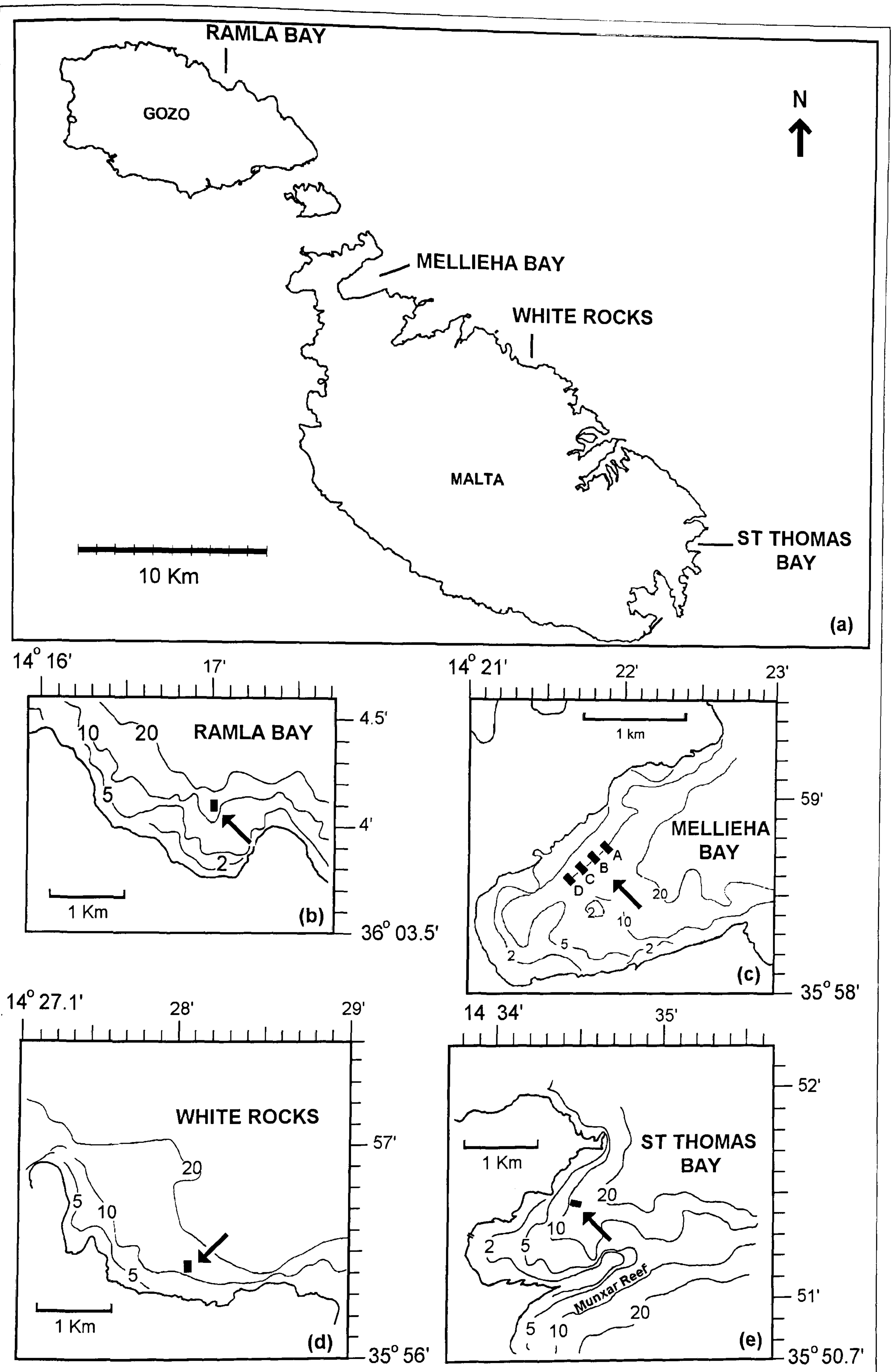


Figure 17. (a) Map of the Maltese Islands showing the four study locations; (b) – (e) maps of the four study locations, indicating the bathymetry (2 m, 5 m, 10 m and 20 m depth contours) and sampling stations.

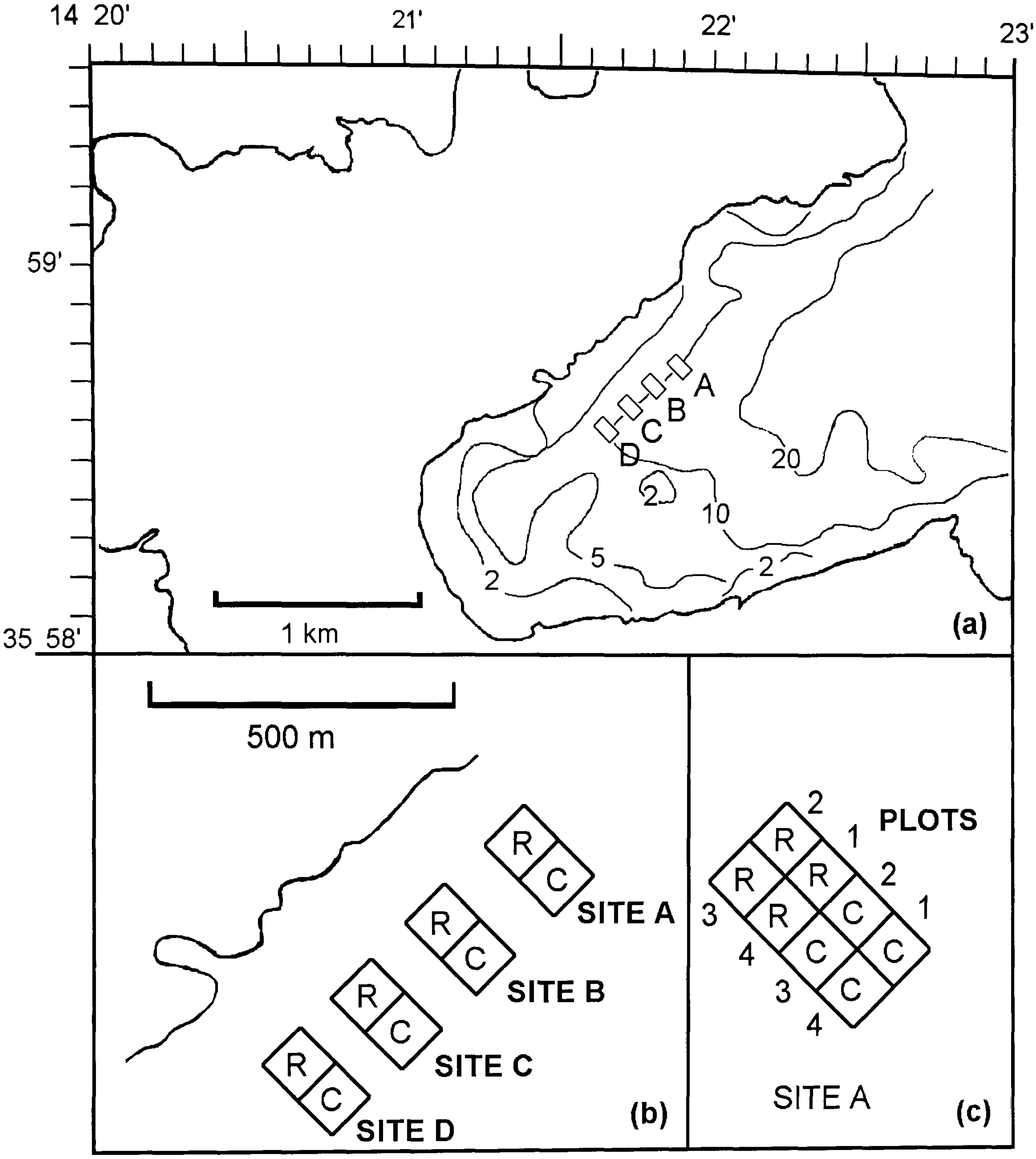


Figure 18. (a) Map of Mellieha Bay showing the bathymetry (2 m, 5 m, 10 m and 20 m depth contours) and the location of the four sites (A to B); (b) the four sites within Mellieha Bay (R = reticulate *Posidonia oceanica* bed and C = continuous *Posidonia oceanica* bed); and (c) the location of the plots within Site A (plots 1 to 4 in each of the two bed types).

the reticulate type meadows), each measuring 25 m x 25 m, were selected within site A in Mellieha Bay (Figure 18c).

3.2.2 Data collection and analyses

To measure seagrass architectural characteristics, twelve orthotropic (vertically-growing) shoots (e.g. Mazzella et al., 1989) were collected from adjacent reticulate and continuous *P. oceanica* beds, at each of the three spatial scales considered. Plants sampled were at least 1 m apart and from at least 1 m inside the bed edge. Shoot density estimates were made in adjacent reticulate and continuous *P. oceanica* beds, at each of the three spatial scales considered, by counting the number of shoots enclosed in four replicate 0.05 m^2 samples taken using the corer (see Chapter 2) designed for the study of associated fauna (Chapter 5). All sampling was carried out between 2nd August and 4th September 1999.

In the laboratory, the leaves of each shoot were counted, and estimates were made of the number of leaves, leaf width and leaf length (± 1 mm) for each shoot sample. Estimates of shoot biomass were obtained by scraping off all epiphytes, drying the leaves for 24 h in an oven at 80°C, and weighing (± 0.001g) the dry leaf and epiphyte fractions separately.

Two-factor ANOVA tests (with alpha set at 0.05) were carried out on the *P. oceanica* architectural data obtained from each of the three different spatial scales, using an orthogonal model in which 'bed type' (two levels) was fixed and 'sampling locality' (four levels) was a random factor. At the large (location) and medium (site) spatial scales, data from site A and plot 1 were respectively selected 'a priori' for use in the analyses. Prior to analyses, data were tested for homogeneity of variances using Cochran's test and, where necessary, appropriate transformation of data was carried out (Underwood, 1997). Analyses were carried out using the PC software package GMAV5 produced at the University of Sydney (GMAV5, 1996). When the ANOVA indicated significant differences, the source of difference was identified using Student Neuman Keuls (SNK) tests Underwood (1997). SNK tests use an estimate of the standard error of the mean in each treatment to make comparisons between all pair combinations of means, after they have been arranged in rank order from the smallest to largest (Underwood, 1981). SNK tests were also used to identify the source of difference when the ANOVA indicated a significant interaction. However, when investigating a significant interaction, rather than using SNK tests that compare the means for the main effects (as can be done when ANOVA does not indicate a significant interaction), means of the levels of one factor were compared within each level of the other factor, and vice-versa (Underwood, 1981).

3.3 RESULTS

Although there were general trends in the seagrass architectural measures taken, there were always exceptions. For example, mean shoot densities were generally higher for continuous than reticulate beds at each spatial scale, but the reverse was found at White Rocks and St Thomas Bay at the large scale, and in plot D at the medium scale (Figure 19 a - c). ANOVA indicated a significant interaction between the two factors at the large scale, while significant differences in shoot density values between the two different bed forms were present only at the small scale. The significant interaction detected at the large spatial level was attributed to significant differences in shoot density: (i) between continuous and reticulate beds at Mellieha Bay and St Thomas Bay (SNK; $p < 0.05$), and (ii) between the continuous bed at Ramla Bay and continuous beds at the other three sites (SNK; $p < 0.01$), and between the reticulate bed at Ramla Bay and the reticulate bed at Mellieha Bay (SNK; $p < 0.05$). The significant difference between the two bed types at the small spatial level was attributed to significant differences in shoot density between the two bed types, averaged over the four plots (SNK; $p < 0.01$) (Table 7).

Shoot biomass values recorded from the two different bed types were similar at the large and small scales. However, at the medium scale, values recorded from reticulate beds were generally higher than those of continuous beds (Figure 19 d - f). ANOVA did not detect any significant differences in shoot biomass values between the two different bed types at any of the three spatial scales. On the other hand, significant differences were detected for the factor 'sampling locality' at the large scale and a significant interaction was detected between the two tested factors at the medium scale. The significant difference in the factor 'sampling locality' at the large scale was attributed to significant differences in shoot

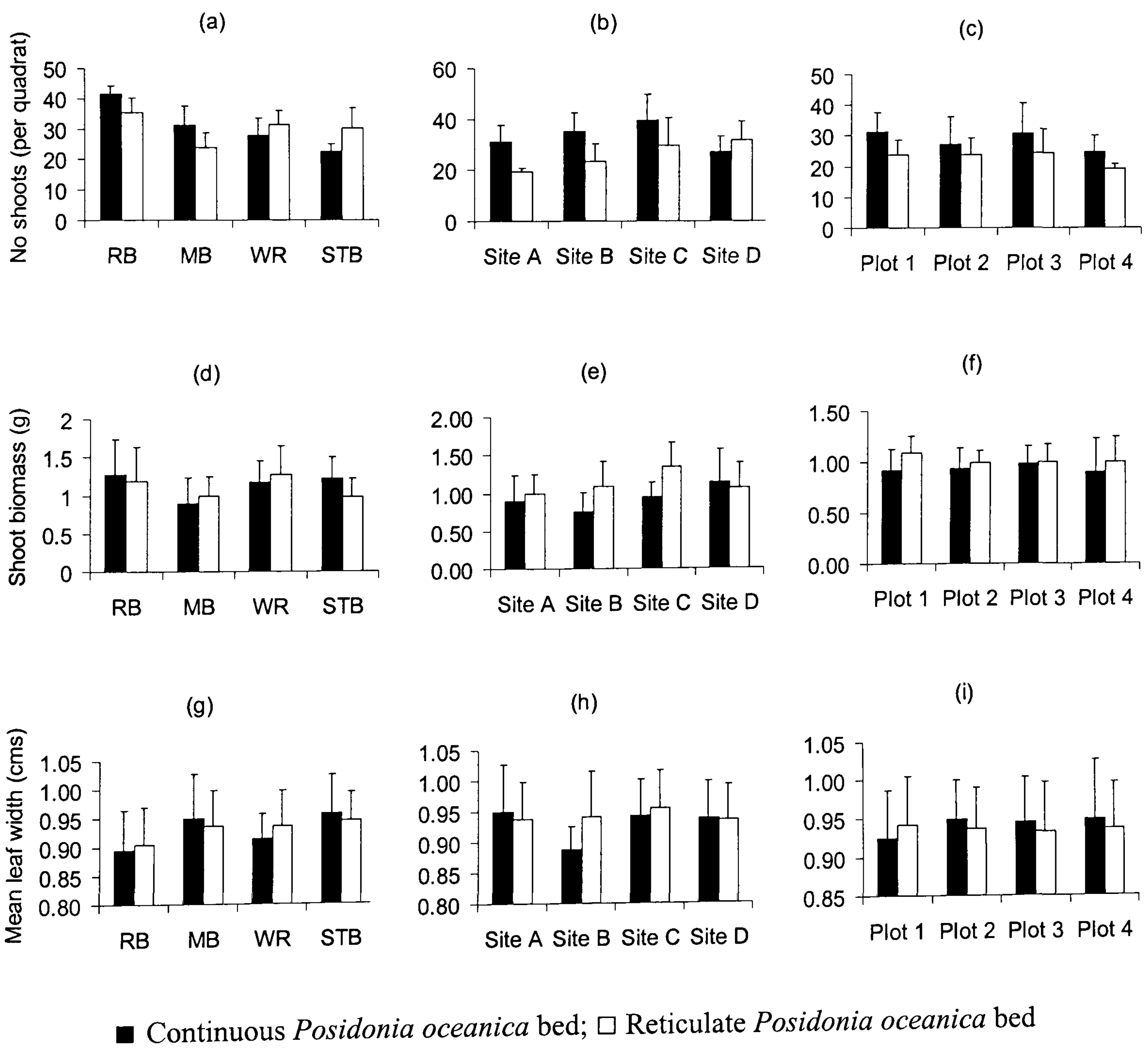


Figure 19. Mean values of shoot density (a – c), shoot biomass (d – f) and leaf width (g - i) at the three spatial levels: large (a, d & g), medium (b, e & h) and small (c, f & i). Error bars are +1 SD.

biomass, averaged over the two bed types: (i) between Ramla Bay and Mellieha Bay (SNK; $p < 0.05$), and (ii) between Mellieha Bay and White Rocks (SNK; $p < 0.05$), with shoot biomass averaged over the two bed types (Table 8). The significant interaction between the two tested factors at the medium scale was attributed to significant differences: (i) between the two bed types at site B (SNK; $p < 0.01$) and site C (SNK; $p < 0.01$); and (ii) between the continuous bed at site B and the continuous bed at site D (SNK; $p < 0.05$), between the reticulate bed at site A and the reticulate bed at site C (SNK; $p < 0.05$), and between the reticulate bed at site B and the reticulate bed at site C (SNK; $p < 0.05$) (Table 8).

Table 7. Summary of ANOVA results for shoot density (per quadrat). The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Spatial level	**Source of variation**	**df**	**Shoot density n = 4** Transformation: none Cochran's test: NS		
			MS	F	p
Large	Bed type (B)	1	2.53	0.02	NS
	Location (L)	3	236.78	9.34	***
	B x L	3	112.11	4.42	*
	Residual	24	25.36		
Medium	Bed type (B)	1	300.12	2.68	NS
	Site (S)	3	75.87	1.24	NS
	B x S	3	111.87	1.83	NS
	Residual	24	61.06		
Small	Bed type (B)	1	258.78	46.09	***
	Plot (P)	3	55.11	1.23	NS
	B x P	3	5.61	0.12	NS
	Residual	24	44.93		

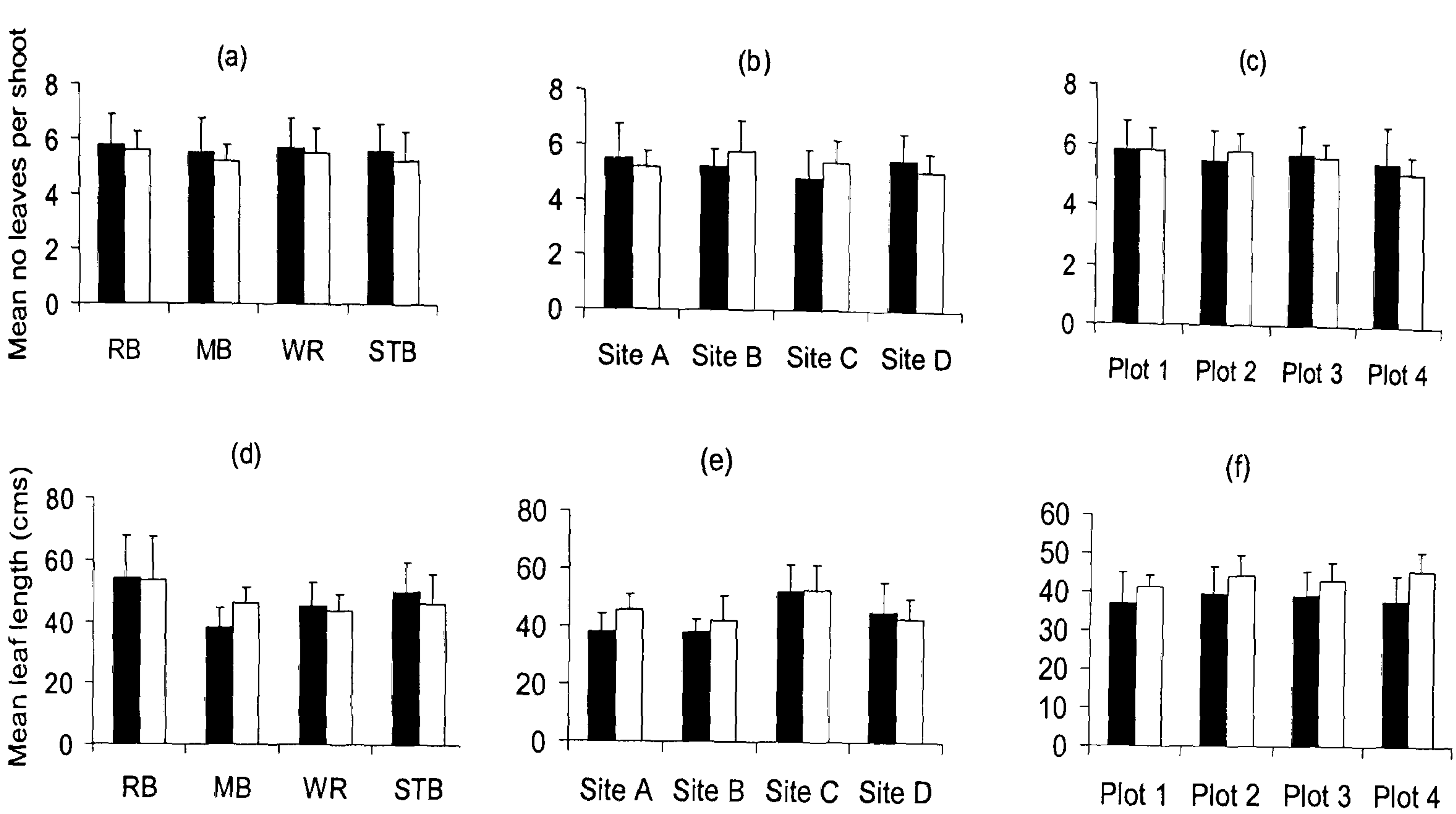
Leaf width values recorded from the two different bed types were similar and no general pattern was evident (Figure 19 g - i); no significant differences were detected by ANOVA between the two different bed types at any of the three spatial scales. Significant differences were, however, detected by ANOVA for the factor 'sampling locality' at the large scale. This was attributed to significant differences in leaf width, averaged over the two bed types, between Ramla Bay and St Thomas Bay (SNK; $p < 0.05$), and between Ramla Bay and Mellieha Bay (SNK; $p < 0.05$) (Table 8).

Generally, the mean number of leaves and the mean leaf lengths were similar, although there was a tendency for the number of leaves per shoot to be larger in continuous beds at the large scale, and for leaves to be longer in reticulate beds at the small scale (Figure 20).

Table 8. Summary of ANOVA results for shoot biomass (g d w per shoot) and mean leaf width (cms). The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Spatial level	**Source of variation**	**df**	**Shoot biomass n = 12** Transformation: none Cochran's test: NS			**Leaf width n = 12** Transformation: none Cochran's test: NS		
			MS	F	p	MS	F	p
Large	Bed type (B)	1	0.0241	0.15	NS	0.001	0.03	NS
	Location (L)	3	0.4230	3.55	*	0.013	3.26	*
	B x L	3	0.1577	1.32	NS	0.002	0.45	NS
	Residual	88	0.1191			0.004		
Medium	Bed type (B)	1	0.9101	3.05	NS	0.004	0.74	NS
	Site (S)	3	0.2909	2.96	*	0.005	1.36	NS
	B x S	3	0.2980	3.03	*	0.005	1.35	NS
	Residual	88	0.0983			0.004		
Small	Bed type (B)	1	0.1828	7.28	NS	0.002	0.21	NS
	Plot (P)	3	0.0147	0.33	NS	0.004	0.11	NS
	B x P	3	0.0251	0.57	NS	0.001	0.29	NS
	Residual	88	0.0442			0.004		

ANOVA detected significant differences between the two different bed forms for number of leaves at the large scale and for leaf length at the small scale. Significant differences in leaf length values were also detected for the factor 'sampling locality' at the large and medium scales. The significant difference in number of leaves detected for 'bed type' at the large scale was attributed to significant differences between the two bed types (SNK; $p < 0.05$), averaged across the four locations. The significant difference in leaf length detected for 'bed type' at the small scale was attributed to significant differences between the two bed types in plot 4 (SNK; $p < 0.05$). The significant difference in leaf length



■ Continuous *Posidonia oceanica* bed; □ Reticulate *Posidonia oceanica* bed

Figure 20. Mean values of number of leaves per shoot (a – c) and leaf length (d – f), at the three spatial levels: large (a & d), medium (b & e) and small (c & f). Error bars are +1 SD.

Table 9. Summary of ANOVA results for mean leaf length per shoot (cm) and mean number of leaves per shoot. The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = p < 0.05; ** p < 0.01; *** = p < 0.001.

Spatial level	**Source of variation**	**df**	**Mean number of leaves n = 12** Transformation: none Cochran's test: NS			**Mean leaf length n = 12** [1]Transformation: Ln (X) Cochran's test: NS		
			MS	F	p	MS	F	p
Large	Bed type (B)	1	1.50	27.00	*	0.0042	0.05	NS
	Location (L)	3	0.55	0.58	NS	0.21	4.57	**
	B x L	3	0.06	0.06	NS	0.093	1.99	NS
	Residual	88	0.96			0.047		
Medium	Bed type (B)	1	0.17	0.10	NS	145.51	1.29	NS
	Site (S)	3	0.57	0.68	NS	747.06	12.17	***
	B x S	3	1.69	2.02	NS	112.61	1.83	NS
	Residual	88	0.84			61.38		
Small	Bed type (B)	1	0.014	0.02	NS	649.47	33.67	*
	Plot (P)	3	1.094	1.51	NS	44.42	1.25	NS
	B x P	3	0.45	0.63	NS	19.29	0.54	NS
	Residual	88	0.72			35.47		

[1]Transformation was only necessary for 'location' data.

detected for the factor 'sampling locality' at the large scale was attributed to significant differences, averaged over the two bed types, between Ramla Bay and Mellieha Bay (SNK; $p < 0.01$), and between Ramla bay and White Rocks (Table 9).

Overall, the results of ANOVA indicated that most of the significant differences detected were associated with the factor 'sampling locality' rather than 'bed type', thereby indicating a general similarity in the foliar architecture between reticulate and continuous bed types of *P. oceanica*. However, significant differences in bed architectural characteristics were detected between different sampling localities at the various spatial scales examined, indicating significant spatial variation in *P. oceanica* bed architecture.

3.4 DISCUSSION

The results of the present study show that there were no consistent patterns in bed architecture between the two different *P. oceanica* bed types. Furthermore, ANOVA indicated that most of the detected significant differences were associated with 'sampling locality', thereby, indicating a predominance of spatial differences in bed architecture rather than consistent differences between the two different bed types. Therefore, the null hypothesis of no differences in architectural characteristics between the two bed types was accepted.

Physical and biotic environmental factors have different magnitudes of influence on different seagrass bed types. For example, currents and strong wave action may be expected to cause greater physical stress on reticulate than on continuous beds, since the former have a greater edge to area ratio (Foncesa et al., 1983; Irlandi et al., 1995). Resuspension of sediment, originating from the sandy patches interspersed amongst the reticulate beds (Gacia & Duarte, 2001), would decrease the amount of light available to plants located in reticulate beds, through a reduction in water transparency, leading to reduced photosynthetic rates and subsequent lower growth rates and changes in plant architectural characteristics (see Hemminga & Duarte, 2000 and references therein). The greater edge to area ratio of reticulate beds may also render plants making this bed type more exposed to physical injury resulting from grazing by fishes and other megafaunal species (Cebrian et al., 1996) that may exert larger feeding pressures along the border of seagrass beds. It may be predicted, therefore, that such environmental and biotic stresses would impact plants within reticulate beds more than those located within continuous beds, resulting in consistent architectural differences between the two different bed types. However, in the case of the *P. oceanica* beds studied, the present results do not support this proposition.

Some differences in *P. oceanica* bed architectural measures were detected between reticulate and continuous beds, but the inconsistency of these differences was highlighted by significant interactions between the two factors 'sampling locality' and 'bed type' for shoot density at the large scale and for biomass at the medium scale. For example, at the large scale, shoot density values were higher for the continuous beds at Ramla Bay and Mellieha Bay, but the reverse was true at White Rocks and St Thomas Bay where shoot density values were higher for the reticulate beds. Significant differences between the two different bed types were detected also for shoot density and leaf length at the small scale, and for number of leaves at the large scale. However, there were no broadly consistent patterns of occurrence of differences over the three spatial scales considered. Furthermore, ANOVA indicated that most of the significant differences detected were associated with the factor 'sampling locality' rather than 'bed type'.

In the present study, the lack of a clear difference in the plant architecture between the two different bed types, over a number of spatial scales, is somewhat unexpected considering the observations of previous studies for other species of seagrass (e.g. *Zostera marina*). For example, Irlandi (1997) noted significant differences in shoot density between small (1 m across) and large (5 – 10 m across) *Zostera marina* patches. Hovel & Lipcius (2001) also found significant differences in the same architectural measure between small (area < 1 m) and large (area = 1000 – 3000 m^2) patches of the same seagrass. However, comparisons of shoot density of the same seagrass between larger patches of different sizes, did not detect significant differences in this architectural measure. For example, Bowden et al. (2001) did not find significant differences in shoot density between patches having a diameter of 15 m and 30 m, while the same held true for the study by Hovel & Lipcius (2001) when comparing this architectural measure between a nearly continuous bed (area = 30,000 m^2) and 'connected' patches (area = 10 – 100 m^2). Therefore, at least for *Zostera marina*, it appears that significant differences in shoot density of healthy seagrass beds are mainly to be expected when comparing very small patches (circa 1 m) with larger patches or continuous stands. On the other hand, spatial differences in architectural characteristics within the same *Zostera marina* bed have been observed (e.g. between different in-patch locations for the same seagrass patch; see Bowden et al., 2001), indicating potential small-scale 'within-bed' variation.

Several studies have indicated that a number of physical and biological environmental characteristics differ between the edge and inner parts of a seagrass bed. These include seagrass bed architecture (e.g. Duarte & Sand-Jensen, 1990; Bowden et al., 2001) and the abundance of associated fauna (e.g. Irlandi et al., 1995; Bologna, 1998). However, such 'edge effects' do not appear to extend to the core of a seagrass bed, unless the latter have a small area (e.g. small patches measuring one or two metres across) such that they consist almost entirely of edge habitat. Consequently, comparisons of bed architectural characteristics between large patchy/reticulate and continuous seagrass beds, based on samples taken away from the edge (as was deliberately planned in the present sampling design to eliminate the potential confounding influence of 'edge effects'), indicate similar physical and biological characteristics. The results for *P. oceanica* beds obtained from the present study support this notion (for bed architectural characteristics).

The present study indicated that most of the detected significant differences in *P. oceanica* bed architectural characteristics were associated with 'sampling locality', thereby indicating a predominance of spatial differences in bed architecture rather than consistent differences between the two different bed types. Although the results obtained from the 'small' and 'medium' spatial scales (inside Mellieha Bay) should not be extrapolated to the three other locations considered in the study, they are consistent with the findings of other workers who examined the spatial variation of *P. oceanica* bed architectural characteristics (e.g. Panayotidis et al., 1981; Scardi et al., 1989; Balestri et al., 2003). For example, in their study of the spatial variation of *P. oceanica* bed architectural characteristics over a number of spatial scales, varying between tens of kilometres and a few metres, Balestri et al. (2003) noted significant differences, with most variability being detected at the following two spatial levels: 'tens of kilometres' and 'few hundred metres'. The present results are comparable with those obtained from the latter study. However, the extent of such variability between different bed types of *P. oceanica* has not been reported elsewhere.

The spatial variations in plant architecture recorded by the present study are due, probably, to differences in the degree of influence exerted by edaphic factors, such as the hydrodynamic regime and the physico-chemical properties of the substratum (e.g. Fonseca

& Bell, 1998). In the present study, the significant difference in plant architecture detected at the large spatial level between *P. oceanica* beds at Ramla Bay and those present in the other locations was due to higher shoot densities, narrower leaf width and higher leaf length values recorded from the former location. It appears, therefore, that the *P. oceanica* beds at Ramla Bay (the location which is most exposed to the predominant northwest winds; Chapter 2) have responded to the higher energy environment, by having longer and narrower leaves. Some Mediterranean workers have noted changes in plant architecture of *P. oceanica* beds located in certain physical environmental conditions (e.g. high energy hyrodynamic regimes and/or bottom geomorphology), to which the seagrass responds by increasing leaf area (e.g. Wittman, 1984; Abbate et al., 2000). Increases in leaf area enable the plants to optimise the photosynthetic yield to meet the high physiological demand required by the seagrass to survive in such conditions. Other studies have shown that the plant architecture of *Zostera marina* beds is influenced by variations in the interstitial ammonium concentrations of the sediment (Short, 1983). However, large variations in sediment chemical properties between the different sampling localities in the present study are not expected.

In general, landscape ecological studies dealing with seagrass habitats are relatively recent and are lacking for *P. oceanica* beds. As far as is known, the present study is the first to examine differences in *P. oceanica* architectural characteristics between different bed types over a range of spatial scales. The results of the present study do not yield any evidence that changes in *P. oceanica* bed types (continuous → reticulate) that may result from anthropogenic or natural habitat fragmentation, affect overall the habitat architecture within the beds. That is, the present results suggest that from a 'within' habitat structure perspective, reticulate and continuous *P. oceanica* should be treated as having broadly similar within bed architectural characteristics and, hence, presumably of similar ecological value for the associated macroinvertebrate fauna. However, it should be remembered that changes in bed type will bring about changes in habitat area and configuration (Hemminga & Duarte, 2000) that will have consequences for some fauna that associate with seagrass (e.g. fish; Bell & Harmelin-Vivien, 1982; Harmelin-Vivien, 1982; Procaccini et al., 2003). Furthermore, the observed spatial variation in *P. oceanica* architecture, that was apparently independent of bed type, may have important implications for the associated faunal assemblages, given that the species richness and abundance of macrofauna inhabiting seagrass beds are known to be influenced by variations in seagrass structural complexity (Heck & Wetstone, 1977; Heck & Orth, 1980a; Tolan et al., 1997; Webster et al., 1998; Lee et al., 2001) that are likely to operate in taxon-specific ways (the 'perception windows' of Attrill et al., 2000). It would be useful, therefore, to examine whether the species richness and abundance of the motile macroinvertebrate biota associated with *P. oceanica* varies with plant architecture (and combinations of architectural attributes, i.e. complexity) and whether this relationship is independent of bed type or not (Chapter 4). The results of such a study would serve to better inform environmental managers of the relative ecological value of reticulate and continuous *P. oceanica* beds.

CHAPTER 4

INFLUENCE OF *POSIDONIA OCEANICA* BED TYPE AND PLANT ARCHITECTURE ON ASSOCIATED MOTILE MACROINVERTEBRATES

4.1 INTRODUCTION

Concern amongst ecologists and conservation biologists about the loss of biodiversity that may result from habitat fragmentation (Wilcox & Murphy, 1985; Wilson, 1992; Hobbs, 1994) has increased in recent years in parallel with increased awareness of human-induced environmental degradation. Habitat fragmentation implies disruption of continuity, especially as it relates to ecosystem processes (Lord & Norton, 1990). As a result, numerous studies have attempted an assessment of the ecological effects of habitat fragmentation through investigations of terrestrial (e.g. Andrén, 1992) and, to a lesser extent, aquatic habitats (e.g. Ward, 1998). The paradigm that habitat fragmentation leads to loss of species richness (see review by Wilcox & Murphy, 1985) is mostly supported by data for terrestrial habitats, for example studies carried out on forests (Andrén, 1992). However, recent detailed reviews of terrestrial habitat fragmentation studies (e.g. Haila, 2002) are critical of the fact that the results obtained sometimes have contradictory implications. Fewer studies of habitat fragmentation have been undertaken for the aquatic environment, with most of these studies targeting intertidal rocky reef habitats (e.g. Keough, 1984; Farrell, 1989; Svane & Setyobudiandi, 1996; Underwood & Skilleter, 1996; Anderson, 1998). Attention has been paid also to the effects of fragmentation of sublittoral habitats, including coral reefs (Riegl & Riegl, 1996; Acosta & Robertson, 2002) and seagrass beds (Irlandi, 1994; 1997; Irlandi et al., 1995; Frost, 1999; Bowden et al., 2001, Hovel & Lipcius 2001; 2002).

Seagrasses form beds, which differ greatly in overall morphology (i.e. bed type) and within bed structure (i.e. plant architectural characteristics), depending on the constituent seagrass species and on the natural physico-chemical and biological characteristics of the particular locality where the beds occur (Fonseca et al., 1983; Kirkman & Kuo, 1990). Natural abiotic factors such as water movement (e.g. Fonseca & Bell, 1998), bottom geomorphology (e.g. Fonseca et al., 2002), physico-chemical properties of the sediment (e.g. Koch, 2001; Terrados et al., 1998) and water quality (e.g. Nienhuis, 1983), together with natural disturbance events, such as storms (e.g. Patriquin, 1975; Kirman & Kuo, 1990) and biotic process such as bioturbation (Suchanek, 1983; Valentine et al., 1994; Townsend & Fonseca, 1998) and grazing (Hovel & Lipcius, 2001; Preen, 1995), may also play a role in influencing the morphology of seagrass beds and their architectural characteristics. As a result, the morphology of seagrass beds varies widely from small patches (e.g. measuring 1 – 20 m in diameter; Irlandi, 1997; Frost et al., 1999; Reusch, 1998; Hovel & Lipcius, 2002) to reticulate beds (beds interspersed with soft sediment or other habitat types (e.g. Holt et al., 1983; Kirkman & Kuo, 1990; Barberá Cebrián et al., 2002) to large continuous 'meadows' (Fonseca et al., 1983; Fonseca & Bell, 1998). Within-bed structure varies depending on plant architectural characteristics (e.g. shoot density, leaf density, leaf length and leaf width) and on the plant's general growth pattern (e.g. simple strap-like or branching leaves; Orth et al., 1984). Moreover, the stability of seagrass beds varies from one locality to another, such that some exhibit changes in size and position, while others are more stable and retain their original configuration over a long period of time (den Hartog & Phillips, 2001).

Differences in bed type and plant architectural characteristics between different seagrass beds over large spatial scales result in varied landscapes and, possibly, in variations in habitat characteristics which are expected to influence the species composition of the associated faunal assemblages (Robbins & Bell, 1994; Reusch, 1998; Hovel & Lipcius, 2002). For example, predation pressure is expected to be higher in reticulate (fragmented) beds than in continuous (non-fragmented) beds, since the presence of bare sand interspersed amongst the former bed type would enable a higher mobility of predators (Holt et al., 1983) and hence more efficient foraging (e.g. Irlandi, 1994; Irlandi et al., 1995; Hovel & Lipcius, 2002).

Besides predation, other biotic factors are expected to result in small changes in the assemblage composition of motile macroinvertebrates between the two different bed types, given that fragmented beds have a much larger edge to area ratio than continuous beds. These include preferential selection for seagrass edges by some species (e.g. mysids; Bárberá Cebrián et al., 2002 and decapods; Eggleston et al., 1998), higher larval settlement at bed borders (McNeill & Fairweather, 1993; Bologna & Heck, 2000; Tanner, 2003) and enhanced food delivery (e.g. for infaunal bivalves; Irlandi, 1996) in fragmented beds. For example, Reusch (1998) found that recruitment of the mussel *Mytilus edulis* Linnaeus was optimal in medium sized (1.6 m across) *Zostera marina* Linnaeus beds. Plant architecture would also be expected to influence the species richness and abundance of associated macrofauna both directly and indirectly. For example, differences in seagrass leaf morphology have been shown to influence directly the abundance of associated motile epifauna, since some seagrasses have an external anatomy that enhances physical complexity more than others (e.g. Schneider & Mann, 1991; Kenyon et al., 1997). Differences in the density of plants and leaves, the total area of leaf surface available, and leaf turnover (which influences the colonisation pattern of leaf epiphytes), are also important in directly determining the diversity of associated macrofauna, since variation of these plant attributes translates to variation of within-bed architectural complexity and, hence, differences in habitat structure (e.g. Lewis, 1984). Furthermore, the dynamic leaf turnover (e.g. Alcoverro et al., 1997a) would influence the structure and composition of the epiphytic assemblages (e.g. Gambi et al., 1992), which may in turn influence the species richness and abundance of macrofauna feeding on the epiphytes. The presence of macroalgae and epiphytes directly imparts additional physical complexity to the seagrass bed, which may enhance habitat space (Schneider & Mann, 1991) or act as an obstacle for some macrofauna (Heck & Orth, 1980a). Differences in bed type and plant architecture also have an indirect influence on the associated biota by exerting different magnitudes of influence on water movement (e.g. Worcester, 1995; van Keulen & Borowitzka, 2000) and on the physico-chemical properties of nearby sediments (Fonseca et al., 1983).

Certain anthropogenic activities, for example trawling (Sánchez Lizaso et al., 1990; Martín et al., 1997; Sánchez Jerez et al., 2000) and deployment of boat moorings (e.g. Hastings et al., 1995) may cause direct physical alterations in the morphology and within-bed structure of seagrass beds. The recent increased awareness of the global decline of seagrasses (Short & Wyllie Echeverria, 1996; Ruckelshaus & Hays, 1998; Green & Short, 2003) has highlighted the urgency of examining whether fragmented seagrass beds support the same species richness and abundance of associated biota as non-fragmented beds. Given the lack of data on the direct consequences of fragmentation of seagrass habitat on the diversity of associated biota (Irlandi, 1994; 1997; Irlandi et al., 1995; Frost, 1999; Bowden et al., 2001, Hovel & Lipcius 2001; 2002), it is useful for ecologists to examine the biotic diversity of different naturally occurring seagrass bed types, so that coastal managers can be provided with the information that will help them predict the consequences of fragmentation of seagrass beds resulting from anthropogenic disturbance. A small number of studies have addressed the likely influence of seagrass bed fragmentation in this manner by comparing the flora and fauna between continuous and patchy beds (Irlandi, 1994; Irlandi et al., 1995; Frost et al., 1999; Hovel & Lipcius, 2001; Hovel & Lipcius, 2002) and between differently sized patches (McNeill & Fairweather, 1993; Bell et al., 2001; Bowden et al., 2001; Irlandi, 1997). Comparisons of motile macroinvertebrate assemblages associated with continuous and reticulate seagrass beds are largely unavailable (but see Hovel & Lipcius, 2001; 2002), despite the possibility that the latter may constitute the first stage in fragmentation of continuous beds (Fonseca & Bell, 1998).

In the Mediterranean Sea, the endemic *Posidonia oceanica* forms beds that are characterised by variable morphology and high structural complexity. *P. oceanica* grows on both soft and hard substrata, and forms several different bed types, including patchy, reticulate and continuous beds (e.g. Colantoni et al., 1982; Sánchez Jerez et al., 1999a; Buia et al., 2000; Barberá Cebrián et al., 2002), and other particular forms (Section 1.3). Reticulate *P. oceanica* beds (frequently referred to as 'intermatte' beds; e.g. Calvo & Frada-Orestanio, 1984) constitute naturally fragmented seagrass beds (Sanchez Jerez et al., 1999a; Barberá Cebrián et al., 2002), whose structure is determined by a complex suite of environmental factors. Because of such large variation in bed morphology, *P. oceanica* beds are ideal candidates for studies that address the influence of seagrass bed type on the diversity of the associated macrofauna. However, their use in such studies has only been recognised by very few workers (e.g. Barberá Cebrián et al., 2002). Thus, it is evident that data collected from different bed types of *P. oceanica* will contribute to our understanding of how seagrass habitat fragmentation may affect the diversity of the associated biotic assemblages. Consideration of different spatial levels in such studies is crucial, given that the distribution patterns of biotic assemblages and the processes influencing them are scale dependent (Wiens et al., 1986; Wiens, 1989; Levin, 1992); hence proper understanding of community dynamics in seagrass habitats can only be achieved by considering more than one spatial scale. Furthermore, selection of the appropriate scales of study ultimately depends on the size(s) of the particular species under study, given that organisms of different sizes have different 'perceptions' of their habitat (the 'perception windows' of Attrill et al., 2000).

Therefore, the first aim of the present study was to establish whether the species richness, abundance and composition of associated motile macroinvertebrates (i.e. excluding sponges, hydroids, bryozoans and foraminiferans), differed between seagrass beds of different type, over a range of spatial scales. To address this aim, the null hypotheses tested were that the species richness and abundance of motile macroinvertebrate assemblages associated with reticulate and continuous *P. oceanica* beds did not differ between the two bed types, over spatial scales varying from kilometres to metres. The second aim was to establish whether seagrass plant architectural characteristics (Chapter 3) had any significant influence on the species richness, abundance and assemblage composition of macroinvertebrates associated with *P. oceanica* beds, again at spatial scales varying from kilometres to metres. To address the latter aim, the null hypothesis tested was that seagrass plant architectural characteristics did not have a significant influence on the species richness, abundance and composition of motile macroinvertebrate assemblages associated with *P. oceanica* beds, over spatial scales varying from kilometres to metres.

4.2 MATERIALS AND METHODS

4.2.1 Study area and experimental design

Surveys have shown that most of the different *P. oceanica* bed types described in the literature from other parts of the Mediterranean also occur around the Maltese islands (Borg & Schembri, 1995a; Borg et al., 1997). Detailed surveys aimed at mapping the occurrence and spatial extent of the different *P. oceanica* bed types present, were carried out at four chosen locations in the Maltese islands: Ramla Bay, Mellieha Bay, White Rocks and St Thomas Bay (Figure 17). The reasons why these locations were chosen and details of the physical environmental characteristics of the four locations are given in Chapters 2 and 3.

To test for differences in motile macroinvertebrate assemblages associated with reticulate and continuous *P. oceanica* bed types over the spatial scale of kilometres (large spatial scale), sampling stations were established within each of the two different bed types, at each of the four different locations. To test for differences between the two *P. oceanica* bed types over a spatial scale of a few hundred metres (medium spatial scale), four sites, separated from each other by a distance of circa 100 m were selected within one of the locations (Mellieha Bay) (Figure 18a). Each site measured 50 x 100 m and comprised continuous and reticulate bed types (Figure 18b). To test for differences over a spatial scale of tens of metres (small spatial scale), eight plots (four plots in the continuous and four in the reticulate beds, each measuring 25 m x 25 m), were selected within a single site (site A in Mellieha Bay; Figure 18c). The overall experimental layout, based on a staggered nested design (Section 2.1.1), is shown in Figure 16 (Section 3.2.1).

4.2.2 Sampling and laboratory analyses

Sampling of *P. oceanica* in the two different bed types was carried out using a specially designed corer having a diameter of 25 cm, to which a 0.5 mm mesh collecting bag was attached. The design, selection, justification and operation of this particular corer are described in Chapter 2. Using this sampler, four replicate cores were collected by SCUBA divers from adjacent reticulate and continuous beds, at each of the three spatial levels considered (i.e. 20 stations x 4 replicates = 80 samples). All sampling stations were located within a narrow depth range (9 – 12 m; see Chapter 3). To reduce edge effects, cores were collected at least 2 m away from bed boundaries. Four replicate samples were also collected from each sampling station using a smaller (10 cm) diameter metal corer, to enable physico-chemical examination of the sediment and of the root-rhizome material. To obtain estimates of epiphyte (algal and sessile fauna) biomass on *P. oceanica* shoots, twelve orthotropic (vertically-growing) shoots were collected from each sampling station located within the adjacent reticulate and continuous beds, at each of the three spatial levels. Plants sampled were at least 1 m apart and located at least 1 m inside the bed edge (see Section 3.2.2 for details of sampling procedure). All sampling was carried out between 10.00 h and 14.00 h during the period 2nd August to 4th September 1999. To avoid variation in the corer sampling technique, samples were collected by the same diver (the author), while the accompanying diver assisted by closing the draw-string of each sample collecting bag, and securing the sample to a line attached to the accompanying boat that was anchored on site.

In the laboratory, samples collected using the 25 cm diameter corer were washed in seawater, the shoots/leaves and root-rhizome matrix separated, examined carefully by eye and the motile macroinvertebrates removed. The number of shoots per core was counted to determine estimates of shoot density. The total shoot/leaf and root-rhizome fractions (separately) were first scraped free from epiphytes and then washed in freshwater and dried at 80°C for 48 h to constant weight (± 0.001g), to obtain biomass estimates. The remaining sediment and washings were passed through a 0.5 mm sieve and the retained material sorted in trays under a x5 magnifying lens to remove any remaining motile macroinvertebrates. The macroinvertebrates were fixed in 10% formaldehyde in seawater and transferred to 70% ethanol prior to identification to species level using microscopy (x12 - x150) and appropriate taxonomic keys (Tortonese, 1965; Fauvel, 1969a; 1969b; Fauchald, 1977; Ruffo, 1982; 1989; 1993; 1998; Cachia et al., 1991; 1996; 2001; Poppe & Goto, 1991; 1993; Falciai & Minervini, 1992). Where identification to species level was not possible, the putative species present were labelled using an alphabetical code (e.g. Cirratulidae sp. A, etc.). All identified macroinvertebrates were enumerated, and the numbers of species and abundance determined per core.

Samples collected for sediment analyses using the 10 cm diameter corer were first sorted to separate the root-rhizome matrix and other plant material from the sediment. Sub-samples of the sediment for the determination of total organic carbon were taken and frozen at -5°C, while the remaining portions for granulometric analysis were dried in air. Analyses to determine total organic carbon in the sediment (Walkley & Black, 1934) and mean sediment grain size (Folk & Ward, 1957) were carried out following Buchanan (1984).

The leaves of the 12 *P. oceanica* shoots collected separately from the core samples shoots/leaves were scraped using a razor blade to remove all the epiphytes present. Epiphytic material was then (separately) dried for 24 h in an oven at 80°C and weighed (± 0.001g) in order to determine the epiphyte biomass per shoot (see Chapter 3). Estimates of epiphyte biomass per core were obtained by multiplying mean epiphyte biomass per shoot by the *P. oceanica* shoot density recorded from each core sample. Estimates of leaf area per core were obtained by multiplying the mean leaf area per shoot (= total leaf length x mean leaf width per shoot; data from Chapter 3) by the *P. oceanica* shoot density recorded from each core sample.

4.2.3 Data analyses

Differences in macroinvertebrate species richness and abundance between continuous and reticulate *P. oceanica* beds, at each of the three spatial levels, were tested using two-factor ANOVA (with alpha set at 0.05), based on an orthogonal model with two factors: 'bed type' (two levels, fixed) and 'sampling locality' (four levels, random). Similarly, differences in shoot biomass, leaf area, epiphyte biomass, root-rhizome biomass, sediment organic content and mean grain size, were tested using the two-factor ANOVA. Prior to analyses, all data were tested for homogeneity of variances using Cochran's test and, where necessary, appropriate transformations of data were made (see section 4.3.1). Analyses were carried out using the software package GMAV5 produced at the University of Sydney (GMAV, 1997). When the ANOVA indicated significant differences, the source of difference was identified using Student Neuman Keuls (SNK) tests Underwood (1997) (see Chapter 3). SNK tests were also used to identify the source of difference when the ANOVA indicated a significant interaction (see Chapter 3).

Where attributes of seagrass architecture and/or sediment demonstrated the same pattern of significant differences as macroinvertebrate species richness and abundance, linear regression analysis was used to investigate the corresponding relationship. Furthermore, to test whether the infauna were masking the relationship between seagrass architecture and the total motile macroinvertebrate assemblages, linear analyses were carried out using the same attributes of seagrass architecture, but with a reduced faunal data set from which the burrowing bivalves had been removed (i.e. the full macroinvertebrate data set, less the burrowing bivalves). Prior to such analyses, all data were checked for normality using the Shapiro-Wilk Statistic (D'Agostino, 1986) and transformation (ln) applied where necessary (Section 4.3). The Shapiro-Wilk Statistic was also used to assess regression residuals for normality (D'Agostino, 1986), while residual variances were checked for homoscedasticity by examining for patterns of increasing or decreasing variance in plots of standardised residuals (Draper & Smith, 1981).

To test for differences in the composition of assemblages associated with the two different *P. oceanica* bed types at each of the three spatial levels, multivariate analyses was carried out on the species-abundance data ($\sqrt{\sqrt{}}$ transformed, to downweight the contribution of dominant species; Clarke & Warwick, 1994) using the PRIMER v5 suite of programs (Clarke & Gorley, 2001). The analyses consisted of Non-Metric Multidimensional Scaling (NMDS) using the Bray-Curtis index to construct the underlying similarity matrix (Clarke & Warwick, 1994). NMDS was chosen on the basis that it is a superior multivariate technique (e.g. compared to Principal Components Analysis) in the analyses of biological data from ecological communities, since it is less affected by the 'imbalances' of data sets resulting from low counts (e.g. abundance) of rare species and/or high counts of dominant species (Digby & Kempton, 1987). Furthermore, NMDS requires fewer assumptions about the nature and quality of the data compared to other ordination methods (Clarke & Warwick, 1994). NMDS uses the rank order of the values in the similarity matrix to depict the samples in space (for example, a two-dimensional plot), such that samples that are most similar are grouped closest together, while those that have a low similarity with the other samples in the set are placed further apart (Clarke & Warwick, 1994).

The significance of differences in assemblage composition between samples grouped according to bed type was assessed using Analysis of Similarity (ANOSIM; Clarke, 1993). The contribution of the different species to the observed similarity within groups of samples taken from the same type of bed, and the dissimilarity between groups of samples taken from a different bed type, were tested using the Similarity Percentages (SIMPER) procedure (Clarke, 1993). SIMPER uses the Bray-Curtis index to compute the average dissimilarity between all pairs of inter-group samples and then breaks the average value into a separate contribution for each species. The program then averages the contribution of each species over all possible sample pair combinations to calculate the contribution of the particular species to the overall dissimilarity between the groups being compared. In this way, SIMPER identifies and ranks species according to their overall contribution to dissimilarity between the various groups of samples (Clarke, 1993), and helps identify the species that are good discriminators. Species are good discriminators when they show large differences in their respective average abundances (between the sample groups compared) and have a high average dissimilarity value and ratio of average dissimilarity to standard deviation of dissimilarity (Clarke, 1993). Knowledge of the biology of the discriminating species can then be used to interpret the observed differences between groups of samples being compared, in the light of possible ecological attributes and mechanisms.

BIOENV analysis was carried out to examine the relationships between the multivariate assemblage composition and measured environmental variables (Clarke & Ainsworth, 1993). BIOENV enables linking of the multivariate assemblage composition to a specified set of environmental variables, by ranking the latter in order of importance, based on the best match with the biotic data. The underlying computation in the BIOENV procedure consists of comparison of the similarity matrix for the species-abundance data with the similarity matrix for the environmental data, using Spearman's rank correlation coefficient ρ_w (Clarke & Ainsworth, 1993). The environmental variables included in the analysis were shoot biomass, root-rhizome biomass, shoot density, leaf area, mean sediment grain size, total organic carbon in sediment and epiphyte biomass.

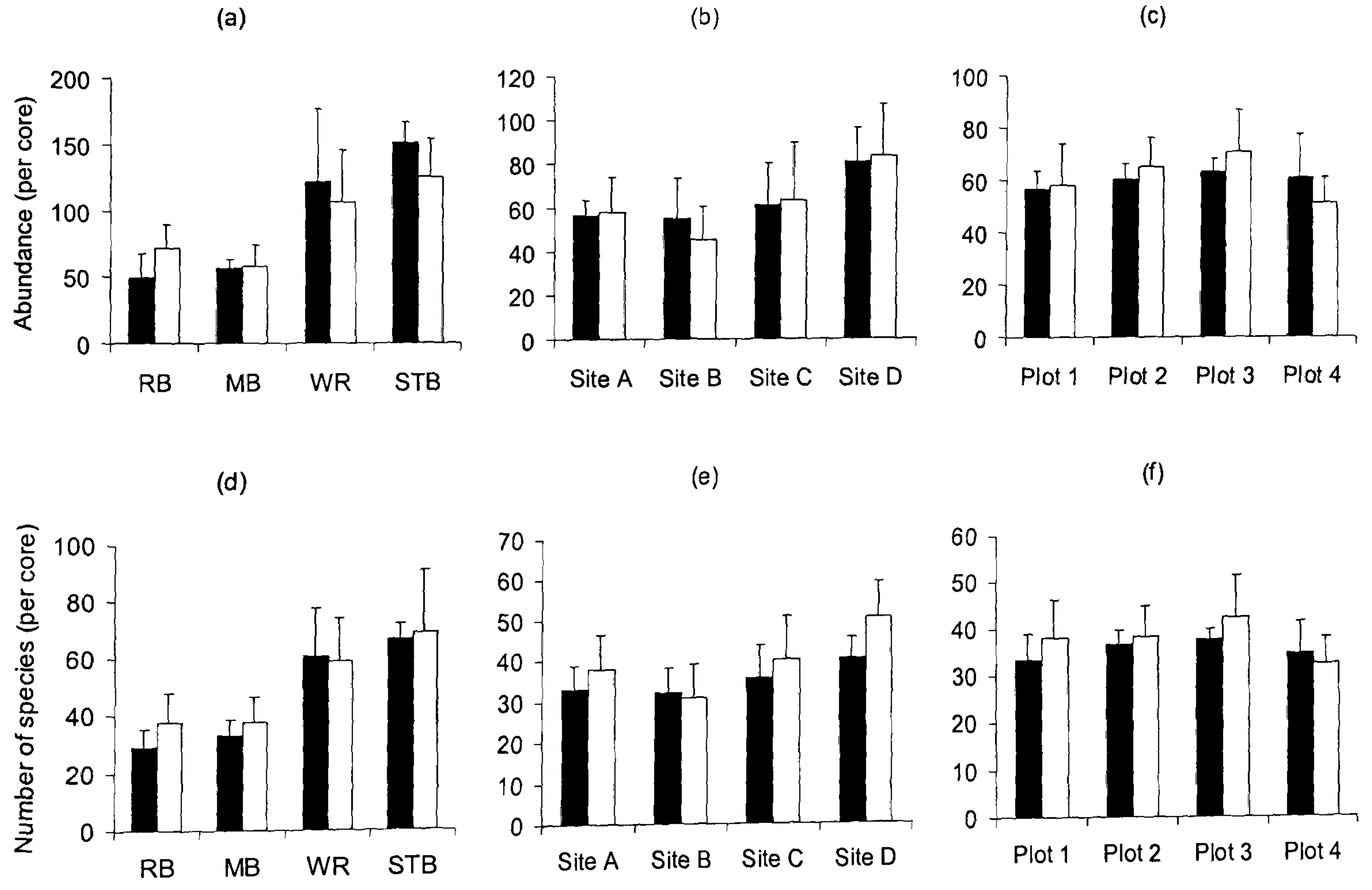
4.3 RESULTS

4.3.1 Univariate analyses

Macroinvertebrates

A total of 6227 individuals were collected (22 nemerteans, 166 sipunculids, 1690 polychaetes, 12 pycnogonids, 3421 crustaceans, 805 molluscs and 111 echinoderms), comprising 316 species of motile macroinvertebrates (3 nemerteans, 3 sipunculids, 71 polychaetes, 2 pycnogonids, 109 crustaceans, 109 molluscs and 19 echinoderms; see Appendix B).

There was no obvious consistent pattern of differences in values of total macroinvertebrate abundance and species richness between continuous and reticulate beds at the three spatial levels and, overall, values recorded from the two different bed types for a given location were somewhat similar (Figure 21). However, higher values of total abundance and species richness were recorded from both continuous and reticulate beds at White Rocks and St Thomas Bay, than at Ramla Bay and Mellieha Bay (Figure 21 a & d). Higher values of total abundance and species richness were also recorded at the medium spatial scale from both continuous and reticulate beds at site D, than at other three sites (Figure 21 b & e). The ANOVA results (Table 10) for total abundance and species richness did not indicate any significant interactions at any of the three spatial levels; however, significant differences were indicated for the factor 'sampling locality' at the large and medium spatial levels respectively. At the large spatial level, total abundance and species richness differed significantly: (i) between the continuous bed at St Thomas Bay and the continuous beds at Ramla Bay (SNK; $p < 0.01$) and Mellieha Bay (SNK; $p < 0.01$), and between the continuous bed at White Rocks and the continuous beds at Ramla Bay (SNK; $p < 0.01$) and Mellieha Bay (SNK; $p < 0.01$); and (ii) between the reticulate bed at St Thomas Bay and reticulate beds at Ramla Bay (SNK; $p < 0.05$) and Mellieha Bay (SNK; $p < 0.05$), and (for species richness only) between the reticulate bed at St Thomas Bay and the reticulate bed at Mellieha Bay (SNK; $p < 0.05$). At the medium spatial scale, total abundance and species richness differed significantly between the reticulate bed at site D and reticulate bed at site B (SNK; $p < 0.05$).



■ Continuous *Posidonia oceanica* bed; □ Reticulate *Posidonia oceanica* bed

Figure 21. Mean values of macroinvertebrate abundance (a-c) and number of species (d-f) at the three spatial levels: large (a & d), medium (b & e) and small (c & f). Error bars are +1 SD.

Table 10. Summary of ANOVA results for total number of individuals and total number of species. The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = $p < 0.05$; ** $p < 0.01$; *** = $p < 0.001$.

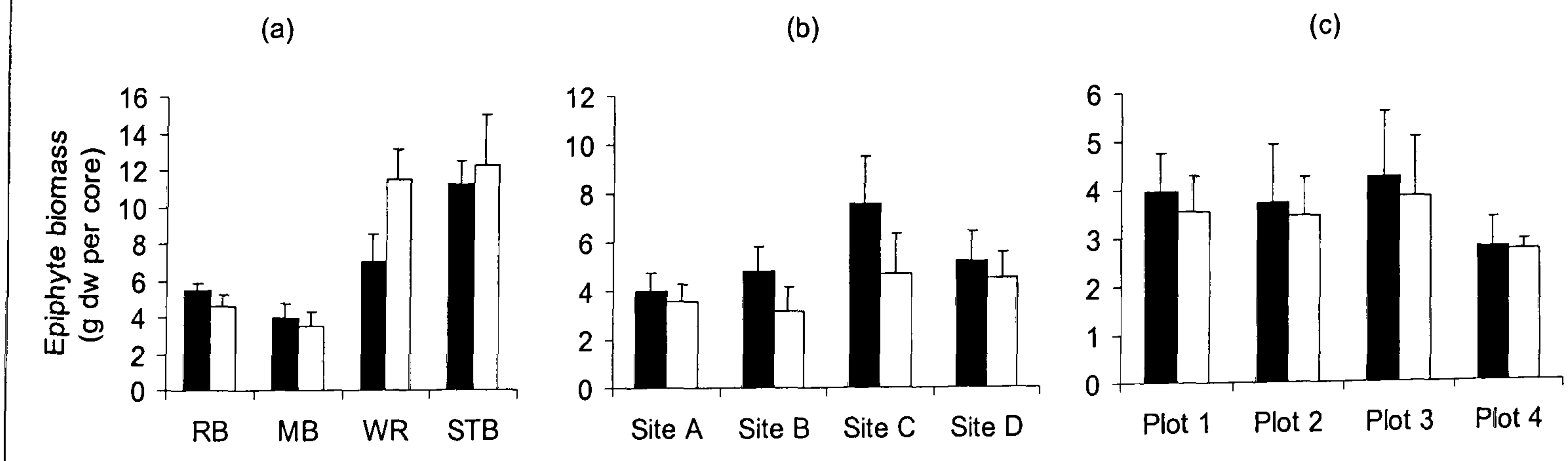
Spatial level	Source of variation	df	Total abundance (per core) n = 4 [1]Transformation: $\sqrt{(x + 1)}$ Cochran's test: NS			Total species richness (per core) n = 4 Transformation: none Cochran's test: NS		
			MS	F	P	MS	F	p
Large	Bed type (B)	1	0.033	0.01	NS	82.28	1.75	NS
	Location (L)	3	34.38	15.58	***	2382.61	14.96	***
	B x L	3	2.48	1.13	NS	46.36	0.29	NS
	Residual	24	2.21			159.22		
Medium	Bed type (B)	1	0.05	0.05	NS	3.78	0.05	NS
	Site (S)	3	4.42	4.42	*	1528.61	4.42	*
	B x S	3	0.21	0.21	NS	73.78	0.21	NS
	Residual	24	84.40			345.82		
Small	Bed type (B)	1	10.12	0.09	NS	40.50	1.84	NS
	Plot (P)	3	202.21	1.45	NS	60.79	1.51	NS
	B x P	3	113.37	0.81	NS	22.00	0.55	NS
	Residual	24	139.5			40.33		

[1]Transformation was only necessary for large spatial level data.

Plant architecture

Although there were some trends in the seagrass architectural measures taken, there was a lack of consistency in differences between the two bed types (Figures 19 & 20, Chapter 3). Overall, the results of two-factor ANOVA for the five plant architectural measures (shoot density, shoot biomass, number of leaves per shoot and mean leaf length and leaf width) did not indicate consistent differences in bed architecture between the two different *P. oceanica* bed types, over the three different spatial levels. Where significant differences were detected by the ANOVA, these were mainly associated with the factor 'sampling locality', thereby, indicating a predominance of spatial differences in within-bed architecture rather than consistent differences between the two different bed types. The results of these analyses have been presented in Chapter 3.

There was no consistent pattern of differences in values of shoot epiphyte biomass between the two different bed types, at the large spatial level. However, values of shoot epiphyte biomass recorded from continuous beds were somewhat higher than those recorded from reticulate beds at both medium and small spatial levels (Figure 22). Furthermore, values recorded from St Thomas Bay and White Rocks (large spatial scale) were much higher than those recorded from Ramla Bay and Mellieha Bay, while values recorded from sites C and D (medium spatial scale) were higher than those recorded from sites A and B (Figure 22 b). The results of two-factor ANOVA for epiphyte biomass (see Table 11) indicated a significant interaction at the large spatial level, but not at the medium and small spatial levels. ANOVA also detected significant differences for the factor 'bed type' at the small spatial level, and for the factor 'sampling locality' at the medium spatial level. The significant interaction detected at the large spatial level was attributed to significant differences: (i) between the two different bed types at White Rocks (SNK; $p < 0.01$) and St Thomas Bay (SNK; $p < 0.01$); (ii) between the continuous bed at White Rocks and the continuous bed at Mellieha Bay (SNK; $p < 0.01$), between the continuous bed at St Thomas Bay and continuous beds at the other three locations (SNK; $p < 0.01$), and between the continuous bed at Ramla Bay and the continuous bed at Mellieha Bay ($p < 0.05$); and (iii) between the reticulate bed at White Rocks and reticulate beds at the other three locations. The significant difference detected for the factor 'sampling locality' at the



■ Continuous *Posidonia oceanica* bed; □ Reticulate *Posidonia oceanica* bed

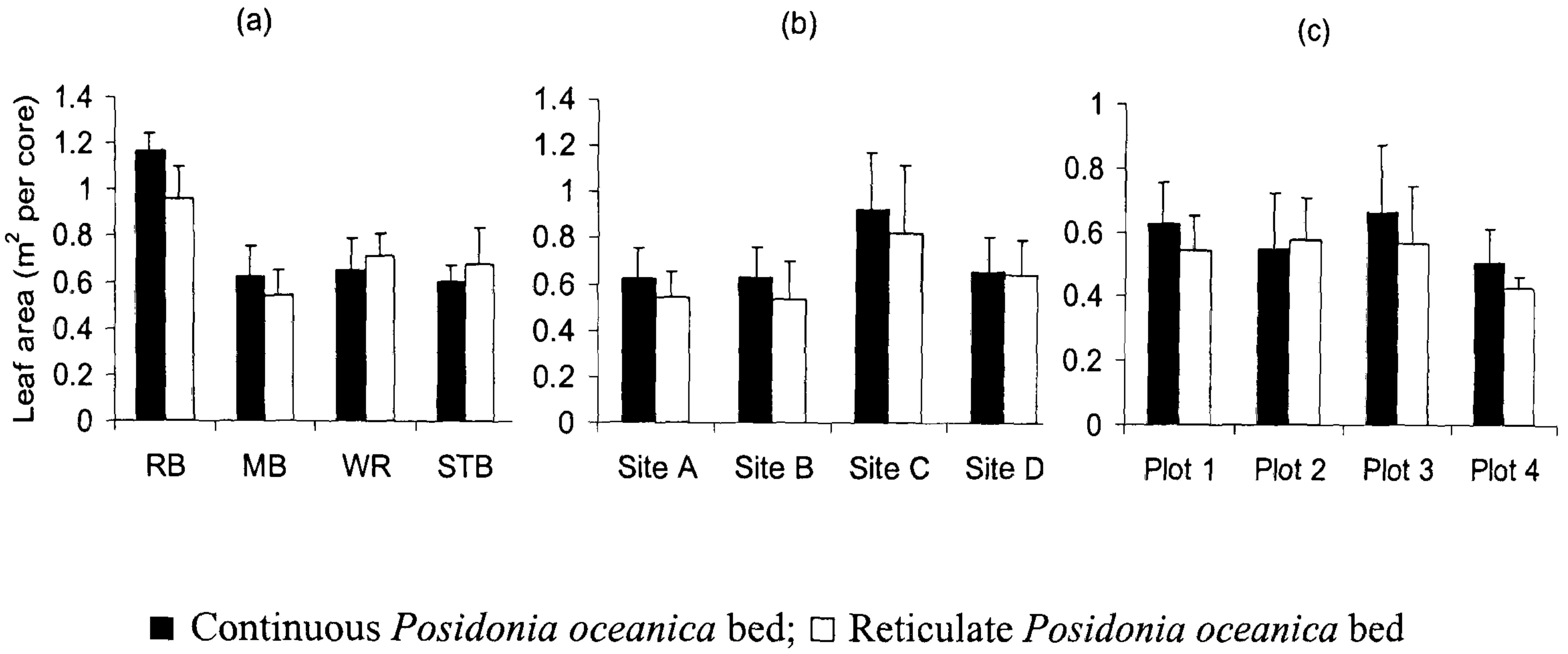
Figure 22. Mean values of epiphyte biomass at the three spatial levels: large (a), medium (b) and small (c). Error bars are +1 SD.

medium spatial level was attributed to significant differences between site C and sites A (SNK; $p < 0.01$) and B (SNK; $p < 0.01$), averaged over the two bed types. The significant difference detected for the factor 'bed type' at the small spatial level was attributed to significant differences between the two bed types, averaged over the four plots (SNK; $p < 0.05$).

Table 11. Summary of ANOVA results for epiphyte biomass. The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Spatial level	**Source of variation**	**Df**	**Epiphyte biomass (g dw per core)** **n = 12** Transformation: none Cochran's test: NS		
			MS	F	p
Large	Bed type (B)	1	6.145	0.15	NS
	Location (L)	3	51.744	48.21	***
	B x L	3	42.223	39.34	***
	Residual	88	1.073		
Medium	Bed type (B)	1	15.839	6.29	NS
	Site (S)	3	9.193	5.85	**
	B x S	3	2.518	1.60	NS
	Residual	88	1.572		
Small	Bed type (B)	1	0.677	13.14	*
	Plot (P)	3	2.474	2.81	NS
	B x P	3	0.515	0.06	NS
	Residual	88			

There was no consistent pattern of differences in values of leaf area between the two different bed types, at the large and small spatial levels. However, values of leaf area were recorded from continuous beds were somewhat higher than those recorded from reticulate beds at the medium spatial level (Figure 23). The results of two-factor ANOVA for leaf area (see Table 12) did not indicate significant interactions at any of the three spatial levels; however, significant differences were indicated for the factor 'sampling locality' at the large and medium spatial levels, and for 'bed type' at the medium spatial level. ANOVA did not detect any significant differences for either of the two factors tested at the small spatial level. The significant difference detected for 'sampling locality' at the large spatial level was attributed to significant differences, averaged over the two bed types, between Ramla Bay and the other three localities (SNK; $p < 0.01$). The significant difference detected for 'bed type' at the medium spatial level was attributed to significant differences between the two bed types, averaged over the four sites (SNK; $p < 0.05$), while the significant difference detected for 'sampling locality' at the same spatial level was attributed to significant differences between site C and the other three sites (SNK; $p < 0.01$), averaged over the two bed types.



■ Continuous *Posidonia oceanica* bed; □ Reticulate *Posidonia oceanica* bed

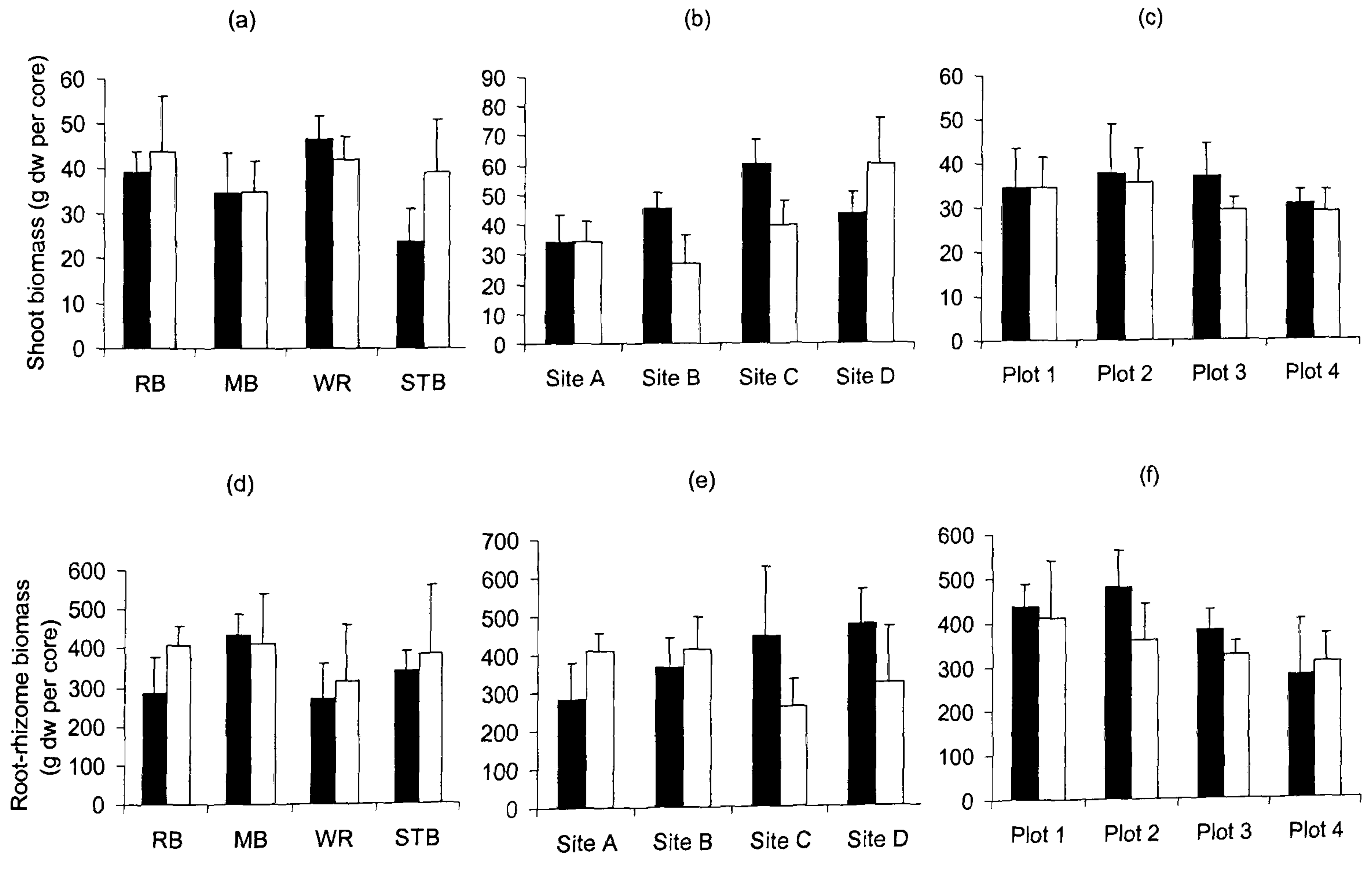
Figure 23. Mean values of leaf area at the three spatial levels: large (a), medium (b) and small (c). Error bars are +1 SD.

Table 12. Summary of ANOVA results for leaf area. The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = $p < 0.05$; ** $p < 0.01$; *** = $p < 0.001$.

Spatial level	**Source of variation**	**df**	**Leaf area (per core) n = 4** Transformation: none Cochran's test: NS		
			MS	F	p
Large	Bed type (B)	1	0.0111	0.30	NS
	Location (L)	3	0.3778	27.45	***
	B x L	3	0.0367	2.66	NS
	Residual	24	0.0138		
Medium	Bed type (B)	1	0.0462	11.82	*
	Site (S)	3	0.1529	4.58	*
	B x S	3	0.0039	0.12	NS
	Residual	24	0.0334		
Small	Bed type (B)	1	0.0262	3.82	NS
	Plot (P)	3	0.0316	1.50	NS
	B x P	3	0.0069	0.33	NS
	Residual	24	0.0210		

Shoot and root-rhizome biomass

There was no consistent pattern of differences in values of shoot biomass (Figure 24 a-c) and root-rhizome biomass (Figure 24 d-f) between the two different bed types, at the three different spatial levels. The results of two-factor ANOVA (see Table 13) for shoot biomass indicated a significant interaction at both large and medium spatial levels, but not at the small spatial level. The significant interaction detected at the large spatial level was attributed to significant differences in shoot biomass: (i) between the continuous bed at White Rocks and continuous beds at the other three locations (SNK; $p < 0.01$), and (ii) between the two different bed types at White Rocks (SNK; $p < 0.05$) and at St Thomas Bay (SNK; $p < 0.05$). The significant interaction detected at the medium spatial level was attributed to significant differences in shoot biomass: (i) between the two different bed



■ Continuous *Posidonia oceanica* bed; □ Reticulate *Posidonia oceanica* bed

Figure 24. Mean values of shoot biomass (a-c) and root-rhizome biomass (d-f) at the three spatial levels: large (a & d), medium (b & e) and small (c & f). Error bars are +1 SD.

types at site C (SNK; $p < 0.01$) and site D (SNK; $p < 0.01$); (ii) between the continuous bed at site C and continuous beds at the other three sites (SNK; $p < 0.05$), and (iii) between the reticulate bed at site D and reticulate beds at the other three sites (SNK; $p < 0.01$).

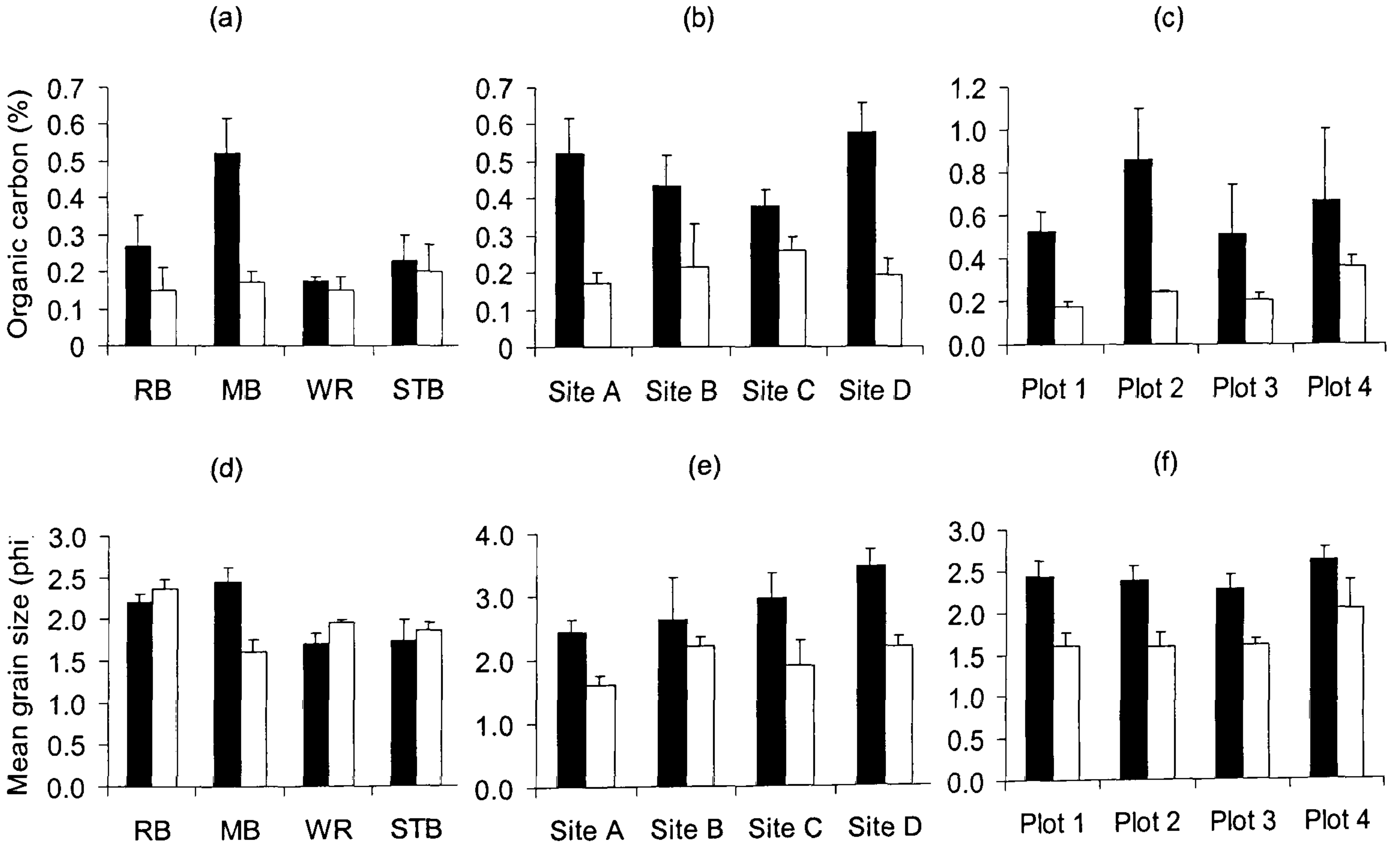
Table 13. Summary of ANOVA results for shoot biomass and root-rhizome biomass. The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Spatial level	**Source of variation**	**df**	**Shoot biomass (per core)** **n = 4** Transformation: none Cochran's test: NS			**Root-rhizome biomass (g) (per core)** **n = 4** Transformation: none Cochran's test: NS		
			MS	F	p	MS	F	p
Large	Bed type (B)	1	12.12	0.04	NS	17632.07	2.39	NS
	Location (L)	3	495.05	6.62	**	23214.93	1.99	NS
	B x L	3	301.83	4.03	*	7373.07	0.63	NS
	Residual	24	74.81			11669.34		
Medium	Bed type (B)	1	236.26	0.38	NS	49980.94	2.12	NS
	Site (S)	3	679.49	8.05	***	6676.82	0.54	NS
	B x S	3	619.53	7.34	**	23580.81	1.90	NS
	Residual	24	84.40			12442.25		
Small	Bed type (B)	1	59.02	2.55	NS	14430.46	1.83	NS
	Plot (P)	3	63.58	1.27	NS	30168.39	4.30	*
	B x P	3	23.17	0.46	NS	7873.24	1.12	NS
	Residual	24	50.07			7015.99		

The results of two-factor ANOVA (see Table 13) for root-rhizome biomass did not indicate any significant interactions at any of the three spatial levels. However, ANOVA detected significant differences for the factor 'sampling locality' at the small spatial level, which was attributed to significant differences between the continuous bed in plot 4 and continuous beds in plots 1 and 2 (SNK; $p < 0.05$).

Sediment characteristics

Values of organic carbon in the sediment were higher in continuous beds than in reticulate beds at Ramla Bay and Mellieha, but were similar between the two bed types at White Rocks and St Thomas Bay (Figure 25 a). Values of organic carbon in the sediment were also higher in continuous beds at both medium (Figure 25 b) and small (Figure 25 c) scales. The results of two-factor ANOVA (see Table 14) indicated significant interactions at the large and medium spatial levels. At the large spatial level, the significant interaction was attributed to significant differences in organic carbon content of the sediment: (i) between the two different bed types at Ramla Bay (SNK; $p < 0.05$) and Mellieha Bay (SNK; $p < 0.01$); and (ii) between the continuous bed at Mellieha Bay and continuous beds at the other three locations (SNK; $p < 0.01$). At the medium spatial level, the significant interaction was attributed to significant differences in organic carbon content of the sediment: (i) between the two different bed types at all four sites (SNK; $p < 0.01$); and (ii) between the continuous bed at site A and the continuous bed at site C (SNK; $p < 0.05$), between the continuous bed at site B and the continuous beds at site D (SNK; $p < 0.05$), and between the continuous bed at site C and the continuous bed at site D (SNK; $p < 0.01$).



■ Continuous *Posidonia oceanica* bed; □ Reticulate *Posidonia oceanica* bed

Figure 25. Mean values of organic carbon content (a-c) and mean sediment grain size of the sediment (d-f) at the three spatial levels: large (a & d), medium (b & e) and small (c & f). Error bars are +1 SD.

The significant difference in the factor 'bed type' at the small spatial scale was attributed to significant differences in organic carbon content of the sediment between the two different bed types, averaged over the four plots (SNK; $p < 0.05$), while the significant difference in the factor 'sampling locality was attributed to significant differences, averaged over the two bed types, between plot D and the other three plots, and between plot B and plot C.

Table 14. Summary of ANOVA results for organic carbon content and mean sediment grain size of the sediment. The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Spatial level	**Source of variation**	**Df**	**Organic carbon in sediment (%)** n = 4 ^{2}Transformation: ln x Cochran's test: NS			**Mean sediment grain size (Phi)** n = 4 Transformation: none Cochran's test: NS		
			MS	F	p	MS	F	p
Large	Bed type (B)	1	0.138	2.97	NS	0.044	0.09	NS
	Location (L)	3	0.050	12.83	***	0.402	20.40	***
	B x L	3	0.046	11.78	***	0.519	26.35	***
	Residual	24	0.039			0.020		
Medium	Bed type (B)	1	0.578	18.86	*	6.381	22.62	*
	Site (S)	3	0.007	1.43	NS	0.864	7.41	**
	B x S	3	0.031	5.87	**	0.282	2.42	NS
	Residual	24	0.005			0.120		
Small	Bed type (B)	1	6.805	33.46	*	4.176	150.31	**
	Plot (P)	3	0.465	5.22	**	0.246	6.65	**
	B x P	3	0.203	2.28	NS	0.028	0.75	NS
	Residual	24	0.089			0.037		

^{2}Transformation was only necessary for small spatial level data.

Values of mean sediment grain size were similar between continuous and reticulate beds in all four locations, except at Mellieha Bay, where Phi values were higher (indicating a predominance of finer sediment) in the continuous beds, (Figure 25 d). Phi values were also higher in continuous beds than in reticulate beds at the medium (Figure 25 e) and small (Figure 25 f) spatial levels. The results of the two-factor ANOVA (see Table 14) indicated a significant interaction for mean sediment grain size at the large spatial level, but not at the medium and small spatial levels. At the large spatial level, the significant interaction was attributed to significant differences in mean sediment grain size: (i) between the two different beds types at Mellieha Bay and at White Rocks; and (ii) between continuous beds in all pair combinations of the four locations (SNK; $p < 0.01$), except between the continuous bed at St Thomas Bay and the continuous bed at White Rocks, and between reticulate beds in all pair combinations of the four locations (SNK; $p < 0.01$), except between the reticulate bed at St Thomas Bay and the reticulate bed at White Rocks. Although the two-factor ANOVA did not indicate a significant interaction at the medium and small scales, significant differences were indicated for both ‘bed type’ and ‘sampling locality’. At the medium spatial scale, values of mean sediment grain size were significantly different: (i) between the two different bed types, averaged over the four sites (SNK; $p < 0.01$), and (ii) between site D and sites A (SNK; $p < 0.01$) and C (SNK; $p < 0.05$), and between site A and site B (SNK; $p < 0.01$), averaged over the two bed types. At the small scale, values of mean sediment grain size were significantly different: (i) between the two different bed types, averaged over the four plots (SNK; $p < 0.01$); and (ii) between plot 4 and the other three plots, averaged over the two bed types (SNK; $p < 0.01$).

Relationship between macroinvertebrates and bed characteristics; full data set

Linear regression carried out using the full macroinvertebrate data set (see Table 15) indicated that at the large spatial level, macroinvertebrate abundance was significantly related to epiphyte biomass (Figure 26 a). Linear regression (see Table 16) also indicated that, at the medium spatial level, macroinvertebrate abundance was significantly related to epiphyte biomass and shoot biomass (Figure 26 b & c). On the other hand, none of the other attributes of seagrass architecture (shoot density, leaf area and shoot biomass) or sediment characteristics (mean grain size and total organic carbon of sediment) had a significant relationship with macroinvertebrate abundance at either of the two spatial levels (Tables 15 & 16).

Linear regression (see Table 17) indicated that, at the large spatial level, macroinvertebrate species richness was related to epiphyte biomass and mean sediment grain size (Figures 27 a & b). Linear regression (see Table 18) also indicated that, at the medium spatial level, macroinvertebrate species richness was related to shoot biomass only (Figures 27 c). On the other hand, none of the other attributes of seagrass architecture (shoot density, leaf area and root-rhizome biomass) or total organic carbon of sediment had a significant relationship with macroinvertebrate species richness at either of the two spatial levels (Tables 17 & 18).

Table 15. Details of regressions for relationships between macroinvertebrate abundance (full data set) and attributes of seagrass architecture and sediment, at the large (location) spatial level. The critical value for the Shapiro-Wilk (S-W) statistic for normality in regression residuals (n = 32) being 0.927 at $p < 0.05$. NS = not significant.

Regression variables	**R^2**	**p-value**	**S-W Statistic**
ln (Shoot density) ln (Abundance)	0.024	NS	/
ln (Leaf area) ln (Abundance	0.016	NS	/
ln (Shoot biomass) ln (Abundance)	0.013	NS	/
ln (Epiphyte biomass) ln (Abundance)	0.555	< 0.001	0.938
ln (Mean sediment grain size) ln (Abundance)	0.095	NS	/
ln (Organic carbon in sediment) ln (Abundance)	0.095	NS	/

Table 16. Details of regressions for relationships between macroinvertebrate abundance (full data set) and attributes of seagrass architecture and sediment, at the medium (site) spatial level. The critical value for the Shapiro-Wilk (S-W) statistic for normality in regression residuals (n = 32) being 0.927 at $p < 0.05$. NS = not significant.

Regression variables	**R^2**	**p-value**	**S-W Statistic**
Shoot density Abundance	0.084	NS	/
ln (Leaf area) ln (Abundance	0.120	NS	/
Shoot biomass Abundance	0.254	< 0.01	0.968
ln (Epiphyte biomass) ln (Abundance)	0.150	< 0.05	0.941
Mean sediment grain size Abundance	0.067	NS	/
Organic carbon in sediment Abundance	0.004	NS	/

Linear regression also indicated a significant relationship between leaf area and epiphyte biomass at the medium scale ($R^2 = 0.865$; $p < 0.001$) (Figure 26d), but not at the large scale ($R^2 = 0.007$; p = NS).

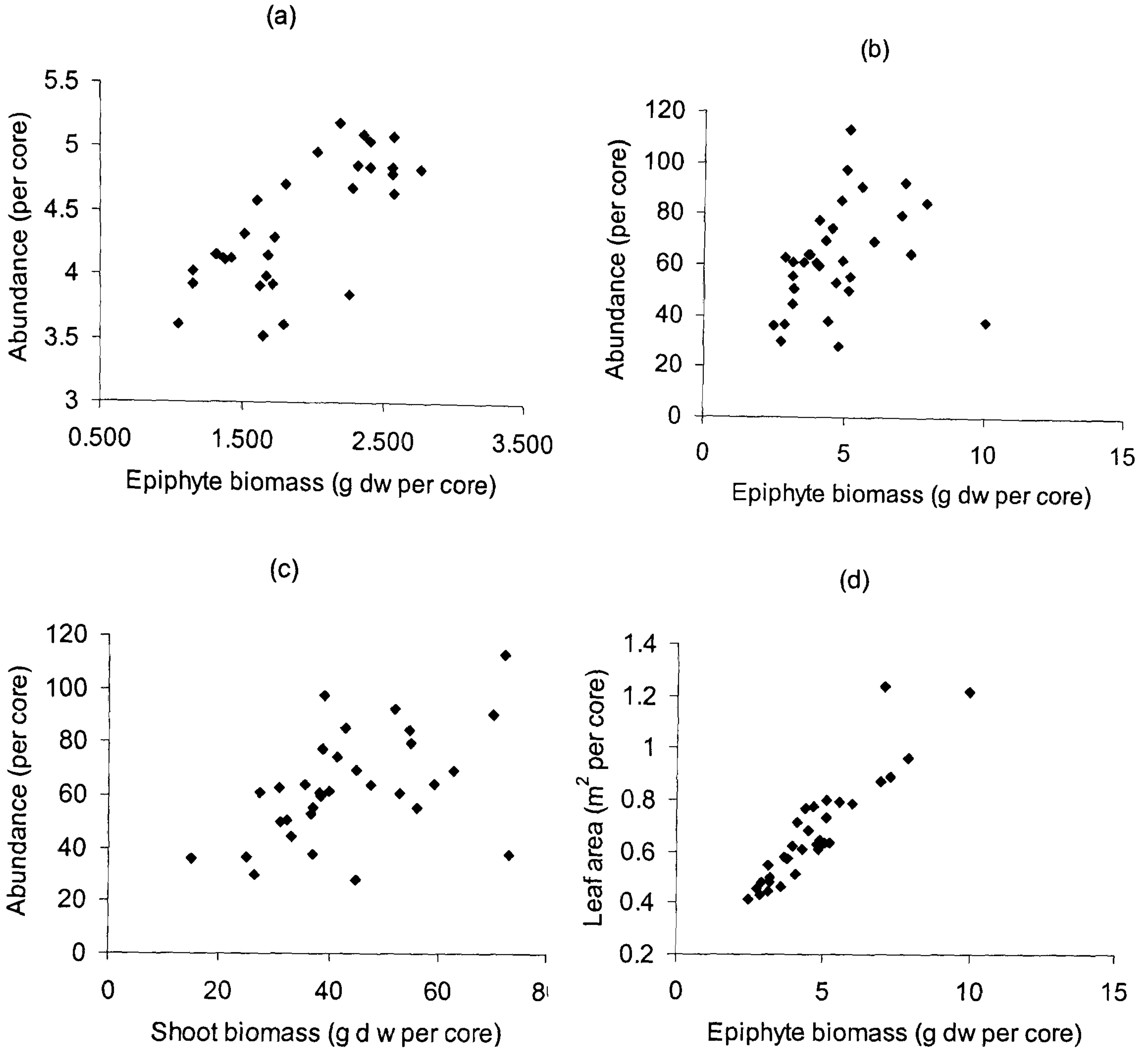


Figure 26. Scatter plots of: epiphyte biomass with (a) macroinvertebrate abundance at the large (location) spatial level; shoot biomass (b) and epiphyte biomass (c) with macroinvertebrate abundance at the medium (site) scale; and leaf area with epiphyte biomass at the medium scale (d).

Table 17. Details of regressions for relationships between macroinvertebrate species richness (full data set) and attributes of seagrass architecture and sediment, at the large (location) spatial level. The critical value for the Shapiro-Wilk test for normality in regression residuals (n = 32) being 0.927 at $p < 0.05$. NS = not significant.

Regression variables	**R^2**	**p-value**	**S-W Statistic**
Shoot density Species richness	0.023	NS	/
ln (Leaf area) ln (Abundance	0.038	NS	/
Shoot biomass Species richness	0.004	NS	/
ln (Epiphyte biomass) ln (Species richness)	0.582	< 0.001	0.947
Mean sediment grain size Species richness	0.172	< 0.05	0.973
ln (Organic carbon in sediment) ln (Species richness)	0.083	NS	/

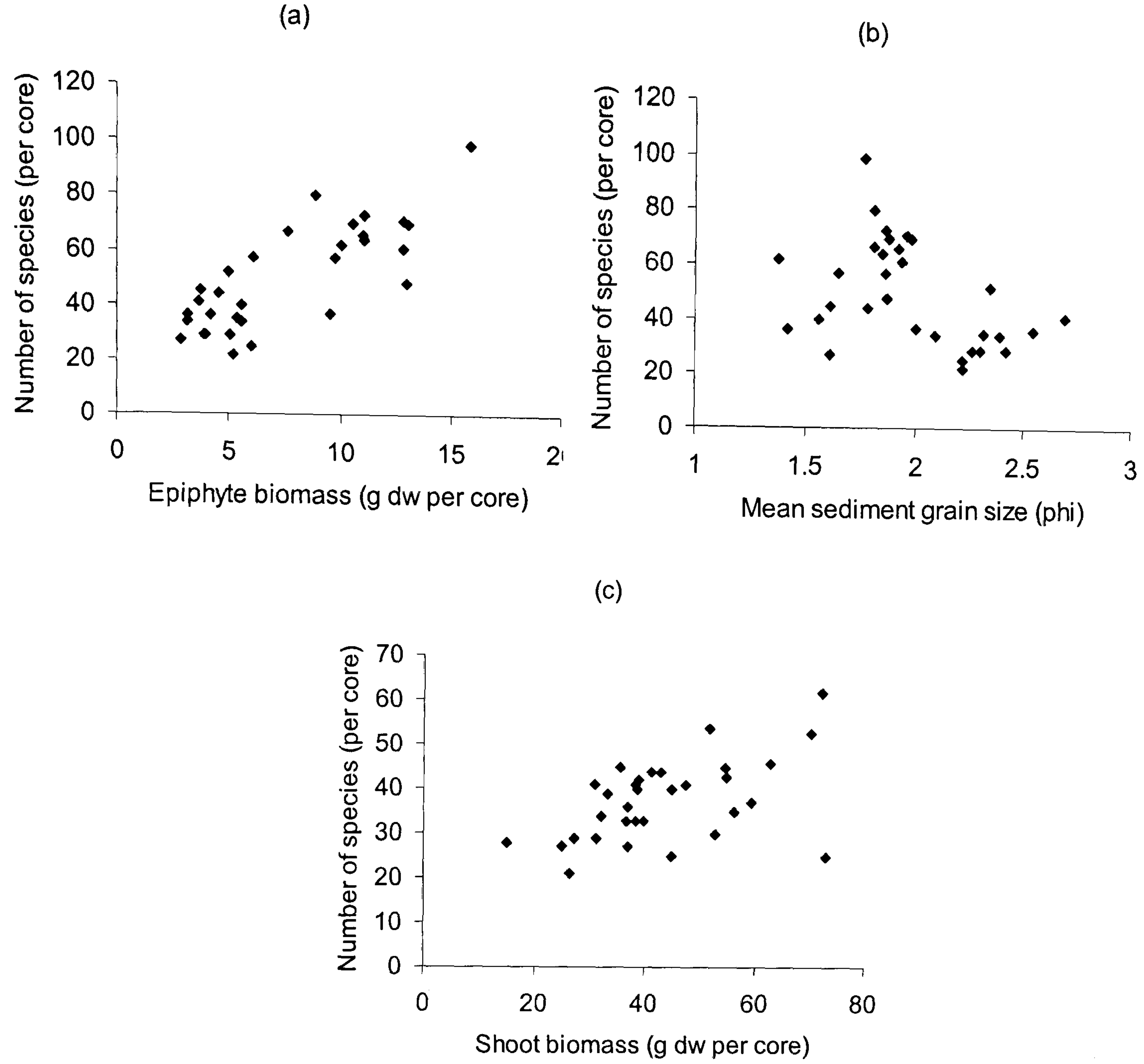


Figure 27. Scatter plots of: epiphyte biomass (a) and mean sediment grain size (b) with macroinvertebrate species richness, at the large (location) spatial level; and shoot biomass (c) with macroinvertebrate species richness at the medium (site) scale.

Table 18. Details of regressions for relationships between macroinvertebrate species richness (full data set) and attributes of seagrass architecture and sediment, at the medium (site) spatial level. The critical value for the Shapiro-Wilk test for normality in regression residuals (n = 32) being 0.927 at $p < 0.05$. NS = not significant.

Regression variables	**R^2**	**p-value**	**S-W Statistic**
Shoot density Species richness	0.049	NS	/
ln (Leaf area) ln (Species richness)	0.080	NS	/
Shoot biomass Species richness	0.261	< 0.01	0.975
ln (Epiphyte biomass) ln (Species richness)	0.073	NS	/
Mean sediment grain size Species richness	0.001	NS	/
ln (Organic carbon in sediment) ln (Species richness)	0.080	NS	/

Relationship between macroinvertebrates and bed characteristics; reduced data set

Linear regression carried out using the reduced macroinvertebrate data set (see Table 19) indicated that at the large spatial level, macroinvertebrate abundance was significantly related to epiphyte biomass. Linear regression (see Table 20) also indicated that, at the medium spatial level, macroinvertebrate abundance was significantly related to epiphyte biomass and shoot biomass. On the other hand, none of the other attributes of seagrass architecture (shoot density, leaf area and shoot biomass) or sediment characteristics (mean grain size and total organic carbon of sediment) had a significant relationship with macroinvertebrate abundance at either of the two spatial levels (Tables 19 & 20).

Table 19. Details of regressions for relationships between macroinvertebrate abundance (reduced data set) and attributes of seagrass architecture and sediment, at the large (location) spatial level. The critical value for the Shapiro-Wilk (S-W) statistic for normality in regression residuals ($n = 32$) being 0.927 at $p < 0.05$. NS = not significant.

Regression variables	R^2	p-value	S-W Statistic
ln (Shoot density) ln (Abundance)	0.011	NS	/
ln (Leaf area) ln (Abundance	0.012	NS	/
ln (Shoot biomass) ln (Abundance)	0.007	NS	/
ln (Epiphyte biomass) ln (Abundance)	0.585	< 0.001	0.930
ln (Mean sediment grain size) ln (Abundance)	0.098	NS	/
ln (Organic carbon in sediment) ln (Abundance)	0.054	NS	/

Table 20. Details of regressions for relationships between macroinvertebrate abundance (reduced data set) and attributes of seagrass architecture and sediment, at the medium (site) spatial level. The critical value for the Shapiro-Wilk (S-W) statistic for normality in regression residuals ($n = 32$) being 0.927 at $p < 0.05$. NS = not significant.

Regression variables	R^2	p-value	S-W Statistic
Shoot density Abundance	0.081	NS	/
ln (Leaf area) ln (Abundance	0.111	NS	/
Shoot biomass Abundance	0.254	< 0.01	0.983
ln (Epiphyte biomass) ln (Abundance)	0.146	< 0.01	0.944
Mean sediment grain size Abundance	0.080	NS	/
Organic carbon in sediment Abundance	0.001	NS	/

Linear regression (see Table 21) indicated that, at the large spatial level, macroinvertebrate species richness was related to epiphyte biomass and mean sediment grain size. Linear regression (see Table 22) also indicated that, at the medium spatial level, macroinvertebrate species richness was related to shoot biomass only. On the other hand, none of the other attributes of seagrass architecture (shoot density, leaf area and root-rhizome biomass) or total organic carbon of sediment had a significant relationship with macroinvertebrate species richness at either of the two spatial levels (Tables 21 & 22).

Table 21. Details of regressions for relationships between macroinvertebrate species richness (reduced data set) and attributes of seagrass architecture and sediment, at the large (location) spatial level. The critical value for the Shapiro-Wilk test for normality in regression residuals (n = 32) being 0.927 at $p < 0.05$. NS = not significant.

Regression variables	**R^2**	**p-value**	**S-W Statistic**
Shoot density Species richness	0.035	NS	/
ln (Leaf area) ln (Abundance	0.059	NS	/
Shoot biomass Species richness	0.005	NS	/
ln (Epiphyte biomass) ln (Species richness)	0.564	< 0.001	0.938
Mean sediment grain size Species richness	0.172	< 0.05	0.973
ln (Organic carbon in sediment) ln (Species richness)	0.074	NS	/

Table 22. Details of regressions for relationships between macroinvertebrate species richness (reduced data set) and attributes of seagrass architecture and sediment, at the medium (site) spatial level. The critical value for the Shapiro-Wilk test for normality in regression residuals (n = 32) being 0.927 at $p < 0.05$. NS = not significant.

Regression variables	**R^2**	**p-value**	**S-W Statistic**
Shoot density Species richness	0.043	NS	/
ln (Leaf area) ln (Species richness)	0.066	NS	/
Shoot biomass Species richness	0.261	< 0.01	0.961
ln (Epiphyte biomass) ln (Species richness)	0.064	NS	/
Mean sediment grain size Species richness	0.002	NS	/
ln (Organic carbon in sediment) ln (Species richness)	0.065	NS	/

Linear regression indicated a significant relationship between leaf area and epiphyte biomass at the medium scale ($R^2 = 0.865$; $p < 0.001$), but not at the large scale ($R^2 = 0.007$; p = NS).

Overall, the results of linear regression obtained from the reduced macroinvertebrate data set, from which the burrowing bivalves (comprising a total of 283 individuals equivalent to 4.5% of the total macroinvertebrate abundance, and 36 species equivalent to 11.4% of the total macroinvertebrate species richness) had been removed, were similar to those obtained from the full macroinvertebrate data set.

4.3.2. Multivariate analyses

None of the NMDS ordination plots for species-abundance data indicated clear separation between samples collected from continuous and reticulate *P. oceanica* beds, showing that motile macroinvertebrate assemblage composition of the two different bed types at all three spatial levels was not dissimilar (Figure 28 a-c). However, the NMDS plot for data collected at the large scale indicated some degree of separation between groups of samples collected from different locations. This separation was especially evident for samples collected from Ramla Bay and Mellieha Bay, which were grouped somewhat distinctly from samples collected form White Rocks and St Thomas Bay. Samples collected from the latter two localities were grouped more closely (Figure 28 a). The stress values of the NMDS plots (0.23 – 0.28) were somewhat high, indicating that caution is required in the interpretation of the ordination results (Clarke & Warwick, 1994).

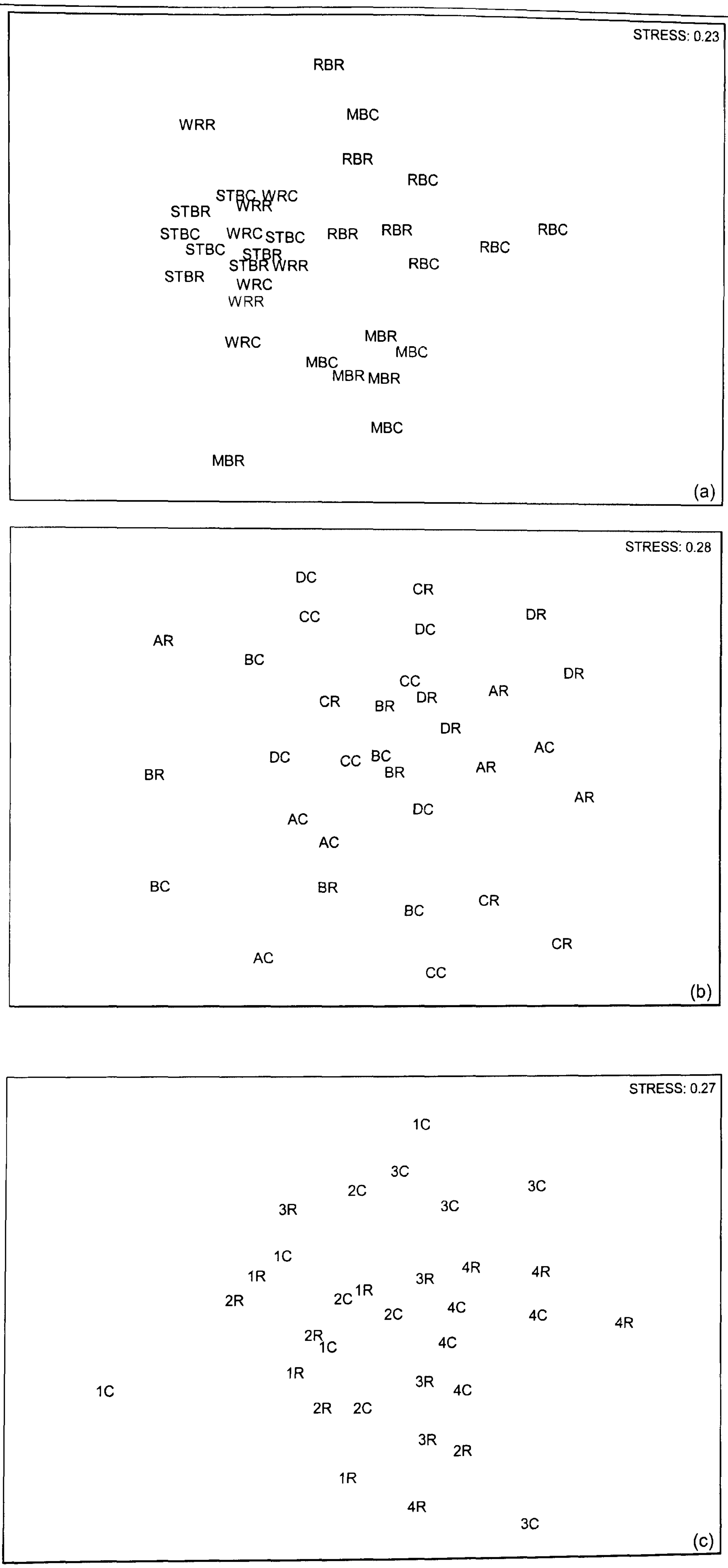


Figure 28. MDS plots produced from the species-abundance data for core samples collected at the three spatial levels: (a) large, (b) medium and (c) small. The last letter denotes the bed type (C = continuous; R = reticulate).

The ANOSIM test indicated that the composition of samples collected from the two different bed types did not differ significantly at any of the three spatial levels (Table 23). However, the test indicated that samples collected from different sampling localities differed significantly at the large (Global R = 0.526; $p < 0.01$) and small (Global R = 0.199; $p < 0.01$) spatial levels, but not at the medium spatial level. At the large spatial level, pairwise ANOSIM indicated significant differences between all four locations (R = 0.439 – 0.652; $p < 0.01$), while at the small spatial level, the same test indicated significant differences between plots 1 and 4 (R = 0.43; $p < 0.01$) and between plots 2 and 4 (R = 0.33; $p < 0.01$).

Table 23. Results of ANOSIM for samples taken from reticulate and continuous beds at the three spatial levels (large, medium and small).

Spatial level	**Statistic value**	**Possible permutations**	**Permutations used**	**Significant statistics**	**Significance level**
Large	-0.013	300540195	999	608	60.9%
Medium	0.05	300540195	999	98	9.9%
Small	0.004	300540195	999	445	44.6%

Table 24 lists the species having the highest contribution to the dissimilarity observed between stations at the large spatial level, which ANOSIM detected significant differences for. The SIMPER analysis showed that the average dissimilarity values between groups of samples taken from the *P. oceanica* beds at different locations were (in order of decreasing value) as follows: 81.65% between Mellieha Bay and White Rocks; 81.48% between Ramla Bay and Mellieha Bay; 81.00% between Ramla Bay and White Rocks; 80.38% between Mellieha Bay and St Thomas Bay; 77.88% between Ramla Bay and St Thomas Bay; and 70.74% between White Rocks and St Thomas Bay. However, despite the relatively high dissimilarity values, no single species had a large contributory influence to the observed dissimilarity for any of the pairwise comparisons; the largest contribution of any one species being 3.77% (the gastropod *Alvania mamillata* Risso; Table 24). A pattern

Table 24. Results of the SIMPER analysis for species having the highest dissimilarity values between groups of samples taken from the four different locations (large spatial level). RB = Ramla Bay; MB = Mellieha Bay; WR = White Rocks; STB = St Thomas Bay. AA = average abundance (number of individuals per core); AD = average dissimilarity; AD/SD = ratio of the average dissimilarity to the standard deviation of dissimilarity for the particular species.

Species	**Stations**		**AA**	**AA**	**AD**	**AD/SD**	**% Contribution**
	X	**Y**	**X**	**Y**			
Alvania mamillata	RB	MB	3.88	0.50	3.07	1.08	3.77
Pagurus chevreuxi	RB	MB	3.75	0.00	3.00	1.14	3.68
Athanas nitescens	RB	MB	4.13	1.75	2.76	1.42	3.38
Amphicteis midas	RB	MB	0.13	2.75	2.41	1.25	2.96
Piromis eruca	RB	MB	0.75	2.38	2.04	1.00	2.50
Hippolyte inermis	RB	MB	0.00	2.00	1.73	1.07	2.12
Maera grossimana	RB	STB	0.75	6.38	2.31	1.42	2.85
Elasmopus brasiliensis	RB	STB	0.00	5.13	2.25	1.83	2.78
Lysianassa costae	RB	STB	0.38	4.63	1.99	1.27	2.45
Maera inaequipes	RB	STB	1.25	5.50	1.96	0.85	2.42
Syllidae sp. A	RB	STB	1.38	4.13	1.82	0.90	2.25
Aora sp.	RB	STB	1.50	4.75	1.77	0.92	2.19
Alvania mamillata	RB	STB	3.88	0.75	1.70	1.06	2.10
Thoralus cranchii	RB	STB	0.63	5.13	1.70	1.19	2.10
Pagurus chevreuxi	RB	STB	3.75	2.75	1.61	1.27	1.99
Athanas nitescens	RB	STB	4.13	2.13	1.25	1.14	1.54
Maera grossimana	MB	STB	0.88	6.38	2.29	1.39	2.80
Maera inaequipes	MB	STB	0.50	5.50	2.03	0.83	2.48
Thoralus cranchii	MB	STB	0.00	5.13	1.95	1.34	2.39
Lysianassa costae	MB	STB	0.75	4.63	1.91	1.22	2.34
Syllidae sp. A	MB	STB	0.50	4.13	1.91	0.91	2.34
Elasmpous brasiliensis	MB	STB	1.00	5.13	1.90	1.55	2.32
Aora sp.	MB	STB	1.13	4.75	1.74	0.89	2.13
Amphicteis midas	MB	STB	2.75	0.25	1.28	1.21	1.56
Hippolyte inermis	MB	STB	2.00	0.75	0.90	1.11	1.10
Piromis eruca	MB	STB	1.75	0.00	0.80	0.70	0.98
Cestopagurus timidus	RB	WR	1.13	5.50	2.56	1.05	3.29
Syllidae sp. A	RB	WR	1.38	4.38	2.21	1.00	2.84
Alvania mamillata	RB	WR	3.88	1.88	2.20	1.00	2.83
Pagurus chevreuxi	RB	WR	3.75	0.38	2.09	1.09	2.68
Athanas nitescens	RB	WR	4.13	2.13	1.94	1.16	2.49
Maera inaequipes	RB	WR	1.25	4.00	1.67	1.26	2.14
Aora sp.	RB	WR	1.50	3.50	1.62	1.34	2.07
Lysianassa costae	RB	WR	0.38	3.13	1.58	1.43	2.04
Galathea bolivari	RB	WR	0.00	2.75	1.52	1.26	1.95
Sabellidae sp. B	RB	WR	0.50	2.50	1.27	1.31	1.63
Cestopagurus timidus	MB	WR	0.00	5.50	2.86	1.15	3.56
Syllidae sp. A	MB	WR	0.50	4.38	2.29	1.00	2.84
Maera inaequipes	MB	WR	0.50	4.00	1.96	1.50	2.44
Amphicteis midas	MB	WR	2.75	0.38	1.62	1.10	2.02
Aora sp.	MB	WR	1.13	3.50	1.56	1.37	1.94
Lysianassa costae	MB	WR	0.75	3.13	1.56	1.40	1.94
Galathea bolivari	MB	WR	0.13	2.75	1.47	1.21	1.83
Piromis eruca	MB	WR	2.38	0.00	1.46	0.84	1.82
Sabellidae sp. B	MB	WR	0.25	2.50	1.29	1.21	1.60
Hippolyte inermis	MB	WR	2.00	0.75	1.15	1.03	1.43
Maera inaequipes	STB	WR	5.50	4.00	1.84	1.10	2.60
Maera grossimana	STB	WR	6.38	1.25	1.83	1.25	2.59
Cestopagurus timidus	STB	WR	2.38	5.50	1.61	1.01	2.27
Thoralus cranchii	STB	WR	5.13	1.13	1.50	1.15	2.13
Elasmpous brasiliensis	STB	WR	5.13	2.13	1.45	1.28	2.05
Lysianassa costae	STB	WR	4.63	3.13	1.32	1.12	1.87
Nereis rava	STB	WR	3.50	0.50	1.21	1.51	1.71
Galathea bolivari	STB	WR	2.00	2.75	0.78	1.21	1.10

of differences in the occurrence and/or abundance of several discriminating species was evident, as follows:

(i) The amphipods *Maera inaequipes* (Costa), *Lysianassa costae* Milne Edwards and *Aora* sp., and the syllid Syllidae sp. A, all of which were more abundant at White Rocks and St Thomas Bay than at Ramla Bay and Mellieha Bay. Particularly large differences in abundance values of these species recorded from the former two locations, compared to those recorded from the latter two locations were evident.

(ii) The gastropod *A. mamillata*, the hermit crab *Pagurus chevreuxi* (Bouvier) and the alpheid shrimp *Athanas nitescens* (Leach), all of which all of which were more abundant at Ramla Bay than at the other three locations.

(iii) The polychaetes *Amphicteis midas* (Gosse) and *Piromis eruca* (Claparède), and the shrimp *Hippolyte inermis* Leach, all of which all of which were more abundant at Mellieha Bay than at the other three locations.

(iv) The hermit crab *Cestopagurus timidus* (Roux), the squat lobster *Galathea bolivari* Zariquiey Alvarez and the sabellid Sabellidae sp. B, all of which all of which were more abundant at White Rocks than at the other three locations.

(v) The amphipods *M. inaequipes* and *Elasmopus brasiliensis* (Dana) and the shrimp *Thoralus cranchii* (Leach), all of which were more abundant at St Thomas Bay than at the other three locations.

SIMPER analysis showed that the average dissimilarity values between the two pairs of 'plot' samples (small spatial level), which ANOSIM detected significant differences for, were as follows: 70.13% between plot 1 and plot 4, and 67.96 between plot 2 and plot 4. However, despite the relatively high dissimilarity values, no single species had a large contributory influence to the observed dissimilarity at any of the two group comparisons;

the largest contribution of any one species being 3.47% (the sipunculid *Phascolion strombi* (Montagu). Overall, the observed differences were due to a broad range of relatively small differences in the abundance values of several species, rather than large difference in the occurrence and/or abundance of one or a few species.

BIOENV indicated that the combination of environmental variables, which best explained the macroinvertebrate assemblage composition observed at the large spatial scale were: leaf area, epiphyte biomass and total organic carbon in sediment ($\rho_w = 0.439$). Values of Spearman's rank correlation coefficient were rather low (< 0.3) for each of the single environmental variables on their own. At the medium spatial scale, a combination of leaf area, root-rhizome biomass, sediment grain size, and total organic carbon in sediment, explained best the macroinvertebrate assemblage composition ($\rho_w = 0.264$). Values of Spearman's rank correlation coefficient were very low (< 0.15) for each of the single environmental variables on their own. At the small spatial scale, relationships between biotic and environmental variables were weak, the highest correlation being from a combination of shoot density and sediment grain size ($\rho_w = 0.096$). Like the combined variables, values of Spearman's rank correlation coefficient were very low (< 0.085) for each of the single environmental variables on their own.

4.4 DISCUSSION

The results of the present study indicated that univariate measures of species richness and abundance, and multivariate measures of the macroinvertebrate assemblage composition did not differ significantly between continuous and reticulate beds of *P. oceanica*, across three spatial levels. Based on these results, the null hypotheses drawn for these measures were accepted. Significant differences in some of the physico-chemical attributes between the two bed types were noted; mean grain size and organic carbon content of the sediment differed significantly between continuous and reticulate beds of *P. oceanica* at the medium and small spatial levels. However, according to the results of multivariate (BIOENV) and linear regression analyses, these two factors did not appear to play a major role in influencing the species richness or abundance of motile macroinvertebrates between *P. oceanica* continuous and reticulate beds.

The similarity in plant architectural features between the two bed types (see also Chapter 3) may account for the lack of significant differences in the diversity of associated macroinvertebrates, given that bed-dependant plant architecture may be important in influencing macrofaunal species richness and abundance (Heck & Wetstone, 1977; Heck & Orth, 1980a; Orth et al., 1984; Tolan et al., 1997; Lee et al., 2001). Therefore, factors that do not necessarily vary with bed type may be more important (e.g. Sogard et al., 1987; Irlandi, 1997; Hovel et al., 2002) in influencing the species richness and abundance of the macrofauna associated with *P. oceanica*. However, it is possible that there is some threshold of *P. oceanica* plant architectural change (Gotceitas & Colgan, 1989; Bartholomew et al., 2000) that can only be attained by large alterations in bed morphology, at which point species number and abundance of associated macroinvertebrate assemblages would be affected (Orth et al., 1984; Worthington et al., 1991). It is noteworthy that while studies into how alteration of seagrass bed structure influences the associated macrofauna have been undertaken for other Mediterranean seagrasses (e.g. *Cymodocea nodosa* (Ucria) Ascherson; Connoly & Buttler, 1996), no such investigations have made on *P. oceanica* beds. Thus, it is reasonable to conclude that continuous and reticulate beds support a similar species richness and abundance, and that any changes in these measures with the fragmentation process are more likely to occur between reticulate and patchy seagrass bed types.

Nevertheless, the possibility that *P. oceanica* bed architecture influences the diversity of associated macrofauna should not be dismissed. Significant differences in species richness and abundance of macroinvertebrates associated with *P. oceanica* were detected for the factor 'sampling locality' at the large (location) and medium (site) spatial levels, while multivariate analyses indicated that the assemblage composition was significantly different for the same factor at the large and small spatial scales. This significant spatial variation in attributes of the macroinvertebrate assemblages associated with *P. oceanica* is concomitant with significant spatial variation in some seagrass architecture and physico-chemical attributes recorded at the same spatial scales.

The results of linear regression for both 'full' and 'reduced' data sets indicated that, at the large spatial level, both macroinvertebrate species richness and abundance were significantly related to epiphyte biomass. Additionally, at the large spatial level, the number of macroinvertebrate species was significantly inversely related to mean sediment grain size. At the medium spatial level, macroinvertebrate abundance was significantly related to epiphyte biomass and shoot biomass, while species richness was significantly related to shoot biomass.

The results of BIOENV indicated that epiphyte biomass was amongst the three environmental variables which best explained the multivariate assemblage composition at the large spatial level, thus supporting the significant relationship obtained by the univariate analyses between this attribute and the macroinvertebrate assemblage. The correlation values obtained by BIOENV at the medium and small spatial level for any single environmental variable or a combination of such variables were rather low (ρ_w = 0.27), hence, these results should be interpreted with caution (Clarke & Warwick, 1994).

Taken together, the results obtained indicate that epiphytes appear to constitute an important factor in influencing both the species richness and abundance of macroinvertebrates associated with *P. oceanica* beds at the large spatial level, while mean sediment grain size also exerts an influence on species richness. Linear regression did not indicate any significant relationships between macroinvertebrate species richness/abundance and leaf area, or between leaf area and epiphyte biomass. Therefore, the observed significant relationship between macroinvertebrate species richness/abundance and epiphyte biomass did not result from a species-area relationship. Thus, the null hypothesis of no relationship between epiphyte biomass and mean sediment grain size, and the species richness and abundance of associated macroinvertebrates at the large scale, was rejected; the diversity of macroinvertebrates associated with *P. oceanica* beds appears to be significantly influenced by the amount of shoot epiphytes present.

The hypotheses of no significant relationship between the abundance of macroinvertebrates and *P. oceanica* shoot biomass and epiphyte biomass, and between the macroinvertebrate species richness and *P. oceanica* shoot biomass at the medium scale were also rejected. However, given that linear regression indicated a significant relationship between shoot biomass and epiphyte biomass, it appears that the significant relationship between macroinvertebrate abundance and epiphyte biomass at this spatial level has resulted from a species-area relationship. In their study of the macroinvertebrate fauna of *Zostera marina* beds, Attrill et al. (2000) noted that seagrass biomass is related to the plant's surface area, and therefore significant relationships between macroinvertebrate species richness and/or abundance and shoot biomass may be attributed to species-area relationships.

The present results add to the recent and growing appreciation that the diversity of macrofauna does not differ consistently between different types of seagrass bed, and other factors not associated with the bed can have an overriding importance in determining the composition of associated fauna. Some workers have noted differences in the associated faunal assemblages between different seagrass bed types, which indicated that fragmentation of seagrass beds may influence the diversity of associated macrofauna. For example, Tolan et al. (1997) and Frost et al. (1999) reported significant differences in the assemblage structure of associated macrofauna between different types of seagrass beds. Bowden et al. (2001) found that the total number of taxa associated with two differently sized patches of *Z. marina* was significantly higher in the larger patch, while the assemblage composition also differed significantly between the two patches. On the other hand, different conclusions have been made by other workers, and recently the consensus appears to be changing. For example, Irlandi (1997) noted that the type and size of seagrass patches were relatively unimportant in influencing the survival of the infaunal clam *Mercenaria mercenaria* (Linnaeus), and concluded that within-bed architectural attributes were more important; the same conclusion was reached by Hovel & Lipcius (2001) for the blue crab *Callinectes sapidus* Rathbun. Turner et al. (1999) noted that the factors structuring the assemblage composition of macroinvertebrates associated with seagrass patches appeared to be independent of patch size, seagrass percentage cover and seagrass biomass. Bell et al. (2001) reported that variation in patch size of *Halodule wrightii* Ascherson did not have any consistent impact on the associated fauna, whilst Hovel & Lipcius (2002) concluded that fragmentation of seagrass beds does not have an overriding influence on juvenile blue crab survival and density. A possible reason for the contrasting results obtained by different workers is that the scale at which most of the cited studies have been carried out may have been inappropriate to reveal consistent differences between different seagrass bed types (McNeill & Fairweather, 1993; Bell et al., 2001; Hovel & Lipcius, 2002). In any case, the more recent conclusions indicate the need to establish a somewhat different paradigm, which is that fragmentation of seagrass beds does not necessarily lead to loss of diversity of the associated macrofauna.

The present findings go some way in identifying the factors that appear to influence the diversity of macroinvertebrates associated with *P. oceanica* beds, and the scale at which different factors may operate. The significant differences in species richness and abundance, and in the assemblage composition between different sampling localities at the large and small spatial scales, suggest that environmental factors operating at local scales are more important in influencing the assemblage composition of associated motile macroinvertebrates. This finding agrees with the observations made by various other workers. For example, Brook (1978) recorded large differences in the species richness and abundance of macrofauna associated with the same type of seagrass beds between and within different sites, which were attributed to large differences in physical environmental characteristics and seagrass bed architectural features. Virnstein & Howard (1987a) found that the species composition of associated macrofauna differed between seagrass beds of the same species that were located in different environmental regimes. Orth (1977) and Pihl (1986) recorded differences in faunal attributes (biomass, secondary production and species composition) within seagrass beds of the same type experiencing different wave exposures and current regimes.

Significantly higher species richness and abundance were recorded from White Rocks and St Thomas Bay at the large spatial scale. However, none of the measured plant architectural features (shoot density, leaf area and shoot biomass) had correspondingly significantly higher values at White Rocks and St Thomas Bay. On the other hand, shoot epiphyte biomass was significantly higher at these two localities, and was also significantly correlated to macroinvertebrate species richness and abundance. The southern half of the Maltese Islands, where White Rocks and St Thomas Bay are located, is more densely populated and supports a higher industrial activity than the northern half, resulting in higher nutrient loading of coastal waters due to the presence of a greater number of sewage outfalls, industrial effluents and harbour activities (Mallia et al., 2002). Therefore, elevated nutrient concentrations off the southern coast of the Maltese Islands (Axiak et al., 2000) may account for the significantly higher values of shoot epiphyte weight recorded from the *P. oceanica* beds at White Rocks and St Thomas Bay.

Several studies have shown the importance of seagrass epiphytes as a food supply for the associated macroinvertebrate assemblages (Orth & van Montfrans, 1984; Alcoverro et al., 1997a; Jernakoff et al., 1996; Jernakoff & Nielsen, 1997; Bologna & Heck, 1999; Moncreiff & Sullivan, 2001). For example, Gambi et al. (1992) highlighted the importance of *P. oceanica* epiphytes in influencing the species richness and abundance of associated motile macroinvertebrates, although they did not provide statistical data that directly showed the positive correlation between epiphytes and macroinvertebrate diversity. However, epiphytes add another dimension to the foliar canopy: they increase physical complexity, thereby enhancing microhabitat space (Heck & Orth, 1980a; Kitting, 1984; Virnstein, 1987; Worthington et al., 1991). Small hermit crabs and other walking crustaceans use epiphytes to climb up into the seagrass foliar canopy by clinging onto the epiphytes, while smaller macroinvertebrates use them as a refuge against predation (e.g. Greening & Livingston, 1982; Leber, 1985; Hall & Bell, 1988). For example, Greening & Livingston (1982) noted that the crab *Neopanope texana* Sayi (Smith) and the shrimp *Alpheus normanni* Kingsley appeared to seek refuge from predators in epiphytic red algae growing on seagrass. Epiphytes may also help the passive settlement of the larvae of some organisms, while tube-building amphipods use them for support (Nelson, 1979; Coen et al., 1981; Worthington et al., 1991). Use of *P. oceanica* epiphytes as a microhabitat would particularly apply to the size range (circa 1 mm – 5 mm) of most of the macroinvertebrates recorded from the study area, since the physical structure of epiphytes (Virnstein, 1987) falls within the 'perception window' (Attrill et al. 2000) for such macrofauna. For example, the species that contributed most to the observed differences and were good discriminators between samples taken from the *P. oceanica* beds at White Rocks and St

Thomas Bay (the two locations having the highest seagrass epiphyte biomass) and samples taken at the other two locations, were the small amphipods *M. inaequipes*, *Aora* sp. and *L. costae*, and the polychaete Syllidae sp. A. These species could be utilising the shoot epiphytes as microhabitat, and may also be feeding on epiphytes, or on particulate organic matter deposited on their surface (e.g. Gambi et al., 1992). In particular, amphipods are known to be important constituents of the mesograzer guild that feed on epiphtes in seagrass beds (Howard, 1982; Jernakoff & Nielsen, 1997; Duffy & Harvilicz, 2001). Higher abundances of *M. inaequipes*, *Aora* sp. and *L. costae* and of other amphipods (for example, *Maera grossimana* (Montagu) and *E. brasiliensis*), and the small shrimp *T. cranchii*, were recorded from *P. oceanica* beds at St Thomas Bay, where shoot epiphyte biomass was significantly higher than at the other three locations. Besides having a small size, and, therefore, possibly using the epiphytes as a microhabitat (Nelson, 1979; Coen et al., 1981; Greening & Livingston, 1982; Leber, 1985; Worthington et al., 1991), the aforementioned suite of species comprise a mixture of herbivores, herbivores-deposit feeders and deposit feeders-carnivores, which may be grazing the epiphytes or feeding on food particles trapped in the fine thalli of algal epiphytes (Marsh, 1973; Scipione, 1989; Scipione, 1999; Gambi et al., 1992).

The motile macroinvertebrates that were more abundant in the *P. oceanica* beds at White Rocks, and which were also identified by SIMPER as having a high contribution to the observed differences between this and the other three locations, included the anomurans *C. timidus*, *G. bolivari* and *Pisidia longicornis* (Linnaeus). These macroinvertebrates are predominantly inhabitants of the *P. oceanica* matte (López de la Rosa & Garcia Raso, 1992), therefore, the higher abundance of these species in the *P. oceanica* beds at White Rocks may be related to some particular property of the matte (e.g. physical structural complexity; Chapter 5) which was not considered in the present study.

In summary, higher nutrient levels at White Rocks and St Thomas Bay (Axiak et al., 2000), appear to enhance epiphyte production, leading to an increased species richness and abundance of macroinvertebrates that use the epiphytes as a refuge from predation and/or as food, and ultimately leading to higher secondary production in *P. oceanica* beds at these localities. The importance of seagrass epiphytes in influencing the diversity of associated macroinvertebrates has been noted earlier by other workers (e.g. Kitting, 1984; Schneider & Mann, 1991; Gambi et al., 1992), but it appears that this observation has not been given due consideration in seagrass ecological studies made so far (Virnstein, 1987). For example, Lewis & Hollingworth (1982) and Hall & Bell (1988) found that abundances of epiphyte and macrofauna were positively correlated in beds of *Thalassia testudinum* Banks & Soland ex Koenig, while Edgar & Robertson (1992) noted that a reduction in seagrass (*Amphibolis*) epiphytes resulted in a corresponding decrease in epifaunal abundance.

In the oligotrophic Mediterranean Sea, nutrient enrichment may serve to enhance secondary production associated with *P. oceanica* beds, as long as nutrient levels are not exceedingly high. For example, Kirkman et al. (1991) found that the species richness and abundance of macrofauna associated with a *Posidonia australis* Hook bed located in eutrophic waters were higher than those recorded from a *Posidonia sinuosa* Cambridge & Kuo bed located in oligotrophic waters. However, excessive nutrient input may cause adverse effects, for example those caused by excessive epiphytic growth, which may lead to inhibition of seagrass photosynthesis (e.g. Sand-Jensen, 1977), or by algal blooms that can eventually lead to bed decline (e.g. Ott, 1980, Silbertein et al., 1986). Such effects have indeed been observed in the Mediterranean. For example, nutrient enrichment originating from an offshore fish farm located in St Paul's Bay, Malta, led to increased species richness and abundance of macroinvertebrates associated with *P. oceanica* beds at a distance of around 50 m from the fish cages, but a lower diversity was recorded closer to the farm where the seagrass bed was very degraded (Dimech et al., 2002). Excessive epiphytic growth may also impede the movement of fauna (Heck & Orth, 1980a), such that macroinvertebrate abundance decreases (Bell & Westoby, 1987). The amount of epiphytes present on seagrass shoots is also indirectly influenced by the hydrodynamic regime of a particular coastal area, since this would influence the supply of nutrients to a particular seagrass bed.

Because of the highly complex mechanisms involved, the direct ways in which variation of the hydrodynamic regime influences the diversity of seagrass-associated macrofauna is not clearly understood. Several authors have proposed variation in effective transport of food and larvae by currents to seagrass beds (e.g. Hovel et al., 2002), and disturbance to the larger macrofauna by strong currents that cause dislodgment (e.g. gastropods; Schanz et al., 2000) as possible explanations. The importance of hydrodynamic factors in influencing the macrofauna of seagrass beds has long been recognised (e.g. O'Gower & Wacasey, 1967; Orth, 1977; Pihl, 1986). Of the four locations considered (at the large scale) in the present study, Ramla Bay was identified as the most exposed, while Mellieha Bay had the lowest exposure (Chapter 2). The species that contributed most to the observed differences (SIMPER analysis) between Ramla Bay and the other three locations were the small gastropod *A. mamillata*, the hermit crab *P. chevreuxi* and the alpheid shrimp *A. nitescens*, all of which were more abundant at the former location. While the latter two species are known to mainly inhabit the *P. oceanica* matte (López de la Rosa & Garcia Raso, 1992), where they may seek shelter from predators and adverse factors such as strong water movement, it is possible that the small gastropod *A. mamillata* is capable of out-competing other macroinvertebrate gazers on the seagrass leaf surfaces by resisting detachment (e.g. Schanz et al., 2000).

Mellieha Bay had the lowest exposure value of the four locations. The species indicated by SIMPER to be high contributors and good discriminators between Mellieha Bay and the other three localities, were the shrimp *H. inermis* and the polychaetes *P. eruca* and *A. midas*. The first species is a typical inhabitant of the *P. oceanica* leaf canopy, where it can have a very high abundance (Pessani et al., 1995; Borg & Schembri, 2000), while the last two species are typical inhabitants of seagrass beds growing on soft bottoms that have a high proportion of fine sediments (Castelli, 1989; Martinelli et al., 1998). The hydrodynamic regime of a particular coastal locality also plays an indirect role in influencing the species composition of benthic macroinvertebrate assemblages present by influencing the sedimentary regime; the general tendency being for high-energy environments to have coarser sediments than low energy environments (Pihl, 1986; Fonseca & Bell, 1998). For the same bay, Drago (1997) concluded that complex hydrodynamic processes, resulting from the presence of an extensive rocky shoal off its mouth, act in concert with the coastal configuration of the area and the seabed topography to inhibit flushing of the inner bay areas by the open sea. Therefore, the particular hydrodynamic properties inside Mellieha Bay apparently favour species that prefer sheltered conditions (e.g. *H. inermis*) and high sedimentation rates (e.g. *P. eruca* and *A. midas*), and may also be responsible for the observed significant differences in values of organic carbon and mean sediment grain size between continuous and reticulate beds.

Interpretation of the significant relationship indicated by linear regression between macroinvertebrate abundance and *P. oceanica* shoot biomass and epiphyte biomass, and between macroinvertebrate species richness and *P. oceanica* shoot biomass at the medium spatial level requires caution. Several workers have related shoot biomass to seagrass bed structural complexity (Heck & Wetstone, 1977; Heck & Orth, 1980a; Stoner, 1980; Gore et al., 1981; Ansari et al., 1991). However, Attrill et al. (2000) showed that the use of seagrass biomass as a measure of bed structural complexity could introduce the confounding effects of sampling area, since shoot biomass is related to the plant's surface area. The significant relationship indicated by linear regression between leaf area and epiphyte biomass at the medium spatial level supports Attrill et al.'s (2000) inference. Therefore, at the medium spatial level, the significant relationship indicated by linear regression between macroinvertebrate species richness and abundance, and shoot biomass and epiphyte biomass probably result from species-area relationships.

The significant differences detected by multivariate analysis (ANOSIM) at the small spatial level were attributed to small differences in abundance of a large number of species, rather than large differences in the abundance of several species. It is therefore probable that the significant difference in the assemblage composition at the small spatial level results from natural patchiness in the distribution of macroinvertebrates associated with *P. oceanica* beds at such scale. Processes that contribute to patchiness at small spatial scales include stochastic settlement of larvae, aggregations caused by colonisation of patchily distributed microhabitats, and small-scale patterns of differences in behaviour (Hughes, 1979; Bell & Westoby 1986b; Jernakoff et al., 1996).

Studies on fragmented *P. oceanica* beds, similar to the present one, are not available for comparison. A study by Barberá Cebrián et al. (2002) on the structure of the mysid assemblages of *P. oceanica* beds in Spain concluded that fragmented seagrass beds supported a higher species richness of mysids than homogeneous beds. However, the study by these authors centered on mosaics formed by two seagrass species, namely *P. oceanica* and *C. nodosa*, both of which were also intermixed with bare sand (Barberá Cebrián et al., 2002). In another study by Accardo-Palumbo et al. (1992), comparison of *P. oceanica* reefs and 'atolls' did not reveal significant differences in the associated prosobranch assemblages between the two different bed types.

While naturally occurring reticulate and continuous *P. oceanica* beds appear, overall, to support similar motile macroinvertebrate assemblages, this finding should be interpreted with caution with respect to the issue of anthropogenic related seagrass bed fragmentation. Certainly the results of the present study do not provide evidence that fragmentation of continuous seagrass beds should be considered as an 'acceptable' change, and hence a pretext for allowing anthropogenic activities to modify continuous beds to reticulate ones. It should be remembered that fragmentation of seagrass habitat leads not only to a change in bed configuration but also to reduced coverage and thus to loss in habitat area (Hemminga & Duarte, 2000), the latter potentially also having consequences for some of the seagrass-associated fauna other than the motile macroinvertebrates (e.g. fish; Sánchez Jerez et al., 1996). Furthermore, fragmentation of continuous seagrass beds to very small-sized patches (e.g. 1 – 10 m across) leads to bed types that essentially consist of edge habitat, which would have implications for the associated macrofauna (Irlandi, 1997, Bowden et al., 2001). Additionally, fragmentation of seagrass beds increases their exposure to colonisation by opportunistic species (e.g. the alien Caulerpales; Ceccherelli et al., 2000).

The present results suggest that reticulate and continuous *P. oceanica* beds have a broadly similar habitat 'value' for macroinvertebrates, when total available area is not considered. In a recent review, Bell et al., (2001) concluded that there is no current overwhelming evidence that fragmentation of seagrass beds has any impact on the associated fauna. Therefore, fragmented beds should receive the same attention as non-fragmented ones, when considering conservation and protection issues (McNeill & Fairweather, 1993). As in the case of terrestrial habitats, fragmented seagrass beds should not be viewed from the island-biogeographic point of view or as 'unitary entities' (Haila, 2002), but as part of a hierarchical arrangement of different bed types in a heterogeneous seagrass landscape (Robbins & Bell, 1994).

In conclusion, reticulate and continuous *P. oceanica* beds appear to support similar assemblages of motile macroinvertebrates and local environmental factors, apparently independent of bed type, including shoot epiphytes (possibly both as food and physical habitat; Virnstein, 1987; Schneider & Mann, 1991; Moncreiff & Sullivan, 2001), sediment grain size (e.g. Frost et al., 1999; Boström & Bonsdorff, 1997), and (albeit indirectly) the hydrodynamic regime (e.g. Hovel et al., 2002) are more important in influencing the diversity of associated motile macroinvertebrates than bed type. However, not all these factors influence the macroinvertebrate assemblages associated with *P. oceanica* at the same spatial scale.

Overall, the present results support the findings of recent workers (e.g. Frost et al., 1999) that began to challenge the earlier paradigm that fragmented habitats support a lower diversity of fauna. It is therefore proposed that fragmentation of continuous to reticulate *P. oceanica* beds does not necessarily lead to alteration of the species richness and abundance of the associated macroinvertebrates and local factors, both natural (e.g. the hydrodynamic regime) and anthropogenic (e.g. nutrient enrichment of coastal waters) are more important in influencing seagrass-associated macroinvertebrate assemblages.

Clearly there is still much research to be undertaken in order to gain a better understanding of the effects of seagrass habitat fragmentation on the associated faunal assemblages. For example, it would be useful to address whether the diversity of macrofauna differs between reticulate beds and discrete patches of *P. oceanica*. Although it appears that such a comparative study is difficult to undertake in Malta, due to the apparent rare occurrence of adjacent reticulate and patchy beds located at the same water depth, it may be possible to make such a study elsewhere in the Mediterranean. Other useful questions that need to be addressed are: Which is the more important role of seagrass epiphytes to the associated macroinvertebrates; as food or as microhabitat? Does complete loss of the foliar canopy lead to loss of diversity of associated macroinvertebrates? The latter study could compare the species richness and abundance of macrofauna associated with dead matte (lacking a foliar canopy) and living matte (having a foliar canopy) of *P. oceanica* (Chapter 5). In the meantime, data generated from the present study will, at the very least, inform conservation biologists and assist coastal managers in formulating appropriate conservation measures for the different naturally occurring bed types of *P. oceanica* in the Maltese Islands.

CHAPTER 5

DIFFERENCES IN MOTILE MACROINVERTEBRATE ASSEMBLAGES OF LIVING AND DEAD *POSIDONIA OCEANICA* MATTE

5.1 INTRODUCTION

Seagrass beds can be divided broadly into different structural compartments, namely the foliar canopy and the root-rhizome matrix (Orth et al., 1984; Mazzella et al., 1992; Buia et al., 2000), which vary in their habitat characteristics and in the biotic assemblages they support (e.g. Bianchi et al., 1989). Although these different compartments are referred to frequently as separate subhabitats supporting different biotic assemblages (Kikuchi & Peres, 1977; Kikuchi, 1980), complex interactions occur between the species associated with each, together with vertical migration by some species (e.g. Sánchez Jerez et al., 1999b), thereby making clear distinction untenable (Mazzella et al., 1986; Baden & Boström, 2001).

A current paradigm in seagrass ecology is that the abundance of motile macrofauna associated with seagrass beds is greater than that of unvegetated habitats (Thayer et al., 1975; Orth, 1977; Virnstein et al., 1983; Lewis, 1984; Pihl, 1986; Kirkman et al., 1991; Curras et al., 1993; Boström & Bonsdorf, 1997). The foliar canopy is utilised by macrofauna as a refuge against predation (e.g. Lee et al., 2001) and as a nursery habitat for larvae and juveniles of many macrofaunal species (Jacobs et al., 1981; Orth et al., 1984; Virnstein, 1987; Bell & Pollard, 1989, Howard et al., 1989; Edgar, 1990). The plants themselves are a rich source of organic matter and detritus (Bach et al., 1986; Mateo & Romero, 1997), while the plant surfaces support a high biomass of epiphytes which serves as food for many grazers (Kitting, 1984; Johnson & Johnstone, 1995; Jernakoff et al.,1996; Jernakoff & Nielsen, 1997) and as microhabitat for small motile macroinvertebrates (Heck & Orth, 1980a; Virnstein, 1987; Hall & Bell, 1988; Worthington et al., 1991). In turn, detritus feeders and grazers serve as prey items for a large number of invertebrates and vertebrates (e.g. decapods and fishes; Brook, 1977; Young & Young, 1978; Heck & Orth, 1980b; Stoner, 1980; Burchmore et al., 1984; Howard, 1984; Leber, 1985; Greenway, 1995). Therefore, it is not surprising that several studies have reported significant differences in the abundance of macrofauna between seagrass beds and unvegetated bottoms, when comparing the seagrass foliar canopy with adjacent 'bare' substrata (e.g. Howard et al., 1989; Edgar et al., 1994; Connolly; 1997). On the other hand, very few studies (e.g. Lewis & Stoner, 1983; Currás et al., 1993) have included the root-rhizome layer when comparing the associated macrofauna of seagrass beds and adjacent bare substrata, and the contribution of the former habitat to the diversity of seagrass-associated macrofauna has not been clearly established, although workers have pointed out that it may play an important role (Orth; 1977; Orth et al., 1984; Virnstein, 1987; Webster et al., 1998; Buia et al., 2000). In principle, given that the root-rhizome matrix has a large proportion of trapped sediment, one may expect that the diversity of macrofauna associated with this subhabitat would not be very dissimilar to that of surrounding bare sand habitats. However, experiments involving reduction of leaf height or complete removal of the foliar stratum of a seagrass bed have shown that the leaf canopy *per se* may not be of overriding importance for associated macroinvertebrates, and other factors, possibly the root-rhizome layer that persists after removal of the foliar canopy, may be involved (Bell & Westoby, 1986a; 1986b; Connoly, 1995). The root-rhizome layer may increase habitat structural complexity by providing cavities and interstices in the mat that can be inhabited by cryptic macrofauna (e.g. García Raso, 1990; Somaschini et al., 1994; García Raso et al, 1996) and protect the infauna against predation (e.g. Blundon & Kennedy, 1982; Peterson, 1982). Additionally, the network of roots and rhizomes prevents the accumulation of toxic compounds (Terrados et al., 1999) and stabilises the mobile sediments (Ward et al., 1984), creating a favourable habitat, which supports a high diversity of associated macrofauna (e.g. Harmelin, 1964; Templado, 1984; Chimenz et al., 1989; Somaschini et al., 1994; Gambi et al., 1995; Borg & Schembri, 2000). The root-rhizome layer also traps sand and other sediment that provides a habitat in itself, while the roots and rhizomes may serve as a source of food for the infauna and cryptic macroinvertebrates (Bellan Santini et al., 1986).

The possible contribution of dead seagrass matte to localised organic enrichment, long after disappearance of the canopy, has been pointed out by Jackson et al. (2001). Thus, it is probable that the root-rhizome compartment supports a substantial amount of the biodiversity of seagrass habitats (Orth et al., 1984; Virnstein, 1987).

Fragmentation of seagrass habitat is a gradual process that may involve slow degradation of large continuous beds into non-continuous ones, and ultimately to smaller bed fragments. In some cases, degradation of seagrass beds leads to complete loss of the foliar canopy, such that only the root-rhizome layer remains (e.g. Meinesz et al., 1988). Therefore, the remaining root-rhizome matrix can be viewed as the lower extreme end of the gradual process of seagrass bed fragmentation and degradation. It would be useful to compare the diversity of macrofaunal assemblages associated with the root-rhizome matrix after loss of the foliar canopy to that of the root-rhizome matrix in seagrass beds having an intact foliar canopy. The data generated from such a study would enable a quantitative assessment of the contribution of the root-rhizome matrix to seagrass bed diversity. In turn, such data will help assess whether the root-rhizome matrix remaining after complete loss and degradation of the foliar canopy of a seagrass bed, has any conservation value.

In the Mediterranean Sea, the endemic *Posidonia oceanica* (Linnaeus) Delile forms beds that constitute one of the most important shallow-water coastal habitats in this sea, through their roles as nurseries, refugia and feeding grounds for many invertebrates and fishes (Mazzella et al., 1992; Boudouresque et al., 1994), and their contribution to physical coastal dynamic processes, including protection against coastal erosion (e.g. Boudouresque & Meinesz, 1982; Jeudy de Grissac, 1984). Because of their high conservation importance, *P. oceanica* beds are listed in the EC Directive 92/43/EEC (the 'Habitats Directive') as a priority natural habitat, whose protection requires the designation of Special Areas of Conservation (EEC, 1992). *P. oceanica* is one of the largest seagrasses, with strap-like leaves sometimes exceeding one metre in length (Drew and Jupp, 1976) and having a width of around 1 cm. Beds of this seagrass are characterised by very high shoot densities (e.g. 1,200 shoots m^{-2} at a depth of 5 m; Mazzella *et al.*, 1992) and a root-rhizome layer consisting of tough lignified roots and rhizomes admixed with sediment, known as 'matte', that has a complex structure and can be several metres thick (e.g. 4-5 m; Romero et al., 1994; Mazzella et al., 1986). The high structural complexity of both leaf canopy and root-rhizome matte of *P. oceanica* beds (Buia et al., 2000) makes them ideal for comparisons of the role of these two compartments in determining the diversity of seagrass-associated macroinvertebrate assemblages. To date, investigations on the total macrofauna have been centered mainly on the leaf canopy (e.g. Mazzella et al., 1989; Scipione et al., 1996; Sánchez Jerez et al., 1999a), while the few available studies on matte macrofauna mainly deal with single taxa (e.g. the polychaetes; San Martin & Vietez, 1984; Willsie, 1986; Somaschini et al., 1994). Only a handful of studies have investigated the total biotic assemblages of the different subhabitats comprising *P. oceanica* beds (e.g. Templado, 1984; Bianchi et al., 1989; Chimenz et al., 1989).

Disturbance from natural processes and events, such as strong currents and wave action (Blanc & Jeudy de Grissac, 1984) and anthropogenic activities, for example, discharge of sewage and harbour activities (Ramos Éspla, 1984), and trawling (Ardizzone & Pelusi, 1984), may lead to death of *P. oceanica* in parts of the bed, exposing the underlying root-rhizome matrix (Meinesz et al., 1988; Mazzella et al., 1986). The remaining root-rhizome matte consists of the compacted remains of the seagrass root-rhizome matrix, having numerous small crevices and other spaces, some of which are filled with sediment, and commonly referred to as 'dead matte' (e.g. Harmelin, 1964; Vaccarella et al., 1981; Willsie, 1983; Salghetti-Drioli et al., 1989; Mazzella et al., 1986). Dead *P. oceanica* lacks the foliar canopy and would therefore be more exposed to currents (Gambi et al., 1989b), and hence to the loss of the interstitial sediments, which are easily resuspended by water movement and eroded from the matte (Terrados & Duarte, 2000). Therefore, one would expect loss of the finer sediments from the dead matte so that the mean grain size of the retained sediments would be larger than in the case of living *P. oceanica* matte. Living matte also has a higher rate of sediment deposition, since the overlying leaf canopy traps suspended fine particles from the water column (Duarte et al., 1999), hence leading to differences in sediment grain size between living and dead matte of *P. oceanica*. The hollow cavities thus produced in dead *P. oceanica* matte may serve as a habitat for cryptic macrofauna (Harmelin, 1964; Vaccarella et al., 1981; Willsie, 1983; Somaschini et al., 1994), while the slowly decomposing root-rhizome matrix may provide a rich source of detritus and organic matter that may serve as food for the associated macrofauna (Bellan Santini et al., 1986; Edgar et al., 1994). However, since dead *P. oceanica* matte lacks the overlying leaf canopy, the surface is easily accessible to predators (e.g. Lee et al., 2001), hence, predation pressure may be higher in this habitat than in the case of living matte. The dead matte surface is often colonised by epiphytes (Vaccarella et al., 1981), which themselves increase structural complexity (Heck & Orth, 1980a; Virnstein, 1987; Worthington et al., 1991) and provide food (Kitting 1984; Jernakoff et al., 1996; Moncreiff & Sullivan, 2001), hence serving as a new microhabitat for other macrofauna. The dead *P. oceanica* matte surface can also become colonised by macroalgae (e.g. Boudouresque et al., 1985b; Meinesz et al., 1988; Salghetti-Drioli et al., 1989; Barberi et al., 1995), and sometimes by the pioneering seagrass *Cymodocea nodosa* (Ucria) Ascherson (e.g. Calvo & Frada-Orestanio, 1984; Mazzella et al., 1986), thereby acting a substratum for other vegetation assemblages and their associated fauna.

Dead *P. oceanica* matte may persist for several years, or even decades (e.g. Meinesz & Lefèvre, 1984), and can have a continuous cover over large areas, or can occur as patches intermixed with living matte (Augier & Boudouresque, 1970; Augier, 1985; Meinesz et al., 1988; Panayotidis & Simboura, 1989). Large areas of dead *P. oceanica* matte have been reported from many parts of the Mediterranean, including Spain (e.g. Ramos Esplá, 1984), France (e.g. Augier, 1986), Corsica (e.g. Meinesz et al., 1988), Italy (e.g. De Metrio et al., 1978; 1980; Vaccarella et al., 1981), Sardinia (e.g. Barberi et al., 1995), Sicily (e.g. Calvo & Frada-Orestanio, 1984) and Greece (e.g. Panayotidis & Simboura, 1989), showing that the occurrence of this habitat is widespread in the region. Given the high conservation importance of *P. oceanica* beds, the widespread occurrence of dead matte is potentially alarming. Where present, dead *P. oceanica* matte is generally viewed as a degraded habitat having a low ecological value (Notiziario S.I.B.M., 2003), but such discrimination is not supported by ample data. Surprisingly, few studies of the ecology of this habitat are available (Harmelin, 1964; De Metrio et al., 1978; 1980; Vaccarella et al., 1981; Willsie, 1983; Abada Guerroui & Willsie, 1984; Bellan Santini et al., 1986; Somaschini et al., 1994). Furthermore, quantitative studies designed specifically to compare the macrofauna of living and dead matte are generally lacking (Harmelin, 1964) and most deal only with single taxa, namely amphipods (e.g. Bellan Santini et al., 1986) and polychaetes (e.g. Somaschini et al., 1994). The available data indicates that dead *P. oceanica* matte may support a high diversity of associated macrofauna, which could possibly be higher than that of living matte (Harmelin, 1964). However, Somaschini et al. (1994) concluded that dead matte of *P. oceanica* did not support a higher diversity of polychaetes than living matte. It would be useful to study the diversity of the whole macrofaunal assemblages associated with *P. oceanica* dead matte and compare them to those of living matte of the seagrass. Data generated from such a study will enable a quantitative assessment of the contribution of dead *P. oceanica* matte to the diversity of associated with seagrass habitats. In turn, such data will help assess whether dead matte resulting from fragmentation and/or degradation of *P. oceanica* beds has any conservation value. Given that dead *P. oceanica* matte sometimes results from natural disturbance, a useful starting point would be comparisons of the diversity, species composition and structure of biotic assemblages associated with naturally occurring dead and living matte.

The present study aimed to establish whether the diversity of associated motile macroinvertebrate assemblages, sampled at a number of spatial scales, differed between living *P. oceanica* matte (supporting living shoots of the seagrass) and dead matte (not supporting living shoots of the seagrass). To address this aim, the null hypothesis tested was that the species richness, abundance, and assemblage composition of associated motile macroinvertebrates did not differ between living and dead *P. oceanica* matte. To examine any possible relationships between macroinvertebrate diversity and environmental variables (namely the organic carbon content and grain size of the sediment, and root-rhizome biomass), the study also aimed to examine for differences in these variables between living and dead *P. oceanica* matte. To address this aim, the null hypothesis tested was that the aforementioned physical attributes examined did not differ between living and dead *P. oceanica* matte.

5.2 MATERIAL AND METHODS

5.2.1 Study area and experimental design

Previous surveys (Borg & Schembri, 1995a; Borg et al., 1997) showed that areas of dead *P. oceanica* matte, interspersed with the living seagrass, occur in several bays and inlets in the Maltese Islands (Central Mediterranean). While in some bays and inlets, large areas of dead *P. oceanica* matte have resulted from degradation of the seagrass due to anthropogenic disturbances, in other places, such regression appears to have resulted from natural events, most probably strong currents and wave action (Blanc & Jeudy de Grissac, 1984; Meinesz et al., 1988). Mellieha Bay, located on the northeastern coast of mainland Malta, is a relatively undisturbed locality. A detailed survey of the bay showed the presence of large patches of dead *P. oceanica* matte interspersed with living matte of the seagrass (Figure 29), predominantly in the 5 – 8 m depth range (see Chapter 2 for details of survey methodology and results). The presence of interspersed living and dead matte of *P. oceanica* provided an opportunity to compare the two habitat types, since water depth and other physical environmental conditions are the same for both, hence enabling unconfounded comparison (Underwood, 1997).

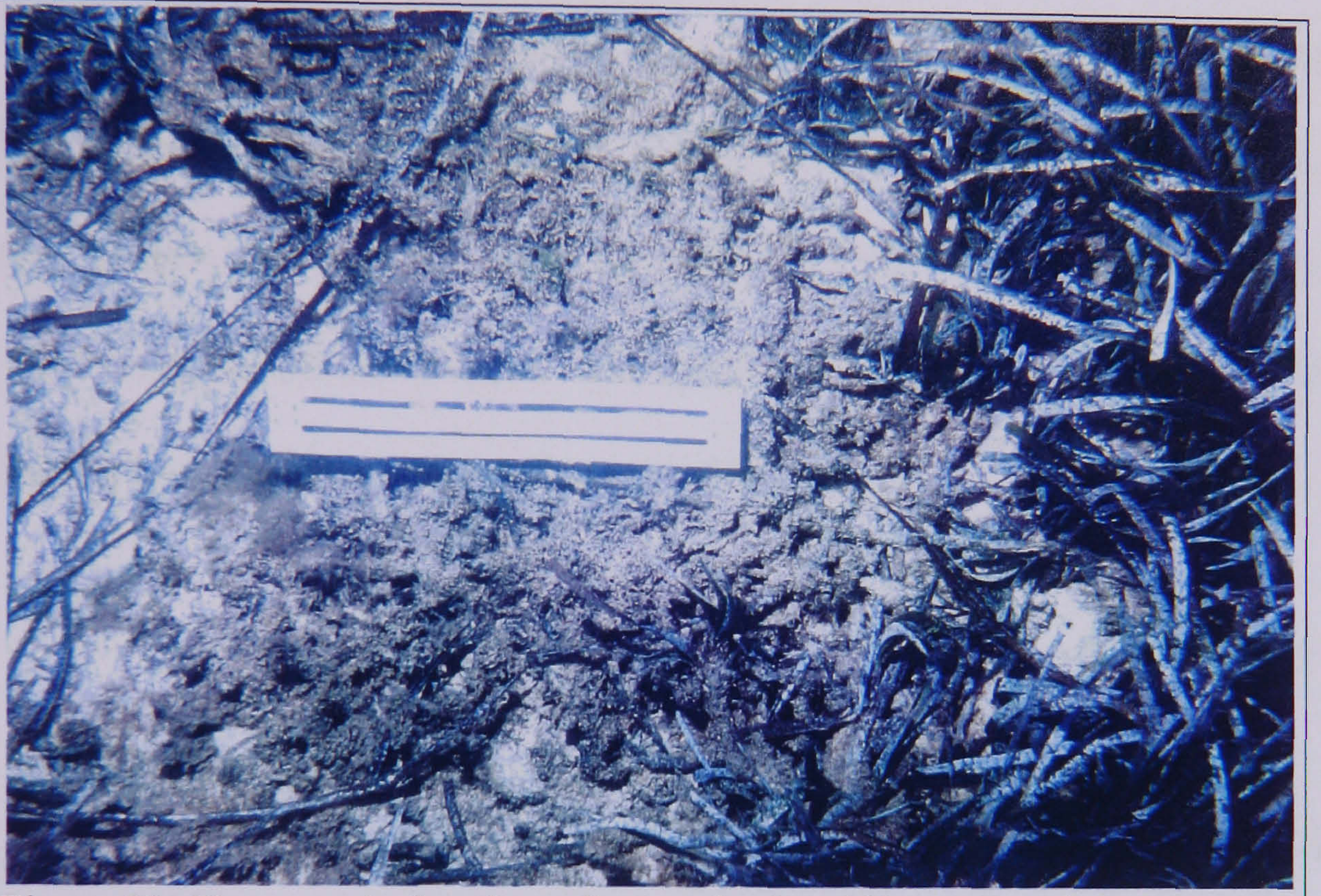


Figure 29. Photograph showing adjacent dead and living *Posidonia oceanica* matte in the study area. The scale shown is 30 cm long.

The experimental design for the present study was based on a randomised spatial layout consisting of four plots, each measuring 60 x 80 m, and located at a depth of 6 m in Mellieha Bay (Figure 30). Adjacent plots were separated from each other by a distance of around 80 m, and each had dense and healthy *P. oceanica* beds interspersed with patches of dead matte which varied in size between 0.05m^2 and 25 m^2. Such a design ensures spatial replication and allows for detection of spatial differences, if any, between live and dead matte between localities (Underwood, 1997).

5.2.2 Sampling and laboratory analyses

Sampling of living and dead *P. oceanica* matte was carried out using a specially designed corer having a diameter of 25 cm, to which a 0.5 mm mesh collecting bag was attached see

Chapter 2). The design, selection, justification and operation of this particular corer are described in Chapter 2. Using this sampler, four cores were collected randomly by SCUBA divers from adjacent areas (each ranging between 8 m^2 and 12 m^2) having the two different matte types, within each of the four plots, such that a total of 32 samples were obtained (4 plots x 2 treatments x 4 replicate samples; Figure 30). Four replicate samples were collected also from each sampling station, using a smaller (10 cm) diameter metal corer, to study physico-chemical properties of the sediment and of the root-rhizome material. To reduce edge effects, all samples were collected at least 2 m away from the boundary between the two different matte types. All sampling was carried out between 10.00 h and 15.00 h, during the first three weeks of August 2000.

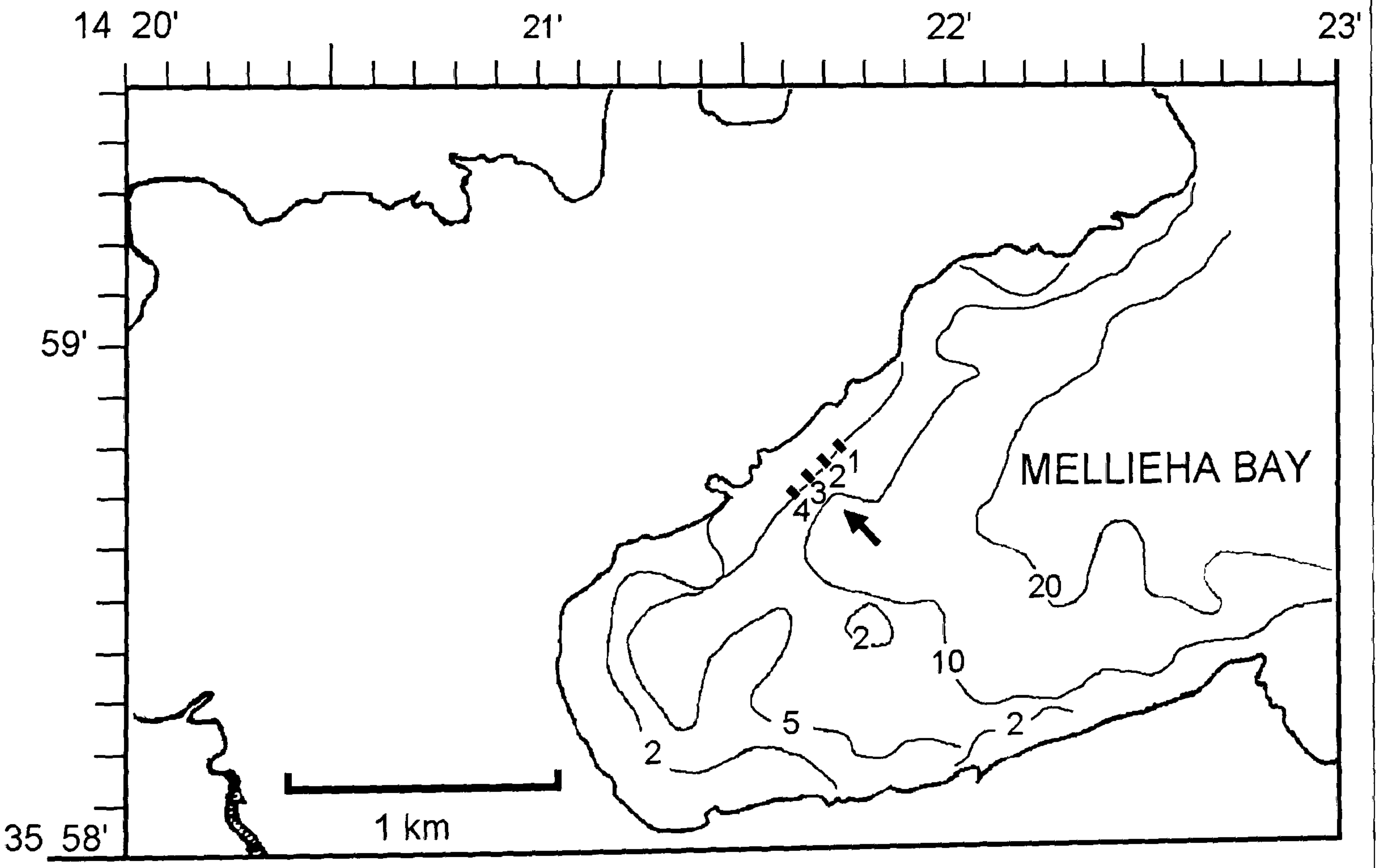


Figure 30. Map of Mellieha Bay showing the location of the four plots (arrow) and bathymetry (2 m, 5 m, 10 m and 20 m depth contours).

In the laboratory, samples collected for faunal studies, using the 25 cm diameter corer, were washed in seawater, and the shoots (for living matte) and root-rhizome matrix separated and examined carefully to remove the conspicuous motile macroinvertebrates.

The remaining sediment and washings were passed through a 0.5 mm sieve and the retained material sorted for any remaining motile macroinvertebrates in trays under a x5 magnifying lens. The macroinvertebrates were fixed in 10% formaldehyde in seawater and transferred to 70% ethanol prior to identification to species level using microscopy (x12 - x150) and appropriate taxonomic keys (see Chapter 4).

The *P. oceanica* shoots collected in cores taken on the living matte were separated from the root-rhizome fraction, and counted to obtain estimates of shoot density. To obtain estimates of biomass the shoots from samples taken on living matte, and the root-rhizome fractions from samples (25 cm diameter core) taken on living and dead matte were washed in tap water and dried at 80°C for 48 h to constant weight (± 0.001g). Samples collected for sediment analyses using the 10 cm diameter corer were first sorted to remove the root-rhizome matrix and other plant material from the sediment. Sub-samples of the sediment for determination of total organic carbon were frozen at -25°C, while the remaining portions were dried in air for granulometric analysis. Analyses to determine total organic carbon in the sediment (Walkley & Black, 1934) and mean sediment grain size (Folk & Ward, 1957) were carried out as given in Buchanan (1984).

5.2.3 Data analyses

Differences in the species richness and abundance of motile macroinvertebrates between the two different matte types were tested using two-way ANOVA (with alpha set at 0.05). Differences in organic content and mean grain size of the sediment, and of the dry weight of the root-rhizome fraction between the two different *P. oceanica* matte types, were tested likewise, using two-way ANOVA. The ANOVA model used was orthogonal, in which 'matte type' (M; two levels) was a fixed factor and 'plot' (P; four levels) was random. Differences in shoot density and leaf biomass between living *P. oceanica* matte in the four plots were tested using one-way ANOVA (with alpha set at 0.05). Prior to analyses, all data were tested for homogeneity of variances using Cochran's test and, where necessary, appropriate transformation of data (see Section 5.3) was made. Analyses were carried out using the PC software package GMAV5 produced at the University of Sydney (GMAV, 1996). When the ANOVA indicated significant differences, the source of difference was identified using SNK tests (Underwood, 1997) (see Chapter 3).

To test for differences in the assemblage composition associated with the two different *P. oceanica* matte types, multivariate analyses were carried out on the species-abundance data ($\sqrt{\sqrt{\ }}$transformed, to downweight the contribution of dominant species; Clarke & Warwick, 1994) using the PRIMER v5 suite of programs (Clarke & Gorley, 2001). The analyses consisted of Non-Metric Multidimensional Scaling (NMDS), using the Bray-Curtis index to construct the underlying similarity matrix (Clarke & Warwick, 1994) (see Chapter 4 for a justification of use of this multivariate ordination technique). Significance of differences in assemblage composition for samples from living and dead matte was assessed using two-way Analysis of Similarity (ANOSIM) (Clarke, 1993). The contribution of the different species to the observed similarity within groups of samples taken from the same type of matte, and the dissimilarity between groups of samples taken from different matte types, were tested using the Similarity Percentages (SIMPER) program (Clarke, 1993). BIOENV analysis was carried out to examine the relationships between the macroinvertebrate assemblage composition and environmental variables measured (Clarke & Ainsworth, 1993). The environmental variables included in the analysis were mean sediment grain size, total organic carbon in sediment and root-rhizome biomass. A brief description of the principles underlying these four different statistical analyses techniques has already been presented in the preceding chapter (Chapter 4).

5.3 RESULTS

A total of 5695 individuals were collected (7 nemerteans, 47 sipunculids, 1447 polychaetes, 12 Pycnogonids, 3680 crustaceans, 416 molluscs and 86 echinoderms) comprising 215 species (1 nemertean, 1 sipunculid, 54 polychaetes, 2 pycnogonids, 84 crustaceans, 67 molluscs and 7 echinoderms; see Appendix B). Of these, 39 species were recorded exclusively from dead matte and 32 exclusively from living matte (Appendix C). In all four plots, the mean total abundance (Figure 31a) and species richness (Figure 31b) were significantly higher in samples collected on dead *P. oceanica* matte than on the living matte (Table 25).

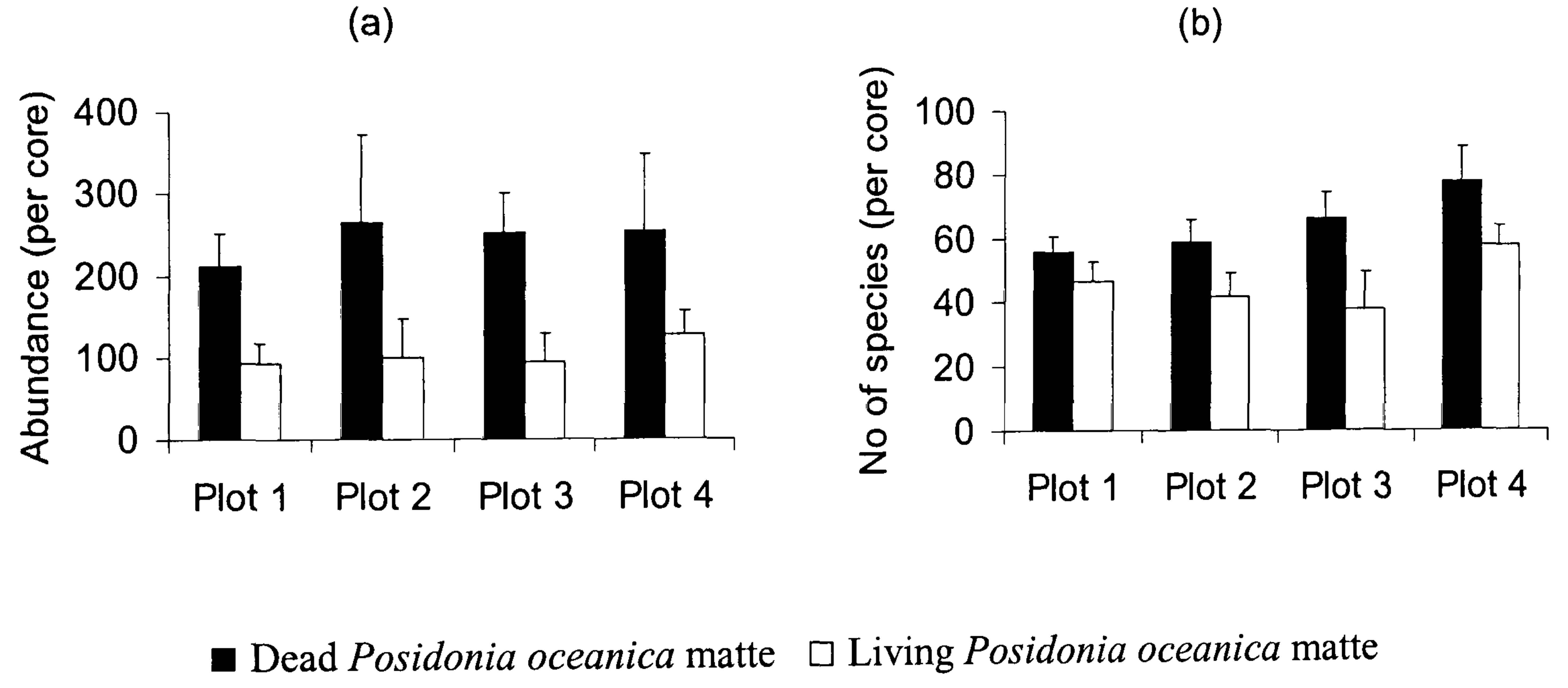


Figure 31. Mean values of abundance (a), number of species (b). Error bars are +1 SD.

Table 25. Summary of ANOVA results for abundance (per core) and number of species (per core). The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Source of variation	**df**	**Abundance** **n = 4** Transformation: none Cochran's test: NS			**Number of species** **n = 4** Transformation: none Cochran's test: NS		
		MS	F	P	MS	F	p
Matte type (M)	1	146746.53	70.04	**	1875.78	10.22	*
Plot	3	1109.86	0.32	NS	202.44	2.55	NS
M x P	3	2095.20	0.60	NS	183.53	2.31	NS
Residual	24	3470.38					

The significant difference in abundance detected for the factor 'matte type' was attributed to significant differences between dead and living matte in all four plots (SNK; $p < 0.01$), while the significant difference in species richness detected for same factor was due to significant differences between the two matte types in plot 2 (SNK; $p < 0.05$) and plot 3 (SNK; $p < 0.01$). Overall, total species richness and abundance recorded for the various major macroinvertebrate phyla were consistently higher on dead *P. oceanica* matte (Figure 32).

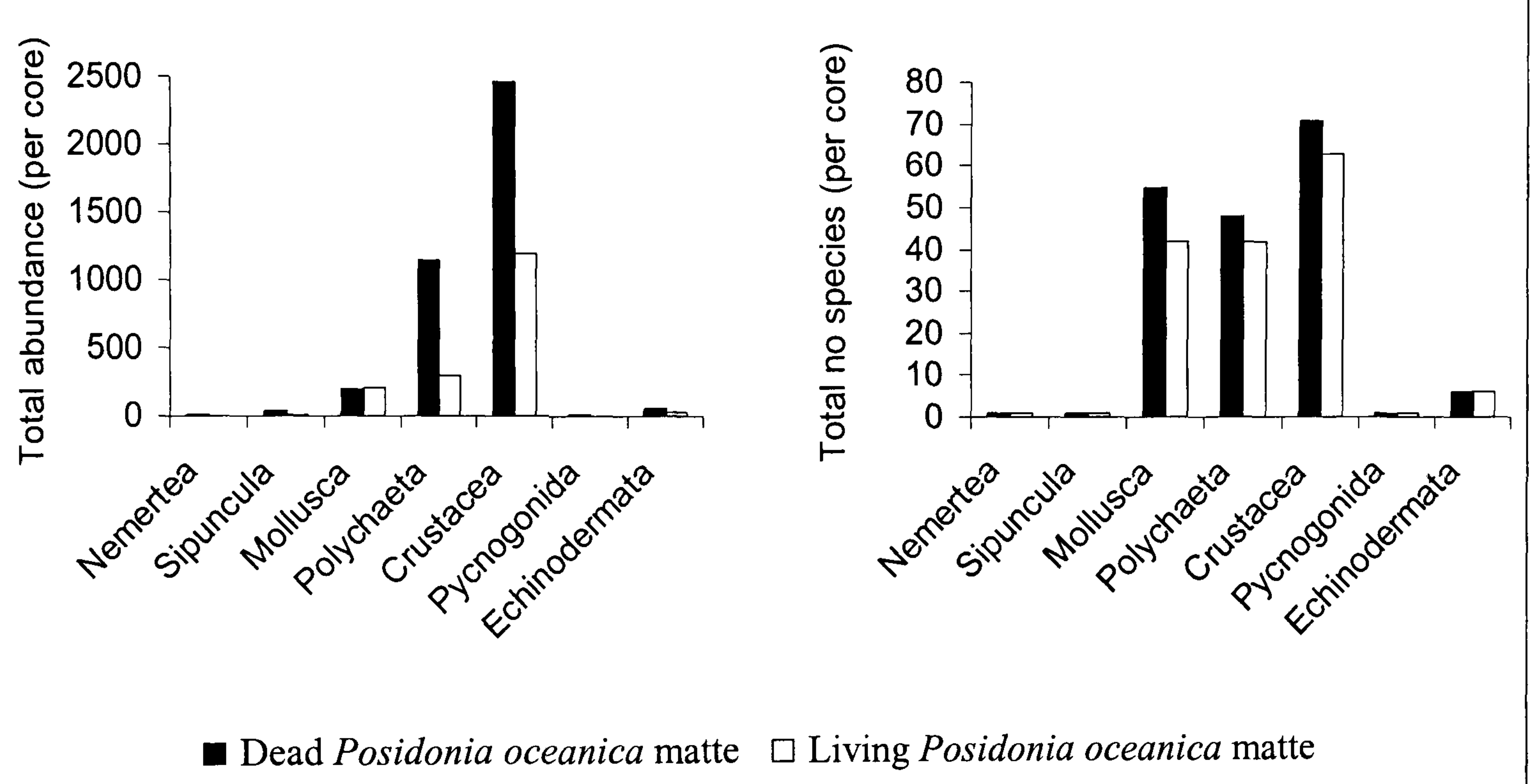
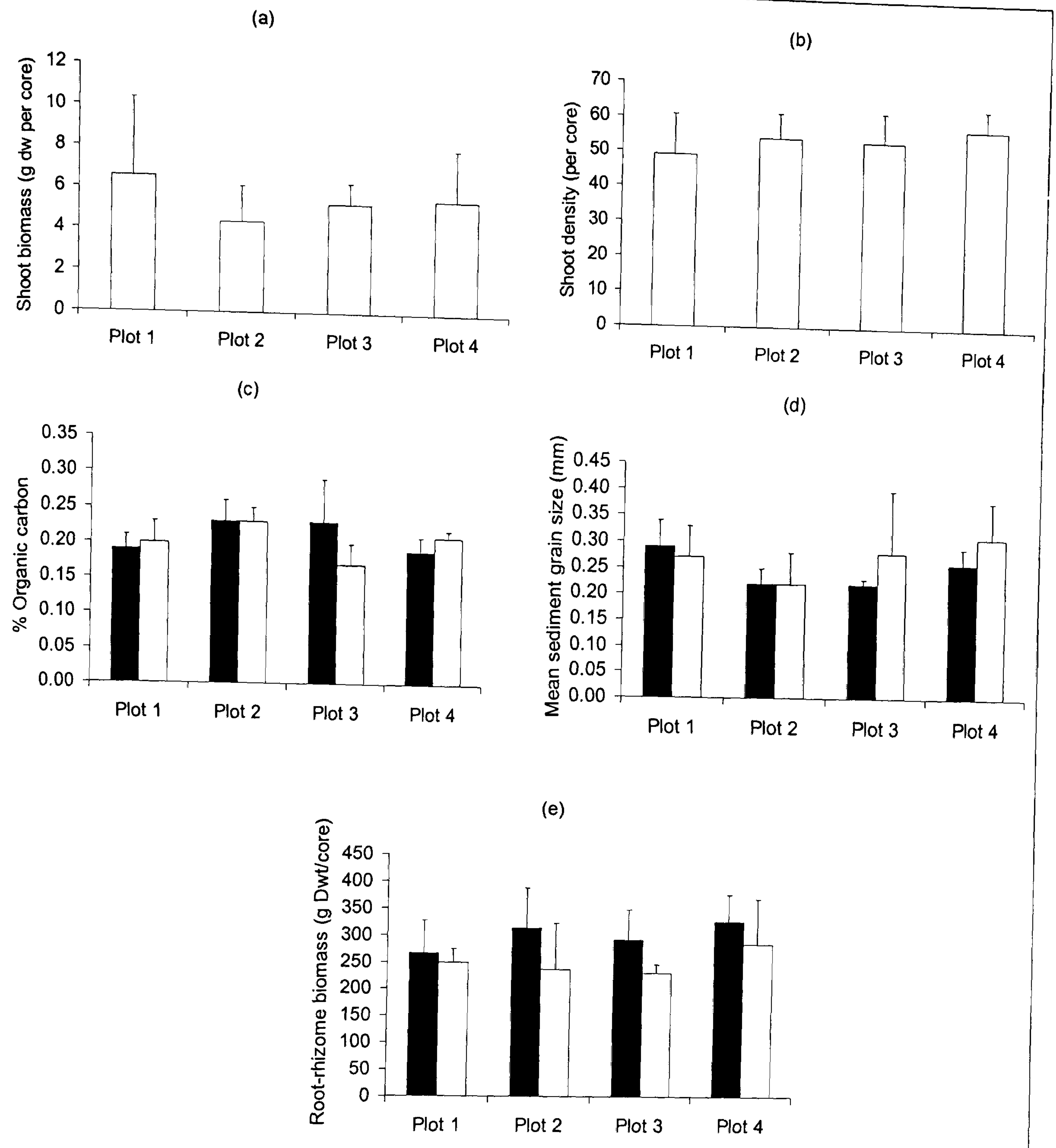


Figure 32. Values of total abundance (a) and total number of species (b) for the major taxa.

One-way ANOVA indicated that leaf biomass (Figure 33a) and shoot density (Figure 33b) were not significantly different between living *P. oceanica* matte in the four plots. No consistent pattern of differences in mean organic carbon content (Figure 33c) and mean grain size of the sediment were evident between living and dead *P. oceanica* matte in the four plots (Figure 33d); the two-factor ANOVA did not indicate any significant differences in these sediment properties between the two matte types (Table 26). Values of dry weight of the root-rhizome fraction of the dead matte were, overall, higher (Figure 33e), although not significantly so (Table 26).



■ Dead *Posidonia oceanica* matte □ Living *Posidonia oceanica* matte

Figure 33. Mean values of shoot biomass (a), shoot density (b), % organic carbon in sediment (c), mean sediment grain size (d) and root-rhizome biomass (e) recorded from the four plots. Error bars are +1 SD.

The NMDS plot gave a clear separation between the two groups of samples collected on living and dead *P. oceanica* 'matte', except for a single sample (L3) taken on living matte, which was an outlier (Figure 34). Furthermore, the NMDS plot indicated that samples collected from living *P. oceanica* matte were less closely grouped together than samples taken on dead matte. The stress level of the NMDS plot (0.11) indicated a god ordination with no prospect of a misleading interpretation (Clarke & Warwick, 1994).

Table 26. Summary of ANOVA results for total organic carbon in the sediment, mean sediment grain size and root-rhizome biomass. The significance of Cochran's test following transformation (where applicable) is indicated. NS = not significant; * = p < 0.05; ** p < 0.01; *** = p < 0.001.

Source of variation	**df**	**% Organic carbon in sediment** n = 4 Transformation: ln(X) Cochran's test: NS			**Mean sediment grain size (mm)** n = 4 Transformation: none Cochran's test: NS			**Root-rhizome biomass (g)** n = 4 Transformation: none Cochran's test: NS		
		MS	F	P	MS	F	p	MS	F	p
Matte type (M)	1	0.151	0.21	NS	0.048	1.73	NS	20034.21	15.30	NS
Plot	3	0.052	2.01	NS	0.007	1.40	NS	4194.55	0.82	NS
M x P	3	0.070	2.73	NS	0.003	0.54	NS	1309.24	0.26	NS
Residual	24	0.026			0.005			5106.46		

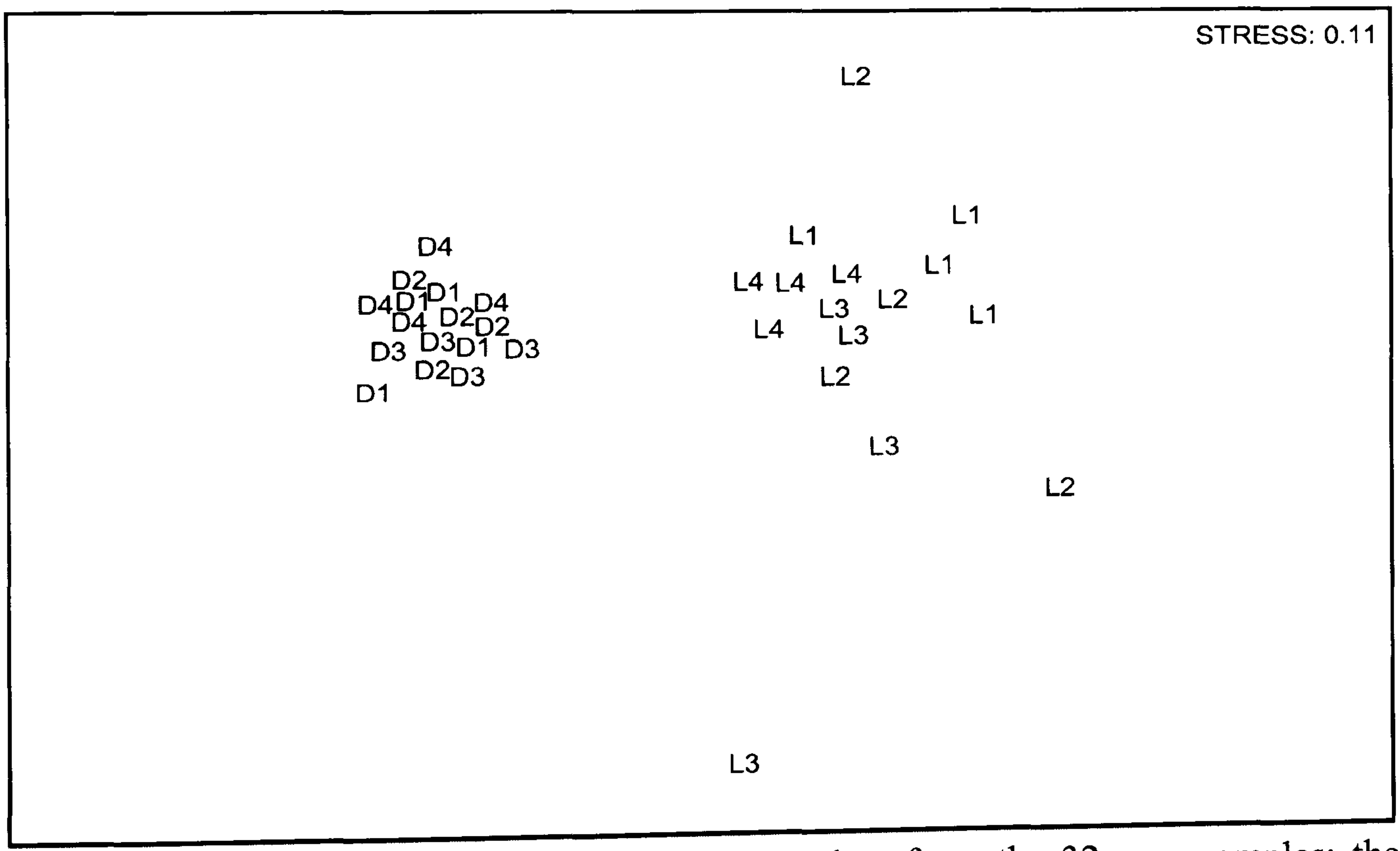


Figure 34. MDS plot for the species-abundance data from the 32 core samples; the letters D and L represent samples taken on dead or living *Posidonia oceanica* matte respectively, while the number indicate the plot from where the respective sample was taken (plots 1, 2, 3 and 4).

The distinct grouping of samples by NMDS was corroborated by the 2-way crossed ANOSIM, which indicated that samples collected on the two matte types were significantly different (Global R = 0.88; p < 0.01). The ANOSIM test also revealed that samples collected from the same type of matte did not differ significantly between the four different plots, for either living or dead *P. oceanica* matte (Global R = 0.054; $p > 0.05$). The species having the highest contribution to the dissimilarity and that discriminate between the two groups of samples taken from the two different matte types, are listed in Table 27. The SIMPER analysis showed that the average dissimilarity value between the two sample groups was 79.81%. The amphipod *Leptocheirus guttatus* (Grube) alone contributed to 11.98% to the dissimilarity, being found only in samples from dead matte. Overall, the observed differences were due to species that were either recorded only from one of the two *P. oceanica* matte types (e.g. the amphipods *L. guttatus* and *Lysianassa costae* Milne Edwards, and the decapod *Galathea bolivari* Zariquiey Alvarez, which were recorded only from dead matte, and the amphipod *Ampelisca* cf. *rubella* A. Costa, which was only recorded from living matte), or to large differences in abundance of species

Table 27. Results of the SIMPER analysis for species having the highest dissimilarity values between the two groups of samples taken from different *Posidonia oceanica* matte types. AA = average abundance (number of individuals per core); AD = average dissimilarity between the two locations being compared; AD/SD = ratio of the average dissimilarity to the standard deviation of dissimilarity for the particular species.

Species	**AA Dead matte**	**AA Living matte**	**AD**	**AD/SD**	**Contribution %**
Leptocheirus guttatus	34.63	0.00	9.56	3.30	11.98
Maera inaequipes	14.50	2.00	3.46	1.46	4.33
Nereis rava	12.88	1.13	3.27	1.89	4.09
Maera grossimana	11.50	2.25	2.63	1.61	3.30
Elasmopus pocillimanus	2.44	8.63	2.31	0.90	2.90
Athanas nitescens	8.94	3.38	1.91	1.08	2.39
Lysianassa costae	6.56	0.00	1.90	1.04	2.38
Anphinomidae sp.	6.69	0.13	1.89	1.88	2.36
Galathea bolivari	5.81	0.00	1.62	1.95	2.03
Syllidae sp. B	7.50	2.25	1.62	1.38	2.03
Aoridae sp.	6.63	8.88	1.58	1.41	1.98
Terebellidae sp.A	5.38	0.25	1.56	1.07	1.95
Cyathura carinata	5.31	0.31	1.39	1.59	1.75
Leptochelia savignyi	5.25	0.50	1.33	1.45	1.67
Leptocheirus bispinosus	5.00	0.38	1.29	1.13	1.61
Alpheus dentipes	5.25	1.00	1.28	1.62	1.60
Liljeborgia dellavallei	0.06	4.13	1.18	1.23	1.48
Pontogenia chrysoscoma	4.63	0.63	1.14	1.47	1.43
Piromis eruca	4.06	0.50	1.09	1.20	1.37
Ampelisca cf *rubella*	0.00	3.75	1.05	1.35	1.32
Amphithoe ramondi	4.13	0.44	1.02	1.34	1.28
Notomastus latericeus	4.13	1.38	0.94	1.01	1.18
Microjassa cumbrensis	1.31	3.69	0.94	1.38	1.18
Cestopagurus timidus	0.44	3.31	0.88	1.17	1.10

between the two matte types (e.g. the amphipods *Maera inaequipes* (Costa) and *Maera grossimana* (Montagu), the decapod *Athanas nitescens* (Leach), and the polychaete *Nereis rava* Ehlers, all of which were more abundant on dead matte, and the amphipod *Elasmopus pocillimanus* (Bate) and *Aora* sp., which were more abundant on living matte) (Table 27).

BIOENV indicated that the environmental attribute that best explained the macroinvertebrate composition was mean sediment grain size ($\rho_w = 0.136$); however, the value of the correlation coefficient was relatively low. On the other hand, no combination of the three environmental attributes achieved a correlation higher than that attained by mean sediment grain size alone.

5.4 DISCUSSION

The present study showed that dead *P. oceanica* matte supported significantly higher species richness and abundance of motile macroinvertebrates than living matte, the observed results being consistent between mattes of the same type across the spatial scale considered. Multivariate analysis indicated that the assemblage composition of the associated motile macroinvertebrates differed significantly between the two matte types, such that many species were recorded exclusively from each of the two habitat types. Based on these results, the null hypothesis of no difference in the species richness and abundance between living and dead matte of *P. oceanica* was rejected. In the study area, *P. oceanica* dead matte supported a higher species richness and abundance of associated motile macroinvertebrates.

Previous studies on the macroinvertebrate assemblages of dead *P. oceanica* matte (Harmelin, 1964; Abada Guerroui & Willsie, 1984; Somaschini et al., 1994) have indicated that the habitat may support a rich macrofauna, both in terms of number of species and abundance. Some of these investigations indicated also that the species composition and structure of the biotic assemblages associated with dead *P. oceanica* matte may vary, depending on matte type and structure (Harmelin, 1964; De Metrio et al, 1978; 1980). For example, De Metrio et al. (1978; 1980) noted differences in the assemblage structure of associated macroinvertebrates between two dead mattes of *P. oceanica* that had different elevation (hence, the two matte surfaces were located at different water depth), while Harmelin (1964) and Abada Guerroui & Willsie (1984) also noted differences in the associated macroinvertebrate assemblages between dead matte located in different water quality regimes.

Univariate analyses indicated that the physical properties of the substratum, namely organic content, grain size and root-rhizome biomass, were not significantly different between the two matte types, nor were these variables strongly correlated with the assemblage composition of macroinvertebrates associated with living and dead matte. Based on these results, the null hypothesis of no difference in the physical attributes examined between living and dead *P. oceanica* matte was accepted. Thus, other factors must be considered to explain the observed difference in the motile macroinvertebrate assemblages of living and dead matte.

The NMDS plot indicated that the motile macroinvertebrate assemblages associated with dead *P. oceanica* matte were more homogeneous than those associated with the living matte. This relative lack of variability between samples could reflect the relatively more 'stable' habitat characteristics of the dead matte. Living *P. oceanica* beds undergo considerable seasonal changes in within-bed structure, characterised by changes in plant growth rates and architectural features (e.g. leaf turnover, biomass etc.; Romero, 1989a), and dynamic epiphyte turnover rates (Alcoverro et al., 1997a), which would influence the structure and composition of associated macrofaunal assemblages accordingly (Gambi et al., 1992). Furthermore, the macrofauna associated with the leaf canopy is expected to be continually exposed to environmental stress, for example hydrodynamic forces cause the shoots to undergo a swaying motion (Fletcher & Day, 1983), which may dislodge the macrofauna, while strong currents may also dislodge and transport small macrofauna away from the bed (Schanz et al., 2000). Exposure to hydrodynamic forces and may also hinder larval recruitment (Luttenton & Rada, 1989). Thus, higher disturbance, leading to a more variable macroinvertebrate assemblage composition associated with the leaf canopy subhabitat (Bianchi et al., 1889; Chimenz et al., 1989) is the probable underlying reason for the observed loose grouping of samples collected from living *P. oceanica* matte. On the other hand, the root-rhizome layer of both dead and living *P. oceanica* matte is less exposed to such environmental stress (Mazzella et al. 1986), although in the case of dead matte, the absence of an overlying leaf canopy may result in greater overall exposure to water movement (e.g. Gambi et al., 1989a).

Other factors then, not considered in the present study, appear to be responsible for the observed significant differences in macroinvertebrate diversity between living and dead matte of *P. oceanica*. Whilst the present results indicate that there is no significant difference between the organic matter content of sediment from living and dead matte, the quality value of this food source for macroinvertebrates could differ between the two bed types. Living *P. oceanica* matte is enriched by detritus resulting from the breakdown of *P. oceanica* leaves (Mateo & Romero, 1997) and from particulate organic matter (POM) suspended in the water column that is intercepted by the leaf canopy, which is thereafter partly deposited on the living matte (Duarte et al., 1999). On the other hand, *P. oceanica* dead matte could be serving as a richer source of detritus for the fauna, for whilst part originates from the leaf canopy of adjacent living seagrass (Mateo & Romero, 1997), organic matter will also originate from the continuously decomposing dead root-rhizome layer (Harrison, 1989; Enríquez et al., 1993). Most of the macroinvertebrates that were recorded in higher abundance from dead *P. oceanica* matte, and which contributed most to the dissimilarity between samples collected from dead and living matte, are predominantly detritivores and deposit-suspension feeders. These include the amphipods *L. guttatus, M. inaequipes, M. grossimana* and *Leptocheirus bispinosus* Norman, the polychaetes *N. rava*, Amphinomidae sp. and Terebellidae sp., the isopod *Cyathura carinata* (Krøyer) and the tanaid *Leptochelia savignyi* (Krøyer) (Wittmann et al., 1981; Scipione, 1999; Gambi et al., 1992). The species identified by SIMPER as high contributors to the samples taken on living *P. oceanica* matte (and good discriminators between living and dead matte) included herbivores and deposit-suspension feeders (e.g. the amphipods *E. pocillimanus*, *Aora* sp., *Liljeborgia dellavallei* Stebbing and *Microjassa cumbrensis* (Stebbing & Robertson); Wittmann et al., 1981; Scipione, 1999). Dead *P. oceanica* matte comprises a high biomass of slowly decomposing roots and rhizomes, part of which would have had its organic composition altered by bacterial action and chemical reactions (Harrison, 1989; Enríquez et al., 1993). Therefore, the resulting chemically modified vegetal matter may be more palatable and readily available for assimilation by the macrofauna (Edgar et al., 1994). Furthermore, burrowing organisms such as the shrimp *Alpheus dentipes* Guérin-Méneville (which was much more abundant in dead *P. oceanica* matte and was identified by SIMPER as an important contributor to the observed differences between the two matte types) may be playing an important role in increasing the amount of detrital matter available for consumption by other macroinvertebrates, through harvesting of seagrass leaves and root-rhizome material, and reworking of the sediment (e.g. Stapel & Erftemeijer, 2000). Since the shrimps ventilate their burrows, they help create an environment rich in organic matter and oxygen, which favours bacterial growth (e.g. Branch & Pringle, 1987) and more rapid decomposition of seagrass (leaf + root-rhizome) tissue to a detrital form that is more palatable and has a higher energy yield for the consumers (the macrofauna of dead matte).

Thus it is possible, as observed in the present study, that there could be no difference in the amount of organic matter between living and dead matte habitat, nor any relationship between simple univariate measures of the associated macroinvertebrate assemblage and the organic matter content, but the dead *P. oceanica* matte habitat would be supplying larger amounts of detritus in a form that is more readily available as food. This may also account for the observed preference of several species (e.g. the decapods *G. bolivari*, *Thoralus cranchii* (Leach)) recorded from the dead matte that usually occur in living *P. oceanica* matte, but which were absent altogether in the latter habitat. These findings suggest that the macroinvertebrates of adjacent living and dead matte of *P. oceanica* may be actively selecting the latter due to the better food supply, but only when the dead matte habitat is immediately adjacent to living matte.

The less compact and spongy texture of the dead *P. oceanica* matte offers much less resistance to burrowers (e.g. the anomuran *G. bolivari* and the shrimp *Upogebia mediterranea* Noël; see Appendix C), while the presence of more hollow spaces and crevices in the dead matte (compared to its living counterpart), will increase microhabitats available to cryptic fauna (Harmelin, 1964; García Raso, 1990; García Raso et al, 1996). For example, the alpheid shrimp *A. nitescens*, the isopod *C. carinata* and the tanaid *L. savignyi*, were all more abundant in samples taken on dead matte, SIMPER indicating these species as high contributors and good discriminators between samples taken on living and dead *P. oceanica* matte. Several workers have emphasised the important role of the physical complexity of the seagrass foliar stratum in enhancing the diversity of associated macrofauna by providing refugia against predation, habitat for larval settlement and growth, and food (see reviews by Heck & Wetstone, 1977; Orth et al., 1984; Virnstein, 1987; Heck & Crowder, 1991; Jernakoff et al., 1996). However, the present results indicate that the root-rhizome layer of *P. oceanica* beds alone (i.e. without the presence of an overlying foliar stratum) can support a very high species richness and abundance of associated macroinvertebrates, possibly because this habitat is characterised by both high structural complexity and stability. Harmelin (1964) had indicated that dead *P. oceanica* matte may support a higher diversity of associated macrofauna by stating that "cette entité biocoenotique est particulièrement bien définie dans le cas des matte mortes qui représentent paradoxalment, le milieau type de la biocoenose". Recently, Somaschini et al. (1994) compared the polychaete fauna of dead and living *P. oceanica* matte, and concluded that dead matte did not support a significantly higher diversity of polychaete fauna than living matte, thereby contending Harmelin's (1964) statement. However, since Somaschini et al.'s study considered only the polychaete taxon, the results of their study cannot be extended to the whole motile macroinvertebrate assemblages associated with dead *P. oceanica* matte. The present findings, however, support the conclusions reached by Harmelin (1964).

The surface of the dead *P. oceanica* matte also serves as a hard substratum, enabling colonisation by algae and other sessile epibiota, whose species composition would resemble that of the photophilic assemblages on hard substrata (e.g. Vaccarella et al., 1981). The epibiota of *P. oceanica* living matte receives less light, being shaded by the overlying leaf canopy, and is therefore sciaphilic in nature (e.g. García Raso et al, 1996). Such differences in the species composition of associated epiphytic assemblages between living and dead matte of *P. oceanica* would be expected to influence the species composition of motile macroinvertebrate grazers that feed on them (Jernakoff et al., 1996; Jernakoff & Nielsen; 1997).

The present results, that dead *P. oceanica* matte resulting from natural disturbance supports a distinct and richer motile macroinvertebrate assemblage than living matte, and which is apparently not correlated to the root-rhizome biomass or physical properties of the sediment (total organic carbon content and grain size) considered in the present study, cannot be generalised to other dead matte habitats which might exist in different environmental conditions (e.g. at different water depths Harmelin, 1964; De Metrio et al., 1978; 1980) or result from death of the seagrass due to pollution (Bellan Santini et al., 1986). The present results do, however, highlight the importance of the matte habitat in its own right (Harmelin, 1964; Vaccarella et al., 1981) and indicate the need for further study to: (i) establish whether the detritus produced by dead matte is more palatable to the associated macrofauna than that originating from living matte; (ii) examine for positive correlations between the structural complexity of dead matte and the species richness and abundance of associated macrofauna; (iii) determine whether the epiphytic assemblages of dead matte provide better habitat or food than living matte; (iv) determine whether dead matte is more suitable for burrowing infauna than living matte; and (v) establish whether the species richness and abundance of macrofauna associated with dead matte varies with distance from living matte of *P. oceanica.*

The unfortunate labelling of one of the *P. oceanica* matte habitat types as 'dead', could easily lead to general acceptance that this habitat type supports a lower biodiversity and is of low conservation importance. Clearly, the present data indicate otherwise. Furthermore, the present results and those of other studies (e.g. Harmelin, 1964; De Metrio et al.; 1980) show that some of the species that occur in dead *P. oceanica* matte are rare, making this habitat of potentially high conservation value. For example, De Metrio et al. (1978; 1980) recorded a number of species from this habitat (e.g. the serpulid polychaete *Hydroides helmatus* (Iroso) and the gastropod *Tectonatica filosa* (Philippi)), which they considered very rare. Loss of the foliar canopy can be considered as the most extreme form of fragmentation of *P. oceanica* habitat. However, the present findings show that even this extreme fragmentation may not necessarily result in a loss of diversity (with respect to number of species) of the associated macrofauna, though clearly the assemblage composition changes.

Seagrass habitats are undergoing a worldwide decline as a result of both natural and anthropogenic disturbances (Short & Wyllie Echeverria, 1996; Green & Short, 2003; Procaccini et al., 2003), and beds of *P. oceanica* are no exception; regression is apparent throughout the Mediterreanean Sea, in particular the western parts (Pérès, 1984; Marbá et al., 1996). Studies that relate to the fragmentation of *P. oceanica* beds and the diversity of associated biota are, therefore, essential to understand the consequences of loss of this habitat and to provide coastal managers with useful data on which to base appropriate management and conservation strategies. Thus, the results of the present study and those of a related study (Chapter 4) can be utilised towards this end.

CHAPTER 6

GENERAL DISCUSSION

6.1 INTRODUCTION

A huge effort has been made to increase knowledge of seagrass biology and of the ecology of seagrass habitats, and the available literature is very vast. However, investigations of the role of seagrass bed structure in influencing the diversity of associated biota have often yielded results that lack agreement. Researchers have proposed that different factors influence the species richness and abundance of macrofauna associated with seagrass beds, including shelter against predation (Heck & Orth, 1980a), use as habitat and nursery areas for settlement of larvae and growth of juveniles (Heck & Thoman, 1984; Bell & Westoby, 1986a, b; Heck et al., 1989) and provision of food (e.g. van Montfrans et al., 1984; Klumpp et al., 1989; Schneider & Mann, 1991; Mateo & Romero, 1997; Nelson, 1997; Vizzini et al., 2002). On the other hand, recent data suggest that the species richness and abundance of macroinvertebrates associated with seagrass beds may follow a simple space-occupancy model in which increase in habitable area (e.g. leaf surface) leads to an increase in macroinvertebrate diversity, hence, a 'sampling artifact' may be present (Attrill et al., 2000).

The lack of concordance of results between different studies may also be attributed to the following: (i) adoption of different sampling techniques, hence hindering comparison of results; (ii) use of inadequate and/or inefficient samplers; (iii) use of experimental designs that are undermined by lack of consideration of spatial variation and/or by the presence of confounding factors; and (iv) lack of acknowledgement of the complex nature of seagrass ecosystems (e.g. Livingston, 1984). In many cases the last has led workers to inappropriately: (a) generalise and extrapolate the conclusions reached for a particular seagrass bed in one geographical area/spatial level to those of seagrass beds of the same or of different species in a different geographical areas/spatial level; and/or (b) attempt to single out 'a main factor' responsible for the observed high biodiversity characterising seagrass beds. Progress towards an understanding of the ecology of seagrass beds, which is essential for the eventual implementation of effective conservation and management of seagrass habitats (Virnstein, 1995; den Hartog & Phillips, 2001), depends on knowledge of the more fundamental aspects of the habitat, such as those underlying the dynamics of seagrass coverage, the processes that determine variation in bed morphology and architecture, the factors that control colonisation and habitat use by the associated biotic assemblages, and the scales at which such factors operate. Data on processes that influence the species composition and structure of biotic assemblages associated with seagrass beds, will, undoubtedly, help in assessing the magnitude of habitat loss and associated biodiversity that may result from anthropogenic disturbance of seagrass ecosystems.

A major concern, that has important direct ecological and economical implications, is the loss of biodiversity that may result from the alteration of seagrass bed structure due to anthropogenic disturbance; for example, those brought about by fragmentation of large continuous beds into smaller patches and the subsequent observed or presumed concomitant changes in within-bed structure (e.g. Lewis, 1984; Robbins & Bell, 1994; Reusch, 1998; Hovel et al., 2002). Well-documented causes of anthropogenic disturbance of seagrass habitats that lead to fragmentation include the deployment of boat moorings (Hastings et al., 1995), anchoring (e.g. Francour et al., 1999), trawling (e.g. Martín et al., 1997) and eutrophication (Nienhius, 1983; Walker & McComb, 1992; den Hartog & Phillips, 2001). While several studies (Irlandi, 1994; 1997; Irlandi et al., 1995; Hovel & Lipcius 2001, 2002; Frost el al., 1999; Bowden et al., 2001; Barberá Cebrián et al., 2002) have addressed the role of fragmentation of seagrass beds on the associated fauna, very few (Frost el al., 1999; Bowden et al., 2001) have considered the 'whole' macrofaunal assemblage associated with both leaf stratum and root-rhizome layer. Where available, the results of such investigations tend to lack agreement as to the degree of influence of fragmentation on seagrass-associated fauna (e.g. Irlandi, 1994; 1997; Frost el al., 1999;

Bowden et al., 2001), possibly because of lack of consideration of more than one spatial level during study (Robbins & Bell, 1994; Bell et al., 2001), or perhaps because other important aspects, such as the degree of isolation of seagrass fragments (e.g. Hovel & Lipcius, 2002), have not been taken into account.

Nevertheless, recent reviews have concluded that published data do not show compelling evidence that fragmented seagrass beds support a lower diversity than non-fragmented ones (e.g. Bell et al. 2001), which potentially supports Haila's (2002) view that habitat fragmentation has received excessive attention and the subject is more of an 'intellectual attractor' than an ecological reality. On the other hand, given the alarming rate at which loss of seagrass habitat is occurring worldwide (Short & Wyllie Echeverria, 1996; Ruckelshaus & Hays, 1998), the possible loss of biodiversity that may result from anthropogenic fragmentation of seagrass habitats cannot be ignored. Knowledge of the composition of biotic assemblages associated with different seagrass bed types and within-bed architecture, and how the relationships between the two vary across spatial (and temporal) scales, will help quantify the loss of biodiversity that may result from the fragmentation of seagrass habitat, and in predicting recovery of biodiversity during attempts at habitat restoration.

The present chapter aimed to (i) integrate the results and interpretations made in the preceding studies with current knowledge of the influence of seagrass bed structure on the associated macrofauna, and (ii) examine current conservation guidelines; hence, enabling assessment of the implications for conservation and management of *Posidonia oceanica* (Linnaeus) Delile beds in the Maltese Islands and the rest of the Mediterranean. The chapter also aimed to present conservation proposals and recommendations for further research, which will help Mediterranean conservation biologists and environmental managers to update current conservation guidelines, propose new conservation measures and identify related issues that require further investigation for *P. oceanica* habitat.

6.2 STUDIES OF THE ROLE OF *POSIDONIA OCEANICA* BED STRUCTURE IN INFLUENCING ASSOCIATED MACRO-INVERTEBRATE ASSEMBLAGES

The present research, which addressed the influence of seagrass bed structure on the diversity of associated motile macroinvertebrate assemblages, was carried out on beds of *P. oceanica* in the Maltese Islands because: (i) this species produces some of the most morphologically and structurally complex seagrass beds worldwide (Buia et al., 2000), including ones found in Malta (Borg & Schembri, 1995b) and, therefore, provides an ideal candidate for investigating the role of seagrass bed type and within-bed structure on the associated fauna; (ii) data comparing plant architecture and the composition of the macroinvertebrate assemblages associated with different bed types of this seagrass are lacking; (iii) the endemic *P. oceanica* forms the largest and most widespread seagrass beds in the Mediterranean, which constitute one of the most important shallow-water habitats in this sea (Boudouresque et al., 1994); and (iv) *P. oceanica* habitats are seriously threatened by the intense anthropogenic activities that prevail in the region (Procaccini et al., 2003), hence, there is an urgent need for the assessment and subsequent implementation of appropriate conservation measures and management strategies for beds of this seagrass.

Ultimately, effective habitat conservation and management (Grumbine, 1994) depend on knowledge of the influence of changes in the structure of *P. oceanica* beds on the associated biotic assemblages, and on assessment of the relative ecological value (e.g. in terms of biodiversity supported) of different bed types of this seagrass. Therefore, the present study addressed the fundamental aspects of the influence of *P. oceanica* bed structure on the associated assemblages of motile macroinvertebrates, namely, whether: (a) continuous (non-fragmented) and reticulate (fragmented) beds of *P. oceanica* differed in their plant architectural characteristics; (b) assemblages of associated motile macroinvertebrates differed between continuous and reticulate beds of *P. oceanica*; and (c) assemblages of associated motile macroinvertebrates differed between *P. oceanica* beds that have been completely defoliated (dead matte) and others that have retained the foliar stratum (living matte).

Given the importance of considering different spatial scales in ecological experiments, the present study was carried out across different spatial levels, which varied between several kilometres to a few tens of metres. Appropriate study locations, which as far as practicality would allow, had similar environmental characteristics and, hence, enabled unconfounded comparison of the different bed types of *P. oceanica* across the chosen spatial levels, were selected following an extensive pilot survey. Furthermore, as part of the pilot study, the construction and testing of a sampler, specifically designed to sample the motile macroinvertebrates of *P. oceanica* beds, enabled efficient and precise sampling of the total associated macroinvertebrate assemblages (Chapter 2).

The absence of significant differences in plant architectural features between the continuous and reticulate beds of *P. oceanica* studied suggests that the presence of bare sand areas interspersed amongst the latter bed type does not influence the growth pattern and plant architecture of the seagrass (Chapter 3), despite the fact that plants in such a bed type would presumably be more exposed to adverse factors such as water movement (Fonseca & Bell, 1998), siltation (Gacía & Duarte, 2001) and grazing by megafauna (Alcoverro et al., 1997a). While reticulate beds have a greater edge: area ratio compared to continuous beds, the present results and data from the published literature indicate that differences in attributes of seagrass architecture resulting from 'edge effects' do not extend to the core of the bed (irrespective of bed type) and, hence, appear to be restricted to the bed periphery, probably within a distance of around 1 m from the latter (Duarte & Sand-Jensen, 1990; Irlandi, 1997; Hovel & Lipcius, 2001; Bowden et al., 2001).

Comparison of macroinvertebrate species richness, abundance, and assemblage composition between continuous and reticulate beds of *P. oceanica* also showed that the associated macroinvertebrate fauna did not differ significantly between the two bed types (Chapter 4), thereby, indicating that fragmentation of continuous seagrass beds to reticulate beds does not necessarily lead to a decrease in the diversity of macrofauna, as has been reported for fragmented terrestrial habitats (e.g. Wilcox & Murphy, 1985; Andrén, 1992). The latter result is not surprising, given the observed similarity in plant architectural features between the two bed types, for seagrass within-bed structure has been shown to be an important determinant of the diversity of associated macrofauna (Heck & Wetstone, 1977; Heck & Orth 1980a; Tolan et al., 1997; Webster et al. 1998). As in the case of plant architecture, despite the greater edge: area ratio of reticulate beds compared to continuous beds, the present results and those obtained by other workers (e.g. Irlandi et al., 1995; Bologna, 1998) indicate that differences in the species richness and abundance of seagrass-associated macroinvertebrates resulting from 'edge effects' do not extend to the core of the bed (irrespective of bed type, and are probably restricted to the bed periphery, probably within a distance of around 1 m from the latter (e.g. Irlandi et al., 1995; Bologna, 1998). However, the results (Chapter 4) indicated also that *P. oceanica* in different localities, but having similar plant architectural characteristics, supported different assemblages of associated macroinvertebrates.

At the large spatial level, macroinvertebrate species richness and abundance were correlated with epiphyte biomass. Epiphytes enhance macrofaunal diversity by increasing micohabitat complexity (Heck & Orth 1980a; Greening & Livingstone, 1982; Hall & bell, 1988; Worthington et al., 1991) and by providing food (van Montfrans et al., 1984; Schneider & Mann, 1991; Jernakoff et al., 1996; Jernakoff & Nielsen, 1997; Bologna & Heck, 1999). The higher abundance of epiphytes recorded from White Rocks and St Thomas Bay (which was significantly related to higher macroinvertebrate species richness and abundance) resulted, possibly, from higher nutrient concentrations in coastal waters in the southern half of the Maltese Islands (Axiak et al., 2000; Axiak & Sammut, 2002). The observed significant correlation between the diversity of macroinvertebrates associated with beds of *P. oceanica* and seagrass epiphyte load has important regional implications. The Mediterranean Sea is oligotrophic (Estrada et al., 1985) and, therefore, moderate increases in nutrient concentrations will increase primary production (in the case of *P. oceanica* beds this would mostly be epiphyte production), therefore, enhancing the physical complexity of microhabitat (the epiphyte layer) and increasing food supply within beds of the seagrass (Jernakoff et al., 1996). In turn, increased epiphyte abundance enhances the diversity of grazer assemblages, leading to enhanced secondary production and efficiency of resource use (Duffy et al., 2003). The increased secondary production has particular implications where crustaceans are involved, since crustacean mesograzers dominate the diets of shallow-water fishes (Edgar & Shaw, 1995); an increase in abundance of crustaceans may enhance trophic transfer up the food chain, hence, potentially increasing fishery yields. However, excessive nutrient loading may lead to excessive epiphytic growth on *P. oceanica*, which may hinder movement of the larger macrofauna within the beds (e.g. Bartholomew et al., 2000), leading to reduced macrofaunal diversity. Severe reduction in the amount of light reaching the seagrass due to shading by epiphytes (Silberstein et al., 1986, Buzzelli & Meyers, 1998), may lead to death of the seagrass and potential loss of the habitat (den Hartog, 1994; Hemminga, 1998; den Hartog & Phillips, 2001; Dimech et al., 2002).

The significant relationship between the species richness of macroinvertebrates associated with *P. oceanica* beds and mean sediment grain size (at the large spatial scale), highlighted the importance of this physical measure in influencing the diversity of seagrass-associated macrofauna, in particular the infauna, as has been indicated by other workers (e.g. Frost et al. 1999). The sediment characteristics of a particular locality are influenced strongly by the hydrodynamic regime (Pihl, 1986; Fonseca & Bell, 1998) and the same applies for other environmental attributes, including supply of nutrients (e.g. Schanz et al., 2000). Therefore, local environmental factors, namely the hydrodynamic regime (O'Gower & Wacasey, 1967; Orth, 1977; Pihl, 1986; Scipione, 1999), epiphyte load and mean sediment grain size, all appear to be important in influencing the diversity of motile macroinvertebrates associated with *P. oceanica* beds, at large spatial levels. At the spatial level of a few hundred metres, the present results indicated that seagrass shoot biomass and epiphyte biomass were important in influencing the abundance of macroinvertebrates associated with *P. oceanica* beds, while shoot biomass on its own was important in influencing macroinvertebrate species richness. However, the significant relationships detected at this spatial level appear to have resulted from species-area relationships and not from the direct influence of seagrass shoot biomass and/or epiphyte biomass on macroinvertebrate species richness and abundance. At the small spatial level of tens of metres, no positive correlation was found for any specific factor. Different factors, therefore, which are independent of bed type, may influence the diversity of macrofauna associated with seagrass beds, depending on the spatial scale considered (Chapter 4).

The results of the comparison of motile macroinvertebrate assemblages between living and dead *P. oceanica* matte indicated a distinct difference between bed types near the extreme ends of the fragmentation gradient and, to some extent, the findings were unexpected. The present findings indicate that assemblage composition of macroinvertebrates associated with dead matte of *P. oceanica* is very dissimilar to that of living matte and that dead matte can support a higher diversity of associated macroinvertebrates. The higher species richness and abundance of macrofauna recorded from dead matte may be due to greater availability of detrital matter and a higher matte structural complexity, however, such propositions remain untested (Chapter 5).

6.3 EVALUATING CURRENT CONSERVATION AND MANAGEMENT PRACTICES FOR *POSIDONIA OCEANICA* BEDS

Because of their high productivity, biodiversity and vulnerability to natural and anthropogenic threats, many countries have adopted strict measures to protect seagrass beds (see Green & Short, 2003, and reviews therein), sometimes in combination with special conservation and management programmes (e.g. Pulich et al., 1997). *Zostera marina* Linnaeus is the most abundant seagrass in the northern hemisphere (Hemminga & Duarte, 2000). The Atlantic coast of Europe supports extensive *Z. marina* beds, which, therefore, constitute the single-most widespread seagrass habitat in many countries of western Europe (den Hartog, 1970). Consequently, some of these countries have adopted conservation measures for *Z. marina* beds. For example, in the United Kingdom, areas with this seagrass habitat are protected in many coastal sites by being included in several Nature Reserves (e.g. Buck, 1997). Furthermore, *Z. marina* beds are included in the UK Habitat Action Plan for seagrass beds, which outlines conservation and protection measures for all seagrass beds in the United Kingdom (e.g. Holt et al., 1997). Indeed, *Z. marina* beds are widely protected throughout Europe since: (i) they are frequently included in Special Protected Areas that have been established under the EU's Bird Directive (79/409/EEC); and (ii) *Z. marina* is a named component of coastal lagoons which constitute a priority habitat under the EU's Habitats Directive (92/43/EEC). Indirectly, it is also protected where it occurs in the following 'Annex I' habitats of the same EU

Directive: (a) shallow sandbanks slightly covered by seawater all of the time; (b) large shallow inlets; (c) estuaries; (d) sandflats not covered by seawater at low water.

Beds of *P. oceanica* have even stricter protection measures than *Z. marina*, since they are listed in Annex I of the EU's Habitats Directive (92/43/EEC) on the Conservation of Natural Habitats and of Wild Fauna and Flora (the 'Habitats Directive'), which require the designation of Special Areas of Conservation, and are further designated as 'Priority Habitat' (EEC, 1992). In addition, *P. oceanica* is included in Appendix I (strictly protected flora) of the Bern Convention on the Conservation of European Wildlife and Natural Habitats and in Annex II (endangered and threatened species) of the Protocol Concerning Specially Protected Areas and Biological Diversity (SPABIM) in the Mediterranean. Despite the diversity of regulations, *P. oceanica* lacks protection in many parts of the Mediterranean since: (i) the EU Habitats Directive does not apply to non-EU countries, and therefore excludes all North African and southeast European Mediterranean countries that also border the Mediterranean Sea; and (ii) not all Mediterranean countries are signatories to the SPABIM Protocol. Furthermore, the general tendency has been for a few Mediterranean states, particularly those that have led *P. oceanica* research (namely: France, Italy and Spain), to formulate their own legislation on an *ad hoc* basis, to protect seagrass beds in their country (Buia et al., 2003).

With regard to the EU regulations for protection of *P. oceanica*, the large variation in seagrass bed morphology of this seagrass poses serious difficulties in interpretation of the regulations, since they do not specify whether they apply to all bed types, nor do they define the way in which a *P. oceanica* 'bed' is defined. For example, while it may seem obvious that continuous and largely homogeneous beds of *P. oceanica* qualify for protection, do the regulations apply also to fragmented beds and patches of the seagrass? A recently published manual on methods for the study of the Mediterranean benthos (Gambi

& Dappiano, 2003) includes a comprehensive review of methods to study Mediterranean seagrasses and seagrass bed habitats (Buia et al., 2003) and a review of the various classifications of *P. oceanica* bed types. Buia et al. (2003) listed four classifications, as follows: (i) according to the substratum on which the seagrass grows, namely sand, rock, or biogenic, the latter mainly referring to the *P. oceanica* matte; (ii) whether monospecific or polyspecific; (iii) according to coverage, namely homogeneous or heterogeneous; and (iv) according to bed morphology. The latter classification includes several bed types that have been described in the literature from various Mediterranean countries (Table 28). However, despite being the most comprehensive classification available in the published literature, Buia & Dappiano (2003) omit the following important *P. oceanica* bed types: (i) patchy beds on sand/matte; (ii) reticulate beds growing on sand/matte; (iv) reticulate beds growing on bedrock; and (v) dead matte.

Table 28. List of different *P. oceanica* bed types, as given in Buia et al. (2003).

***Posidonia oceanica* bed type**	**Description**
Continuous	Continuous bed growing on homogeneous matte
Sugar loaf	Continuous bed growing on a non-homogeneous matte, such that different parts of the bed are more elevated than others.
Terraced	Continuous bed growing on matte, but having a terraced relief
Cordon	Beds having a cordon morphology in which the *P. oceanica* alternates with sand channels and usually aligned perpendicular to the shore
Striped (or banded) beds	Similar to cordon beds, but their orientation is usually parallel to the shore
Patchy beds (on rock)	Patches of seagrass growing on bedrock (and sometimes on large boulders)
Hillocks	Small, hill-shaped patches growing on matte, surrounded by bare sand
Barrier reef	Bed forming a continuous reef structure in shallow waters close to the shore, sometimes enclosing a body of water between the shore and the reef which has lagoon-type characteristics
Fringe barrier reef	The precursor of a *Posidonia* barrier reef, distinguished from the latter by the absence of a lagoon
Atoll	A ring-shaped bed growing on matte, having sparse seagrass toward its centre

The RAC/SPA[1] bioceonosis classification scheme used for the SPABIM protocol, which is based on one elaborated for French Atlantic and Mediterranean coasts (Dauvin, 1994),

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[1] Regional Activity Centre for Specially Protected Areas. The RAC/SPA scheme was prepared by a meeting of experts on Mediterranean marine habitat types convened by RAC/SPA and held in Hyères (18-20 November, 1998). It was subsequently finalized by the Fourth Meeting of Focal Points for Specially Protected Areas (Tunis, 12-14 April 1999) and was ultimately adopted by the Eleventh Meeting of the Contracting Parties (Malta, 27-30 October 1999).

revised and adapted for the specificities of the French Mediterranean zone and then extended to the whole of the Mediterranean Sea to meet the needs of SPABIM, lists the following *P. oceanica* bed types:

- Ecomorphosis (≅ bed type) of *P. oceanica* striped meadows.
- Ecomorphosis (≅ bed type) of *P. oceanica* 'barrier reef' meadows.
- Ecomorphosis (≅ bed type) of *P. oceanica* dead matte without much epiflora.
- Association (≅ bed type) of *P. oceanica* meadows with *Caulerpa prolifera* (Forsskal) Lamouroux.

Clearly, the above classification is far from complete, especially when compared to Buia et al.'s (2003) list and the findings of this study (Chapter 2). The incompleteness of the RAC/SPA scheme was acknowledged recently by a number of delegations at the RAC/SPA Meeting of Experts held in Rome[2]. As it is the only available international classification that lists different bed types of *P. oceanica*, the RAC/SPA scheme is frequently referred to and expanded upon, when Mediterranean seagrass ecologists and coastal managers raise the subject of conservation and protection of different bed types of this seagrass. For example, in their report on alignment of marine habitat data to the requirements of the EU Habitats Directive, Borg & Schembri (2002) used the RAC/SPA scheme for different bed types of *P. oceanica*, but emphasise several problems with this. Borg & Schembri (2002) noted that, of the four *P. oceanica* bed types listed in the RAC/SPA scheme, only three occurred in the Maltese Islands, the striped (or banded) beds had not yet been recorded locally. Furthermore, Borg & Schembri (2002) noted that a number of other distinctive so-called 'ecomorphoses' (bed types) that occurred in the

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[2] Meeting of experts for the finalisation of the Standard Data-Entry Form (SDF) for national inventories of natural sites of conservation interest. Rome, 23-24 March 2000.

Maltese Islands, were not listed in the official RAC/SPA classification, and new categories were added for local use, as follows:

- Ecomorphosis of continuous *P. oceanica* meadows on bedrock with enclaves of photophilic algae.
- Ecomorphosis of continuous *P. oceanica* meadows on sand with enclaves of bare sand.
- Ecomorphosis of reticulate *P. oceanica* meadows on sand with enclaves of bare sand.
- Ecomorphosis of continuous *P. oceanica* meadows on bedrock with enclaves of sciaphilic algae.
- Complex of: Ecomorphosis of reticulate *P. oceanica* on bedrock with enclaves of bare sand, mixed with the Association of *Peyssonnelia squamaria* (Gmelin) Decaisne and *Flabellia petiolata* (Turra) Nizamuddin.
- Complex of: Ecomorphosis of reticulate *P. oceanica* on bedrock with enclaves of bare sand, mixed with the Association of *Dictyopteris polypodiodes* (De Candolle) Lamouroux.
- Complex of: Ecomorphosis of reticulate *P. oceanica* on bedrock with enclaves of bare sand, mixed with the Association of *Cystoseira* spp.

In particular, these authors found difficulty in defining a unit that consists of what is effectively a mixture of two distinct habitat types (for example, an association of macroalgae on rock interspersed with a particular *P. oceanica* bed type). To solve this problem, Borg & Schembri (2002) introduced the concept of a 'complex of habitats', as in the last four listed above. In another example, the set of proposed recommendations for the classification of different *P. oceanica* bed types, published in the official bulletin of the Italian Marine Biological Society (Notiziario S.I.B.M., 2003), following the 2003 National Convention of the same society, refer to the *P. oceanica* bed types listed in the RAC/SPA scheme and include an additional classification of the various bed types of this seagrass according to value (Table 29). While the recommended valuation scheme gives equal ecological status to the different listed bed types of *P. oceanica*, and this is supported by the findings of the present study, it gives a much lower value to dead matte of *P. oceanica*; which is contrary to the findings of the present study.

Table 29. Evaluation criteria proposed during the 2003 meeting of the Italian Marine Biological Society for different bed types of *P. oceanica* listed in the RAC/SPA scheme. V = vulnerability; VP = ecological/heritage value; R = degree of rarity; Es = aesthetic value; Ec = Economic value; C = classification (D = key habitat; R = habitat considered important; NR = habitat of low importance). 1 = high; 2 = medium; 3 = low.

P. oceanica bed type	V	VP	R	Es	Ec	C
'Praterie a *Posidonia oceanica*' = *P. oceanica* beds.	1	1	2	1	1	D
'Facies dei rhizomi morti (mattes mortes) di *Posidonia oceanica* senza epiflora' = ecomorphosis of dead matte of *P. oceanica* without epiflora.	2	3	2	3	3	NR
'Ecomorfosi di praterie a bande' = ecomorphosis of striped (or banded) beds of *P. oceanica.*	1	1	2	1	1	D
'Ecomorfosi di praterie a barriera' = ecomorphosis of *P. oceanica* reefs.	1	1	2	1	1	D

A main problem underlying the formulation of such classification schemes is the lack of data on the ecological value of different seagrass bed types, while adoption of these classification schemes for local use in various countries poses difficulties due to the unavailability of a comprehensive classification of different bed types of *P. oceanica* for the whole Mediterranean. Attempts at giving a 'face value' to different bed types of the seagrass appears to be premature at present, given the dearth of ecological data on different bed types. While the reasons underlying such value-weighting classifications are well intended, there are dangers, since such an exercise could be misleading or even counter-productive if there is insufficient information on which to base them. The present findings suggest that the various bed types (continuous, reticulate, dead matte) of *P. oceanica* all appear to have a high ecological value, yet all form an integral part of a heterogeneous dynamic landscape having interchangeable components. For example, in unfavourable conditions, living matte of *P. oceanica* may change to dead matte, but the latter may eventually be recolonised by living shoots when favourable conditions return. Hence, an equal effort should be directed at protecting and conserving different bed types of *P. oceanica*, and in restoring them following damage.

Overall, the present study has provided information for drawing conservation and management programmes for beds of *P. oceanica*, and for the revision of existing ones, including international ones, such as that administered by RAC/SPA. Besides continuous *P. oceanica* beds, reticulate beds and dead matte of the seagrass support a high biodiversity, although the latter is in many respects a temporary habitat, presumably moving towards bare sand. Using the present results, Mediterranean coastal managers can argue in favour of adopting conservation measures for reticulate beds and dead matte of *P. oceanica* that are similar to those proposed for continuous and living matte of the seagrass (Notiziario S.I.B.M., 2003). Current international schemes listing different bed types of *P. oceanica* having a high ecological value should be amended to include ones (e.g. reticulate beds and dead matte) that have been indicated by the present study as being equally important, hence requiring equal protection.

In the more local context, the present study has contributed valuable data for a better understanding of the ecology of *P. oceanica* beds in the Maltese Islands. Few studies of the ecology of the macrofauna associated with local *P. oceanica* beds are available (Borg & Schembri, 2000; Howege, 1998), and none deals with the 'whole' macroinvertebrate assemblages. Generally, the motile macroinvertebrate assemblages recorded from the present study are similar to those recorded from Italian (e.g. Mazzella et al., 1989; Gambi et al., 1995; Scipione, 1999) and Spanish (e.g. García Raso, 1990; Sánchez Jerez at al., 2000) *P. oceanica* beds. The present findings have confirmed the similar ecological and economic value of continuous and reticulate beds of *P. oceanica*, which has traditionally been recognised also by local fishermen, who consider both bed types as important fishing grounds (hence, an indication of their high productivity). In general, members of the local community have viewed fragmented beds as having a lower ecological value than continuous beds. However, the general public sector is less likely to have a developed understanding of seagrass habitats than fishermen. Community knowledge of traditional uses of seagrasses and of the socio-cultural values of seagrass bed habitats, such as that obtained from fishermen, may form the basis for increased success in efforts to protect the habitat (Wyllie Echeverria et al., 2002). In Malta, coastal managers have frequently requested advice on the 'relative ecological value' of the two different bed types, particularly when required to make decisions on coastal development projects that would directly affect fragmented beds located inshore, but their requests could not be met. The present results will, therefore, help local managers to make more informed decisions when dealing with coastal projects that may affect beds of *P. oceanica* by considering fragmented beds and 'dead' matte as having a high ecological value, as has been acknowledged to date for non-fragmented beds of the seagrass.

The present findings will also help in formulating mitigation measures and restoration programmes for *P. oceanica*. Mitigation measures should apply to any bed type of the seagrass, given the similar ecological value of the various bed types. Once a particular anthropogenic activity is identified as having a significant adverse impact on *P. oceanica* beds, the source of disturbance should be eliminated or reduced to a level that does not cause further damage to the habitat. Where damage has already occurred, for example, where a continuous bed has been transformed to a reticulate one, or where only dead matte remains, the altered bed should not considered as lost completely and efforts at restoration (den Hartog, 2000) are still worth attempting. Restoration should, therefore, not be necessarily aimed solely at regenerating areas where homogenous or continuous beds were once present, especially given the low rates of success in regenerating seagrass beds in areas where environmental conditions have been appreciably altered (den Hartog, 2000). The difficulties in regenerating beds of slow-growing seagrasses such as *P. oceanica*; regeneration of seagrass patches or reticulate beds, may equally lead to a valuable habitat. In the case of dead *P. oceanica* matte, restoration attempts through transplantation may yield better results than have been achieved to date on sandy substrata, since the root-rhizome matte may offer better anchorage for newly-transplanted shoots until they have taken root and established themselves.

In conclusion, present results indicate that fragmented seagrass beds should not be viewed as isolated habitat fragments, but as part of a hierarchical arrangement of different bed types in a heterogeneous seagrass landscape (Robbins & Bell, 1994). Continuous and reticulate beds of *P. oceanica* appear to have broadly similar plant architectural features and support a similar biodiversity of associated motile macroinvertebrate assemblages. While plant architecture may be important in influencing the diversity of macroinvertebrates associated with other seagrass beds, edaphic factors have also been identified has having a potentially overriding importance (Hemminga & Duarte, 2000). Local environmental factors, including nutrient concentrations in the water column and hydrodynamic processes (O'Gower & Wacasey, 1967; Orth, 1977; Pihl, 1986; Fonseca & Bell, 1998), appear to be more important in influencing the diversity of macrofauna associated with *P. oceanica* beds, leading to spatial variation in the faunal assemblage structure. It is possible, that for those seagrasses having a high structural complexity including *P. oceanica,* alteration of plant architectural features may not necessarily have the same impact on the associated biota as would physical changes in seagrass beds having a lower structural complexity as, for example, *Z. marina* beds. The present findings indicate that the influence of the root-rhizome compartment of seagrass beds on the associated diversity of macrofauna may be considerable, especially for seagrass beds that have a very thick matte, such as *P. oceanica*. Classifications of different bed types of *P. oceanica* in categories according to 'ecological value' appear to be counterproductive and should be avoided, since all bed types form part of a heterogeneous dynamic landscape (Fonseca & Bell, 1998) that incorporates interchanges and transitions between different seagrass bed forms, hence, an equal conservation effort should be directed at them all. Given the current lack of success in restoration of seagrass habitat by transplantation where

P. oceanica beds have been adversely impacted and degraded by anthropogenic activities, appropriate legislation should be enacted to ensure that the source of disturbance is removed, or reduced to a level that is acceptable for ensuring health and survival of *P. oceanica* as a habitat of great importance to the coastal ecosystem of the Mediterranean Sea.

6.4 RECOMMENDATIONS

In view of the present findings, the following recommendations for future research are proposed:

1) Reviews of the published data (e.g. Bell et al., 2001), and the results of this study, indicate that, in general, fragmented and non-fragmented seagrass beds (i.e. beds of different morphology) appear to have similar ecological value. However, to ascertain whether this proposition is generally true, it is necessary to conduct studies of biotic assemblages in different geographical areas. Further study also needs to be made since the conclusions reached based on investigations of natural fragmentation of seagrass beds may necessarily hold true for human-induced habitat fragmentation, since much depends on: (i) the period over which the change in habitat configuration occurs, and (ii) the type and permanency of the anthropogenic disturbance. For example, a single disturbance event leading to direct physical fragmentation of seagrass beds (e.g. damage caused by boat propellers) would be expected to cause changes in the associated macrofaunal assemblages that are different from those caused by fragmentation resulting from long-term pollution caused by a sewage outfall. Ideally, long-term observational studies of fragmentation of seagrass habitats caused by natural or anthropogenic disturbance should be carried out over multiple spatial scales, while manipulative

experiments would enable the gathering of more precise data on the effects of rapid fragmentation of seagrass beds on associated assemblages and subsequent rates of habitat and assemblage recovery. There is also the need for more detailed studies on the extent of 'edge effects' in seagrass beds, i.e. the distance from the bed periphery to the core of a seagrass bed, within which attributes of plant architecture and the associated fauna are different from those found further inside.

2) The present findings highlight the importance of avoiding generalisation in seagrass ecological studies. For example, what may be applicable to a *Z. marina* bed in nutrient-rich waters may not hold true for beds of the same seagrass in a different locality having lower nutrient concentrations. More so, what may be concluded for beds of a particular seagrass (e.g. *Z. marina*) in one locality with a given set of environmental characteristics may not hold true for beds of a different seagrass (e.g. *P. oceanica*) present in a another geographical locality having a completely different environmental regime. Furthermore, the present findings highlight the need for consideration of spatial scale when undertaking ecological studies of seagrass beds; the influence of different factors on seagrass-associated faunal diversity varies depending on scale, while the influence resulting from a particular factor at one scale may be different from that of the same factor operating at a different scale. The incorporation of adequate spatial replication in seagrass ecological research, as has already been emphasised by other workers (e.g. Turner et al., 1999) is therefore crucial.

3) The present finding that the species richness and abundance of motile macroinvertebrates associated with *P. oceanica* beds are positively correlated with the amount of seagrass epiphytes has been previously suspected (e.g. Gambi et al., 1992), but quantitative data to support the observation (as supplied in the present

study) was lacking. Since excessive epiphyte load may be detrimental to the seagrass (Sand-Jensen, 1977; Sibertein et al., 1986; den Hartog, 1994; Hemminga, 1998; den Hartog & Phillips, 2001), experiments are needed to establish the upper thresholds at which the amount of epiphytes present will impact the seagrass bed adversely. It would also be useful to identify whether *P. oceanica* epiphytes are more important as food or as habitat for the associated macroinvertebrates. Studies aimed at identifying the herbivores that feed on the *P. oceanica* epiphytes will help in understanding the role of herbivory in controlling epiphyte load on the seagrass.

4) With regard to the implications for conservation and management *P. oceanica*, there is an urgent need for gathering data on the various bed types formed by this seagrass to evaluate their relative contribution to the whole ecosystem. Regulations for the conservation and management of *P. oceanica* beds should include clear descriptions of the various existing bed types. Reference to some bed types, but not to others, leads to ambiguities as to whether a particular bed type is important to protect or not. Morphological distinctions between different bed types should be formalised and the distribution of the various *P. oceanica* bed types in the Mediterranean Sea ascertained. Thereafter, it would be useful to examine for differences in the faunal assemblages of bed types not yet compared. Such investigations would provide results to support or refute the suggestion made by the present study that, for conservation purposes, non-fragmented and fragmented beds should not be discriminated. For the time being, restoration and mitigation efforts should be directed at treating the various different bed types of *P. oceanica* as habitats of equal potential ecological value. Where alteration of a particular bed type has occurred, even if this is of an extreme form (e.g. complete loss of the seagrass shoots, leading to dead matte), every effort should be made at restoration; no bed should be 'written off' as having a low ecological value. Where *P. oceanica*

beds have been completely altered to dead matte, there is a need to establish whether the latter can be re-colonised by living *P. oceanica*, hence, possibly, using it as a substratum for restoration of seagrass habitat.

5) The possibility of the existence of a threshold of bed fragmentation of *P. oceanica* below that of the fragmented (reticulate) bed type examined, which may influence the diversity of associated macrofauna, cannot be excluded. Furthermore, *P. oceanica* beds that have been fragmented to patches may have within-bed architectural attributes (shoot density, number of leaves, leaf length etc.) that differ from those of the reticulate and continuous beds considered in the present study, which may, therefore, have an important influence on the associated macroinvertebrate diversity (e.g. Tolan et al., 1997; Webster et al. 1998). Such propositions could be considered by examining the relationship between the bed structural and biodiversity attributes of patchy *P. oceanica* beds.

6) Manipulative field experiments are needed to establish whether alteration of within bed plant architecture of *P. oceanica* influences the diversity of associated macrofauna. The present findings, and those of other workers, indicate that *P. oceanica* plant architecture may not be as important for the associated macrofauna as in the case of beds formed by other seagrasses having a lower structural complexity. However, if this assertion generally holds true, it could still be that there exists a particular threshold of alteration of *P. oceanica* architecture that would result in changes in the diversity of associated macrofauna (the 'threshold' hypothesis of Gotceitas & Colgan, 1989; see also Heck & Crowder, 1991 and Bartholomew et al., 2000). Studies to determine if such an architectural threshold exists, and what factors cause changes past the threshold, would contribute to an

understanding of the degree of alteration of within bed seagrass architecture that would start affecting the associated diversity adversely.

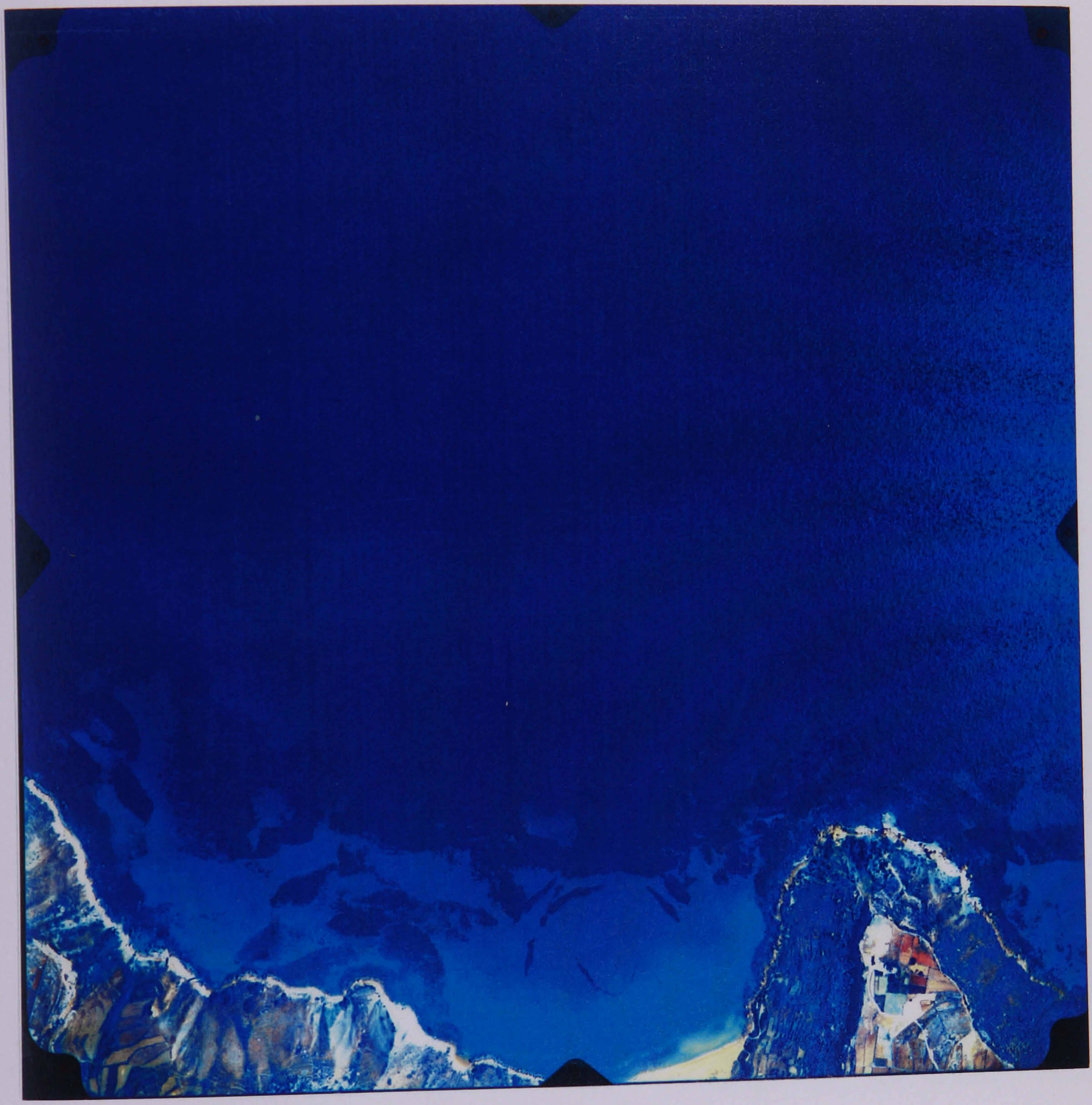
7) The case of *P. oceanica* dead matte requires special attention. Ecological studies of dead matte occurring in different environmental regimes (e.g. water depth, degree of isolation, location, type of disturbance leading to their occurrence etc) are required in different parts of the Mediterranean to gain a better understanding of the characteristics of this habitat. The somewhat inconclusive results obtained from the present study indicate the need for further investigations. In particular there is a need to establish: (i) whether the high diversity associated with dead *P. oceanica* matte is due to a greater of availability of detritus (originating from the dead root-rhizome matrix) that may be more palatable to the associated macrofauna than that originating from living matte: (ii) whether the dead *P. oceanica* matte has a higher structural complexity than living matte, which may, therefore, be significantly correlated with the observed higher diversity of associated macroinvertebrate assemblages; (iii) whether the epiphytic assemblages of dead matte differ from those present on living matte, hence, possibly, providing better habitat and food than living matte; and (iv) the stability and 'longevity' of this habitat type. In the meantime, use of the term 'dead' matte for this habitat may be misleading, since it implies a habitat with low ecological value; use of the more appropriate term 'bare' matte is recommended.

8) Last, but not least, there is a need for better understanding of the biology of key macroinvertebrate species associated with seagrass beds, in particular their feeding habits, trophic status, larval dispersal and recruitment patterns. Such information is particularly useful for interpreting differences in macroinvertebrate assemblage composition between different seagrass bed types and/or seagrass beds located in

places having different environmental characteristics, and hence better understand the influence of seagrass bed structure on the associated macroinvertebrate assemblages.

APPENDIX A

Aerial photographs used to determine the spatial distribution of *Posidonia oceanica* and other benthic habitats in the four study locations. Scale = 1: 16,000. Courtesy of Data Trak Ltd (Malta).

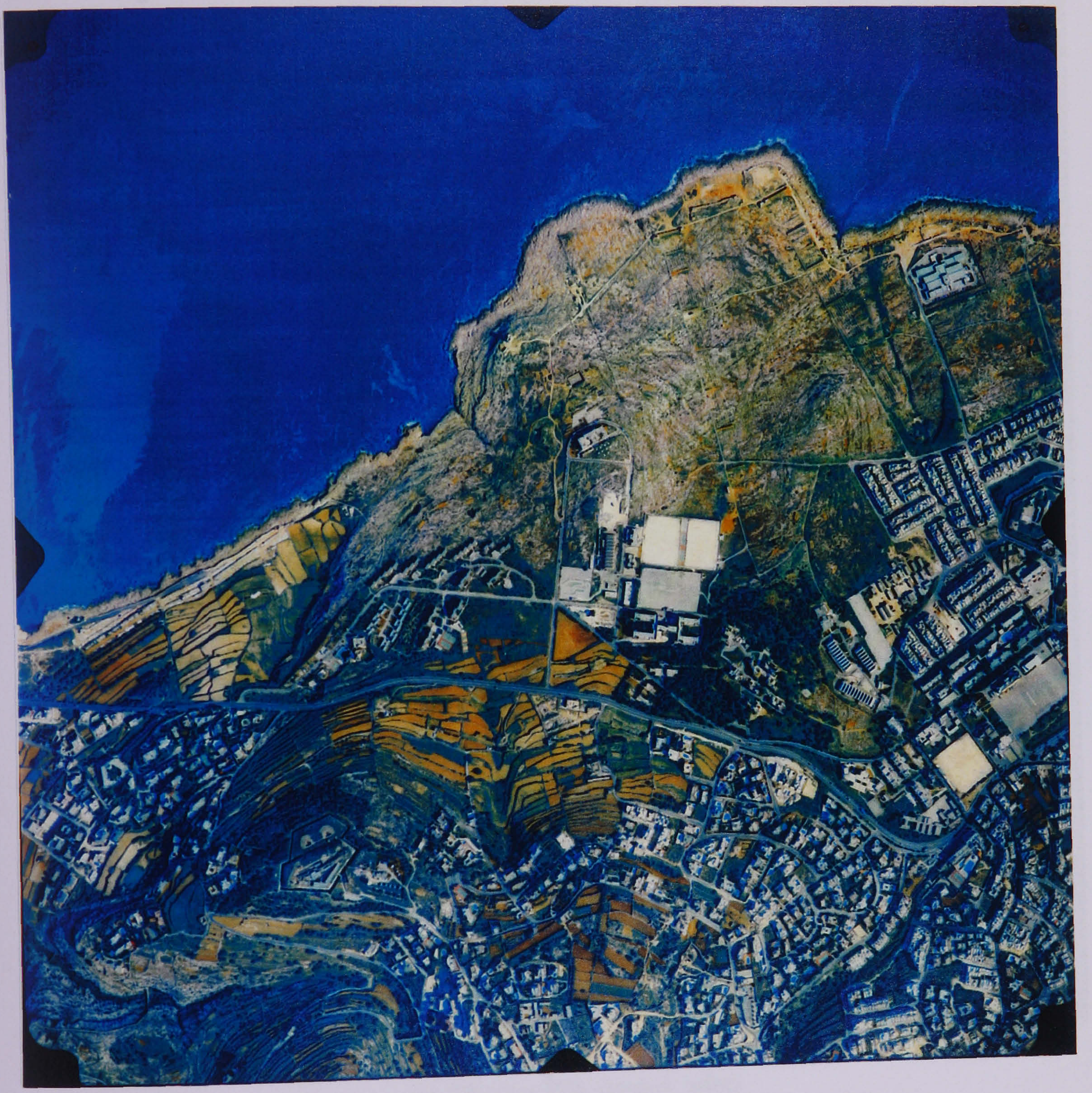


Ramla Bay

APPENDIX A (continued)

Mellieha Bay

APPENDIX A (continued)



White Rocks

APPENDIX A (continued)

St Thomas Bay (larger inlet)

Appendix B

Classified list of species, indicating the respective sub-study/s from which the respective species were recorded (●).

Species	Selection of sampler size and minimal sampling area (Chapter 2)	Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)	Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)
NEMERTEA			
Nemertea sp. A	●	●	●
Nemertea sp. B		●	
Tubulanus sp.	●	●	
SIPUNCULA			
Aspidosiphon muelleri Diesing, 1815		●	
Phascolion strombi (Montagu, 1804)	●	●	●
Golfingia vulgaris (de Blainville, 1827)	●	●	
POLYCHAETA			
Ampharetidae sp.	●		
Amphicteis midas (Gosse, 1855)	●	●	●
Amphinomidae sp.		●	●
? *Amphitrite* sp.		●	
Aphroditidae sp.		●	●
Arabella sp.		●	●
Aricidea sp.	●	●	●
Capitellidae sp.		●	●
Chaetozone setosa Malmgren, 1867	●	●	●
Cirratulidae sp. A		●	●
Cirratulidae sp. B		●	
Dasybrachus gajolae Eisig, 1887	●	●	
Diopatra sp.		●	●
Dorvilleidae sp. A	●	●	●
Dorvillidae sp. B		●	
Eunice torquata Quatrefages, 1865	●	●	●
Eunice vittata (Delle Chiaje, 1828)	●	●	●
Glycera sp.		●	●
Goniada emerita Audouin & Milne-Edwards, 1833	●	●	●
Hesionidae sp.	●		
Kefersteinia cirrata Keferstein, 1862	●	●	●
Lacydoniidae sp.		●	
Lepidonotus squamatus (Linnaeus, 1758)	●	●	●
Lumbriclymene cf *minor* Arwidsson, 1907	●	●	●
Lumbrineris sp.		●	
Lumbrineris impatiens (Claparède, 1868)	●	●	●
Lumbrineris latreilli Audoin & Milne-Edwards, 1834	●	●	●
Lysibranchia paucibranchiata Cantone, 1983		●	

Appendix B (continued)

Species	Selection of sampler size and minimal sampling area (Chapter 2)	Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)	Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)
Lysidice cf *collaris* Grube, 1870	●	●	●
Lysidice ninetta Audouin & Milne-Edwards, 1833	●	●	●
Maldanidae sp. A	●	●	●
Maldanidae sp. B	●	●	●
Maldanidae sp. C	●	●	●
Marphysa cf *bellii* Audoin & Milne Edwards, 1833		●	
Marphysa fallax Marion & Bobretzky, 1875	●	●	
Marphysa sanguinea (Montagu, 1815)	●	●	●
Nematonereis unicornis (Grube, 1840)	●	●	●
Nepthydae sp. A	●	●	●
Nepthydae sp. B	●		●
Nereis rava Ehlers, 1868	●	●	●
Nereidae sp. A	●	●	●
Nereidae sp. B		●	●
Nereidae sp. C		●	
Notomastus sp.	●	●	●
Notomastus latericeus M. Sars, 1851	●	●	●
Opheliidae sp.		●	●
Orbiniidae sp.		●	
Palola siciliensis (Grube, 1840)	●	●	
Pectinariidae sp.	●	●	●
Pherusa monilifera (Delle Chiaje, 1841)	●	●	
Phyllodocidae sp. A	●	●	●
Phyllodocidae sp. B		●	●
Phyllodocidae sp. C		●	
Piromis eruca (Claperède, 1870)	●	●	●
Polynoinae sp. A	●	●	●
Polynoinae sp. B		●	●
Polyopthalmus sp.	●	●	●
Pontogenia chrysocoma (Baird, 1865)	●	●	●
Psammolyce arenosa Delle Chiaje, 1841	●	●	●
Sabellidae sp. A	●	●	●
Sabellidae sp. B	●	●	●
Sabellidae sp. C		●	
Scalibregmatidae sp.	●	●	
Serpulidae sp.	●	●	●
Spionidae sp.		●	
Spirorbis sp.	●		
Sthenelais sp.	●	●	●
Syllidae sp A	●	●	●
Syllidae sp B	●	●	●
Syllidae sp C	●	●	●

Appendix B (continued)

Species	Selection of sampler size and minimal sampling area (Chapter 2)	Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)	Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)
Syllidae sp D		●	●
Syllidae sp E		●	
Terebellidae sp. A	●	●	●
Terebellidae sp. B	●	●	●
Terebellidae sp. C		●	●
MOLLUSCA			
Polyplacophora			
Acanthochitona fascicularis (Linnaeus, 1767)	●	●	
Chiton corallinus (Risso, 1826)		●	
Lepidochitona africanus (Nierstrasz, 1906)		●	
Lepidochitona furtiva (Monterostato, 1879)	●	●	●
Lepidopleurus cajetanus (Poli, 1791)		●	●
Leptochiton bedulli Dell' Angelo & Palazzi, 1986	●	●	●
Leptochiton cancellatus (Sowerby, 1840)			●
Gastropoda			
Aclis ascaris (Turton, 1819)			●
Alvania discors (Allan, 1818)		●	●
Alvania lineate Risso, 1826		●	
Alvania mamillata Risso, 1826		●	●
Ascobula fragilis (Jeffreys, 1856)			●
Barleeia unifasciata (Montagu, 1803)		●	
Berthella cf *plumula* (Montagu, 1803)	●	●	●
Berthella cf *stellata* (Risso, 1826)	●	●	●
Bolma rugosa (Linnaeus, 1767)		●	
Bittium lacteum (Philippi, 1836)		●	
Bittium latreillii (Payraudeau, 1826)		●	●
Bittium reticulatum (da Costa, 1778)		●	
Buccinulum corneum (Linnaeus, 1758)		●	●
Bulla striata Bruguière, 1792		●	●
Calliostoma dubium (Philippi, 1844)		●	●
Calliostoma zizyphinum (Linnaeus, 1758)		●	●
Cerithium vulgatum Bruguière, 1792		●	●
Clanculus jussieui (Payraudeau, 1826)	●	●	●
Clathromangelia granum (Philippi, 1844)		●	
Columbella rustica (Linnaeus, 1758)		●	●
Colubraria reticulata (de Blainville, 1826)			●
Conus mediterraneus Hwass in Bruguière, 1792		●	●
Crepidula unguiformis Lamarck, 1822	●	●	
Emarginula octaviana Coen, 1939		●	●
Emarginula tenera Locard, 1892		●	
Epitonium sp.		●	
Erosaria spurca (Linnaeus, 1758)		●	

Appendix B (continued)

Species	Selection of sampler size and minimal sampling area (Chapter 2)	Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)	Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)
Euspira guillemini (Payraudeau, 1826)		●	
Euspira nitida (Donovan, 1804)		●	
Gibberula caelata (Monterosato, 1877)		●	●
Gibberula miliaria (Linnaeus, 1758)			●
Gibbula ardens (Von Salis, 1793)	●	●	●
Gibbula fanulum (Gmelin, 1791)		●	
Gibbula guttadauri (Philippi, 1836)			●
Gibbula turbinoides (Deshayes, 1835)		●	
Gibbula umbilicaris (Linnaeus, 1758)	●	●	●
Gibbula varia (Linnaeus, 1758)		●	
Haliotis lamellosa Lamark, 1822	●	●	
Haminoea hydatis (Linnaeus, 1758)		●	●
Hexaplex trunculus (Linnaeus, 1758)		●	●
Jujubinus exasperatus (Pennant, 1777)	●	●	●
Jujubinus striatus (Linnaeus, 1758)		●	
Mangelia sp	●	●	●
Mangiliella caerulans (Philippi,1844)		●	
Mangeliella taeniata (Deshayes, 1835)	●	●	●
Metaxia metaxae (delle Chiaje, 1828)		●	
Mitra corniculum (Linnaeus, 1758)			●
Mitrella minor (Scacchi, 1836)			●
Mitrella cf *scripta* (Linnaeus, 1758)		●	●
Mitrolumna mediterranea Mifsud, 2001		●	
Muricopsis cristata (Brocchi, 1814)		●	
Nassarius cuvieri (Payraudeu, 1826)		●	●
Ocinebrina aciculata (Lamarck, 1822)		●	●
Ocinbebrina edwardsi (payraudeau, 1826)			●
Odostomia conoidea (Brocchi, 1814)			●
Payraudentia intricata (Donovan, 1804)		●	●
Parvioris anderswareni Van Artsen & Savelli, 1991		●	●
Philine aperta (Linnaeus, 1767)			●
Pollia dorbignyi (Payraudeau, 1826)		●	●
Raphithoma cordieri (Payraudeau, 1826)		●	●
Raphitoma linearis (Montagu, 1803)		●	
Raphitoma philberti (Michaud, 1829)		●	●
Rissoa sp.		●	
Rissoa auriscalpium (Linnaeus, 1758)	●	●	●
Rissoa labiosa (Montagu, 1803)		●	
Rissoa variabilis (Von Mühlfeldt, 1824)		●	
Rissoa ventricosa Desmarest, 1814	●	●	
Rissoa violacea Desmarest, 1814	●	●	
Rissoina bruguieri (Payraudeau, 1826)	●	●	●
Smaragdia viridis Linnaeus, 1758	●	●	

Appendix B (continued)

Species	**Selection of sampler size and minimal sampling area (Chapter 2)**	**Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)**	**Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)**
Tricolia pullus (Linnaeus, 1758)	●	●	●
Tricolia speciosa (Von Mühlfeldt, 1824)	●	●	●
Tricolia cf *tenuis* (Michaud, 1829)	●		
Trivia cf *pulex* (Solander in J. E. Gray, 1828)		●	●
Turbonilla jeffreysii (Jeffreys, 1848)		●	●
Turbonilla lactea (Linnaeus, 1758)			●
Turbonilla striatula (Linnaeus, 1758)		●	
Turridia sp.		●	
Vexillum ebenus (Lamarck, 1811)		●	●
Vexillum savignyi (Payraudeau, 1826)			●
Vitreolina philippi (Rayneval & Ponzi, 1854)		●	●
Volvarina mitrella (Risso, 1826)		●	
Bivalvia			
Abra alba (Wood W., 1802)		●	
Anodontia fragilis (Philippi, 1836)	●		●
Arca noae Linnaeus, 1758	●	●	
Arca tetragonal Poli, 1795		●	
Arcopagia balaustina Linnaeus, 1758	●	●	
Callista chione (Linnaeus, 1758)		●	
Chlamys varia (Linnaeus, 1758)		●	
Ctena decussata (O.G. Costa, 1829)	●	●	●
Glans aculeata (Poli, 1795)		●	●
Glans trapezia (Linnaeus, 1767)	●	●	●
Gouldia minima (Montagu, 1803)		●	
Irus irus (Linnaeus, 1758)		●	
Lamellaria perspicua (Linnaeus, 1758)		●	
Lima hians (Gmelin, 1791)	●	●	●
Limaria inflate Link, 1807		●	
Lissopecten hyalinus (Poli, 1795)	●	●	
Loripes lacteus (Linnaeus, 1758)	●	●	
Loripes lucinalis (Lamarck, 1818		●	●
Modiolus barbatus (Linnaeus, 1758)	●	●	●
Musculus costulatus (Risso, 1826)	●	●	
Myrtea spinifera (Montagu, 1803)		●	
Nucula nitidosa Winckworth, 1930	●	●	●
Nucula nucleus (Linnaeus, 1758)		●	
Paphia aurea (Gmelin, 1791)	●		
Plagiocardium papillosum (Poli, 1795)	●	●	
Parvicardium scriptum (Bucquoy, Dautzenberg & Dollfus, 1892)	●	●	●
Parvioris microstoma (Brusina, 1864)	●		
Petallifera petallifera (Rang, 1828)		●	
Pinctada radiata (Leach, 1814)		●	

Appendix B (continued)

Species	Selection of sampler size and minimal sampling area (Chapter 2)	Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)	Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)
Pinna nobilis (Linnaeus, 1758)		●	
Pitar rudis (Poli, 1795)		●	
Solemya togata (Poli, 1795_		●	
Striarca lactea (Linnaeus, 1758)		●	●
Tellina balaustina (Linnaeus, 1758)		●	●
Thracia papyracea (Poli, 1791)			●
Venericardia antiquata (Linnaeus, 1758)	●	●	
Venus verrucosa Linnaeus, 1758	●	●	
Cephalopoda			
Sepia sp.		●	●
ARTROPODA			
Pycnogonida			
Achelia sp.		●	●
Ascorhynchus sp.		●	
Cumacea			
Cumacea sp. A		●	●
Cumacea sp. B			●
Leptostraca			
Nebalia bipes (O. Fabricius, 1780)		●	●
Tanaidacea			
Apseudes cf *talpa* Montagu, 1808	●	●	●
Leptochelia savingyi (Krøyer, 1842)	●	●	●
Mysidacea			
Gastrosaccus sanctus (van Beneden, 1861)	●	●	●
Siriella clausii G. O. Sars, 1877	●	●	●
Isopoda			
Ancyroniscus sp.		●	
Cirolanidae sp.	●	●	●
? *Cyathura carinata* (Krøyer, 1847)		●	●
Cymodoce truncata Leach, 1814	●	●	●
Dynamene tubicauda Holdich, 1968	●	●	●
Eurydice sp.		●	●
Gnathia sp.	●	●	●
Idotea sp.			●
? *Janira* sp.	●		
Jaeropsis sp.	●	●	●
Synisoma lancifer (Miers, 1881)			●
Zenobiana prismatica (Risso, 1826)		●	●
Amphipoda			
Ampelisca cf *rubella* A. Costa, 1864	●	●	●
Ampelisca typica (Bate, 1856)	●	●	●
Ampelisca unidentata Schellenberg, 1936	●	●	●
Amphilochus neopolitanus Della Valle, 1893		●	●

Appendix B (continued)

Species	Selection of sampler size and minimal sampling area (Chapter 2)	Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)	Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)
Amphithoe helleri G. Karaman, 1975	●	●	●
Amphithoe ramondi Audouin, 1826		●	●
Aora sp.	●	●	●
Apherusa chiereghinii Giordani-Soika, 1950	●	●	●
Atylus guttatus (Costa, 1851)		●	●
Atylus vedlomensis (Bate & Westwood, 1862)		●	●
Caprella sp.		●	●
Caprella acanthifera Leach, 1814		●	●
Ceradocus orchestiipes Costa, 1853		●	
Ceradocus semiserratus (Bate, 1862)		●	
Cheirocratus sundevallii (Rathke, 1843)	●	●	
Corophium sp.		●	
Dexamine cf *spiniventris* (A. Costa, 1853)	●	●	●
Dexamene spinosa (Montagu, 1813)	●	●	●
Elasmopus sp.		●	
Elasmopus brasiliensis (Dana, 1855)		●	●
Elasmopus pocillimanus (Bate, 1862)		●	●
Gamarella fucicola (Leach, 1814)		●	●
Harpinia sp.		●	●
Hyale sp.		●	●
Hyale pontica Rathke, 1837		●	
Iphimedia eblanae Heller, 1867		●	
Iphimedia minuta G.O. Sars, 1864	●	●	●
Isaeidae sp.		●	
Lepidepicreum sp.		●	
Leptocheirus bispinosus Norman, 1908		●	●
Leptocheirus guttatus (Grube, 1864)		●	●
Leptocheirus cf. *longimanus* Ledoyer, 1973		●	
Leptocheirus pectinatus (Norman, 1869)	●	●	●
Leucothoe richiardsii Lessona, 1865	●	●	●
Liljeborgia cf. *dellavallei* Stebbing, 1906	●	●	●
Lysianassa costae Milne Edwards, 1830	●	●	●
Lysianassa longicornis Lucas, 1849	●	●	●
Lysianassa pilicornis (Heller, 1866)		●	●
Maera grossimana (Montagu, 1808)	●	●	●
Maera hirondellei Chevreux, 1900		●	●
Maera inaequipes (Costa, 1857)		●	●
Melita hergensis Reid, 1939		●	●
Microjassa cumbrensis (Stebbing & Robertson, 1891)		●	●
Monoculodes sp.		●	●
Orchomene humilis (Costa, 1853 = *O. batei*, Costa, 1853)		●	●
Peltocoxa cf. *marioni* Catta, 1875		●	

Appendix B (continued)

Species	Selection of sampler size and minimal sampling area (Chapter 2)	Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)	Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)
Pereionotus tesudo (Montagu, 1808)			●
Phoxocephalidae sp. A	●	●	●
Phoxocephalidae sp. B		●	
Phoxocephalidae sp. C		●	
Pontocrates arenarius (Bate, 1858)		●	
Psammogammarus caecus Karaman, 1955		●	●
Socarnes filicornis (Heller, 1866)	●	●	●
Sthenothoe sp.		●	●
Urothoe elegans Bate, 1857	●	●	
Urothoe cf *intermedia* Bellan Santini & Ruffo, 1986	●	●	●
Decapoda			
Achaeus cranchii, Leach, 1817		●	
Achaeus gracilis O.G. Costa, 1839	●	●	●
Alpheus dentipes Guérin-Méneville, 1832	●	●	●
Alpheus macrocheles (Hailstone, 1835)	●	●	●
Anapagurus sp.		●	●
Athanas nitescens (Leach, 1814)	●	●	●
Calcinus tubularis (Linnaeus, 1767)		●	●
Cestopagurus timidus (P. Roux, 1830)	●	●	●
Dromia personata Linnaeus, 1758		●	
Ebalia edwardsi O.G. Costa, 1838	●	●	●
Eurynome aspera (Pennant, 1777)		●	
Galathea bolivari Zariquiey Alvarez, 1950	●	●	●
Galathea sp.		●	
Galathea squamifera Leach, 1814		●	
Gnathophyllum elegans (Risso, 1816)		●	
Gourretia denticulata (Lütze, 1937)	●	●	●
Herbstia condyliata (Fabricius, 1787)		●	
Hippolyte garciarasoi d'Undekem d'Acoz, 1996	●	●	●
Hippolyte inermis Leach, 1815	●	●	●
Hippolyte leptocerus (Heller, 1863)	●	●	●
Hippolytidae sp.	●		
Ilia nucleus (Linnaeus, 1758)	●	●	●
Liocarcinus arcuatus Leach, 1814		●	
Lysmata seticaudata (Risso, 1816)		●	
Macropodia czernjawskii (Brandt, 1880)	●	●	
Paguristes cf *eremita* (Linnaeus, 1767)	●	●	●
Pagurus anachoretus Risso, 1827	●	●	
Pagurus chevreuxi (Bouvier, 1896)	●	●	●
Palaemon xiphias Risso, 1816	●	●	●
Parthenope massena (Roux, 1830)		●	
Philocheras fasciatus (Risso, 1816)			●
Pilumnus hirtellus (Linnaeus, 1761)	●	●	●

Appendix B (continued)

Species	Selection of sampler size and minimal sampling area (Chapter 2)	Macroinvertebrate assemblages of reticulate and continuous *Posidonia oceanica* meadows (Chapter 4)	Macroinvertebrate assemblages of living and dead *Posidonia oceanica* meadows (Chapter 5)
Pisa muscosa (Linnaeus, 1758)		●	●
Pisa nodipes (Leach, 1815)		●	
Pisa tetraodon (Pennant, 1777)		●	
Pisidia longicornis (Linnaeus, 1767)		●	●
Pontonia cf *flavomaculata* Heller, 1864		●	
Processa sp.	●	●	●
Sirpus zariquieyi Gordon, 1953	●	●	●
Thoralus cranchii (Leach, 1817)	●	●	●
Upogebia mediterranea Noël, 1992	●	●	●
Xantho incisus Leach, 1814			●
ECHINODERMATA			
Ophiuroidea			
Amphipholis squamata (Chiaje)		●	●
Amphiura chiajei Forbes, 1843	●	●	●
Ophioderma longicaudum Retzius, 1805	●	●	
Ophiocomina nigra (Abilgaard, 1789)		●	
Ophiomyxa pentagona (Lamarck, 1816)		●	●
Asteroidea			
Asterina gibbosa (Pennant, 1777)	●	●	●
Astropecten spinulosus (Philippi, 1837)	●	●	
Echinoidea			
Brissus unicolor (Leske, 1778)		●	
Echinocyamus pusillus (O. F. Muller, 1776)		●	
Genocidaris maculata A. Agassiz, 1869	●	●	●
Paracentrotus lividus (de Lamarck, 1816)	●	●	●
Psammechinus microtuberculatus (de Blainville, 1825)	●		
Spatangus purpureus O. F. Muller, 1776		●	
Holothuroidea			
Holothuria helleri Marenzeller, 1878		●	
Holothuria mammata Grube, 1840		●	
Holothuria polii Delle chiaje, 1823	●	●	●
Holothuria tubulosa Gmelin, 1788	●	●	
Leptosynapta minuta (Becher, 1906)		●	
Tachythyone tergestina (M. Sars, 1857)		●	
Trochodota venusta (Semon, 1887)		●	

APPENDIX C

List of invertebrate species and respective total abundance that were recorded exclusively from either dead or living *Posidonia oceanica* matte (Chapter 5).

Taxon	Dead matte	Living matte
Polychaeta		
Aphroditidae sp.		2
Arabella sp.	4	
Capitellidae sp.		1
Diopatra sp.		7
Eunice sp.	3	
Glycera sp.	8	
Goniada emerita Audouin & Milne-Edwards, 1833	2	
Lepidonotus squamatus (Linnaeus, 1758)	2	
Lumbriclymene cf *minor* Arwidsson, 1907	2	
Lysidice ninetta Audouin & Milne-Edwards, 1833		1
Marphysa sanguinea (Montagu, 1815)	1	
Nepthys sp.	3	
Nepthydae sp. A		1
Nereidae sp. B	1	
Polyopthalmus sp.	1	
Phyllodocidae sp. A	1	
Phyllodocidae sp. B	1	
Serpulidae sp.		2
Mollusca		
Leptochiton cancellatus (Sowerby, 1840)		1
Lepidopleurus cajetanus (Poli, 1791)		1
Aclis ascaris (Turton, 1819)	3	
Alvania discors (Allan, 1818)		25
Berthella sp.		1
Bittium latreillii (Payraudeau, 1826)	1	
Bulla striata Bruguière, 1792	1	
Cerithium vulgatum Bruguière, 1792	4	
Colubraria reticulata (de Blainville, 1826)	1	
Emarginula octaviana Coen, 1939	1	
Gibbula guttadauri (Philippi, 1836)	2	
Gibbula umbilicaris (Linnaeus, 1758)		3
Haminoea hydatis (Linnaeus, 1758)	23	
Hexaplex trunculus (Linnaeus, 1758)		2
Mangelia sp.	1	
Mangiliella taeniata (Deshayes, 1835)	5	
Mitra corniculum (Linnaeus, 1758)	1	
Mitrella minor (Scacchi, 1836)	6	
Ocinebrina edwardsi (Payraudeau, 1826)	1	
Odostomia conoidea (Brocchi, 1814)	1	
Parvioris anderswareni Van Artsen & Savelli, 1991		1
Philine aperta (Linnaeus, 1767)	2	
Raphitoma codieri (Payraudeau, 1826)	1	
Raphitoma philberti (Michaud, 1829)	1	
Thracia papyracea (Poli, 1791)	1	
Tricolia speciosa (Von Mühlfeldt, 1824)		11
Trivia pulex (Solander in J. E. Gray, 1828)	1	
Turbonilla jeffreysii (Jeffreys, 1848)	1	
Turbonilla lactea (Linnaeus, 1758)		1
Viteolina philippi (Rayneval & Ponzi, 1854)		1
Ascobulla fragilis (Jeffreys, 1856)	1	
Glans aculeata (Poli, 1795)	3	
Lima hians (Gmelin, 1791)	6	
Loripes lucinalis (Lamarck, 1818)		2
Modiolus barbatus (Linnaeus, 1758)	1	
Tellina balaustina (Linnaeus, 1758)	1	
Sepia sp.		1

APPENDIX C (continued)

Taxon	**Dead 'matte'**	**Living matte**
Crustacea		
Cumacea sp. B		2
Nebalia bipes (O. Fabricius, 1780)		8
Ampelisca cf *rubella* A. Costa, 1864		60
Amphithoe helleri G. Karaman, 1975	11	
Atylus guttatus (A. Costa, 1851)		5
Atylus vedlomensis (Bate & Westwood, 1862)		3
Caprella acanthifera Leach, 1814	45	
Dexamine cf *spiniventris* (A. Costa, 1853)	1	
Harpinia sp.	1	
Iphimedia minuta G.O. Sars, 1864		3
Leptocheirus guttatus (Grube, 1864)	554	
Lysianassa costae Milne Edwards, 1830	105	
Lysianassa longicornis Lucas, 1849	46	
Melita hergensis Reid, 1939		
Pereionotus testudo (Montagu, 1808)	3	1
Phoxocephalidae sp.	2	
Stenothoe sp.	3	
Urothoe cf *intermedia* Bellan Santini & Ruffo, 1986	2	
Dynamene tubicauda Holdich, 1968	1	
Eurydice sp.		2
Gnathia sp.	13	
Idotea cf *emarginata* (Fabricius, 1793)		1
Synisoma cf *lancifer* (Miers, 1881)		1
Zenobiana prismatica (Risso, 1826)		2
Alpheus macrocheles (Hailstone, 1835)	4	
Anapagurus sp.	4	
Galathea bolivari Zariquiey Alvarez, 1950	93	
Gourretia denticulata (Lütze, 1937)	3	
Ilia nucleus (Linnaeus, 1758)	1	
Paguristes cf *eremita* (Linnaeus, 1767)	1	
Palaemon xiphias Risso, 1816		2
Philocheras fasciatus (Risso, 1816)		4
Thoralus cranchii (Leach, 1817)	14	
Upogebia mediterranea Noël, 1992	15	
Echinodermata		
Ophiomyxa pentagona (lamarck, 1816)	5	
Asterina gibbosa (Pennant, 1777)		9
Total number of exclusive species in respective 'matte' type	**39**	**32**

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Role of *Posidonia oceanica* bed structure in determining the diversity of associated macroinvertebrate assemblages

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