2003

Importance of seagrass beds as a habitat for fishery species around Jersey

Jackson, Emma Louise

http://hdl.handle.net/10026.1/521

http://dx.doi.org/10.24382/3262
University of Plymouth

Importance of seagrass beds as a habitat for fishery species around Jersey

by

Emma Louise Jackson

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological Sciences
Faculty of Science

In collaboration with the
States of Jersey Department of Agriculture and Fisheries

November 2003

Importance of seagrass beds as a habitat for fishery species around Jersey

Emma Louise Jackson

Abstract

Worldwide, seagrass habitats have been identified as important nursery areas, refugia and feeding grounds for many faunal species, including those of commercial and recreational value. Their importance as both permanent and temporary habitats has been recognised in UK fisheries management and conservation strategies; however, it must be emphasised that current knowledge of the roles of seagrass habitats originates mostly from research carried out outside the UK. Also, the subtidal distribution of *Zostera* around the British Isles has not been rigorously quantified at many locations. Local studies are essential for providing the relevant information required by fishery agencies to make valued judgements of the importance of seagrass beds. This study reports the spatial and small-scale temporal utilisation of previously unsampled and unmapped subtidal seagrass (*Zostera marina*) beds by large mobile fauna in the coastal waters of Jersey, English Channel (49°00N 02°00W). The focus was on the value of the seagrass beds as a habitat for exploited species.

A map of the distribution and structure of the seagrass beds was produced, using a combination of aerial photography and acoustic survey methods. Landscape metrics enabled the configuration of the seagrass beds to be quantified and compared. The main factors affecting seagrass distribution and configuration were exposure and depth, with seagrass growing predominantly on the north-eastern, eastern and southern coasts, down to depths of 6m. Such depths limit the use of standard quantitative methods (e.g. throw traps). The bias of five alternative sampling methods was examined in terms of species composition, length-frequency distributions and operational efficiency (time cost). The influence of sampling at different times of day and tidal state was also assessed. Results indicated that a combination of trawl and beach seine sampling (day and night) best represented the mobile macro-fauna present in the seagrass bed examined.

To date, seagrass studies have identified that patterns of faunal assemblages associated with small-scale, seagrass bed characteristics weaken when studies move from local to larger geographical scales. Current knowledge is derived largely from beds within estuaries or sheltered bays, but the island of Jersey possesses coastal seagrass beds and is surrounded by an intensified anticlockwise current. Spatial scale was assessed initially using a three factor nested ANOVA, with six random sites nested within geographic location (north east/ south of the island), and sampled during the day and at night. The aim was to examine whether local-scale variability in large mobile fauna between beds was superseded by variability at a larger scale (the coastal location of the seagrass beds). Gross measures of total abundance indicated that location of the site was not as important as the variability between individual sites. However, ANOVA on individual species showed that patterns were not only site but species specific. Detailed mapping of the seagrass beds identified that the landscape configurations of the seagrass beds varied significantly with site. Habitat characteristics of ten seagrass beds were examined as potential influences on fish, decapod and cephalopod mollusc distributions. Seagrass habitat variables were derived from aerial photographic analysis (e.g. core area, edge density), acoustic data (e.g. depth, leaf height) and diver surveys of the beds (e.g. epiphyte index, density). The contributions of these variables as predictors of properties of the fauna were evaluated using multiple linear regression models. Results indicated that deeper seagrass habitats supported greater species diversity and species density than the shallower beds. More fragmented seagrass beds were not consistently found to support lower species diversity; after an initial decline with increasing fragmentation diversity increased, possibly due to the diverse mosaic of seagrass, algae and sand. However, juvenile density of larger, exploited fish species showed a negative relationship with increased fragmentation of the seagrass beds. In addition to landscape configuration and depth, smaller-scale structural changes in both canopy height and epiphytal load appeared to influence densities of smaller decapod crustaceans and small and cryptic fish densities. The density of both groups increased with increasing seagrass complexity.

Table of Contents

Study aims and objectives 1

1 The Importance of Seagrass Beds as a Habitat for Fishery Species 3
  1.1 Introduction 4
  1.2 Permanent residents of seagrass beds 7
  1.3 Temporary residents of seagrass beds 9
    1.3.1 Foraging 9
    1.3.2 Refuge from predation 10
    1.3.3 The nursery role 12
  1.4 Seagrass detritus as the basis of the coastal fisheries food chain? 19
  1.5 The relative value of seagrass to fishery species compared with other habitats 20
  1.6 The importance of scale 22
    1.6.1 Spatial scales of variability 23
    1.6.2 Temporal scales of variability 30
  1.7 Limitations of sampling methodologies 33
  1.8 Conclusions and recommendations for conservation 34

2 *Zostera marina* landscapes around the coast of Jersey 37
  2.1 Introduction 38
    2.1.1 Objectives 42
  2.2 Materials and Methods 42
    2.2.1 Study Location 42
    2.2.2 Remote sensing using aerial photographs 44
    2.2.3 Acoustic survey 48
    2.2.4 Calculation of seagrass landscape metrics 51
    2.2.5 Measurement of biological and environmental site variables 52
  2.3 Results 54
    2.3.1 Large-scale seagrass distribution 54
    2.3.2 Seagrass landscape attributes 59
    2.3.3 Seagrass bed attributes 59
    2.3.4 Environmental setting of seagrass beds 62
    2.3.5 Relationship between environmental setting and seagrass attributes 63
  2.4 Discussion 67

3 Assessment of gear suitability for sampling mobile macro-fauna of subtidal seagrass (*Zostera marina*) beds and adjacent sand 73
  3.1 Introduction 74
    3.1.1 Aim 76
  3.2 Materials and Methods 76
    3.2.1 Study site 76
    3.2.2 Selection of gear for present study 78
    3.2.3 Sampling design and sample treatment 80
    3.2.4 Methods for specific gears 82
    3.2.5 Data Analysis 85
  3.3 Results 88
    3.3.1 Effect of habitat, time and tide 88
    3.3.2 Species selectivity 96
    3.3.3 Size selectivity 108
    3.3.4 Cost 113
  3.4 Discussion 114
    3.4.1 Conclusions 118

4 Spatial and temporal variability of large mobile fauna in seagrass beds (Jersey, English Channel) 120
4.1 Introduction 121
4.1.1 Aims 123
4.2 Materials and Methods 124
4.2.1 Study location 124
4.2.2 Sampling method 126
4.3 Results 129
4.3.1 Spatial patterns of distributions 129
4.3.2 Temporal patterns of distribution 144
4.4 Discussion 160
4.4.1 Summary 171
5 Habitat characteristics and spatial arrangement affecting fish and decapod assemblages of seagrass (*Zostera marina*) beds around the coast of Jersey (English Channel) 172
5.1 Introduction 173
5.2 Aims and Objectives 179
5.3 Materials and Methods 180
5.3.1 Study location and site selection 180
5.3.2 Estimation of habitat variables 181
5.3.3 Sampling the fauna 187
5.3.4 Statistical analysis 189
5.4 Results 190
5.4.1 General description of assemblages 190
5.4.2 Comparison of trawl and beach seine samples 196
5.4.3 Faunal assemblage variability in trawl sampled seagrass landscapes 197
5.4.4 Determination of similar seagrass habitats 199
5.4.5 Multiple regression models of the effects of habitat variables 201
5.5 Discussion 208
5.5.1 Influence of habitat variables on daytime fauna 209
5.5.2 Influence of habitat variables on night-time fauna 214
5.5.3 Other influencing factors and study limitations 215
5.5.4 Conclusions 217
6 Summary 218
6.1 Summary 219
6.2 Limitations and suggestions for further work 223
6.3 Recommendations for management of Jersey seagrass beds 225
7 References 236
7.1 References 237

Table of Figures

Figure 1.1 A summary of the scales of spatial patterns that may affect seagrass fishery relationships and examples of recent studies that have addressed them. 25

Figure 1.2 A summary of the scales of temporal variability that may affect seagrass fishery relationships and examples of recent studies that have incorporated and identified them. 31

Figure 2.1 (a) Geographical Location of Jersey. Red arrows indicate the intense anticlockwise gyre. The 20m isobath of the French continental shelf is shown in blue. (b) Percentage frequencies of hourly wind direction measured at Jersey Airport from 1971 to 2000. Source: Jersey Meteorological Office, 2000. (c) Aerial photo coverage of Jersey coastline. 43

Figure 2.2 The equipment and setup of the Biosonics DT4000^{TM} system; a) Transducer attached to a pole and fixed to the side of the Fisheries enforcement boat; b) Onboard sounder electronics, linked to laptop computer, collating positional information from a DGPS receiver c) Biosonics set up on a smaller research vessel 49

Figure 2.3 Accuracy of the final map. The Kappa statistic for individual photographs and mosaics, where seagrass occurred is given. 55

Figure 2.4 Distribution of *Zostera marina* (in green) around the coast of Jersey, English Channel. 56

Figure 2.5 Bar charts of the larger-scale variables in configuration and exposure of seagrass landscapes around the coast of Jersey. a) REI, Relative exposure index (x10^6); b) edge density; c) total area of seagrass (*Zostera marina*); d) largest patch index; e) % of adjacent habitat that is rock; f) core area of seagrass as a percentage of the landscape (CPLAND). The names of the sites can be located with reference to Figure 2.4. 57

Figure 2.6 Typical Biosonics ™ DT4000 echogram, from the seagrass near to Elizabeth Castle on the south Coast of Jersey. The vertical axis corresponds to depth in metres and the horizontal axis to ping report numbers (equivalent time or distance travelled at a constant speed). 60

Figure 2.7 Relationship between leaf height (mm) recorded using Biosonics DT4000^{TM} echo-sounder and in situ SCUBA diver measurements. Correlation $r = 0.809$, $p < 0.05$. $y = 193.14 + (1.1127)x$. Dotted red line represents 95% confidence limits. 60

Figure 2.8 Box plots of seagrass plant variables at the different sites around the coast of Jersey. a) Depth and b) Seagrass leaf height as measured using the Biosonics DT4000^{TM} echo sounder system; c) Epiphyte Index; d) Mean Particle Grain Size; e) Leaf height; f) Shoot density, collated from SCUBA diver collections. See Figure 2.4 for locations 63

Figure 2.9 Linear regressions and 95% confidence limits for area weighted mean core area index versus (a) Relative Exposure Index (REI), (b) Depth, (c) Percentage of adjacent habitat that is rock; and for (d) Largest Patch Index versus REI; and Edge density versus (e) Depth and (f) Slope. 64

Figure 2.10 Linear regressions and 95% confidence limits for (a) Relative Exposure Index (REI) versus Shoot density m^{-2}, and depth versus (b) leaf length and (c) Epiphyte index. 66

Figure 2.11 Section of the seagrass bed at St Catherine Bay illustrating the unvegetated sand patches caused by dragging mooring chains (taken from a helicopter). 70

Figure 3.1 Study area on the north-west coast of Jersey (English Channel). Areas of bare sand and seagrass (hatched) delimited within St Catherine Bay 77

Figure 3.2 The 1.5m beam trawl (10mm mesh and 6mm mesh cod end liner) used in the study. The odometer is visible on the near side shoe. 82

Figure 3.3 The small (5.5m) open boat with a 40HP 4-stroke petrol engine used in the deployment of trawl, pots and divers. 83

Figure 3.4 Design used to asses the variability in trawl sample composition between habitat, time and tide (all factors are orthogonal and fixed, n = 6). 83
Figure 3.5 Design used to asses the variability in push net, beach seine and diver survey sample composition between habitat, time and tide (all factors are orthogonal and fixed, n = 3). 84
Figure 3.6 MDS ordination computed from the similarities between log (x+1) species densities of different sampling methods over sand and seagrass. (Stress = 0.17). Bubble size is indicative of the number of species sampled. 96
Figure 3.7 Plotted Strauss indices for various size classes of different species of fish sampled by different gears in seagrass and sand habitats conditioned against total catch from all gears. Values > 0 indicate selection for the specific size class, < 0 against and 0 no bias. ■ seagrass beach seining; □ sand beach seining; O sand push netting; ● seagrass push netting; Δ sand trawl; ▲ seagrass trawl; ◆ seagrass potting; ◊ sand potting 110
Figure 3.8 Plotted Strauss indices for various size classes of different species of decapod sampled by different gears in seagrass and sand habitats conditioned against total catch from all gears. Values > 0 indicate selection for the specific size class, < 0 against and 0 no bias. ■ seagrass beach seining; □ sand beach seining; O sand push netting; ● seagrass push netting; Δ sand trawl; ▲ seagrass trawl; ◆ seagrass potting; ◊ sand potting. 112
Figure 3.9 Combinations of gear and the percentage of species sampled in seagrass (conditioned against catch from all gears) versus cost in person hours. Potting (P), beach seining (B), trawling (T), Diver survey (D) and push netting (N). 114
Figure 4.1 Distribution of seagrass (dark green) around Jersey and locations of the sites sampled in the present study. 125
Figure 4.2 Common small and cryptic fish, identified as permanent residents within the seagrass beds. Clockwise from top left: *Syngnathus typhle* (from Froese & Pauly, 2003 with permission from C.L. Hernández-González). *Syngnathus acus* (from Froese & Pauly, 2003 with permission from J. Jensen), *Spinachia spinachia* (from Froese & Pauly, 2003 with permission from J. Jensen) and *Pomatoschistus microps* (Froese & Pauly, 2003). 132
Figure 4.3 MDS ordination computed from the similarities between log (x+1) species densities at different seagrass sites on the north-east (La Coupe, St Catherine Bay and Flicquet) and south coasts (Violet, Les Elavees and Elizabeth Castle) of Jersey, English Channel Islands. (Stress = 0.15). 132
Figure 4.4 Spatial patterns in total species numbers for north and south seagrass beds on the coast of Jersey, English Channel Islands during the day and at night. Bars represents a significant difference (* = P <0.05, ** = P <0.01). 133
Figure 4.5 Spatial patterns in total densities for north and south seagrass beds on the coast of Jersey, English Channel Islands during the day and at night. Bars represents a significant difference (* = P <0.05, ** = P <0.01). 134
Figure 4.6 Spatial patterns in fish species numbers for north and south seagrass beds on the coast of Jersey, English Channel Islands during the day and at night. Bars represents a significant difference (* = P <0.05, ** = P <0.01). 135
Figure 4.7 Spatial patterns in fish densities (minus *Gobiusculus flavescens*) for north and south seagrass beds on the coast of Jersey, English Channel Islands during the day and at night. Bars represents a significant difference (* = P <0.05, ** = P <0.01). .135
Figure 4.8 Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for fish a) *Labrus bergylta*, b) *Symphodus melops*, c) *Callionymus lyra* sampled from six seagrass on the north East and south coast of Jersey, during September 2000. 141
Figure 4.9 Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for decapods a) *Palaemon serratus*, b) *Processa edulis*

crassipes, c) *Liocarcinus arcuatus* sampled from six seagrass on the north East and south coast of Jersey, during September 2000. 143

Figure 4.10 MDS ordination computed from the similarities between log (x+1) species densities at three different seagrass beds during May, July and September 2000. (Stress = 0.18). 146

Figure 4.11 Diel patterns in total species numbers for seagrass beds at La Coupe, Flicquet and St Catherine Bay, on the north east coast of Jersey, English Channel Islands. Bar represents a significant difference (** = $p < 0.01$). 147

Figure 4.12 Monthly total species numbers for seagrass beds at La Coupe, Flicquet and St Catherine Bay. Bars represent significant differences (* = $p < 0.05$; ** = $p < 0.01$). 148

Figure 4.13 Monthly total densities (m^{-2}) for day and night samples from all three seagrass beds (La Coupe, Flicquet and St Catherine Bay, on the north east coast of Jersey, English Channel Islands). Bars represent significant differences (** = $p < 0.01$)...... 149

Figure 4.14 Diel variation in total species of fish for seagrass beds at La Coupe, Flicquet and St Catherine Bay, on the north east coast of Jersey, English Channel Islands. Bars represent significant differences (* = $P < 0.05$; ** = $P < 0.01$). 149

Figure 4.15 Monthly variations in total number of fish species for seagrass beds at La Coupe, Flicquet and St Catherine Bay. Bars represent significant differences (* = $p < 0.05$; ** = $p < 0.01$). 150

Figure 4.16 a) Variations in total fish densities between the seagrass beds at La Coupe, Flicquet and St Catherine Bay. b) Monthly variations in total fish densities between the seagrass beds. Bars represent significant differences (* = $p < 0.05$; ** = $p < 0.01$). 151

Figure 4.17 Variations in number of decapod species between a) months, b) sites and c) day/night. Bars represent significant differences (* = $p < 0.05$; ** = $p < 0.01$). 151

Figure 4.18 Monthly and diel variations in total decapod densities across all seagrass beds (La Coupe, Flicquet and St Catherine Bay) Bars represent significant differences (** = $P < 0.01$). 152

Figure 4.19 Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for fish a) *Callionymus lyra*, b) *Spondyliosoma cantharus*, c) *Pollachius pollachius* d) *Gobiusculus flavescens* sampled from three seagrass on the north east coast of Jersey, during May, July and September 2000. 157

Figure 4.20 Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for decapods a) *Palaemon serratus*, b) *Processa edulis crassipes*, c) *Liocarcinus arcuatus* sampled from 3 seagrass on the north East coast of Jersey, during May, July and September 2000. 160

Figure 4.21 Cuttlefish (*Sepia officinalis*) eggs attached a seagrass shoot in St Catherine Bay on the north East Coast of Jersey, English Channel. 162

Figure 5.1 Representations of two models predicting the responses of fish (a and b) and macroinvertebrates (b) at a landscape level (a) (adapted from Salita, 2000) and plant level (b) (adapted from Heck and Orth, 1980). 175

Figure 5.2 Distribution of seagrass around Jersey and the locations of the sites sampled in the present study. 181

Figure 5.3 Example of a Biosonics DT4000^{TM} derived, bathymetric map with seagrass bed overlaid at Flicquet Bay on the north east coast of Jersey 182

Figure 5.4 A close up image of the sort of habitat edges encountered 186

Figure 5.5 Length-frequency distribution of fish (minus Gobidae or Syngnathidae) sampled using trawls during the day and night. 193

Figure 5.6 Length-frequency distribution of fish (minus Gobidae or Syngnathidae) sampled using beach seine during the day and night. 193

Figure 5.7 Multidimensional scaling plot of trawl and beach seine samples from Les Elavees and St Catherine Bay seagrass beds. MDS is based on Bray-Curtis similarity matrix of log (x+1) transformed density data. 196

Figure 5.8 Multidimensional scaling plot of day-time trawl samples from eight seagrass landscapes around Jersey. MDS is based on Bray-Curtis similarity matrix of log (x+1) transformed density data. 198

Figure 5.9 Multidimensional scaling plot of night-time trawl samples from eight seagrass landscapes around Jersey, English Channel. MDS is based on Bray-Curtis similarity matrix of log (x+1) transformed density data. 198

Figure 5.10 The distribution of the eight seagrass beds sampled using the trawls, against the first two principal component axes in Table 5.6. PC1 represents fragmentation of the seagrass bed as illustrated by the example areas from the binary thematic images *green is seagrass, yellow is unvegetated sand....... 200

Figure 5.11 Linear regressions and 95% confidence limits for depth versus daytime (a) total species number, (b) total density (m^{-2}), (c) total diversity (H'), (d) fish species number, (e) density of fish (m^{-2}), (f) fish diversity (H'), (g) decapod species number, (h) density of decapods (m^{-2}), (i) decapod diversity (H'). 205

Figure 5.12 (a) Regression of total species diversity against increasing transect heterogeneity, with 95% confidence limits (b) 2nd-order polynomial regression equation of total species number against PC1 (representative of increasing seagrass habitat fragmentation). 209

Table of Tables

Table 1.1 Examples of commercially exploited species that have been linked to seagrass beds. 5

Table 1.2 Seagrass species that are the focus of seagrass/ fishery relations with a brief description of their morphology and geographical range (compiled from various sources; Den Hartog, 1970; Phillips & Meñez, 1988). 7

Table 2.1 Stepwise multiple linear regression of seagrass landscape attributes loaded on REI, Depth (m), % of adjacent habitat that is rock and slope. F to enter was set at $p < 0.10$ and all values are significant at $p < 0.10$. Values shown are the semi partial correlation coefficients (sr^2) and the adjusted r^2 for the model......65

Table 2.2 Stepwise multiple linear regression of seagrass plant attributes loaded on REI, Depth (m), % of silt in sediment, mean particle grain size and slope. F to enter was set at $p < 0.10$ and all values are significant at $p < 0.10$. Values shown are the semi partial correlation coefficients (sr^2) and the adjusted r^2 for the model......65

Table 3.1 Analysis of variance results for trawls. Three factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 'time' has 2 levels is orthogonal and is fixed (Day/ Night), factor 3 is tide and has two levels, orthogonal and fixed (Low/High). n = 4. * $P < 0.05$, **, $P < 0.01$, *** $P < 0.001$ 89

Table 3.2 Analysis of variance results for beach seine. Two factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 'time' has 2 levels is orthogonal and is fixed (Day/ Night). n = 3. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. 90

Table 3.3 Analysis of variance results for push netting. Two factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 'time' has 2 levels is orthogonal and is fixed (Day/ Night). n = 3. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ .91

Table 3.4 Analysis of variance results for Dive survey. Two factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 'time' has 2 levels is orthogonal and is fixed (Day/ Night). n = 3. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ .92

Table 3.5 Analysis of variance results for potting. Four Factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 has 2 levels is orthogonal and is fixed (Day/ Night), factor 3 is Pot type has two levels and is orthogonal and fixed (Inkwell/ D-pot), factor 4 is bait type, which has four levels is orthogonal and is fixed (1=Scad, 2=White tile, 3= Light stick, 4=No Bait). Number of replicates = 4. F values at $_{(1,96)}$ degrees of freedom unless the effect includes the bait type factor ($F_{(3,96)}$)......94

Table 3.6 Densities (ha^{-1}) of species sampled using the five different methods in seagrass and their rank......99

Table 3.7 Seagrass: Results of a one-way ANOVA ($F^{3,26}$) with unequal sample sizes, (on log (x+1) transformed data where necessary to meet assumptions) for effects of different gear type. Area standardised density data (individuals ha^{-1}) of each species caught at low tide, day/night pooled. Standard error are indicated in parentheses; rare species, species absent from two gear types and data showing heterogeneous variance are excluded from the analysis; ^{a} exploited species; n.s. not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Also showing the summarised results of *post hoc* means tests where a significant effect of gear was observed. 102

Table 3.8 Densities (ha^{-1}) of species sampled using the five different methods in sand and their rank. 103

Table 3.9 Sand: Results of a one-way ANOVA ($F_{(3,26)}$) with unequal sample sizes, (on log (x+1) transformed data where necessary to meet assumptions) for effects of different gear type. Area standardised density data (individuals ha^{-1}) of each species caught at low tide, day/night pooled. Standard error are indicated in parentheses; rare species, species absent from two gear types and data showing heterogeneous variance are excluded from the analysis; ^{a} exploited species; n.s. not significant, * $p < 0.05$, **

$p<0.01$, *** $p< 0.001$. Also showing the summarised results of *post hoc* means tests where a significant effect of gear was observed. 107

Table 4.1 Mean densities ($100m^{-2}$) of fish, decapod crustaceans and cephalopod molluscs at three north-eastern and three southern sites of seagrass. Standard errors of the mean are given in parentheses. Exploited species are highlighted with '*'. 130

Table 4.2 ANOVA on dominant fish and decapod species (> 1% of total catch). Three factor mixed model ANOVA, Factor 1, Location (Lo, fixed, 2 levels; north, south), Factor 2, Site [random, nested in location, Si(Lo)], Factor 3 is time of sampling (Ti), fixed and orthogonal, with 2 levels (n = 4). * = P < 0.05, ** = P < 0.01, n.s. = not significant. Location codes: LC = La Coupe, StC = St Catherine Bay, F= Flicquet, V = Violet, LE = Les Elavees, EC = Elizabeth Castle. Species underlined: less than 5 % of the total abundance of a species recorded in southern locations. 137

Table 4.3 ANOVA on proportions of fish resident groups. Three factor mixed model ANOVA, Factor 1, Location (Lo) is fixed, with 2 levels (north, south), Factor 2, Site is random and nested in Location [Si(Lo)], Factor 3 is Time of sampling (Ti), fixed and orthogonal, with 2 levels (n = 4). * = P < 0.05, ** = P < 0.01, n.s. = not significant. Location codes: LC = La Coupe, StC = St Catherine Bay, F= Flicquet. 139

Table 4.4 Monthly mean densities ($100m^{-2}$) of cephalopod molluscs, fish, decapod crustaceans from three north eastern isolated seagrass beds. Standard errors of the mean are given in parentheses. Exploited species are highlighted with '*'...............144

Table 4.5 ANOVA on dominant fish and decapod species (> 1% of total catch). Three factor, orthogonal ANOVA, Factor 1, Month (Mo, fixed, 3 levels; May, July and September), Factor 2, Time of sampling (Ti, fixed, two levels day/night), and Factor 3 is site (fixed with 3 levels) (n = 4). * = P < 0.05, ** = P < 0.01, n.s. = not significant. Location codes: LC = La Coupe, StC = St Catherine Bay, F= Flicquet. 153

Table 5.1 Trawl specific, seagrass landscape specific and physical variables used to explain distributions of fish and decapod assemblages. † entered as an independent variable into multiple regression models. 184

Table 5.2 List of fish species collected during beach seining and trawling with information on their total abundance, frequency of occurrence in samples and range of total lengths. * = exploited species. 191

Table 5.3 List of decapod species collected during beach seining and trawling with information on their total abundance, frequency of occurrence in samples and range of total lengths. * = exploited species. 194

Table 5.4 List of cephalopod mollusc species collected during beach seining and trawling with information on their total abundance, frequency of occurrence in samples and range of total lengths. * exploited species. 194

Table 5.5 Species absent from trawl samples but present in beach seines at same sites. Table shows the frequency of occurrence of the species in beach seine samples (out of n = 12) and whether or not the species was sampled at other sites using the trawl...197

Table 5.6 Principal component analysis evaluations from seagrass bed landscape variables and Coefficients in the linear combination of variables making up Principal components. Highest variable weights area given in red. † entered as an independent variable into multiple regression models. 199

Table 5.7 Results of the two-factor ANOVA carried out on trawl-specific variables Factor one (Time) was fixed and had two levels (day and night). Factor two (Site) again fixed, was orthogonal to Time and had eight levels (St Catherine Bay, Flicquet, La Coupe, Les Elavees, Violet, Karame, Icho and Elizabeth Castle). 201

Table 5.8 Results of stepwise multiple regression of habitat variables on ensemble variables of fish and decapod assemblages from daytime trawl samples (n = 32). Values given are the squared semi-partial correlation coefficients (sr^2, the correlation between the unadjusted dependent variable with the respective variable after controlling for all independent variables in the equation). Only those variables entered into the final equation are listed, all others did not meet a criteria of $p = 0.05$ for entry. Those dependent variables marked with a '*' indicate variables which could not be transformed to give a normal distribution and were therefore not analysed using multiple linear regression. All Multiple R-values of final equations were significant at $p< 0.01$. Negative signs indicate a negative relationship. 203

Table 5.9 Results of stepwise multiple regression of habitat variables on ensemble variables of fish and decapod assemblages from night-time trawl samples ($n = 32$). Values given are the squared semi-partial correlation coefficients (sr^2, the correlation between the unadjusted dependent variable with the respective variable after controlling for all independent variables in the equation). Only those variables entered into the final equation are listed, all others did not meet a criteria of $p = 0.05$ for entry. Those dependent variables marked with a '*' indicate variables which could not be transformed to give a normal distribution and were therefore not analysed using multiple linear regression. All Multiple R-values of final equations were significant at $p< 0.01$. Negative signs indicate a negative relationship. 204

Table 5.10 Results of non-parametric correlations (Gamma coefficient) between fish resident groups and the independent variables. Only Gamma significant at $p < 0.05$ are shown. 206

Table 5.11 Results of stepwise multiple regression of habitat variables on ensemble variables of fish and decapod assemblages from night and daytime trawl samples ($n = 32$). Values given are the squared semi-partial correlation coefficients (sr^2, the correlation between the unadjusted dependent variable with the respective variable after controlling for all independent variables in the equation). Only those variables entered into the final equation are listed, all others did not meet a criteria of $p = 0.05$ for entry. Those dependent variables marked with a '*' indicate variables which could not be transformed to give a normal distribution and were therefore not analysed using multiple linear regression. All Multiple R-values of final equations were significant at $p< 0.01$. Negative signs indicate a negative relationship. 208

Table 6.1 Table illustrating the various factors impacting seagrass beds, their sources, influence on the fauna (based on models developed in Chapter 5) and threats to seagrass beds, and suggestions for management 230

Acknowledgements

This work was supported by the States of Jersey Department of Agriculture and Fisheries and the University of Plymouth.

I would first like to thank my supervisory team, Dr Ashley Rowden (NIWA, New Zealand), Prof Mal Jones and Dr Martin Attrill (University of Plymouth), Dr Simon Bossy (States of Jersey DAF), for their advice, support and perspective.

The fieldwork for this thesis would not have been possible without the help of the States of Jersey Department of Agriculture Fisheries Officers (Greg Morel, Neil Hutton and Mike Smith), Lizzie Jolley and Mark Torode. I am very grateful especially for those people involved in the 3 o'clock in the morning shifts. Thank you to Andrew Syvret for his 'back of hand' knowledge of Jersey's intertidal zone. Also my thanks go to CEFAS (Lowestoft) for the loan of sampling gear.

Many thanks to Paul Tucker, Ian Robinson and the Armed Forces Pilots; Peter Brindle and Martin Patterson, for making the extra helicopter reconnaissance possible. A special thank you to Steve Gibson (NERC Remote sensing Unit, University of Plymouth), Pauline Framingham and Allan Jones (University of Plymouth) for their advice and guidance with the GIS software.

Special thanks must go to Louise McAbendroth for her words of wisdom and understanding. Also, to Matt Frost for sharing experiences and for his useful facts mind and to Angus Jackson for coming to my rescue with the binding. But to all my friends in MBERG, thank you for all your support, encouragement and discussion.

A big thank you to my parents (Anne-Marie and Norman Jackson), for their unlimited support and to my brother Adam for keeping me smiling. Finally, to William Debois, thank you for putting up with the worst and sharing the best, "I should have been a professional whistler".

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

This study was financed with the aid of a studentship from the States of Jersey Department of Agriculture and Fisheries and Plymouth University.

A programme of advanced study was undertaken, which included research modules on the scientific method and research environment, and a staff development course on statistical methods. Tutoring in the use of image analysis and Geographic Information Systems was also carried out.

Relevant scientific seminars and conferences were regularly attended at which work was presented; external institutions were visited for consultation purposes and several papers prepared for publication.

Publications:

Jackson, E.L., Rowden, A. A., Attrill, M. J., Bossy, S. F. and Jones, M. B. (2002). Comparison of fish and mobile macroinvertebrates associated with seagrass and adjacent sand at St. Catherine Bay Jersey (English Channel): Emphasis on commercial species. *Bulletin of Marine Science*, **71**(3): 1333-1341.

Jackson, E.L., Rowden, A. A., Attrill, M. J., Bossey, S. F. and Jones, M. B. (2001). The importance of seagrass as a habitat for fishery species. *Oceanography and Marine Biology: An Annual Review*. **39**: 269-303.

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S. F. (2000). Seagrass or bare sand: which is more important for English Channel fisheries? *Biologia Marina Mediterranea*: Proceedings of the Fourth International seagrass Biology Workshop, 7(2): 381-384.

Wyllie-Echeverria S., Gunnarsson K., Mateo M.A., Borg J.A., Renom P., Kuo J., Schanz A., Hellblom F., **Jackson E.**, Pergent G., Pergent-Martini C., Johnson M., Sanchez-Lizaso J., Boudouresque C.F., Aioi K. (2002). Protecting the seagrass biome: Report from the traditional seagrass knowledge working. *Bulletin of Marine Science*, **71**(3): 1415-1417.

Presentation and Conferences Attended:

Jackson, E.L. (2002). Habitat characteristics affecting fish assemblages of seagrass (*Zostera marina*) beds around the coast of Jersey. July 2002, Fisheries Society of the British Isles, Annual Symposium, Hull, UK. (Poster presentation).

Jackson, E.L. (2002). Habitat characteristics affecting fish and decapod assemblages of seagrass (*Zostera marina*) beds around the coast of Jersey. March 2002, 31st Benthic Ecology Meeting, Florida. (Oral presentation)

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S. F. (2001). Variability of large mobile fauna in seagrass beds (Jersey, English Channel): which scale is most important? March 2001, 30th Benthic Ecology Meeting, Durham (New Hampshire), USA. (Oral presentation). April 2002 MBA Postgraduate Workshop, Plymouth (Oral Presentation).

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S. F. (2000). Seagrass or bare sand: which is more important for English Channel fisheries? September 2000, 4th International Seagrass Biology Workshop, Balagna (Corsica), France. (Oral presentation)

Jackson, E.L., Attrill, M. J, Bossy, S. F., Jones, M. B. and Rowden, A. A., (2000). What to use and when to use it: sampling the large mobile fauna of seagrass (*Zostera marina*) beds. March 2000, 29th Benthic Ecology Meeting, Wilmington (north Carolina), USA. (Oral presentation)

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S.F. (1999) Mapping and sampling seagrass (*Zostera marina*) beds in Jersey, English Channel. December 1999, Linnean Meeting on Remote Sensing of the Littoral Marine Environment, Linnean Society, London, UK. (Poster presentation).

External Contacts:

Dr. C. Hily.Institut Université de Bretagne Occidentale, France.
Dr. S Wyllie-Echeverria, School of Marine Affairs, University of Washington, USA.
Dr. C. Simenstad, Wetland Ecosystem Team, University of Washington, USA.
Dr. Glen Hyndes, Centre for Ecosystem Management, Edith Cowan University, Australia.

Signed ....

Date .....04 MAR 04.....

Study aims and objectives

The overall aim of this thesis is to assess the importance of seagrass beds around Jersey to fishery species and biodiversity. Specific objectives of this study were:

1. To provide a large-scale distribution map of the seagrass habitats around Jersey.
2. To carry out small-scale mapping at selected sites to identify seagrass habitat structure and landscape configuration.
3. To assess the diversity of fish, decapod crustaceans and cephalopod molluscs at selected sites and their relationship with local fisheries.
4. To elucidate links between attributes of seagrass and fish/decapod communities.
5. Construct simple predictive models of the fish/ decapod supported by seagrass habitats around Jersey.
6. Suggest management objectives for conservation of the seagrass landscapes.

The review in Chapter 1 aims to identify, from previous studies, where the potential value of seagrass beds as habitats lies, by reviewing the roles of such habitats for different species. The aim was also to look at how these roles vary both temporally and spatially and identify where there are gaps in the present knowledge (both theoretical and geographical).

The seagrass beds around the island of Jersey (English Channel) were previously unstudied and unmapped. Chapter 2, therefore, provides a distribution map of the seagrass beds around Jersey to focus further study. The aim was also to quantify the landscape configuration and structure of the seagrass beds and assesses the factors potentially affecting them. Due to the depths to which seagrass around Jersey grows, standard quantitative methods could not be used, therefore in Chapter 3 five alternative sampling methods and the influence of sampling at different times of day and tidal state are examined. Results from Chapter 3 were used to identify suitable sampling methods and times, which were used to address the main aims of the thesis.

The Chapter 1 shows that patterns of faunal assemblages associated with small-scale, seagrass bed characteristics (density, biomass or bed heterogeneity) weaken when studies move from local to larger geographical scales. It is therefore important to assess larger scales of variability (both temporally and spatially) in order to put smaller scales into context. Chapter 4 examines whether local scale variability in large mobile fauna between beds is superseded by variability at a larger scale. Finally, Chapter 5 assesses in detail the seagrass habitat characteristics of ten seagrass beds as potential influences on fish, decapod and cephalopod mollusc distributions. The knowledge gained will allow fishery managers to focus conservation and restoration efforts. In Chapter 6 the findings of the study are summarised and suggestions for management provided.

1 The Importance of Seagrass Beds as a Habitat for Fishery Species

Part of this Chapter was published:

Jackson, E.L., Rowden, A. A., Attrill, M. J., Bossy, S. F. and Jones, M. B. (2001). The importance of seagrass as a habitat for fishery species. *Oceanography and Marine Biology: An Annual Review.* **39**: 269-303

1.1 Introduction

The proposal by Petersen and Boysen-Jensen (1911) that beds of the coastal seagrass *Zostera marina* were the basis of all life in the sea was seriously undermined when the devastating effects of the 1930s seagrass wasting disease on these plant communities (see review by Rasmussen, 1977) failed to produce the envisaged catastrophic collapse of fisheries. Although the fundamental links between fishery species and seagrass beds may not be as simple and direct as that proposed by Petersen and Boysen-Jensen (1911), there are many examples of associations between fishery species and seagrass beds. These associations have supported the idea that seagrass beds are important for fishery species (Table 1.1). There is some support for Petersen and Boysen-Jensen's (1911) theory that fisheries may depend on these marine meadows and a number of reports have correlated diminishing seagrass cover to declining fish catches. Examples include the King George whiting (*Sillaginodes punctata*) in Westernport Bay Victoria, Australia (Kikuchi, 1974, Bell & Pollard, 1989) and soft-shell blue crab (*Callinectes sapidus*) in Chesapeake Bay, USA (Shabmann & Capps, 1985). Bell and Pollard (1989) commented that fisheries are likely to depend heavily on seagrass only where harvests are made in very enclosed estuaries and bays, where seagrass provides the only shelter and where the exploited species spawns within the bay or estuary. These comments appear to contradict the general statement that now introduces much of the current seagrass faunal literature, that seagrasses are "well known" as important habitats for many economically valuable fishes and decapods, particularly in their juvenile stages. This rather limitless declaration appears to be based on Bell and Pollard's review (1989), which, although thorough, focused on Australian studies.

The same comment of regionality may also be applied to the recent review of Connolly *et al.* (1999), which examined fisheries sustainability. Such general statements of seagrass importance, based on scientific studies, can often lead to inaccurate assumptions when extrapolated to, for example, different geographical locations, fishery species or seagrass species. For this thesis, and to avoid any confusion, some commonly-used terms need to be defined. Firstly, what constitutes a fishery species? For the purpose of this thesis, a fishery species is one that is either destined directly for sale, an important target for recreational fishing or captured for mariculture. Caution is needed, however, because in some cases, juveniles of a particular species may utilise seagrass beds in regions where they are not exploited, only to migrate to other locations where they may be fished. Of course other species may have an indirect importance by being, for example, the dominant prey of a more directly exploited species. Studies involving such organisms will be identified where appropriate.

Table 1.1 Examples of commercially exploited species that have been linked to seagrass beds.

	Species	**Location**	**Examples of recent literature**
Fish	*Sillaginodes punctata* (King George Whiting)	Victoria south Australia	Connolly, 1994b Jenkins *et al.*, 1997b, 1998
	Sciaenops ocellatus Red Drum	Gulf of Mexico Texas	Holt *et al.*, 1983 Rooker *et al.*, 1998a,b, 1999
	Spondyliosoma cantharus Black bream	Mediterranean	Guidetti, 2000 Francour, 1997
	Paralabrax nebulifer Barred Sand Bass	California, United States	Valle *et al.*, 1999
	Syphraena barracuda (Barracuda)	Florida, United States	Schmidt, 1989
	Theragra chalcogramma Walleye pollock	Washington, United States	Sogard & Olla, 1993
	Gadus morhua Atlantic cod	Newfoundland	Tupper & Boutilier, 1995 Gotceitas *et al.*, 1997
	Meuschenia frycineti Six spined leather jacket	Victoria, south Australia	Edgar & Shaw, 1995a Jenkins *et al.*, 1997b
	Haletta semifasciata Blue rock Whiting	Victoria, south Australia	Edgar & Shaw, 1995a Jenkins *et al.*, 1997b
Mollusc	*Argopecten irradians* Bay Scallop	north Carolina, United States	Irlandi, *et al.*, 1995 Pohle *et al.*, 1991
	Mytilus edulis Blue Mussel	Netherlands Western Baltic Sea	De Jonge & De Jong, 1992 Reusch, 1998
	Mercenaria mercenaria Quahog	north Carolina,.United States	Irlandi & Peterson, 1991 Irlandi, 1996
	Sepia officianalis Cuttlefish	East Coast, United Kingdom	Sea fish Industry Authority, 1996
Decapod	*Callinectes sapidus* (Blue Crab)	East Coast United States	Perkins-Visser *et al.*, 1996. Ryer *et al.*, 1990.
	Penaeus esculentus Brown Tiger Prawn	Gulf of Carpentaria, north Australia	Loneragan *et al.*, 1998
Echinoderm	*Sphaerechinus granularis* Sea urchin	north East coast of France	Guillo & Michel, 1993

Secondly, seagrass itself is a general term, representing a group of species with a variety of leaf shapes, lengths, rhizome thickness, densities and areal coverage. Different seagrass species often have contrasting and specific environmental requirements, and exhibit particular geographical distributions. Whilst there are over 57 recorded species of seagrass, the majority of work has focused on only nine. Table 1.2 summarises these species, their common names, morphology and distribution (see Phillips & Meñez, 1988). This Chapter focuses largely on the temperate/subtropical species *Zostera marina*, but other species are also discussed and, to avoid falling into the trap of generalisation, the seagrass species involved will be identified.

Although Kikuchi (1974) divided the mobile fauna of seagrass beds into four categories (permanent residents, seasonal residents, temporary visitors which forage in a wider area than the seagrass bed, and occasional migrants), the present review uses a broader division and considers the fishery species found in seagrass habitats as either permanent or temporary residents. The section dealing with temporary residents is subdivided on functional response rather than temporal pattern of use.

In addition to examining direct links between seagrass habitats and exploited species, the indirect roles of seagrass to fishery success, such as trophic subsidy, are not neglected. Several studies have examined the relative habitat value of seagrass beds to fishery species by comparisons with other habitats, such as kelp forests (Wheeler, 1980), mangroves (Ronnback, 1999), salt marshes (Boesch & Turner, 1984), coral reefs (Jones, 1991) and bare sand (Gibson *et al.*, 1998); these comparsions will be reviewed. Perception of temporal and spatial scales of variability are also important to the understanding, modelling and management of ecological systems such as seagrass beds, whilst the sampling gear employed can have confounding effects on the comparability of studies.

Both scale and sampling methods will be assessed in terms of their potential influence on the interpretation of results from seagrass–fisheries studies. The overall aim of this Chapter, however, is to present evidence that supports or challenges current theories on the processes and links between seagrass beds and fishery species. By highlighting these theories, and the gaps and limitations of current literature on seagrass fisheries, the review also aims to suggest what further information is required for effective conservation efforts or to predict the impacts of further seagrass loss on fishery species.

Table 1.2 Seagrass species that are the focus of seagrass/ fishery relations with a brief description of their morphology and geographical range (compiled from various sources; Den Hartog, 1970; Phillips & Meñez, 1988).

Species	Common names	Brief morphology and biology	Distribution
Zostera marina	Eelgrass	Leaf length up to 2 m, up to 12 mm width Euryhaline	Northern Hemisphere Pacific and Atlantic Oceans to Arctic circle
Zostera muelleri	None	Leaf length 0.05 to 0.3 m long, 1 to 2 mm wide. Euryhaline.	South Eastern Australia, Tasmania.
Zostera capricorni	None	Leaf length up to 0.5m 2 to 5 mm long. Principally marine and subtidal.	East Coast Australia, New Zealand.
Heterozostera tasmanica	None	Leaves up to 0.25m long, 2.5mm wide. Mean low water spring tide to shallow subtidal.	Western Australia to New South Wales, Tasmania and Chile.
Posidonia australis	None	Leaf length 0.3 to 0.6 m long, 6 to 20 mm wide. Euryhaline, subtidal.	South Coast Australia, Tasmania.
Posidonia oceanica	None	Leaves up to 0.5m 5 to 9 mm wide. Steno-haline, subtidal, moderately sheltered to exposed coasts.	Mediterranean
Halodule wrightii	Shoal grass	Leaf length up to 0.32 m long, 2.2 mm wide. Lower intertidal to upper subtidal.	Western Tropical Atlantic and Atlantic Coast of Africa
Syringodium filiforme	Manatee grass	Leaf length up to 0.3 m and 2mm wide. Purely subtidal, often in mixed stands with *Thalassia testudinum*	Western Tropical Atlantic
Thalassia testudinum	Turtle grass	Leaf length up to 0.3m and 3 to 10mm wide. Subtidal.	Western Tropical Atlantic

1.2 Permanent residents of seagrass beds

Species that may be expected to exhibit the strongest relationship with seagrass habitats are those that inhabit the beds all year round and throughout their entire life history. However, apart from burrowing animals, the protection provided by seagrass is often limited to small and cryptic species (Edgar & Shaw, 1995a). Generally, permanent residents are small in size and, as a result, are of minimal importance in terms of commercial and recreational exploitation (Kikuchi, 1974). There are exceptions, for example, *Thalassia* and *Halodule* beds in Florida (USA) support a large number of pinfish (*Lagodon rhomboides*) which are indirectly valuable to fisheries. Pinfish are used for bait in long line and sport fishing (Jordan *et al.*, 1996). They are also the main prey item of a number of commercially valuable species, such as sea trout, known to forage in these seagrass beds (Jordan *et al.*, 1996). Other examples include the blue crab in the *Zostera marina* beds of Central and south America and brown tiger prawns (*Penaeus esculentus*) in northern Australian seagrass beds (Bell & Pollard, 1989; Loneragan *et al.*, 1998). O'Brien (1994) suggested that adult brown tiger prawns preferred seagrass (*Zostera capricorni*) as food but juveniles progressively changed their diet from diatoms to seagrass as they grew.

Some seagrass beds are home to both the adults and juveniles of certain species; for example, the six-spined leather jacket (*Meuschenia frycineti*) and blue rock whiting (*Haletta semifasciata*) identified by Edgar and Shaw (1995a) in southern Australian seagrass beds (*Heterozostera tasmanica* and *Zostera muelleri*). In the Mediterranean *Posidonia oceanica* beds, Guidetti (2000) identified different age classes of both annular bream (*Diplodus annularis*) and black bream (*Spondyliosoma cantharus*). Such examples may make the species candidates for classification as permanent residents, but require more study. Identifying which species are permanent residents requires seasonal sampling, analysis of length-frequency distributions and age classes or novel methods such as tagging techniques.

Even when permanent residents can be identified they are rarely exclusive to seagrass beds. Instead, the seagrass habitat is merely one of a number of local structures or refugia from which to choose (Heck *et al.*, 2003). For example, in Mediterranean *Posidonia oceanica* beds, conger eels (*Conger conger*), more commonly associated with rock and boulder habitats, concealed themselves in the thick rhizome mat (Francour, 1997). Karnofsky *et al.* (1989) found that lobster (*Homarus americanus)* in a Massachusetts bay (USA) dug shelters not only under rocks and boulders, habitats with which they are usually associated, but also under seagrass (*Zostera marina*). Although the rock shelters probably afforded better protection, they had to be of a suitable size, whereas the *Zostera* shelters could be modified and therefore made more permanent.

The loss of seagrass habitat would probably have an immediate and observable impact on the survival of these 'permanent residents', particularly if the relationship is an obligate one, and therefore their identification by fisheries managers is an important consideration.

Despite the few examples given above, the majority of commercially important species only use seagrass beds for either a small part of their life history, as a temporary foraging area or a short-term refuge from predation. They fit into Kikuchi's (1974) category of 'temporary residents'.

1.3 Temporary residents of seagrass beds

1.3.1 Foraging

Seagrass beds are often quoted as important foraging sites for a number of species, including those of fishery value (Schmidt, 1989; Edgar & Shaw, 1995b; Buckel & Stoner, 2000). There are even a few examples of exploitable species that feed directly on seagrass. Francour (1999) found that Mediterranean saup (*Sarpa salpa*) fed primarily (although not exclusively) on *Posidonia oceanica* and the adults of the commercially fished echinoid *Sphaerechinus granularis* also feed directly on *Zostera marina* in northern France (Guillou & Michel, 1993). However, it is proposed that the main reason that commercial species forage in seagrass beds is the high density of potential faunal prey items present (Adams, 1976b; Webb, 1991; Tupper & Boutilier, 1995). Simple foraging models suggest that many fish swim (with or without a pattern) until they find food, stop to eat it, then swim again until more food is found. Under this scenario, fish will spend more time where there is food (Connolly, 1997). Prey items, such as harpacticoid copepods, amphipods and polychaetes, which form a major part of the diet of many fish species associated with shallow inshore areas (Klumpp *et al.*, 1989; Webb, 1991), are often found in greater abundance within seagrass. However, swim-search patterns may not be the optimal foraging behaviour for predators in seagrass beds. A predator swimming through seagrass would have difficulty in detecting a prey item because the moving vegetation would interrupt visual cues. Hover searches, where the predator remains static and waits for the prey to move may be more successful (Diana, 1995).

The adults of some commercially valuable species may incorporate the seagrass beds into a larger foraging area (Heck & Thoman, 1984; Blaber *et al.*, 1992), although the possibility of higher densities of prey organisms is likely to make seagrass a more important component than other areas. Seagrass beds may not always support higher densities of prey items than other areas or the density of certain species may depend on the structure of a particular bed (Connolly, 1994a). Brook (1977) concluded that the majority of fish captured in *Thalassia* beds (Florida, USA) were foraging over a wide area because stomach contents analysis revealed a significant proportion of non-seagrass fauna.

Connolly (1994b) suggested that the link between King George whiting juveniles and *Zostera muelleri* habitat is due to food supply and that the importance of seagrass beds may depend on the abundance of associated fauna. Jordan *et al.* (1996) observed that a variety of recreationally valuable predators, such as red drum (*Sciaenops ocellata*), crevelle jack (*Caranx hippos*), spotted seatrout (*Cynoscian nebulosus*), southern hake (*Urophycis floridanus*) and gulf toadfish (*Opsanus beta*) feed on the pinfish that inhabit the seagrass beds of the Gulf of Mexico. Pinfish growth rates have been observed to vary with seagrass (*Thalassia testudinum*) density (Spitzer *et al.*, 2000) and it may be that this variability in prey size is reflected in the density of predators.

To determine which fishes or decapods are temporary foragers may require detailed analysis of stomach contents. This information can then be used to assess the importance of the seagrass bed as a foraging area for a particular species and aid in the construction of both energy budgets (Adams, 1976b) and trophic pathways. These help fisheries managers in assessing the relative value of seagrass beds in terms of the production of particular species and the larger implications of seagrass loss or restoration. Many studies have tried to evaluate the food selectivity of fishes quantitatively by using the ratio of food in their stomachs to the available food in the environment (Thayer *et al.*, 1975; Schmidt, 1989; Edgar & Shaw, 1995b). Thayer *et al.* (1975) collected 33 species of fishes from a north Carolina (USA) seagrass bed and found that guts contained crustaceans, gastropods and polychaetes of species associated commonly with seagrass and occasional pieces of *Zostera marina*. Schmidt (1989) correlated the diets of young barracuda with dominant seagrass infauna and again found fragments of seagrass (*Halodule* and *Thalassia* species) in the stomach contents analysed. Other studies have utilised stable carbon isotope analysis to assess trophic linkages in seagrass beds (e.g. Klumpp & Nichols, 1983; Thresher *et al.*, 1992).

With the apparent enhanced food abundance in seagrass beds, increased growth would be expected but is not always observed (Spitzer *et al.*, 2000). Perkins-Visser *et al.* (1996) proposed that the abundance and quality of the food, as well as the time available for foraging, determined the actual energy yield from a particular habitat. This foraging time is very much dependent on the time spent avoiding predation.

1.3.2 Refuge from predation

Seagrass beds are often quoted as offering good protection from predation (Orth *et al.*, 1984; Main, 1987; Rooker *et al.*, 1998a; Hindell *et al.*, 2000). Although many studies support this role, the level of protection available varies with the structure of the seagrass bed and is often limited to particular fish size classes (smaller species and juveniles) or cryptic species. Gaining an understanding of the degree of protection provided by seagrass for particular exploited species may help in determining which seagrass beds in a region provide the optimum protection or foraging conditions for that species. Lower predation pressure means less time and energy is required for hiding or escaping, and more time can be spent foraging, gaining energy and growing faster (Fraser & Gilliam, 1987; Bax, 1998). There is often a balance between the benefits and costs of the structural complexity of seagrass habitats. Complexity benefits some smaller fish by providing refugia, yet is detrimental to visual predators by concealing their prey (Edgar & Shaw, 1995a). Organisms, therefore, might be faced with a trade-off between levels of habitat complexity suitable for protection and for foraging (Werner & Hall, 1988; Burrows, 1994). One way of minimising predation risk whilst maximising foraging may be to utilise heterogeneous habitats. Holt *et al.* (1983) hypothesised that this type of heterogeneity was important for juvenile red drum. They found red drum to be more abundant in patchy areas than in homogenous stands of *Halodule wrightii* and suggested that this greater abundance was related to the juvenile fishes' requirements for open feeding areas adjacent to seagrass that provided nearby protection from larger predators.

Predator–prey relationships have represented a large portion of the literature on seagrass fisheries in the past (see Orth *et al.*, 1984 for a review of the earlier literature). Studies have assessed the variability in predation pressures between bare sand and seagrass, the majority identifying greater refuge provision in seagrass beds (Rozas & Odum, 1988; Ryer *et al.*, 1990). For example, Ryer *et al.* (1990) showed that the moulting activity of blue crab was greater in a *Zostera marina* and *Ruppia maritima* beds than in an adjacent marsh creek. The protection from predation offered by the seagrass during this vulnerable stage has also been demonstrated in the laboratory (Heck & Thoman, 1981), in the field (Ryer *et al.*, 1990) and in tethering studies (Shabmann & Capps, 1985; Heck & Wilson, 1987; Wilson *et al.*, 1987).

Perhaps of greater significance than comparisons with bare sand are the patterns in predator–prey relationships that are observed at different scales of seagrass complexity. It is often assumed that the protection afforded increases with the structural complexity of the seagrass bed. If seagrass beds do offer protection from predators, and this protection does increase with complexity of the habitat, it may also be expected that predator growth rates will be high in low complexity seagrass habitats and decline with increasing seagrass complexity irrespective of prey densities. Buckel and Stoner (2000) demonstrated that large predatory fish such as blue fish (*Pomatomus saltatrix*) are less able to prey upon juvenile striped bass (*Morone saxatilis*) with increasing seagrass (*Zostera marina*) density. Similar results were noted by Savino and Stein (1982), who further attributed these effects to increases in visual barriers for predators. Heck and Orth (1980) hypothesised that in open marine systems, predator success would be inversely proportional to plant surface area and that, due to the constant immigration of possible prey items, there would be no over-exploitation at lower densities. This prediction was supported by Spitzer *et al.* (2000) in a study on the growth rates of the pinfish inhabiting *Thalassia* beds in Florida. However, the relationship between seagrass complexity and predation success may not be a simple linear one (Heck & Thoman, 1981; Lipcius *et al.*, 1998). Nelson (1979) hypothesised a threshold effect, whereby, protection from predators was significantly greater above a particular plant density. Gotceitas *et al.* (1997) demonstrated that *Zostera marina* increased significantly the time required by a predator to catch 0+ age cod (*Gadus morhua*). They tested this refuge role in a laboratory study where 0+ cod were given the choice of safe and unsafe bottom substrata and Artificial Seagrass Units (ASUs). Below shoot densities of 720 m^{-2} there was no difference between bare sand and seagrass. This result enforced the threshold hypothesis proposed by Nelson (1979) (see also Orth & van Montfrans, 1982; Savino & Stein, 1982).

One way to test the role of predation in structuring seagrass communities is by measuring the response to its removal. Perkins-Visser *et al.* (1996) showed that juvenile blue crabs grew faster in predator-free enclosures within *Zostera marina* than those in similar enclosures deployed outside the beds. Connolly (1994a) tested the importance of canopy to small fishes by removing it, finding that fish abundance over the habitat where *Z. marina* had been removed was not significantly lower than in distant seagrass habitats or controls. All these studies highlight the difficulties in determining whether predation (top down) or food availability and competition (bottom up) controls the overall dynamics of marine ecosystems (Rosaz & Odum, 1988; Bax, 1998).

1.3.3 The nursery role

By far the most studied, and frequently quoted, role of seagrass beds is as a nursery ground for many marine species, including those of commercial and recreational value (Bell & Pollard, 1989; Heck *et al.*, 1989; Gray *et al.*, 1996; Jenkins *et al.*, 1997a,b; Rooker *et al.*, 1998a,b). This role has been defined from studies that have identified high concentrations of juveniles and larval stages within the beds. For example, Valle *et al.* (1999) reported that juveniles of the barred sand bass in Alamitos Bay, California, USA, were found almost exclusively in *Z. marina*. Similarly, in the Gulf of Mexico, several species of Sciaenidae (drums) that are vital to the recreational fishery exploit *Halodule wrightii* and *Thalassia testudinum* meadows during their early life stages (Stoner, 1983; Rooker *et al.*, 1998a,b). Thayer and Chester (1989) stated that up to 90% of the harvestable species in the Gulf of Mexico depended on coastal wetlands and submerged seagrass meadows (*Zostera marina*) for at least part of their life cycles. Perkins-Visser *et al.* (1996) found that, where the seagrass *Z. marina* occurs, the juvenile benthic stages of blue crab occur almost exclusively within them. Whilst larval stages of a number of commercial species, including blue rock whiting and leather jackets, were observed living in a Westernport (Australia) seagrass bed (Jenkins *et al.*, 1997b). In some areas, the preferential settlement of *Mytilus edulis* (blue mussel) (Connolly, 1994a) and *Argopecten irradians* (bay scallops) veligers (Connolly, 1994a; Irlandi, 1996) makes seagrass beds the target of spat collection for aquaculture (De Jonge & De Jong, 1992). The question posed, and often answered, by such studies is whether seagrass beds merely concentrate juveniles, or whether the residents actually gain a selective advantage over individuals inhabiting other habitats. Seagrass may improve survival by providing shelter and food. They may also promote the settlement of planktonic larvae and, for those species that do not have a pelagic larval phase, they may act directly as spawning areas. The following sections review the studies that have supported, opposed and explored these possible nursery functions of seagrass beds.

1.3.3.1 Seagrass beds as spawning grounds

Commercially valuable species that are known either to brood or produce demersal eggs, potentially spawn directly within seagrass beds. One example is the annular bream (*Diplodus annularis*), which inhabits seagrass (*Posidonia oceanica*) beds when spawning (Francour, 1997). Some species may even attach eggs directly to the seagrass blades, for example the cuttlefish (*Sepia officinalis*) on *Zostera marina* beds (Blanc & Daguzan, 1998).

However, inshore spawners are relatively uncommon in temperate regions, and the majority of juvenile fish and decapods within seagrass beds are ocean-spawned species that have been transported inshore by ocean currents. Whereas juvenile and adult fishes of seagrass beds have been well studied, little is known about the importance of this habitat for fish eggs and larvae (Olney & Boehlert, 1988).

1.3.3.2 Offshore-spawned larvae supplying seagrass beds

Most temporary residents of commercial importance that utilise seagrass beds are species that settle from the plankton and, after spending the initial portion of their lives in seagrass beds, often emigrate to another habitat (Middleton *et al.*, 1984). However, finding a suitable habitat for settling may be crucial for the survival of newly-recruited juveniles, and both size and quality of the chosen habitat may determine the carrying capacity of an area (Gotceitas & Brown, 1993; Carr, 1994; Gibson, 1994). A pertinent question is whether the association of a species with a particular type of seagrass bed is a result of active choice or whether initial settlement is random and patterns of distribution are a result of post-settlement processes (Jenkins *et al.*, 1997a, 1999; Worthington *et al.*, 1991). To answer this, factors influencing the larvae before and after settlement to the seagrass beds have to be addressed (Sale *et al.*, 1984; Worthington *et al.*, 1992a).

1.3.3.2.1 Pre-settlement processes

Larval transport

Bell *et al.* (1987) and Levin *et al.* (1997) suggested that, whereas the associations of fishes within seagrass meadows can be explained by either larval supply or selection of habitat, the emphasis is very much on variability in the supply of recruits. The pattern of offshore spawning followed by a pelagic larval stage, where the young fish drift inshore and undergo a benthic stage, is common to many fish species regularly associated with seagrass beds. Eckman (1987) suggested that predation is less important than hydrodynamics in determining the abundance and distribution of early juvenile stages in seagrass beds (see also Eckman & Nowell, 1984; Olney & Boehlert, 1988; Boström & Bonsdorff, 1997; Jenkins *et al.*, 1997b, 1999; Hannan & Williams, 1998; Loneragan *et al.*, 1998). Whilst investigating spatial variability in larval supply and settlement, Rooker *et al.* (1998b) upheld Eckman's (1987) hypothesis and reported a positive correlation between densities of sciaenids and tidal flow rates. In addition, Bell *et al.* (1988) suggested that temperature and salinity tolerances are the ultimate causes of larval settlement in estuaries, whereas spawning location, nature of eggs, length of pelagic larval phase and larval behaviour are proximate causes. Knowledge of all these factors, and the consideration of life-history strategies, may aid in the judgement of the relative importance of a seagrass bed to juveniles of particular commercial species (Sogard *et al.*, 1987; Tolan *et al.*, 1997).

Settlement on seagrass beds: passive or active?

Settlement of exploitable species to seagrass beds may be through either active selection of a seagrass bed (Worthington *et al.*, 1991) or passive settlement (Eckman, 1987). Bell *et al.* (1987) speculated that it is the availability of competent larvae that determines the value of a habitat and that larger structures (in their experiment predator exclusion cages) will receive more individuals than smaller habitats, a speculation supported by Hannan and Williams (1998).

Seagrass beds slow currents and enhance the deposition of fine sediments (Fonseca & Fisher, 1986). In a similar process, seagrasses are thought to enhance the passive settlement of meroplankton and the rate of this settlement may vary, not only with the species of seagrass, but also with certain aspects of plant morphology (Fonseca & Fisher, 1986). In seagrass beds, zooplankton densities are twice that of offshore environments (Robertson *et al.*, 1988). Grizzle *et al.* (1996) noted that *Zostera marina* blades undergo large amplitude synchronous waving at current speeds exceeding 10 cm s^{-1}, a phenomenon that they termed "monami" (Japanese for "aquatic wave"). These authors suggested that the increased movement of seagrass tips through the water column may enhance larval mussel (*Mytilus edulis*) settlement by increasing the likelihood of contact between leaf blade and larva.

Alternative hypotheses for greater larval settlement at the tips of leaves could be that larvae are attracted to, or caught by, the greater epiphyte cover (Newell *et al.*, 1991) or that the pattern was a result of differential post-settlement predation (Pohle *et al.*, 1991). It has even been suggested that post-larval blue crabs detect and respond to chemical cues from *Zostera* (Forward *et al.*, 1994). Assuming that fish larvae are able to 'recognise' seagrass habitat, Worthington *et al.* (1991) used Artificial Seagrass Units (ASUs) to test whether there was a threshold leaf density important for recognition. At low leaf densities, an epiphyte growing on the ASUs lowered the threshold but at high seagrass densities the added complexity of the epiphytic growth impeded fish settlement (Worthington *et al.*, 1991). Settlement processes are species specific but understanding whether the settlement of the larvae of a fishery species is an active or passive process may be valuable if decisions are to be made on the relative value of different seagrass beds. If settlement is a result of active selection, then seagrass beds of a particular morphology or structure may be the priority for protection. Alternatively, if settlement is passive, the location of the beds (for example their position in relation to the mouth of the estuary or depth) may be a more important consideration (Hannan & Williams, 1998, see also section 1.6.1).

Settle and stay?

In a model proposed by Bell and Westoby (1986a), it was hypothesised that the pelagic larvae of fishes and decapods are distributed patchily and settle indiscriminately on the first seagrass habitat that they encounter. These authors further proposed that individuals do not leave a seagrass bed soon after settling, but redistribute to suitable micro-habitats within that bed (Bell & Westoby, 1986a). Therefore, a seagrass bed that may have been identified as a more valuable habitat (for example, due to leaf height and/or density providing greater predator protection) may support fewer individuals of a species, only because a small number of individuals arrived there. If this hypothesis is true and larval settlement is the driving force, then sites in the same location should show similar distributions of juveniles, assuming that settlement patterns are maintained. Principal component analysis supported this prediction (Bell & Westoby, 1986a). Other advocates of the 'settle indiscriminately and stay' hypothesis include Rooker *et al.* (1998a) and Valle *et al.* (1999). Valle *et al.* (1999) assessed differential habitat use by Californian halibut (*Paralichthys californicus*), barred sand bass and other juvenile fishes in Alamitos Bay, California. In addition, they emphasised that seagrass bed characteristics (in this case *Zostera marina*) only affected fish abundance at a local scale and that over larger scales it was the location of the bed within the bay that had an effect. The majority of the evidence indicates that recruitment to seagrass beds shows strong responses to seagrass bed structure at local scales (Orth *et al.*, 1984; Bell & Westoby, 1986b). At larger scales, recruitment may be more influenced by the availability of planktonic larvae (Jenkins *et al.*, 1998).

1.3.3.2.2 Post-settlement processes

Whilst important, knowledge of the settlement patterns of a particular exploited species is often insufficient information for predicting the value (in terms of their survival) of a seagrass bed. A pertinent question is whether these settlement patterns can be maintained. Summerson and Peterson (1984) suggested that, due to the increased survival of fish and decapods that have 'settled and stayed' on seagrass beds (over those that may have re-entered the plankton or migrated to other habitats), patterns can indeed be maintained (see also Jones, 1991; Tupper & Hunte, 1994).

The post-settlement importance of seagrass beds is thought to revolve around two nursery functions discussed earlier: refuge from predators (Savina & Stein, 1982; Lipcius *et al.*, 1998) and increased foraging efficiency (Heck & Thoman, 1984; Perkins-Visser *et al.*, 1996). However, when evaluating the importance of seagrass beds to fishery species, it must be questioned whether the seagrass offers improved growth and increases the chance of survival of its juvenile inhabitants, compared with other habitats. Tupper and Boutilier (1995) hypothesised that the complexity of the seagrass (*Z. marina*) community meant that there was a greater range of prey items available to young-of-the-year cod, which resulted in better growth and better survival after leaving the seagrass bed. Similarly, Valle *et al.* (1999) suggested that the occurrence of juvenile barred sand bass almost exclusively within *Z. marina* was due to greater prey availability, enabling faster growth to a size that is less vulnerable to predation. In Limfjord (Denmark), hatchery-reared cod were released to seagrass (*Zostera marina*) beds to improve their initial survival (Støttrup *et al.*, 1994). However, if faster growth within seagrass beds is a result of greater prey availability, then growth rates would be expected to be correlated with food supply. Levin *et al.* (1997) questioned whether food supply limited the number, or growth rates, of fish recruits in different habitats of a Texan lagoon. They focused on the pinfish and found that recruitment to ASUs was 300 % greater than to sand habitats, regardless of whether they supplemented sand habitats with food. Whilst food supply was not the limiting factor, they suggested that supplies may be more effectively utilised in seagrass beds, allowing juvenile fish to grow faster and exceed the food size-range of various predators (Levin *et al.*, 1997; Bax, 1998).

The quality of the food as well as the time available for foraging (linked to predator avoidance) probably determines the actual energy yield from a particular habitat (Perkins-Visser *et al.*, 1996). Olney and Boehlert (1988) questioned whether seagrass affords predator protection for early life-history stages of fishes. They remarked that any degree of protection would be afforded only to those individuals able to orientate to the seagrass blades. They also pointed out that seasonally high densities of planktivorous fishes, such as silver side, spot and silver perch, may be a result of seagrass beds serving as a sink for pelagic eggs and early larvae. However, other studies have illustrated the suitability of seagrass as a refuge from predation (see earlier, p. 9). When exploited species take advantage of this protection, and of the elevated prey densities, their survival is likely to be high and initial settlement patterns may be maintained (as proposed by Summerson & Peterson, 1984), but not indefinitely. The juveniles of most commercially important species inhabit seagrass beds only temporarily. Kikuchi (1974) reported that when juvenile fishes appear in *Z. marina* beds in spring, they feed upon minute pelagic and epiphytic crustaceans, whilst in summer, young sub-adults feed mainly on bryozoans and polychaetes. Other authors have found similar ontogenetic changes in feeding habits (Carr & Adams, 1973; Adams, 1976b; Brook, 1977; Gillanders, 1995; Pardieck *et al.*, 1999;

Valle *et al.*, 1999). Valle *et al.* (1999) observed that in Alamitos Bay, California, high densities of small juvenile barred sand bass were restricted to *Z. marina*, whereas larger juveniles and adults were more abundant among rocks and over sandy bottoms. In Newfoundland, Gotceitas *et al.* (1997) reported that 1+ cod shifted from *Z. marina* to rock and macro-algae. In many situations, this movement of juveniles from the seagrass bed is related to size and predation. In general, as individual size increases, the effectiveness of the seagrass habitat as a refuge declines and species will move to a more suitable habitat. Pile *et al.* (1996) suggested that this shift out of the seagrass would occur when the risk of predation inside the bed is higher than the energetic value gained by remaining in the habitat. This has important implications in assessing the importance of a seagrass bed to specific juveniles in terms of food availability and in explaining possible periods of residency within the bed.

It is important to note that lower densities of a certain size class of juveniles may result from either selection of an alternative habitat or greater predation rates. A laboratory test of field-identified habitat preferences of the pinfish by Jordan *et al.* (1996) found that, in the absence of predators, juvenile pinfish used seagrass and sand equally and they proposed that the observed patterns were due to predator-mediated selection of habitat. However, Jordan *et al.* (1996) admitted that their study may have been confounded by an edge effect and proposed that the use of available sand habitat may decrease with increasing distance from seagrass cover. The relative importance of differential predation (Stoner, 1983) and predator mediated habitat selection (Main, 1987; Sogard & Olla, 1993; Jordan *et al.*, 1996) needs to be explored in greater detail for individual species.

Finally, it should be recognised that despite the plethora of statements that seagrass beds are important nursery habitats, some studies have questioned this role. Heck *et al.* (1989) found little evidence that juveniles of commercially important fishes and shellfishes used *Z. marina* as nursery grounds in the Nauseate System (Massachusetts, USA), suggesting that the importance of seagrass to fisheries varies with latitude (a view that is explored in greater detail later in the review). Contrary to other evidence, Halliday (1995) found that die-back of *Z. capricorni* and *Halophila* species in Queensland (Australia) was associated with an increase in juvenile prawn densities, rather than resulting in the expected decline of juvenile commercial prawn (*Panaeus plebejus*). In general, however, studies contradicting the view that seagrasses are important fisheries nursery grounds are rare.

1.4 Seagrass detritus as the basis of the coastal fisheries food chain?

Thresher *et al.* (1992) reported that the food chain supporting the larvae of the blue grenadier (*Macruronis novaezelandiae*) was not based on either phytoplankton or terrestrial organic matter. Instead, stable carbon isotope analysis showed that it was based on microbial decomposition of seagrass (*Zostera marina*) detritus. Others have used stable isotopes (outlined by Fenton & Ritz, 1988) as a way of tracking seagrass in food web dynamics (McConnaughey & McRoy, 1979). Dauby *et al.* (1998) measured $^{13}C/^{12}C$ ratio ($\delta^{13}C$) of over 100 species of plants and animals along the Brittany coast (France) and traced the input of carbon from distinct producer groups, particularly *Z. marina*. Using multiple stable isotope analysis in a tropical Australian estuary, Loneragan *et al.* (1997) showed that $\delta^{13}C$ values of juvenile prawns (*Penaeus esculentus*, *P. semisculatus* and *Metapenaeus*) closely matched values of seagrass of various species and seagrass epiphytes. However, these authors also noted that the strength of the similarity was dependent not only on the proximity of other habitats but also on the season (wet or dry), highlighting the caution needed in interpreting these kinds of studies. Similarly, Fry (1981) found that whilst $\delta^{13}C$ values in the brown shrimp (*Penaeus aztecus*) from Texan (USA) seagrass beds matched that of seagrass, shrimp found in open bays of the estuary had ratios closer to that of phytoplankton. Despite this example of trophic subsidy rather than trophic dependence, Fry (1981) noted that most of the shrimp caught on the ebb tides at the estuary entrance had $\delta^{13}C$ comparable with seagrass and suggested that these habitats supplied more shrimp to the fisheries overall.

Seagrass detritus may form the basis of, or at least contribute to, coastal nutrient cycles and indirectly promote the health of a fishery. Wood *et al.* (1969) stated that seagrasses provide large quantities of detrital matter to coastal ecosystems. Bach *et al.* (1986) demonstrated that the export of *Zostera marina* detritus in a Beaufort (north Carolina, USA) estuary equalled, if not exceeded, that of *Spartina alterniflora*. Adams (1976b) also suggested that the basis of the fish food chain in *Zostera* beds was detritus and its associated microbial community, whilst Brook (1977) bridged the gap between detritus and higher trophic level predators (including valuable commercial and sport fishes) by identifying a number of transient foragers.

Much seagrass detritus would appear to settle on/in nearby sediments, Ferrell and Bell (1991) found that the number of fishes on sand adjacent to *Z. capricorni* was significantly higher than sand distant from seagrass. It has also been suggested that the presence of seagrass may lead to organic enrichment of unvegetated sediments nearby, thereby enhancing food production for fishes (Shaw & Jenkins, 1992). Jenkins *et al.* (1993) reported that juvenile greenback flounder (*Rhombosolea tapirina*) may benefit indirectly from seagrass through organic enrichment of sediments and corresponding elevation of food production. Overall, the evidence suggests that the probable role of seagrass detritus in nutrient cycling should not be neglected, as such cycles may represent an important input to coastal fisheries.

1.5 The relative value of seagrass to fishery species compared with other habitats

When considering the importance of seagrass beds to fisheries, one of the first questions asked is: do the fishery species inevitably need this habitat to sustain their populations? Proposals at the International Seagrass Workshop led to a large number of comparative studies (McRoy, 1973), many of which assessed the relative importance of seagrass meadows to fishery species. Seagrass communities have been compared with a number of other inshore habitats, particularly unvegetated ones (Ferrell & Bell, 1991; Heck *et al.*, 1995; Boström & Bonsdorff, 1997; Connolly, 1997; Sheridan, 1997; Gray *et al.*, 1998; Arrivillaga & Baltz, 1999; Guidetti, 2000). These studies often assumed (perhaps incorrectly) that natural densities of fishery species would be a quantitative measure of habitat quality, with higher densities reflecting either a behavioural selection or higher level survival relative to other habitats. Very few studies have attempted to understand the mechanisms producing the patterns (but see Levin *et al.*, 1997). The studies addressing the complexities of these processes were discussed earlier in this chapter.

Usually, and somewhat predictably, higher numbers of fishery species are identified in seagrass beds compared with bare sand habitats (for example Arrivillaga & Baltz, 1999) and the species compositions tend to differ markedly between the two (see Gray *et al.*, 1996). In contrast, overall fish densities are not always higher in seagrass beds compared with adjacent bare sand (Edgar & Shaw, 1995a). In general, species with small individuals, juveniles or those with cryptic habits dominate seagrass beds, whereas large mobile fishes or species able to school, burrow, or camouflage themselves against the seabed are more abundant on bare sand. Therefore, whilst species composition and species number can be variable between habitats, differences in total abundance are often less apparent (Edgar & Shaw, 1995a; Jackson *et al.*, 2002).

Instead of concentrating on differences in composition and abundance of fishes between bare sand and seagrass, Edgar and Shaw (1995a) attempted to quantify the difference in production between the two. Their study, which addressed the consequence of seagrass (*Heterozostera tasmanica* and *Zostera muelleri*) loss, found that most of the juveniles of fishery species were distributed equally between seagrass and bare sand. However, production values were comparable with north American studies, and seagrass values surpassed those of bare sand habitats (Adams, 1976a; Lubbers *et al.*, 1990; Edgar & Shaw, 1995a).

Perhaps of greater significance than comparisons with non-vegetated habitats are those with different forms of submerged aquatic vegetation (Heck *et al.*, 2003). Any form of vegetation increases the complexity of a habitat, thereby providing a higher availability and variability of microhabitats, which in turn support a more diverse fauna (Wheeler, 1980). Gotceitas *et al.* (1997) examined whether juvenile Atlantic cod utilise *Z. marina* as a habitat in Newfoundland (Canada). They assessed different habitat types commonly found in the area and established that juvenile cod were almost exclusive to the *Zostera* beds. Sogard and Able (1991) compared *Z. marina*, the marine alga *Ulva lactuca* and marsh creeks as habitats for epibenthic fishes and decapods. They found that both vegetation habitats were preferred to unvegetated sediment but that *Zostera* was a superior habitat to *Ulva* for epibenthic fishes. However, *Ulva* provided a significant refuge from predation and supported faster growth than the *Zostera* habitat. They concluded that *Ulva* is, therefore, an important habitat in areas lacking seagrass but cannot be considered an equivalent substitute. Continuing the theme in a laboratory-based study, Borg *et al.* (1997) showed that, given the choice, juvenile cod preferred vegetated habitats of *Zostera marina*, the brown alga *Fucus vesiculosus* and algae of the genus *Cladophora* to bare sand. However, this preference was only apparent during the day. These authors proposed that the shelter provided by the macrophytes was not necessary at night. Differences were evident between vegetation types in terms of the size of juveniles; small juveniles were able to utilise all the vegetation types provided but larger individuals were restricted to *Fucus* (Borg *et al.* 1997). In a review of over 200 papers reporting the role of seagrass beds as nursery habitats, Heck *et al.* (2003) found that few significant differences existed in abundance, growth or survival when seagrass meadows were compared to other structured habitats (for example, macroalgal beds).

Seagrass is not always the most important habitat. Heck and Thoman (1984) in a study of submerged aquatic vegetation in Chesapeake Bay (USA) found that *Zostera marina* was not regarded as an important nursery area for fishes because it did not support more individuals than bare substrata. The results of Heck and Thoman (1984) may have been due to the close proximity of the studied bare substrata to seagrass beds. Ferrell and Bell (1991) found that areas of bare sand adjacent to *Z. capricorni* beds constituted a specific habitat for a number of species, and supported higher fish densities than areas some distance from seagrass. One theory put forward for this difference was that the export of seagrass detritus may lead to organic enrichment of nearby non-vegetated sediments, thereby, enhancing food production for fishes (Sogard, 1989; Shaw & Jenkins, 1992; see also p. 20). Some species may use unvegetated areas as long as a refuge is available nearby (Summerson & Peterson, 1984). If this assumption is true, then comparisons of seagrass and adjacent bare sand may be inappropriate for predicting changes in fish assemblages after the loss of the seagrass. The incorporation of near and far bare sand habitats is important in any comparison with this purpose. Ferrell and Bell (1991) pointed out that areas adjacent to seagrass should be managed as carefully as the seagrass itself and the appropriate area of this 'buffer' should be assessed.

The location of the seagrass bed can also influence species composition and fish densities. Jenkins *et al.* (1997b) showed that species diversity was greatest in seagrass compared with bare sand. However, when compared with bare sand, a greater total abundance was not evident in the shallow *Heterozostera* sites, but only in the deeper *Posidonia* beds. This study led Jenkins *et al.* (1997b) to propose that the loss of both intertidal and subtidal seagrass would result in a significant decline in species diversity but that the loss of seagrass in deeper subtidal areas would have a greater consequence for fish densities than loss in the intertidal zone. Hanekom and Baird (1984) found no significant difference in the numbers of fish species at *Zostera marina* and non-*Zostera* sites. However, they attributed this similarity to the turbidity of the estuary they studied, which they proposed might have aided predator evasion, thus reducing the attraction of *Zostera* as a refuge (see also Blaber & Blaber, 1980). It would appear that habitat choice depends on the requirements of an individual during a particular life stage, season or even time of day (Jansson *et al.*, 1985; Sogard & Able, 1991; Borg *et al.*, 1997). Whether habitat selection is an active or passive process, it may be worthwhile to assess the range of habitats available to a species in a given area in addition to seagrass.

1.6 The importance of scale

The studies discussed in previous sections highlight one of ecology's most crucial questions, that of scale. Both the attributes of seagrass habitats and the recruitment of fishes are highly variable in space and time. To provide useful information the temporal and spatial context of any study must therefore be explicit (Mason & Brandt, 1999).

1.6.1 Spatial scales of variability

Bell and Westoby (1987) were among the first to identify that patterns in fish assemblages associated with small scale, seagrass bed characteristics (for example density, biomass or bed heterogeneity) weakened when studies moved from local to larger geographical scales (Figure 1.1). For example, the importance of seagrass beds to commercially important fishes and shellfishes may vary with latitude. Heck *et al.* (1989) found the nursery function and species composition of *Z. marina* meadows at Cape Cod (northern Atlantic coast of the USA) to be strikingly different from Chesapeake Bay and north Carolina further south. A similar latitudinal difference was identified by Sogard and Able (1991), who compared the faunal communities of New Jersey seagrass beds with other *Z. marina* ecosystems along the east coast of the USA. They found that juvenile blue crab did not exhibit the preference for *Zostera* that was evident in Chesapeake Bay (Heck & Orth, 1980; Orth & van Montfrans, 1987) and two Texan bays (Zimmerman & Minello, 1984; Thomas *et al.*, 1990). Other large-scale disparities have been identified and Sogard *et al.* (1987) questioned the assumption that seagrass (*Z. marina*) meadows were important nursery grounds for warm temperate to tropical systems. They proposed further that the proportion of permanent residents in a seagrass bed would increase with decreasing latitude as the extent of winter migrations outside the bed decline.

In 200 studies reviewed by Heck *et al.* (2003), data suggested that seagrass beds in the northern Hemisphere might be more important as nursery areas than those in the southern Hemisphere, a conclusion also reached by Butler and Jernakoff (2000). Either author proposed no explanation and the data originated from just two study hot spots, North America and Australia. However, Heck *et al.* (2003) propose that greater global coverage of seagrass fauna investigations are needed and that specific studies should assess this apparent difference. These regional differences in functional relationships and inter-specific interactions emphasise both the importance of local studies and the need for caution in comparing seagrass beds from different regions. At large geographical scales, it is possible to identify variation not only in the range of certain species of seagrass (see Table 1.1, Phillips & Meñez, 1988) and zoogeographical species pools, but also in the concentrations of studies that address seagrass fisheries relationships. These study 'hot spots', most notably in Australia and north America, are evident in Table 1.2. The majority of studies directly relating seagrasses to fisheries appear to be Australian, including two thorough reviews (Bell & Pollard, 1989; Connolly *et al.*, 1999). Both reviews concluded that specific seagrass meadows represent important habitats for many Australian fishery species (including various species of king and tiger prawn, blue swimmer crab (*Portunus pelagicus*) and the western rock lobster (*Panulirus cygnus*).

Connolly *et al.* (1999) highlighted many gaps in the present understanding of the links between seagrass and fisheries, including the relationships between finfishes and seagrasses (much of the work in Australia being on decapods) and gave comprehensive recommendations for future research. The majority of the ideas, conclusions and suggestions of Connolly *et al.* (1999) have application in other parts of the world and should not be overlooked because of their apparent focus on Australian seagrass beds.

Reducing the scale further, coastal location may be another factor in determining the value of a seagrass bed to fishery species. Many of the studies substantiating the claims of seagrass importance to fisheries are based on beds within estuaries or sheltered coastal regions that, even in the absence of seagrass beds, may be important nursery areas (Boesch & Turner, 1984; Baltz *et al.*, 1993). In particular, there seems to be a focus on shallow seagrass beds within estuaries (Sogard & Able, 1991; Szedlmayer & Able, 1996; Rosaz & Minello, 1998) with a few notable exceptions (e.g. Pihl & Rosenberg, 1982). Therefore, since estuaries are already established as nursery areas in the literature, is the perceived importance of seagrass beds confounded by their estuarine location? The answer is obviously site specific. Detailed habitat comparisons are required to determine the relative value of the seagrass bed compared with other habitats (see p. 20). This need to assess relative importance applies not only to habitats within the same estuary, but also to those within the same shallow coastal regions and bays because these areas are also noted for their nursery importance, even when unvegetated (Gibson *et al.*, 1998).

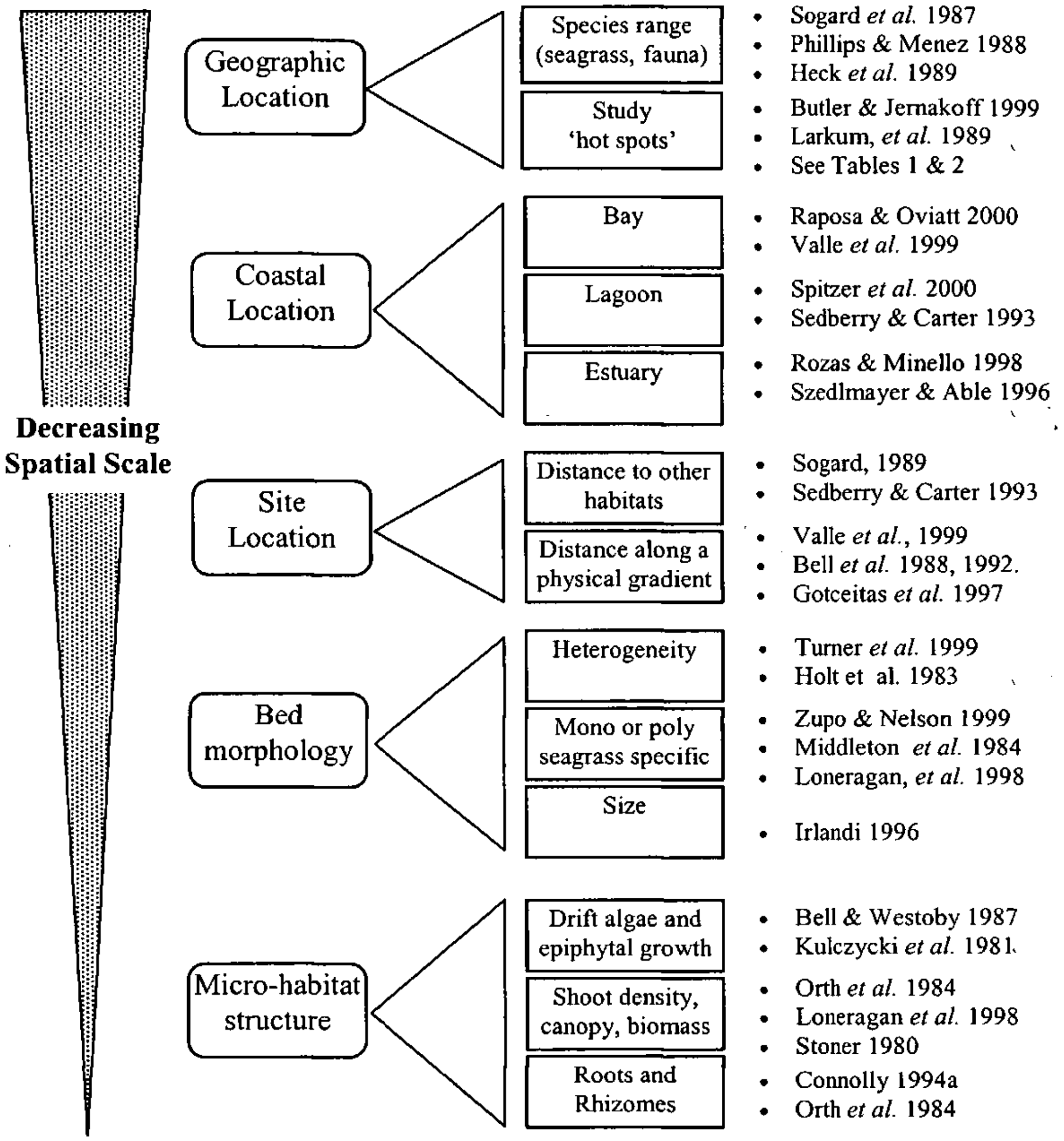


Figure 1.1 A summary of the scales of spatial patterns that may affect seagrass fishery relationships and examples of recent studies that have addressed them.

As the previous section indicated, the depth of the seagrass bed is another important consideration. Bell *et al.* (1992) examined differences in fish assemblages in deep and shallow margins of the seagrass *Posidonia australis* in New south Wales, Australia. For the majority of locations, they reported significantly more fishes in deep seagrass than shallow seagrass during late spring and early summer. The mean shoot density was lower in the deeper beds, however, it was proposed initially that the difference in assemblage may be due to greater numbers of bare-sand species able to utilise the deeper beds. Further investigation revealed that deep *Posidonia* assemblages were more similar to shallow *Posidonia* assemblages than those of deep bare substrata (Bell *et al.*, 1992). In French *P. oceanica* beds, however, Francour (1997) identified lower fish densities in deeper meadows compared with shallow beds. In shallow seagrass beds, the refuge status may be related to both the complexity of the seagrass and the depth of the bed. Not only is the vulnerability of larger piscivores to avian predation thought to be greater in shallow waters, but these larger fishes may also have difficulty moving and foraging and must tolerate higher fluctuations in temperature and oxygen (Ruiz *et al.*, 1993; Pardieck *et al.*, 1999).

Bell and Harmelin-Vivien (1982) found that juveniles of many species were more abundant in shallow sublittoral rocky reefs than *Posidonia* beds at depths of 15 to 20m. They suggested that this difference was due to pelagic larvae being driven to the shore by currents and settling on the most readily available shelter. Most larval settlement studies (see p. 16) have documented patterns within individual beds and have not considered whether recruitment affects the patterns observed over larger geographic areas. This lack of larger spatial consideration needs to be addressed in order to elucidate the links between seagrass beds as juvenile habitats and the productivity of the fisheries to which the juveniles recruit.

The proximity to other habitats may influence the relative importance of one seagrass bed over another. Sedberry and Carter (1993) looked at possible nursery habitats that were available to juvenile stages of economically important reef fishes (including the seagrass *Thalassia testudinum*) adjacent to a coral reef in a Central American lagoon. They found that the over-riding factor in determining the abundance of juveniles was distance to the main reef and its piscivorous predators. Similarly, Raposa and Oviatt (2000) explored the variability in nekton community structure between *Zostera marina* beds at a small geographical scale (within the same bay), by quantifying the effects of neighbouring shoreline type, distance to the shoreline and the biomass of vegetation. They found that both the distances to the shore and the shore type affected nekton assemblages.

Not only has the coastal location of the bed been shown to influence its value as a refuge, foraging site or nursery ground but also its particular position within a bay, lagoon or estuary (Livingston, 1984; Sogard *et al.*, 1987; Bell *et al.*, 1988; Sogard, 1989; Worthington *et al.*, 1995; Hannan & Williams, 1998; Valle *et al.*, 1999). Bell *et al.* (1988) suggested that the location within an estuary may affect distributions and abundance of recently settled fishes and decapods, and hypothesised that this location effect was because larvae of different species occur in different parts of an estuary when competent to settle.

These distributions, they proposed, were the result of not only the site of spawning but also the temperature and salinity tolerances of their eggs and larvae (Bell *et al.*, 1988). This hypothesis was supported by Hannan and Williams (1998), who found the number of ocean-spawned fish settling within seagrass (*Z. capricorni*) habitats decreased with distance from the mouth of a New South Wales lagoon. Monthly length-frequency data gathered over the course of the study season indicated that progressively larger juveniles where found at these distant sites. Valle *et al.* (1999) observed an analogous pattern in Alamitos Bay, California (USA) and found that, although community composition was similar between sites, the abundance of juveniles of the barred sand bass species and California halibut (*Paralichthys californicus*) decreased with increasing distance from the mouth of the bay. The consideration of which areas of seagrass would be the first to be met by ocean-dispersed fry and larvae is, therefore, important in any study, particularly when sites are located in lagoons or estuaries with poor circulation. These examples highlight the inadequacies of studies restricted to only one sand or one seagrass habitat, one site or to one bay or estuary.

Understanding and predicting patterns at large-scales is therefore difficult. As Bell and Westoby (1987) identified, it is only at smaller scales (for example, individual bed morphology) that patterns in species assemblages are more obvious. Like so many habitats, a 'typical' seagrass ecosystem is difficult to define. Many beds exist as vegetational units of various shapes and sizes or have unvegetated zones such as sand-bars interspersed among more homogenous areas (Robbins & Bell, 1994; Turner *et al.*, 1999). This heterogeneity does, however, make them a model system to test how spatial patterning of habitats influences ecological processes (McNeill & Fairweather, 1993; Robbins & Bell, 1994; Irlandi *et al.*, 1995).

Firstly, the size of the seagrass bed, degree of heterogeneity or 'patchiness' may influence its value as a habitat to certain exploitable species. Irlandi *et al.* (1995) assessed the survival and growth of the bay scallop (*Argopecten irradians*) in plots of *Zostera marina* and *Halodule wrightii* varying in heterogeneity. Keeping shoot density, biomass and blade length the same, they showed that simple spatial patterning can alter the roles of predation, with more scallops lost to predation in very patchy seagrass beds. Whereas commercial production of the scallops may be reduced in patchy beds, Irlandi *et al.* (1995) comment that this reduction production also implies greater transfer to higher trophic levels in these beds, potentially supporting larger numbers of other fishery organisms that prey on the juvenile scallops (for example, the blue crab). Such factors should be considered prior to any preferential protection of higher density, homogeneous beds. In a later study, Irlandi

(1996) examined the effects of seagrass patch size and energy regime on the growth of the suspension feeding bivalve *Mercenaria mercenaria*, cultured as a commercial substitute for oysters. Small *Mercenaria* survival did not differ with patch size but larger clams were affected significantly because current flow rates differed between patches. The influence of patch size was not limited to sedentary species (Holt *et al.*, 1983). Jenkins *et al.* (1997b) showed that juvenile King George whiting in a south Australian bay preferred the patches between seagrass, although Connolly (1994c) found that recruits in another south Australian inlet were only caught within the seagrass beds themselves. Once again, variation with locality was evident. Connolly (1994c) attributed this variability to the availability and vulnerability of prey items in each habitat; these interactions have been explored earlier in the review (p. 9).

A question often asked in the literature is whether refuge function of seagrass is correlated with mesoscale variables (for example, patch size) or with microscale variables (such as shoot density). Since the 1980s, seagrass research has focused on the role of the small-scale structural complexity in determining species richness and density (Heck & Orth, 1980; Stoner, 1980; Bell & Westoby, 1986a,b; Bell *et al.*, 1987; Sogard *et al.*, 1987; Ansari *et al.*, 1991; Irlandi, 1996; Loneragon *et al.*, 1998). Complexity has been variously measured as percentage cover, density, biomass, biovolume and plant species diversity in the case of polyspecific seagrass beds (Stoner & Lewis, 1985), although some of these variables may represent seagrass area rather than complexity (Attrill *et al.*, 2000). Variations in morphology and growing conditions (for example, depths) may result in different species of seagrass in the same location hosting contrasting fish species of economic value, or similar species at significantly different densities. *Zostera* and *Posidonia* beds in Botany Bay, Australia were found to serve different functions for juveniles; five species of economic importance were found exclusively in *Zostera* as recently-settled juveniles, whereas none was found only in *Posidonia* (Scott, 1981; Middleton *et al.*, 1984). Apparently, *Zostera* provides an area for initial settlement for several of these species (arguably due to depth and position of the beds), whereas *Posidonia* is utilised later in their life cycles. Rooker *et al.* (1998b) also investigated two types of seagrass (*Halodule wrightii* and *Thalassia testudinum*) and found that particular species of juvenile sciaenids showed a preference for one or the other. Many other studies have found differences in the communities from meadows dominated by different seagrass species (Kulczycki *et al.*, 1981; Martin & Cooper, 1981; Huh, 1984; Middleton *et al.*, 1984; De Troch *et al.*, 1996; Tolan *et al.*, 1997; Loneragan *et al.*, 1998; Zupo & Nelson, 1999).

Orth *et al.* (1984) suggested that the abundance of many species was correlated positively with two distinct aspects of plant morphology; the root rhizome mat and the plant canopy. To test this suggestion, they cleared patches of *Zostera muelleri* canopy in south Australia. The resulting faunal community was more similar, although not identical to, unvegetated areas. Although this similarity may be explained by the short-term nature of the study, Connolly (1994a) proposed that the canopy was not the overriding factor that determined the difference between patches with and without *Zostera*. Rhizomes produced microhabitats and bound the sediment making it more stable but they may also prevent a predator from accessing a prey species or increase prey escape time by impeding the burrowing of the predator (Orth *et al.*, 1984).

Increased abundance and diversity of fishes associated with seagrass meadows have frequently been linked positively to the complexity of the seagrass canopy (Heck & Orth, 1980; Bell & Westoby, 1986b; Ansari *et al.*, 1991). Stoner (1980) found that, irrespective of sediment type or hydrodynamic effects, seagrass biomass was an important factor in the regulation of species abundance, dominance, diversity and trophic organisation. However, Loneragan *et al.* (1998) reported that, although reduced numbers of juvenile tiger prawns were found in the lower biomass seagrass beds due to their areal extent, these beds were still the main nursery area for the valuable northern Australian prawn fishery.

The length, biomass and density of leaves are not the only factors influencing physical complexity of seagrass habitats; epibiota can provide an additional level of complexity (Attrill *et al.*, 2000). Bell and Westoby (1987) found that a bloom of the alga *Giffordia* sp. was correlated with a reduction in decapod and fish abundance, which was attributed to impedance of movement. In contrast, Kulczycki *et al.* (1981) suggested that large clumps of unattached drift algae were a prominent feature of many seagrass ecosystems and may enhance food and shelter provision by further increasing the complexity of the habitat.

When evaluating the relative importance, or perhaps predicting the carrying capacity of, different seagrass and non-seagrass habitats, these sources of variation need to be accounted for, which can cause logistical problems (for example finding a sampling method which does not differ in its efficiency between habitats). There are, however, studies that do incorporate many of these factors. Sogard *et al.* (1987) investigated the relative contribution of physical and vegetation variables in determining densities of fishes on Florida Bay Banks. In addition to measuring a whole suite of seagrass variables (including standing crop, canopy height, shoot density [of each of the seagrass species in the polyspecific bed they studied], blade density, seagrass litter and drift algal biomass), they also determined percentage silt, organic carbon, depth, temperature range and salinity. All sampling was done during both day and night. Multiple regression analysis indicated that although seagrass variables were often interrelated, their differential importance to an individual species indicated that fishes were discriminating between different structural aspects of the seagrass canopy. Resource maps and geographical information systems (GIS) detailing the factors such as the sediment, depth, salinity, temperature and habitat type (including various seagrass variables) of a region, are an important and useful tool and should be considered as a first step in any assessment.

1.6.2 Temporal scales of variability

In addition to the spatial components of variability, other studies have identified strong temporal patterns in both the seagrass bed structure and the composition of their fauna. Geographic location and latitudinal position can affect seasonal patterns, day lengths and tidal amplitude. In short, the functioning of any seagrass bed incorporates strong temporal patterns, which need to be accommodated in any study wishing to decipher their importance to fisheries (Figure 1.2). Long-term fluctuations are now an accepted feature of natural systems and interannual variations are evident in the seagrass fishery literature (Nelson, 1997). Climatic changes influence primary production and thus annual levels of fishery recruitment and production (Caddy, 1986). It may be assumed that the longer the study the more valuable the information (of a predictive nature) will be. Unfortunately long-term data sets are rare (but see Meng & Powell, 1999). In a 3-y study comparing *Zostera capricorni* and *Posidonia australis*, Young (1981) concluded that the differences in the vagile fauna between the two seagrass species were controlled by external events such as seasonal sea temperatures, which led to variable recruitment success. Anderson (1989) analysed a 27-y data set of blue crab catches and a 20-y index of seagrass (*Zostera marina*) areal coverage from the Virginian section of Chesapeake Bay, reporting a strong correlation between the two when the seagrass data were lagged one year (to match juvenile occupation), although a causal link was not established.

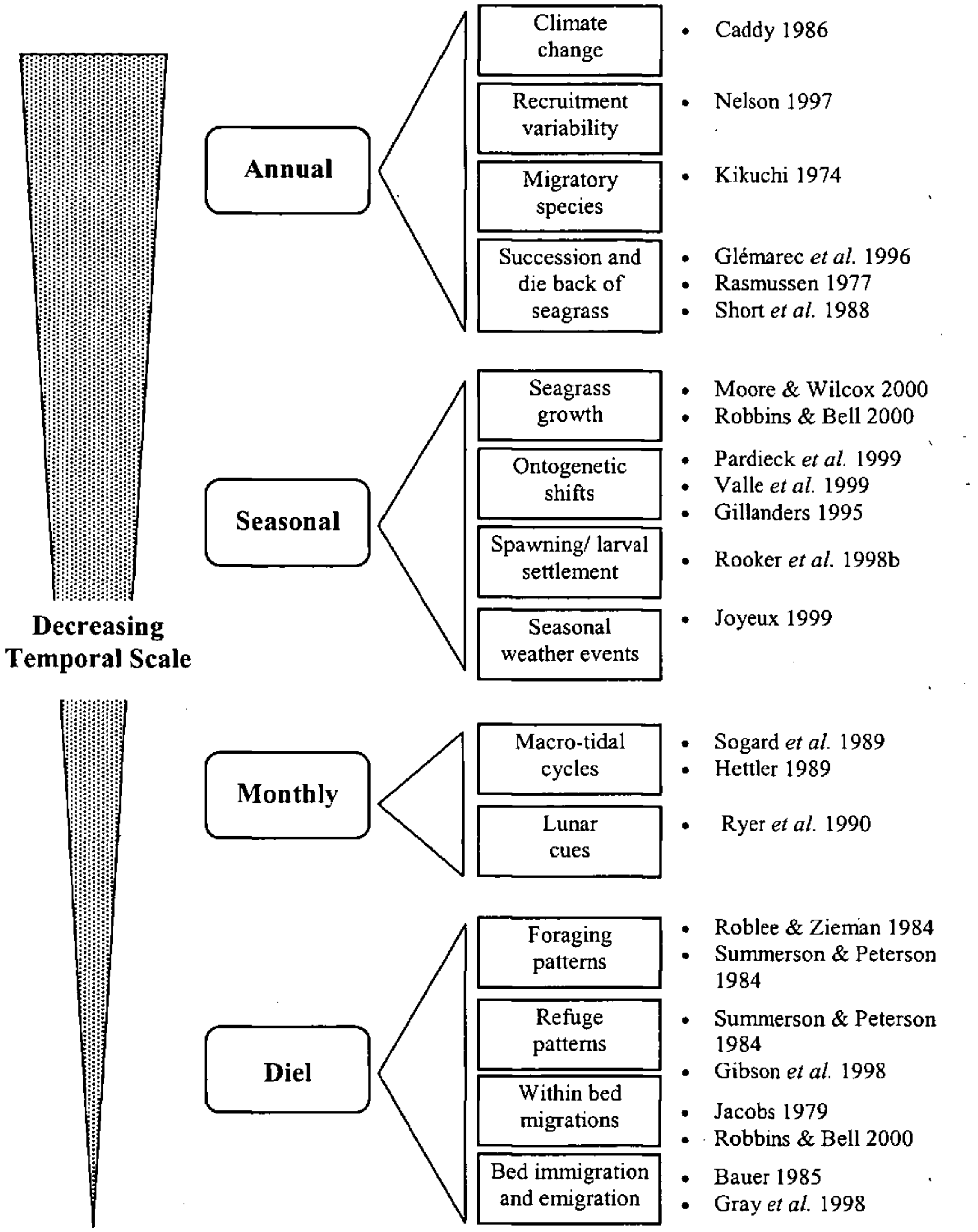


Figure 1.2 A summary of the scales of temporal variability that may affect seagrass fishery relationships and examples of recent studies that have incorporated and identified them.

Seasonal patterns of seagrass bed fauna can be influenced by species-specific spawning times, larval dispersal patterns and ontogenetic shifts within the year. For example, each of five species of sciaenids inhabiting *Halodule* and *Thalassia* beds of a Texan estuary showed distinct settlement periods that rarely overlapped (Rooker *et al.*, 1998b). Also, optimal growth and survival of juvenile red drum (*Sciaenops ocellatus*) within estuarine seagrass meadows (Texas) was observed for mid-season cohorts but the nursery conditions experienced by cohorts early and late in the season did not favour survival in early life (Rooker *et al.*, 1999). Such seasonal patterns are complicated further by the incorporation of monthly weather events and tidal patterns that may produce favourable current conditions for larval transport (Joyeux, 1999). Sampling at different states of the tide, Sogard *et al.* (1989) found no significant tidal differences between the numbers of epibenthic fishes, but a significant difference in the number of water column species. In a large amplitude tidal system, Hettler (1989) illustrated that estuarine-dependent residents and transients moved regularly between flooded salt marsh and adjacent subtidal habitats, and there was no reason to assume that a similar pattern did not occur in intertidal seagrass beds. High tides may make alternative, and perhaps preferred, habitats such as salt marsh available to certain species (Rosaz & Minello, 1998). Thus, if sampled during high tide, seagrass beds may appear temporarily less important to more mobile species. Conversely, at high tide, shallow subtidal and intertidal seagrass beds may become accessible to foragers, or those seeking refuge, and larger predators may enter these beds without risking avian predation. Monthly patterns can also be observed, including the lunar rhythm of ecdysis in blue crabs, during which the crabs utilise seagrass beds as a refuge during this vulnerable period (Ryer *et al.*, 1990).

In addition to tidal variations in assemblages, other diel patterns are evident. Many reports concerning seagrass habitats supporting different and more diverse fish assemblages are based on daytime sampling programmes, even though many estuarine and coastal species of fish display strong diel rhythms of activity (Adams, 1976a; Greening & Livingston, 1982; Sogard *et al.*, 1989; Stoner, 1991). For those studies that have assessed diel variation in seagrass beds, similar strong patterns are evident (Robblee & Zieman, 1984; Bauer, 1985; Edgar & Shaw, 1995a; Rountree & Able, 1997; Mattila *et al.*, 1999). Gray *et al.* (1998) examined whether habitat associations of juveniles of economically important species changed between day and night. A greater number of species was collected over seagrass (combined day and night) but a significant diel variation in the structure of sand-associated assemblages was also observed. Summerson and Peterson (1984) suggested that seagrass beds may serve as refugia in a manner similar to coral reefs because species use seagrass as a shelter by day and forage over sand under the protection of night. Hindell *et al.* (2000) looked specifically at the spatial, diel and tidal variability in the abundance of piscivorous fishes and their prey within an Australian *Heterozostera tasmanica* meadow.

The Western Australian salmon (*Arripis truttacea*) was just one of the species to show strong temporal patterns in its foraging behaviour. If samples are not taken both day and night and at different tidal states, important temporary residents may be missed and the role of the bed inaccurately assessed (Ferrell & Bell, 1991). Unfortunately, the impracticalities of night sampling may prevent the implementation of an ideal sampling programme.

In view of the variability and number of confounding factors that may exist, many scientists have moved toward the use of ASUs (Orth & van Montfrans, 1987; Sogard, 1989; Levin *et al.*, 1997). Jenkins *et al.* (1998) used replicate ASUs adjacent to natural seagrass beds to examine recruitment of King George whiting on the south coast of Australia. The advantage of the ASUs was that density and size of the 'seagrass' could be standardised at all five sites along the 50 km of coastline used in the study.

1.7 Limitations of sampling methodologies

Current perceptions of seagrass–fishery relationships may be clouded not only by the particular spatial and temporal scales of studies, but may also be limited by the particular sampling methods employed. Despite attempts to standardise sampling gear and methods (Phillips & McRoy, 1990), the variability of environments where seagrasses are found often makes this standardisation difficult. The type of sampling gear used, and the temporal and spatial scales at which it is used, all affect the perception of the processes of specific seagrass beds, and hence the roles proposed.

Many techniques have been developed and adopted for sampling the mobile fauna associated with seagrass, including diver observations (Tupper & Boutilier, 1995; Francour *et al.*, 1999; Guidetti, 2000), poisoning (Weinstein & Brook, 1983; Bell & Westoby, 1987), beach seining (Gotceitas *et al.*, 1997; Jenkins *et al.*, 1997b) and beam trawling (Worthington *et al.*, 1992b; Szedlmayer & Able, 1996). As a result, studies have been carried out to assess the relative suitability of these techniques in different situations (Lewis & Stoner, 1981; Orth & Moore, 1983; Gray & Bell, 1986; Rosaz & Minello, 1998; Francour, 1999). Most of the methods used are qualitative and, although quantitative techniques are available (for example drop nets and throw traps), they do have certain limitations, the most significant being the depth at which the gear can be used (Rosaz & Minello, 1997). The majority of seagrass fishery studies are carried out on shallow-water seagrass beds (that are less than 2 m), and this is reflected in the proposed standardised sampling protocols which promote the use of drop nets, throw traps and suction sampling techniques (Gilmore, 1990). Seagrass beds are not, however, limited to depths of 2 m. Francour (1999) reviewed critically fish sampling techniques in *Posidonia oceanica* seagrass beds in the Mediterranean, which can extend to depths of 40 m, and commented that these beds prohibit the use of throw traps or drop nets (due to depth) and trawls (due to high structural complexity). He concluded that the clarity of the water promoted the use of visual census.

In addition to the applicability of sampling method to the seagrass type and location, different methods may be biased to a particular group of organisms (for example, benthic or pelagic, schooling or solitary). A combination of methods and a range of qualitative and quantitative approaches may be needed to describe the macrofaunal communities associated with seagrasses. Without a range of sampling gear, it may be that inferences on species inhabiting the area are limited to the selectivity of the gear. Rosaz and Minello (1997) gave a comprehensive and thorough account of sampling design and gear selection for estimating densities of small fishes in shallow estuarine habitats. They noted that many studies assessing the value of seagrass beds involved inter-habitat comparisons. For an unbiased evaluation, the same gear should be used throughout the study. In addition, the use of gear that characteristically exhibits large and unpredictable variation in catch efficiency makes habitat comparisons unreliable and decreases the ability to detect statistical differences. Rosaz and Minello (1997) emphasised that the ease of standardisation (i.e., being able to make a piece of gear function similarly each time it is used) was an important quality of a sampling gear to prevent variation in catch efficiency.

1.8 Conclusions and recommendations for conservation

Seagrasses are vulnerable to a number of disturbances and require management. With growing fears that stock restoration efforts are being compromised more by habitat loss from coastal development, adverse fishery activities and pollution than by over-exploitation, conservation of habitats (such as seagrass beds) is becoming an important part of fisheries management. The priority of such management has been to determine which habitats represent: "geographically or physically distinct areas that one or more species finds indispensable for its survival at some phase in its life history" (Langton *et al.*, 1996). Seagrass beds are becoming increasingly identified as such habitats (Den Hartog, 1970; McRoy & Helfferich, 1977; Phillips & McRoy, 1980; Larkum *et al.*, 1989), mostly with regard to their role as nursery grounds. Examples supporting this claim are numerous (see Table 1.1) but understanding why seagrass habitats have a significant influence on fisheries requires more detailed information. It is clear that fish recruitment to temperate zone seagrasses shows strong responses to habitat structure at local scales but, at larger scales, recruitment is linked more to the availability of planktonic larvae. Such patterns of scale should be borne in mind when selecting sites for comparative studies or conservation. For example, which site may be the first to receive ocean-spawned larvae? In addition, sites should be selected with a view to minimising the impacts of other variables such as salinity, sediment type and turbidity. Alternatively, these variables should be measured and accounted for, or the use of experimental manipulations and ASUs considered. The spatial patterns identified in initial surveys that may influence the beds functioning must be incorporated into any further study at a level appropriate to the questions posed.

Recent studies have highlighted the temporal variability of the seagrass meadow fauna, and most commercially valuable species appear to be seasonal or temporary seagrass residents. Therefore, survey protocols must take into account seasonal and annual variations in seagrass standing stock, spawning periods, annual recruitment, and the diel and tidal migrations. Once the commercial species using the beds are identified, an understanding of their biology, including detailed ecological assessments of habitat requirements during different stages in their life history, is needed. Ontogenetic or functional phases in a species life history must be integrated with large-scale seagrass distribution (geographical location, larval dispersal, depth, distance from shore, distance to other habitats) and local habitat characteristics (seagrass biomass, density, substratum and drift algal biomass). With this life-history information and a detailed understanding of local seagrass resources, effective conservation and management of the fisheries–habitat complex is possible. However, to assess whether seagrass beds merely concentrate species, or whether the residents gain a selective advantage over individuals inhabiting non-seagrass beds, or seagrasses beds of a different size or morphology, more detailed studies on seagrasses are required. This undertaking requires assessment of growth and survival rates and the many processes defining the community composition of a seagrass bed. In addition to the spatial and temporal patterns, these processes include adult-larval interactions, adult competition, macrofaunal-meiofaunal relationships and migration for reproduction, foraging, and response to predators or strong physical gradients (Stoner, 1980). Clearly, further studies are required to identify which seagrass characteristics are important and at what scales they are evident. Understanding the processes identified above will allow managers to predict the value of seagrass beds, ensure their protection (i.e. protecting the right beds at the right time) and allow sustainable fishing activities. Detailed maps of the seagrass beds will allow consideration of the fact that whilst a particular 'type' of bed morphology may benefit one fishery species more than another, greater areal cover of a less-optimal 'type' may make it significant when directing conservation effort.

The less obvious ways which seagrasses may benefit fisheries also require more study. First, to what extent do seagrass beds form the basis of coastal detritus cycles? Do root systems continue to release detritus and protect other inshore habitats such as salt marshes long after the canopy has been lost to disturbance? Improvements in multiple stable isotope analysis mean that trophic pathways can be mapped more accurately. Offshore migrations may obscure direct links but greater understanding of recruitment patterns and the use of electronic tagging will help to identify possible benefits of seagrass beds to commercial fisheries.

It is apparent that seagrass beds potentially have a high importance for some fishery species and, wheras some attempts have been made to investigate the economic and environmental benefits of restoring seagrass beds (e.g. Shabmann & Capps, 1985; Anderson, 1989), further studies assessing the relative advantages of protecting (via seasonal and areal closures), conserving (by the designation of marine protected areas and no-go zones) or restoring seagrass beds (via transplantation techniques) are needed.

Finally, seagrass research tends to be concentrated in particular geographical 'hot spots', however, latitudinal variation is an important consideration in determining the roles and value of seagrass beds to fisheries. It is clear that future research is needed to identify and quantify the importance of seagrass as a nursery area, refuge and feeding ground for commercially important species in all parts of the world where seagrasses exist. This information needs to be collected using standard sampling methods to enable the true global role of seagrass beds to fishery species to be recognised.

The present Chapter has highlighted that the importance of seagrass habitats varies at different spatial and temporal scales. It also identified how the perception of the roles of seagrass habitats can be distorted by the sampling methods used and the time a study is carried out. Local studies are essential for providing the relevant information required by fishery agencies to make valued judgements and to build up a global view of the role of seagrass habitats.

2 *Zostera marina* landscapes around the coast of Jersey (English Channel Islands)

Part of this Chapter was presented:

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S.F. (1999) Mapping and sampling seagrass (*Zostera marina*) beds in Jersey, English Channel. December 1999, Linnean Meeting on Remote Sensing of the Littoral Marine Environment, Linnean Society, London, UK. (Poster presentation).

2.1 Introduction

In order to manage resources, aid conservation, monitor change and direct sampling for scientific studies, the mapping of marine benthic habitats is of paramount importance, and seagrass beds are no exception (Rasmussen, 1977; Thomas *et al.*, 1990b; Sabol *et al.*, 1996; Kirkman & Kirkman, 2000; CCL, 2000; Forqurean *et al.*, 2001). With growing fears that fish stock restoration efforts are being compromised more by habitat loss from coastal development, adverse fishery activities and pollution, than by over-exploitation, conservation of habitats is becoming an important part of fisheries management (Butler & Jernakoff, 2000; Rosenberg *et al.*, 2000). The priority of such management has been to determine which habitats represent "geographically or physically distinct areas that one or more species finds indispensable for its survival at some phase in its life history" (Langton *et al.* 1996). Seagrass beds are becoming increasingly identified as habitats that require mapping because of their ecological significance (Den Hartog 1970; McRoy & Helfferich 1977; Costanza *et al.*, 1997; Duarte, 1999; Connolly, *et al.*, 1999). Due to their shallow, coastal distribution, seagrass beds are particularly vulnerable to a number of disturbances both natural and anthropogenic (Thayer *et al.*, 1975; Sabol *et al.*, 1996; Short & Wyllie-Echeverria, 1996; Glemarec *et al.*, 1997). As a result of these perceived threats, the inclusion of seagrass beds in the management, research and development objectives of governmental bodies and conservation agencies world-wide (Gubbay, 1993; Council of the European Community, 1992; Costello, 1994; Leadbitter *et al.*, 1999) is now common, even in regions where the role of such habitats have not fully been investigated. In the United Kingdom (UK), areas of seagrass (of the genus *Zostera*) are included in some coastal Sites of Special Scientific Interest (SSSI), Ramsar sites (i.e. an area that has been designated a 'Wetland of International Importance' as defined by the 'Ramsar Convention' of 1971), Special Protected Areas (SPAs) under the EC Birds Directive, Marine Nature Reserves and Voluntary Marine Conservation Areas (VMCAs) and marine Special Areas of Conservation (SACs) (Holmes, 1983; Davison, 1997). The objectives of most UK Regional Biodiversity Action Plans include the maintenance of the extent, quality and distribution of seagrass beds in UK waters (UK Biodiversity Steering Group, 1995), and this requires knowledge of their present distribution.

The seagrass *Zostera marina* (commonly referred to as eelgrass), the predominant species found around the coast of the United Kingdom and the Channel Islands, is essentially a subtidal species. It grows in temperate, sheltered coastal waters of the northern Pacific and north Atlantic, extending as far north as the Arctic Circle (Den Hartog, 1970; Phillips & Meñez, 1988). *Zostera marina* is renowned for the variety of substrata, salinities, temperatures and current regimes it is able to colonise and tolerate (Phillips, 1969; Biebl & McRoy, 1971; Mann, 1972; Burrel & Schubel, 1977; Hootsman, *et al.*, 1987; Cleator, 1993). Such a range of possible areas of occupation not only creates difficulties in predicting the large-scale distribution of *Zostera,* but can also influence the various hierarchical structural characteristics of the beds themselves, and therefore the faunal communities inhabiting them (Turner *et al.*, 1999). Mapping of seagrasses is not only important from a management viewpoint but it is also with regards to the understanding of their ecology. One fact, which has been highlighted by past studies, is that there are significant differences in the habitat roles of seagrass beds in relation to their morphology and location (see review by Jackson *et al.*, 2001). When evaluating the relative importance, or predicting the carrying capacity of, different seagrass habitats, these sources of variation need to be accounted for and there is an increasing move toward the characterisation of seagrass meadows using the concept of landscape ecology (Robbins & Bell, 1994). Resource maps and Geographical Information Systems (GIS) detailing environmental and biological habitat variables are important tools, and should be considered as a first step in any assessment of faunal habitat relationships (Robinson & Levings, 1995; Jackson *et al.*, 2001).

The development of methodologies to meet different marine mapping requirements has come a long way in the past three decades (Walker, 1988; Kirkman, 1996; Thomas *et al.*, 1990; Green *et al.*, 2000). Numerous techniques exist, which can be categorised for ease of description as optical remote sensing, acoustic survey and physical survey. The purpose of the mapping determines the resolution required and the appropriate operational procedures, but detailed comparisons of the cost and accuracy of these and other methods are available (Orth & Moore, 1983; Mumby, *et al.*, 1997; Green *et al.*, 2000).

Orth (1976) described aerial photography as an excellent but expensive method of mapping seagrass beds. Compared with satellite imagery, the expense is great but the accuracy is significantly better with aerial photographs (Chavaud *et al.*, 1998). Recently, more advanced techniques have been utilised. For example, Mumby *et al.* (1997) measured seagrass standing crop using a variety of techniques (including satellite sensors and aerial photography) and found that the delineation of seagrass beds was significantly more accurate using the digital, self geo-rectifying, remote sensing unit, Compact Airborne Spectrographic Imager (CASI) (see also Bajjouk *et al.*, 1996). Although prices and availability are improving, this method is often too expensive to acquire in the first instance, particularly for small-scale studies (see Table 19.2 in Mumby *et al.*, 2000; and Table 5.7 in Green *et al.*, 2000).

Remote sensing via non-commercial satellites is less expensive than aerial photography and CASI (Ferguson & Korfmacher, 1997; Green *et al.*, 2000). Early information obtained by satellite imagery was of limited value due to the large pixel size. For example, for the French Satellite Pour l'Observation de la Terre (SPOT) and Landsat Thematic Mapper (TM), 1 pixel was equivalent to 20 and 30m respectively (see Mumby *et al.*, 1997). More recently, with the launch of new generation commercial, high spatial resolution satellites such as IKONOS (launched 24 September 1999), 1m panchromatic and 4m multi-spectral data are now available at prices comparable to aerial photography acquisition (Tanaka & Sugimura, 2001). Optical images, whether satellite digital or aerial photographs, have the advantage of being direct observations and give continuous detailed coverage. However, use is limited by certain environmental conditions. Most authors agree that the images should be taken at low tide with a sun angle of greater than 35 degrees, without wind or clouds obscuring the view, at the peak of the seagrass growing season and after a period of low wind and rainfall (Orth & Moore, 1983; Green *et al.*, 2000). For the present study, the choice of aerial photography over satellite imagery was based on the scale of the project. The proposed study area has a coastline of 96 km and local knowledge indicated that the seagrass beds ranged in size from approximately 5m to 200m in diameter and, therefore, suitable resolution was not available from satellite data (at the time of the study). In addition, two-year-old aerial photographs, which fitted the criteria required to map seagrass, were freely available which removed the high financial cost usually associated with acquiring aerial photographs.

Acoustic surveys of the seabed offer particular benefits where environmental conditions, such as water depth or clarity, limit the use of optical techniques, or logistical considerations rule out physical surveys (Miner, 1993; Hundley, 1994; Sotheran, *et al.*, 1997; Lee Long *et al.*, 1998; Munro & Nunny, 1998). The ability to detect the seagrass acoustically is thought to be attributable to the air filled lacunae along the length of the seagrass blades, which create back scatter in the echo signal that is greater than the background water noise (Sabol *et al.*, 1997; Siljeström *et al.*, 2001, abstract only). This capability has the potential to provide greater detail regarding the architectural structures of the seagrass (for example leaf height, density, standing crop).

Many of the acoustic techniques used today for mapping seagrass habitats were first developed for mapping freshwater aquatic vegetation (Maceina *et al.*, 1984; Thomas *et al.*, 1990; Sotheran *et al.*, 1997). Acoustic systems range from off-the-shelf depth sounders (Maceina & Shireman, 1980) to specially developed Acoustic Ground Discrimination Systems, which link echo-sounder to Global Positioning Systems (GPS) and onboard Personal Computers (PCs), automating data acquisition for direct processing into a GIS format (Sabol & Melton, 1995; Lee Long *et al.*, 1998). Such systems include side scan sonar (Burret & Chuter, 1991; Pasqualini *et al.*, 1998), Biosonics DT4000™ (Sabol & Melton, 1995), Quester Tangents QTCView™ and Marine Micro System's RoxAnn™ (Hamilton *et al.*, 1999; Foster Smith *et al.*, 2001). Each acoustic system has its own advantages and disadvantages for habitat mapping depending on the specific study objectives, resources and the characteristics of the environment to be mapped. Munro and Nunny (1998) used side scan sonar to map marine biotopes (including seagrass) around the Isles of Scilly (east Atlantic Ocean). They found that, whilst the side scan sonar clearly demarcated dense *Zostera marina* stands with eroding margins, it was insensitive to sparse patches (Munro & Nunny, 1998). Although complete spatial coverage is generated quickly without the need for interpolation, side scan sonar was relatively expensive and could be difficult to deploy (Sabol *et al.*, 1997). In shallow waters, the narrowness of the swath width for side scan sonar was such that the advantages of this system in terms of generating continuous coverage were outweighed (Morrisey, 1998).

In general, echo sounder transects are quick and easy to carry out, require minimal post processing (compared to diver transects), and are considered both more objective and easier to accurately geo-reference than diver surveys (Morrisey, 1998). Whilst some dives are necessary to ground truth the aerial photograph maps and the acoustic readouts, to gather the same amount of information through dive surveys alone would potentially be difficult due to small slack tide windows, unpredictable weather and cost.

For the present study, the automated acoustic array, Biosonics DT4000, was chosen. This system, developed originally by the US Army Corps of Engineers to detect problem aquatic vegetation in navigation channels, consists of digital hydro-acoustics, GPS and GIS components. Since its development, it has been used successfully to assess the character, extent, condition and potential impacts of proposed dredging operations on seagrass beds (Sabol *et al.*, 1996). The transducer used in conjunction with the Biosonics DT4000 system has a very narrow beam width (6°) compared to other systems, which with larger beam widths exhibit significant footprint width variability with depth (for RoxAnn 80% of the depth; Hamilton *et al.*, 1999). Also, because return echoes are digitised at a high frequency (41.67 kHz), a cross section of the transect area with a resolution of about 2 cm is produced which allows accurate and quantitative measures of seagrass attributes such as leaf height and cover (Sabol *et al.*, 1996).

2.1.1 Objectives

There were three main aims for the present seagrass mapping study. The first was to analyse aerial photographs to produce a basal area coverage map of the distribution of previously unmapped seagrass (*Zostera marina*) beds around the island of Jersey in the English Channel. The distribution map will act as a baseline for future monitoring of the seagrass beds, and also identify areas of seagrass potentially at risk from anthropogenic disturbance that may require management or protection.

The second aim was to undertake a more detailed acoustic survey of a number of seagrass beds identified and chosen randomly from the aerial photography produced distribution map. Data resulting from this survey were used to quantify the morphology of Jersey seagrass beds at a number of spatial scales.

The third aim was to examine the relationship between seagrass distribution, landscape and bed characteristics and a number of environmental variables measured during the mapping study. Such an investigation will identify which factors are important for the occurrence and maintenance of seagrass beds, and provide information for evaluations of any future changes in the characteristics of seagrass around the coast of Jersey.

2.2 Materials and Methods

2.2.1 Study Location

Jersey is one of the larger islands in the Normano-Breton Gulf (English Channel) with a coastline measuring approximately 96 km. The island lies just off the coast of France and is within the 20m isobath of the French coastal shelf (Figure 2.1a). Depth, exposure and temperature have all been found to influence the colonisation and growth of *Zostera marina* (Hootsman *et al.*, 1987). Simultaneously, studies have shown how colonisation of seagrass can influence the environment; for example, current velocity and sediment stability (Fonseca *et al.*, 1983). Average water temperatures around Jersey range from 7.9°C in winter (minimum in February) rising to 19.5°C during summer (maximum in August, Jersey Met Office, 2000). Due to tidal mixing, the water column remains well mixed throughout the year and sea surface temperatures are representative of the whole water column (Pingree *et al.*, 1985). Tidal streams in the Channel Islands rotate anticlockwise and numerical models also indicate that tidal transport exceeds wind driven components in the region (Pingree *et al.*, 1974; Pingree & Mardell, 1987). On the whole, Jersey experiences relatively fast tidal currents (up to 5m sec.$^{-1}$), although currents close to the shore are influenced by the shape of the coastline, with prominent headlands increasing the speed of tidal currents and causing gyres within adjoining bays (Barne *et al.,* 1995). In addition to strong tidal currents, Jersey also experiences large tidal ranges, which are approximately 11m during spring tides.

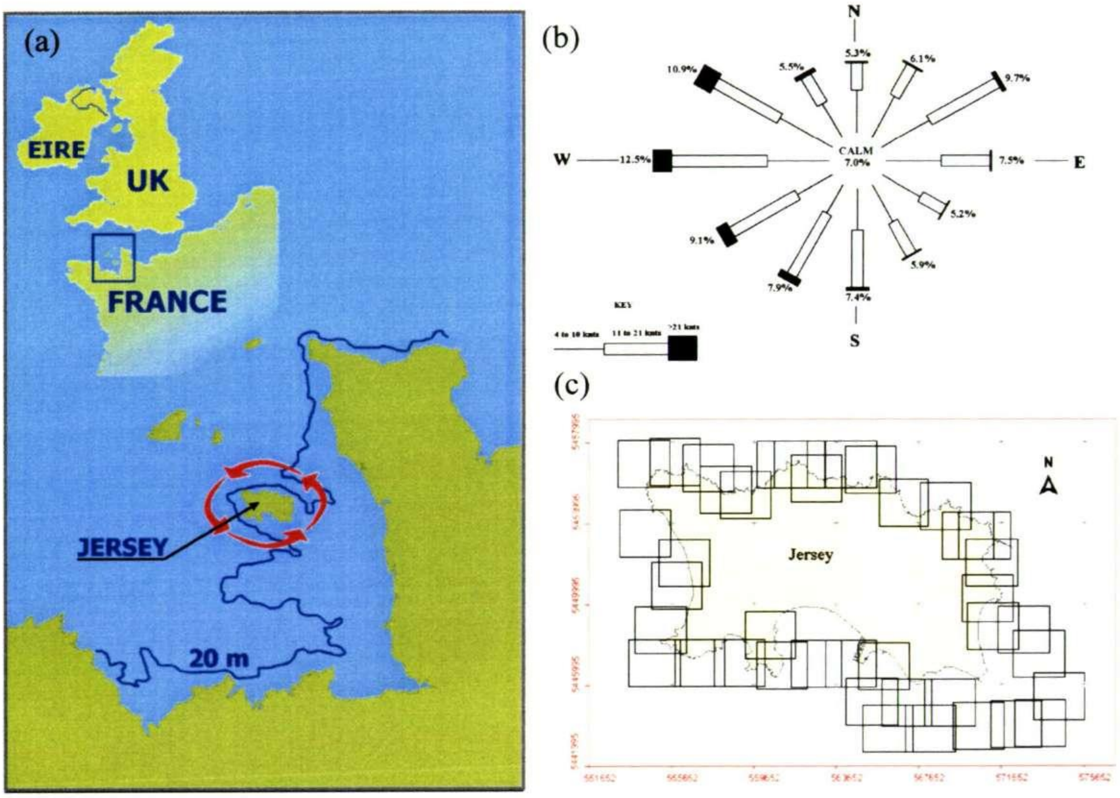


Figure 2.1 (a) Geographical Location of Jersey. Red arrows indicate the intense anticlockwise gyre. The 20m isobath of the French continental shelf is shown in blue. (b) Percentage frequencies of hourly wind direction measured at Jersey Airport from 1971 to 2000. Source: Jersey Meteorological Office, 2000. (c) Aerial photo coverage of Jersey coastline.

In terms of exposure, reports exist of *Zostera* growing in wave-stressed environments (Mann, 1972). However, severe wave action may result in increased mobility of sediments, dislodging and blanketing seagrass and hence sheltered habitats are more favourable (Den Hartog, 1970; Burrel & Schubel, 1977). In Jersey, the predominant wind direction is westerly, where winds reach over 10 kph approximately 10% of the time (Figure 2.1b). In comparison, the south-eastern part of the island is relatively sheltered from prevailing winds. The northern coast is also relatively sheltered, but the topology of Jersey is such that the land falls off sharply on this coast, resulting in greater water depths closer to the shore and coarser and more mobile substrata caused by tidal scour.

Two species of seagrass have been recorded in Jersey, *Zostera noltii* is apparently sparsely distributed in middle and lower intertidal areas, whilst the more abundant and widely distributed *Zostera marina* has been observed from the low intertidal to shallow subtidal (Sinel, 1906; Le Sueur, 1967; Crutchley, 1997). Around Jersey, *Zostera marina* exhibits a diverse range of habitat configurations, from large continuous areas of seagrass to fragmented, smaller patches surrounded by or forming a mosaic with sand and macro-algal habitats (Syvret, A., pers. comm., 1998; Bossy, S.F., pers. comm., 1998; Roper, A., pers. comm. 1999).

2.2.2 Remote sensing using aerial photographs

The aerial photographs used, although not taken for the purposes of the present study, conformed to the ideal criteria suggested for seagrass mapping (stated in Introduction, Orth & Moore, 1983; Mumby & Green, 2000). Photographs were taken using AGFA Avicolor 100 film in a Wield RC20 camera on the 21st July 1997, between 1400 and 1512 (with a spring tide of 1.06m occurring at 1452 British Summer Time). All photographs were digitised by scanning at a resolution of 400 dpi and saved as a 24 bit tagged image file format (TIFF) to CD-ROM. Density level information was stored in 3 bands for each pixel (red, green and blue), that at 24 bit gave a possible 256 density levels.

2.2.2.1 Pre-processing

Unless mentioned below, all processing of digital imagery was carried out using ERDAS Imagine™ version 8.3, which was 'spectral pattern recognition' based (Lillesand & Kiefer, 2000). Pre-processing of the aerial photographs involved image selection, mosaic creation, geo-rectification and land masking. As in most aerial surveys, a great deal of overlap between photos is apparent. Such overlap allows areas of sun glare to be masked by photos taken at a different angle and prevents seagrass beds that span images from being split. Photographs were viewed and relevant images selected and sketched onto a large-scale map to illustrate coverage (Figure 2.1c). The best combinations of images were amalgamated with a feather overlap function within the mosaic tool.

Geo-rectification of the image corrects distortions caused by factors such as the roll of the aircraft, altitude, curvature of the earth, surface atmospheric refraction and non-linearity in the run of the camera's inherent field of vision (Orth & Moore, 1983; Green *et al.*, 2000). An Ordnance Survey map of Jersey (UTM International 1909, Zone 30, with European 1950 datum) was digitised using a digitising table and handheld LC Series II Digitiser™ connected to a PC running the software package ARC. Coastline, buildings, roads and field boundaries were 'traced' to form vectors (lines ending in nodes). The coastline (mean high water spring tide mark) of the island was adjusted to form polygons (using ArcInfo™ version 8 software), which were used to mask out land areas. The vector-based map was used to geometrically correct the aerial images. A polynomial model was applied to a minimum of 30 reference points (or Ground Control Points, GCP's) between the digital image and the previously digitised and projected coastline, road and field coverage. Careful attention was given to dispersing GCPs evenly throughout the image, where feasible. A residual mean square (RMS) error of up to 10 was considered acceptable for this aerial base map. GCPs with a RMS error greater than ten and that contributed significantly to the final morph were removed from the final transformation. Nearest neighbour resampling of pixels was used, as this method transfers original data values rather than averages. After geo-rectification, the pixel size of each of the images was resampled using a bilinear technique to produce a consistent pixel size of $1m^2$. The seaward limit of the area of interest was set at the edge of the image (if less than 10m water depth) or the 10m isobath, where deep water was close inshore (as is the case on the north coast). The choice of this 10m depth was based on the apparent limit to the visibility of the seabed features, and the belief that seagrass does not occur around Jersey at depths greater than 10m.

2.2.2.2 Unsupervised classification

Initial classifications of the processed images were unsupervised, with combined data from the red, blue and green bands used to objectively classify pixels into categories containing similar values for each of the three variables (Chuvieco & Congalton, 1988; Sotheran, *et al.*, 1997; Pasqualini *et al.*, 1998). For a number of images, the variable histograms were viewed to assess spectrally homogenous groups and from this a standard of 30 classes was decided upon (Green *et al.*, 2000). Classes were identified using the ISODATA algorithm (Iterative Self-Organising Data Analysis Technique). This clustering method uses the minimum spectral distance formula to form clusters and classifies pixels repetitively (in this case a maximum of 6 iterations specified), each time redefining the criteria for each class (for example cluster means) to eventually reveal spectral distance patterns in the data (Lillesand & Kiefer, 2000). Once the pixels had been characterised by a similar spectral signature the unsupervised classification was available to be compared to the ground situation.

2.2.2.3 Ground truthing of aerial imagery data

Ground truthing was carried out in two stages. In August 1999, initial ground truthing was carried out to validate the clusters from the unsupervised classification and identify training sites for the supervised classification (see below). In August of the following year ground truthing was carried out to assess the 'thematic' accuracy of the final supervised classifications of images (Mumby & Green, 2000). For both sets of ground validation, class stratified random positions, generated using ERDAS accuracy assessment processor, were identified in the field using Differential Global Positioning Satellite (DGPS) system on board a research vessel. Accurate positioning during ground truthing is important and the use of DGPS that has a working error of 2 to 5m has become indispensable (Green *et al.*, 2000). When the system was first introduced, miscalculations were programmed into GPS transmissions to limit the accuracy of non-military GPS receivers, known as Selective Availability (SA). However, SA was cancelled in May 2000 and a noticeable improvement in the accuracy of the onboard GPS has been observed (Dana, 2000). Fortunately, this preceded ground truthing for the accuracy assessments of the final map. Positions were re-projected from UTM to decimal degrees under the World Geodetic System 1984 (WGS-84). Due to the cost in time and resources incurred by sampling high numbers of truly random sites, driving the vessel in the proximity of a smaller number of randomly generated sites with periodic stops was deemed adequate (Mumby & Green, 2000). At each ground truth position, the presence or absence of seagrass was identified, in shallow water (< 3m) by either snorkelling or glass-bottomed box (using a hand held GPS in a waterproof case), and in deep water (> 3m) by SCUBA diving or a real time drop video camera.

2.2.2.4 Supervised classification of aerial imagery data

Following ground identification of the unsupervised clusters, informational classes were chosen to meet the objectives of the study. These classes were seagrass, 'macro-algae', 'unvegetated sand' and 'unvegetated rock'. In some cases, field validation identified clusters that either did not represent sufficiently certain classes or described two or more classes. Therefore, a hybrid classification method was adopted (Lillesand & Kiefer, 2000) by augmenting the unsupervised with a supervised classification. Supervised classification was implemented using regions (training areas) delimited during the initial ground truthing phase, which are representative of the different habitat classes. The relevant pixels were selected on the images and their spectral information used to specify 'signatures' (numerical descriptors for processing algorithms) of the different classes present in the image scene. Adhering to currently accepted protocol (for example, Lillesand & Kiefer, 2000; Green *et al.*, 2000), a minimum of 10 training areas per class throughout the image was used to obtain a representative sample of the spectral range of each class.

Before the final supervised classification was carried out, signatures underwent an iterative process of refinement. Band plots were assessed to check that the signatures were essentially normally distributed, and image alarm masks and contingency matrices were used to evaluate whether they were sufficiently spectrally separable. In all cases, appropriate recompilation, merging and deleting were employed. In cases where certain spectral classes were poorly represented, further training areas were identified and ground truthed.

The final signature set was entered into a maximum likelihood classification program, which assigned each pixel to a class according to the similarity of the data of that pixel, to a particular signature. The maximum likelihood classification calculates the mean vector variance and correlation for each theme class from the training data and describes the spread of pixels around each mean vector using a probability density function. Pixels are then allocated a class based on the highest probability of membership (see Curran, 1985; Lillesand & Kiefer, 2000). A threshold was conducted on the distance image histogram of the classified image to eliminate pixels that are most likely to be classified incorrectly at a 95% level of probability.

The overall accuracy of the final classification was assessed using error matrices, whereby, each row and column represents each classification category (Mumby & Green, 2000). For the present study, an equal number of accuracy assessment sites (ten) was randomly selected from each class per image (or mosaic). The numbers of correctly and incorrectly classified pixels were used to determine the probability of a pixel misclassification (user accuracy; Janssen & van der Wel, 1994). In addition to user accuracy for each class (only the class 'seagrass' is reported here), a measure of accuracy of the whole image across all classes was calculated using the the multivariate Khat statistics (K, otherwise known as the Kappa coefficient) was calculated using the equation;

$$K = \frac{N\sum_{i=1}^{r} x_{ii} - \sum_{i=1}^{r} (x_i + \cdot x_{+i})}{N^2 = \sum_{i=1}^{r} (x_i + \cdot x_{+i})}$$

(from Mumby & Green, 2000)

where 'r' is the number of rows in the matrix, 'x_{ii}' is the number of observations in the *i*th row of the *i*th column, 'x_{i+}' and 'x_{+i}' are the row and column totals and N is the total number of observations (ten per class) (Green & Mumby, 2000). The Khat statistic represents the proportion of error reduced by the classification compared to the image being classified completely at random (Erdas Inc., 1991).

Isolated seagrass patches less than $100m^2$ were mapped as separate beds of seagrass when the distance between one bed and another was greater than the diameter of the bed. As resources did not allow more detailed mapping of all seagrass areas identified by the final map, a number of seagrass beds was selected at random for further survey using an acoustic system.

2.2.3 Acoustic survey

The Biosonics DT4000 system, an amplitude based digital hydro-acoustic sounder with a high frequency 420kHz narrow beam (6°) transducer, was used to survey nine seagrass bed sites on the east and south coast of Jersey (La Coupe, Flicquet, St Catherine Bay, Ann Port, Grande Haise, Les Elavees, Karame, Violet, Icho, Elizabeth Castle). The transducer of the acoustic system was attached to a pole fixed to the side of the research vessel (Figure 2.2). This fixed (as opposed to towed) arrangement of the transducer allowed uncompromised vessel manoeuvrability, an important consideration in Jersey where some of the seagrass beds occurred on soft sediment areas within rocky reefs. The transducer was linked to onboard sounder electronics through a laptop computer that collated positional information from the vessel's DGPS receiver (Figure 2.2). The transducer (vertically aimed at the seabed) generated short pulses (set at 0.1 ms), the return echoes of which were recorded and digitised at a high frequency (41.67 kHz, corresponding to a depth increment of about 18 mm). Software on the computer (Visual Acquisition v4.0) linked this hydro-acoustic data stream with position reports from the DGPS (Sabol & Burczynski, 1998).

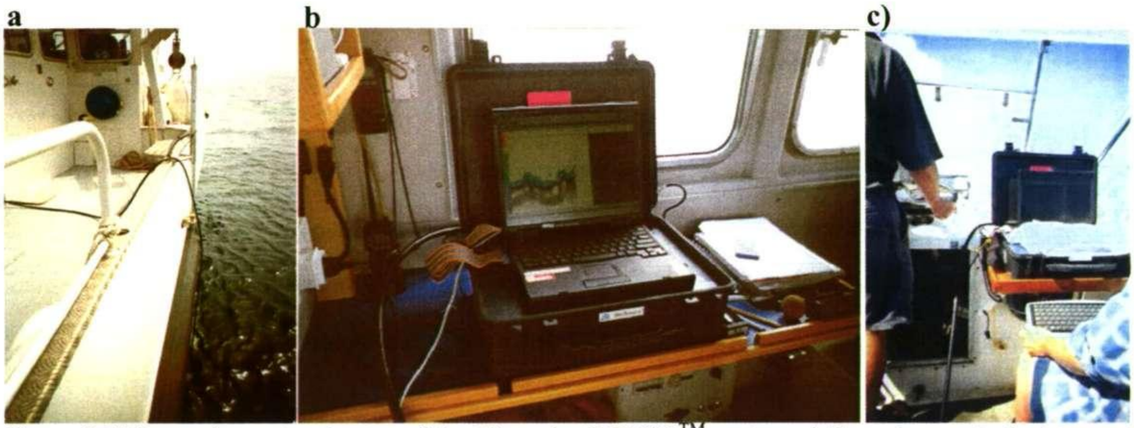


Figure 2.2 The equipment and setup of the Biosonics DT4000^{TM} system; a) Transducer attached to a pole and fixed to the side of the Fisheries enforcement boat; b) Onboard sounder electronics, linked to laptop computer, collating positional information from a DGPS receiver c) Biosonics set up on a smaller research vessel.

With the assumption that depth would influence vegetative changes in the seagrass, transects for the acoustic survey were located perpendicular to the shore. The pre-selected near linear transects were traversed at each study site, using the vessel-mounted acoustic system at a speed of 2.5 ms^{-1} (such a slow speed was maintained to avoid cavitations, which would increase the surface noise levels of the echo return). Transects were carried out at slack water to avoid underestimating seagrass leaf height and overestimating cover, due to the 'flattening out' of seagrass caused by high current speeds (Miner, 1993; Sabol *et al.*, 1996; Sabol *et al.*, 1997). Whilst traversing, returning echoes were displayed as a echogram using the acquisition software, allowing real-time monitoring of transect progress. Initial spacing of transects was approximately 50m, however, this was reduced or increased if the bed was, respectively, more or less homogenous.

2.2.3.1 Processing

The collected hydro-acoustic and position data files (in Biosonics proprietary format) were processed using the specifically designed software BioPlant© Version 1.0 (Biosonics Incorporated, 2000) and written to an ASCII file. The signal processing software used in the Bio Plant program takes advantage of the features described in detail in Sabol and Burczinski (1998). By examining a group of approximately 10 pings (returning echoes) between successive DGPS reports, the seabed is detected and tracked (for more detail see Sabol & Melton, 1995). Algorithms are then employed to examine the spatial distribution of above 'noise' signals in the region immediately above the bottom (Sabol & Melton, 1995). The software produces files of geographical position, bathymetry and attributes seagrass presence/absence, leaf height and seagrass percent cover (see Sabol *et al.*, 1996; Sabol & Melton, 1995). Point coverage was generated from the DGPS positions using

ArcInfo™ (Version 8) and projected to the UTM (Universal Transverse Mercator) co-ordinate system (International 1909, Zone 30, with European 1950 datum). Although the tide was slack during all transects, sometimes the surveys were carried out at low tide and at other times during high tide. Therefore the software Tide Plotter™ was used to estimate the height above chart datum at the times the surveys were carried out and this was subtracted to standardise the depth (Belfield, 1999).

Corrected bathymetry and seagrass attributes were tabulated in Microsoft® Excel, saved as a comma separated text file and joined (using ArcTools version 8.0.2) with their associated position point coverage. Bathymetric and seagrass attribute maps were generated from this point coverage using the triangulated irregular network (TIN) spatial interpolation option within Workstation ArcTools version 8.0.2. Since interpolation does not allow for small gaps between transects, the area of seagrass identified from the aerial photographs and converted to attribute polygons were used as a 'hard-clip' (ArcTools Tin Builder) to mask these areas from interpolation.

Slope was calculated as the arctangent of the difference in depth between the start and finish of each Biosonics transect (m) divided by transect length (m). Slope values from each transect were used to calculate mean slope for each seagrass bed.

2.2.3.2 Ground truthing

The seagrass attributes identified by the acoustic survey were validated using SCUBA diving. Random points along each transect were identified using Biosonics Visual Analyser software (see echogram readout from this software in Figure 2.6) and the location of each position marked. These positions were identified in the field using DGPS and a shot line deployed from the research vessel. A team of two SCUBA divers carried out shoot density counts and leaf length measurements (mean based on measurements of 5 leaves) in a $0.25m^2$ quadrat placed immediately north of the shot mark. In addition to gathering these data for validating acoustic measurement of seagrass bed attributes, samples were taken of other site variables. Above ground biomass samples were collected by placing a $0.0625m^2$ quadrat with a 2mm mesh bag attached. Making sure all the material was inside the bag, the shoots were cut at the water sediment interface before the bag was sealed (the sample was always taken from the same corner of the larger quadrat). A plastic core (50mm diameter) was pushed into the seabed within the large quadrat to a depth of 200mm to recover a sediment sample.

Upon return to shore, seagrass samples were washed with seawater using a 1mm mesh sieve, and all material placed, initially, in labelled plastic bags and kept in a refrigerator until processed (all processing was initiated within 12 h of collection). Sediment samples were frozen until granulometric analysis could be carried out.

2.2.4 Calculation of seagrass landscape metrics

For each of the nine study sites chosen to be surveyed by the acoustic system seagrass landscape patterns were evaluated using the spatial statistics software FRAGSTATS version 3.3 (McGarigal *et al.*, 2002). A buffer zone of 100m was built around the core area of seagrass at each site (evaluated as the largest continuous patch of seagrass in each region, which was assumed to be the site of most stable seagrass colonisation over time). The area within the buffer was clipped from the original image and converted to an ASCII file of rows and columns of pixel values (at a resolution of $1m^2$). Unclassified or boundary regions were assigned the value '-1' to remove them from analysis. Descriptor files were written to describe the pixel value classifications for each image ASCII file. The spatial composition and configuration of each defined seagrass landscape was quantified, using threee metrics, after first calculating the total area (ha) of the identified landscape. To allow comparisons between the different sized landscapes to be made, all metrics were size independent (Jaeger, 2000). As a comparative measure of the relative extent of seagrass within each location, the area of largest patch of seagrass expressed as a percentage of the total area of landscape was calculated (McGarigal & Marks, 1995). This largest patch index (LPI) only provides information on the landscape composition, therefore, measures of configuration are also required. Edge density (mha^{-1}) is the sum of the lengths (m) of all seagrass edge segments, divided by the total landscape area, and is a per unit area standardised substitute for the commonly used measure of total perimeter of seagrass (McGarigal & Marks, 1995). Measures of relative edge can be a good indication of the fragmentation and complexity of the seagrass landscape, and may also be related directly to the susceptibility of the plants to being dislodged or damaged. Edge density, however, is not spatially explicit and, therefore, does not give any indication of shape or form; that is, landscapes of long, thin seagrass patches potentially can have similar edge density to more compact patches. To differentiate between such bed forms, core area of seagrass (in the present study edge depth limit was set at the minimum of 1m) as a percentage of the total landscape area, was calculated. This core area percentage of landscape (CPLAND) index integrates seagrass patch area, shape and edge effect distance (McGarigal *et al.*, 2002). The CPLAND index can have a value between 0 (no core area) and 100 (mostly core area).

2.2.5 Measurement of biological and environmental site variables

2.2.5.1 *Seagrass shoot density, length and width*

In the laboratory, samples of the above ground biomass collected *in situ* (which had been stored at 4 °C for up to 12 h) were rinsed with distilled water on a 1mm mesh sieve to remove the salt and prevent uptake of water by the cell walls (Gessner, 1971). The vegetative shoots of *Zostera marina* were then counted. The length and width of each blade was measured in the laboratory to the nearest mm to allow calculation of the epiphyte index.

2.2.5.2 *Seagrass epiphyte index*

Each seagrass leaf blade of the counted shoots was scraped with a razor blade to remove epiphytes (algal and faunal). The epiphytes were wet weighed and then dried to constant weight at a temp of 100°C. For each sample, an epiphyte index was calculated as the epiphyte weight divided by the sum of the mean leaf length, width and number.

2.2.5.3 *Sediment grain size analysis*

The sediment samples taken during the ground truthing (which had been frozen for storage) were defrosted, oven dried at 105 °C to a constant weight and the dry weight noted. Samples were then wet sieved using a 63μm sieve to seperate the silt clay fraction. After further drying of the remaining fraction, the weight of the sediment retained was subtracted from the original dry weight to give the silt-clay fraction. The sand fraction (> 63 μm) was graded using dry sieving, with the pre-weighed sample sieved (using a mechanical shaker for 15 minutes) using a standard Wentworth series of sieves. After shaking the material on each sieve was weighed and noted. Mean particle grain size and percentage silt were calculated using the software Sed-Stat version 5.1 (Hartley, 1998).

2.2.5.4 *Relative water depth*

The depth at which seagrass existed at each study location was measured using the Biosonics DT4000 acoustic system and processed using the BIOPLANT version 1.0 software, with depth corrected to chart datum (see details earlier in methods). The resulting ASCII file was imported to Microsoft EXCEL™ and the records not identifying seagrass removed prior to calculations of depth distributions of seagrass growth.

2.2.5.5 *Wave Exposure*

To estimate the amount of wind exposure experienced by each of the study segrass bed locations, a relative exposure index (REI) was calculated following the methods of Keddy (1982) adapted by Fonseca and Bell (1998), which used the equation:

$$\mathrm{REI} = \sum_{i=1}^{8}(V_i \times P_i \times F_i)$$

where i is ith compass heading (eight readings, 45° increments), V is mean monthly maximum wind speed (ms^{-1}), P is the percent frequency at which wind occurred from the ith direction and F is the effective fetch (m). Percent frequency and maximum daily wind speed data (between 1991 and 2000) were obtained from the Jersey Met office and had been recorded using a Munro - IM146 Cup anemometer, with an effective wind height of 10m above the ground (Pallot, A., pers. comm., 2002). Effective fetch (defined as the distance from the centre of the seagrass bed to land) was measured using tools within ArcMap™ and with the seagrass beds overlaid onto the digitised Bartholomew map of Europe, for each of the 8 main compass headings.

2.2.5.6 *Data analysis*

2.2.5.6.1 *Validation of acoustic data*

After testing that the assumptions of normality were met, Pearson's product moment correlation was carried out between the data recorded by the Biosonics™ DT4000 system (seagrass leaf height and percent cover) and those corresponding measurements collected in situ (seagrass leaf length and shoot density) from the $0.25\mathrm{m}^2$ quadrat.

2.2.5.6.2 *Differences between study sites*

A one-way ANOVA (unequal sample sizes) was performed to assess whether there were significant differences between the water depth, slope, percent seagrass cover and seagrass height, as recorded using the Biosonics DT4000™ echo sounder. Differences between mean grain size, percent silt-clay fraction, shoot density, leaf length and epiphyte index of seagrass (seagrass (as measured from the $0.0625\mathrm{m}^2$ quadrat) at the different sites were tested using a fully balanced one way ANOVA. Data were ln (x+1) transformed (with the exception of data presented as ratios, which were arcsine transformed) where appropriate, to meet assumptions of homogeneity of variance (tested using Cochran's C test) and α was set to 0.01 to compensate for the increased likelihood of Type 1 error (Underwood, 1981). *Post hoc* comparisons to determine the significant differences between group means were carried out using the Tukey Unequal N HSD test, a modification of the Tukey HSD test (Winer, 1985) and *post hoc* SNK tests. The software STATISTICA (StatSoft Inc. 1998) was used for all analyses.

2.2.5.6.3 Factors influencing seagrass attributes

A correlation matrix was used to identify and remove co-correlates, and the remaining attributes were transformed appropriately and normalised. Simple linear regression and 95% confidence limits were determined using STATISTICA for landscape and seagrass habitat attributes for all sites versus physical conditions present at each site. The Pearson product moment correlation coefficient was used, with the different beds classed as independent observations. The dependent variables, shoot density (m^{-2}), leaf height (m), epiphyte index and edge density (mha^{-1}), were regressed against MPGS, percentage silt, slope, depth and REI. The landscape variables CPLAND and largest patch index were regressed against depth, slope, REI and the percent of adjacent habitat that was rock (in order to determine whether the seagrass growth patterns area restricted by areas where the seagrass cannot grow). Finally, stepwise multiple linear regressions were employed to evaluate the relative influence of environmental variables for predicting specific seagrass landscape and plant attributes.

2.3 Results

2.3.1 Large-scale seagrass distribution

In total, 41 photographs were used and coverage of the target area was complete with the exception of two small regions (one in the north-west corner of Jersey and one in St Aubin's Bay) where, despite image merging attempts, sun glare blanked out the regions. The region in the north-west of Jersey is not only highly exposed to prevailing winds and large waves, but the steep depth profile is such that seagrass colonisation is not possible. In St. Aubin's Bay, sun glare masks areas of potential seagrass cover, however, ground validation using drop camera and diver survey yielded no positive identification of seagrass presence.

Figure 2.3 illustrates the reliability of the final map showing the kappa statistic (shading) of the proposed seagrass map. Only those photographs where seagrass was identified are shown in the accuracy assessment. The accuracy shows unavoidable variability between photographs, due mainly to light levels. Lower accuracies on the north coast are attributable to depth and also confusion between seagrass and algae only at deeper depths. Thorough ground truthing of potential locations using divers and drop camera found no seagrass, suggesting that although the accuracy is lower it is unlikely that seagrass growth occurs in these areas.

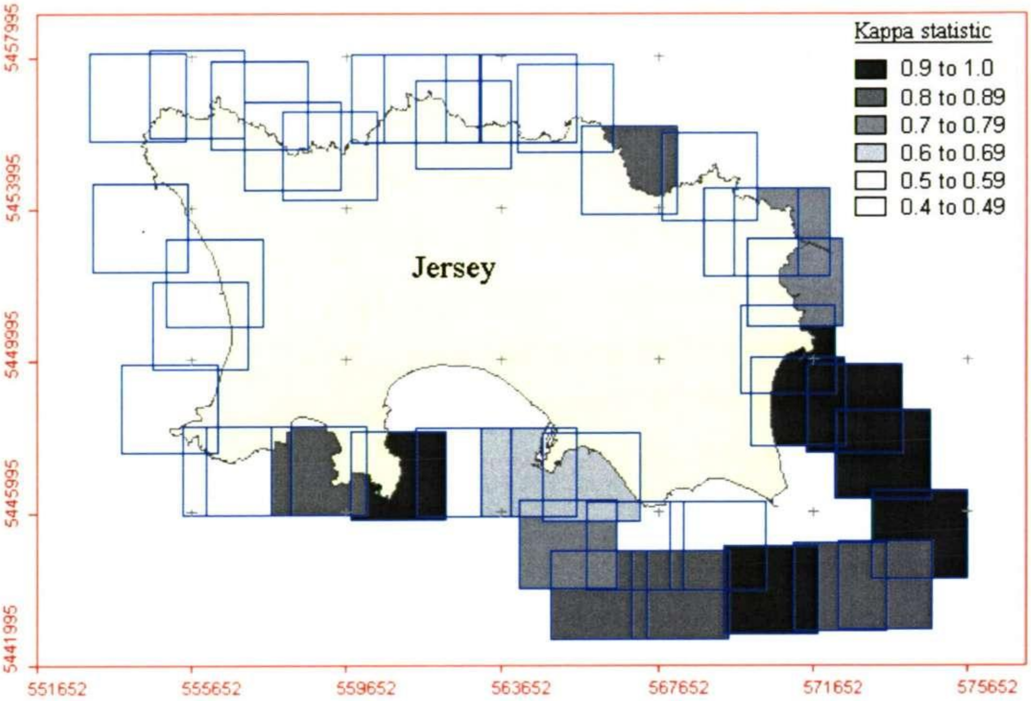


Figure 2.3 Accuracy of the final map. The Kappa statistic for individual photographs and mosaics, where seagrass occurred is given.

Estimates based upon aerial photographs suggest that *Zostera marina* covers 129.07 ha of the shallow subtidal around the coast of Jersey. Predominantly, seagrass beds are found on the east and south coasts of the island, although some small (less than 0.5 ha) isolated patches occur on the north-east coast, restricted to easterly facing bays and rocky gullies (Figure 2.4). The largest expanses of seagrass occurred on the east coast at St Catherine Bay (571379, 54452242 UTM), and on the south coast between rocky outcrops at Les Elavees (572852, 5444996, UTM) and within the Violet Channel (572000, 5443845 UTM), with an estimated coverage of 27.39, 13.42 and 11.54 ha respectively.

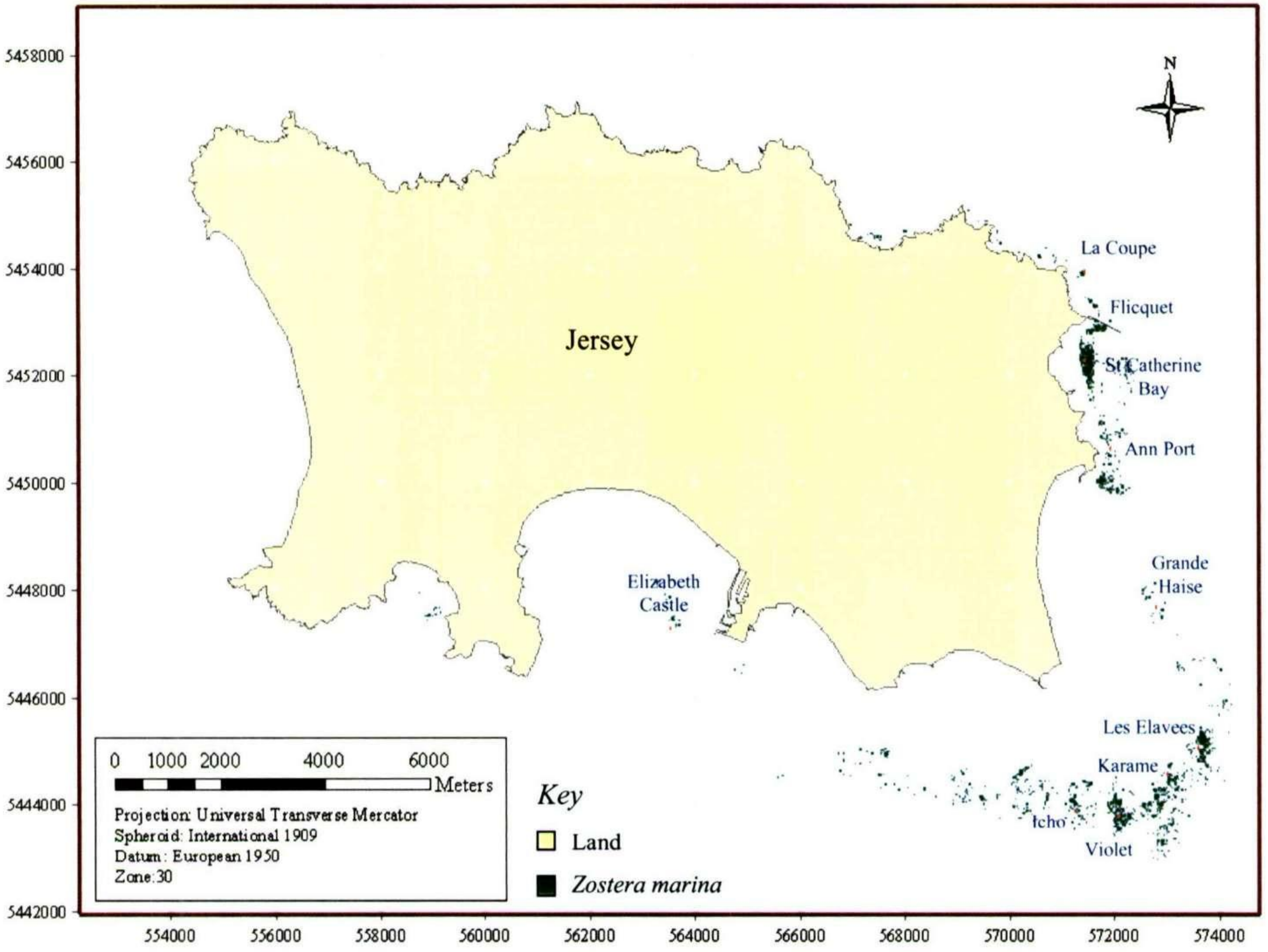


Figure 2.4 Distribution of *Zostera marina* (in green) around the coast of Jersey, English Channel.

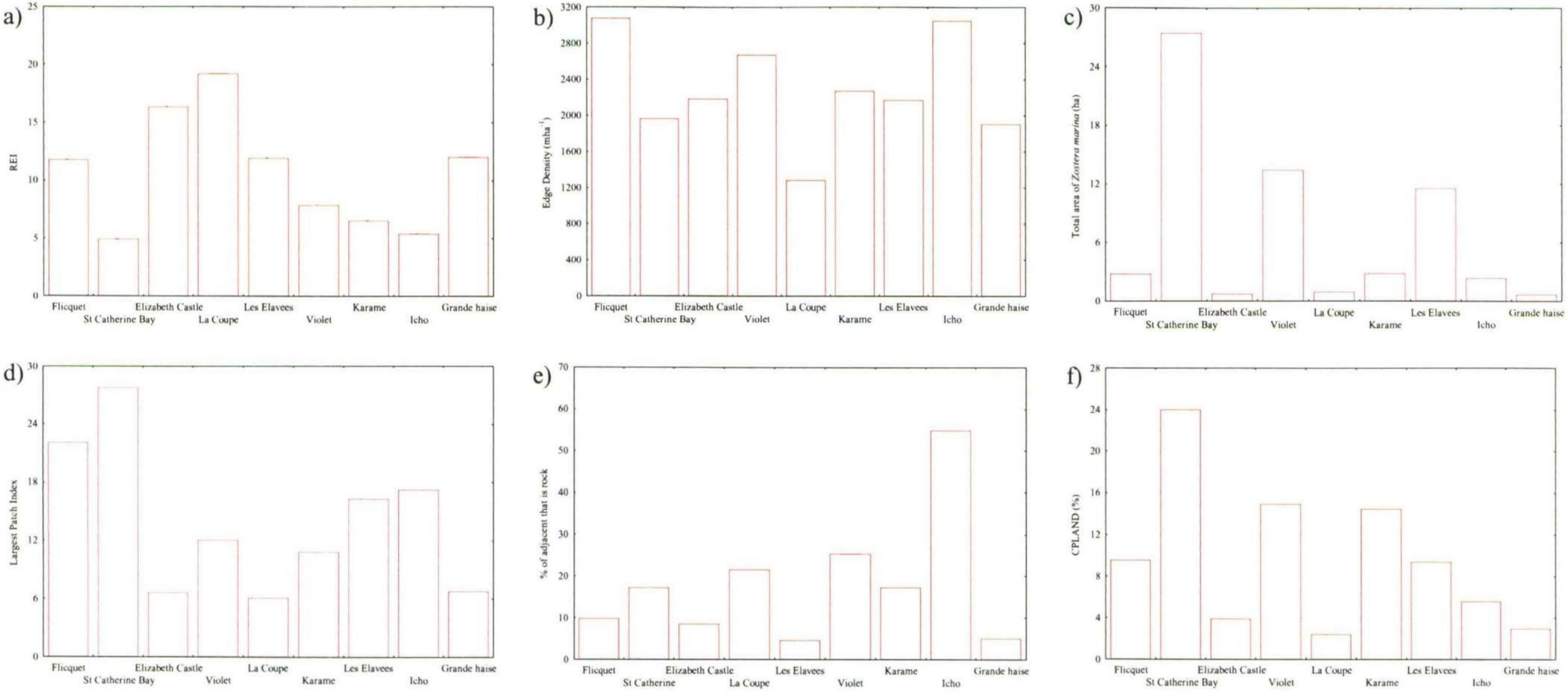


Figure 2.5 Bar charts of the larger-scale variables in configuration and exposure of seagrass landscapes around the coast of Jersey. a) REI, Relative exposure index (x10^6); b) edge density; c) total area of seagrass (*Zostera marina*); d) largest patch index; e) % of adjacent habitat that is rock; f) core area of seagrass as a percentage of the landscape (CPLAND). The names of the sites can be located with reference to Figure 2.4.

2.3.2 Seagrass landscape attributes

The landscape patterns of seagrass distribution varied significantly between the sites studied (Figure 2.5). Across all sites, the mean largest patch index (LPI) was 14.0% of the landscape. Four of the seagrass landscapes had LPIs above this average: St Catherine Bay (LPI; 27.7%), Flicquet (22.1%), Icho (17.2%) and Les Elavees (16.3%) (Figure 2.5d). In comparison Elizabeth Castle (6.6%), La Coupe (6.0%) and Grande Haise (6.8%) all had LPIs well below the average (Figure 2.5d). In terms of the edge density, Flicquet (3074.3 mha^{-1}), Icho (3044.74 mha^{-1}) and Violet (2663.38 mha^{-1}) were all above the average (2282 mha^{-1}) for the area. Lowest edge densities were found at La Coupe (1279.42mha^{-1}) (see Figure 2.5b). The mean core area of seagrass as a percentage of landscapes was relatively small (9.64%) for the study sites. Highest CPLANDs were calculated for St Catherine Bay (23.95 %), Violet (14.88%) and Karame (14.43%) (see Figure 2.5f). Sites with the lowest percentage of seagrass core area (well below the average) were observed at La Coupe (2.36%) and Grande Haise (2.94%).

2.3.3 Seagrass bed attributes

Figure 2.6 is an example of one of the resulting echograms; in this case, from the seagrass bed near Elizabeth Castle on the south coast. Some of the visible features are highlighted. The echogram represents depth along the vertical axis and ping report numbers (equivalent time or distance travelled at a constant speed) along the horizontal. The echo return level is a coloration of voltage squared in decibels (db). Surface noise is due to small bubbles entrained in the water from waves, turbulence or boat propeller causing multiple scattering of the signal. The *Zostera marina* is visible in the echogram as a thick layer of medium level echo returns (approximately -30 to -60db) immediately above the seabed. The top of the canopy varies more than the bottom due to the patchiness and variability in plant height (on this echogram ranges from 0.2 to 1.2m). The bottom typically exhibits the strongest echo (of about -20 db) return and, at the frequency used, there is negligible penetration into the sediment.

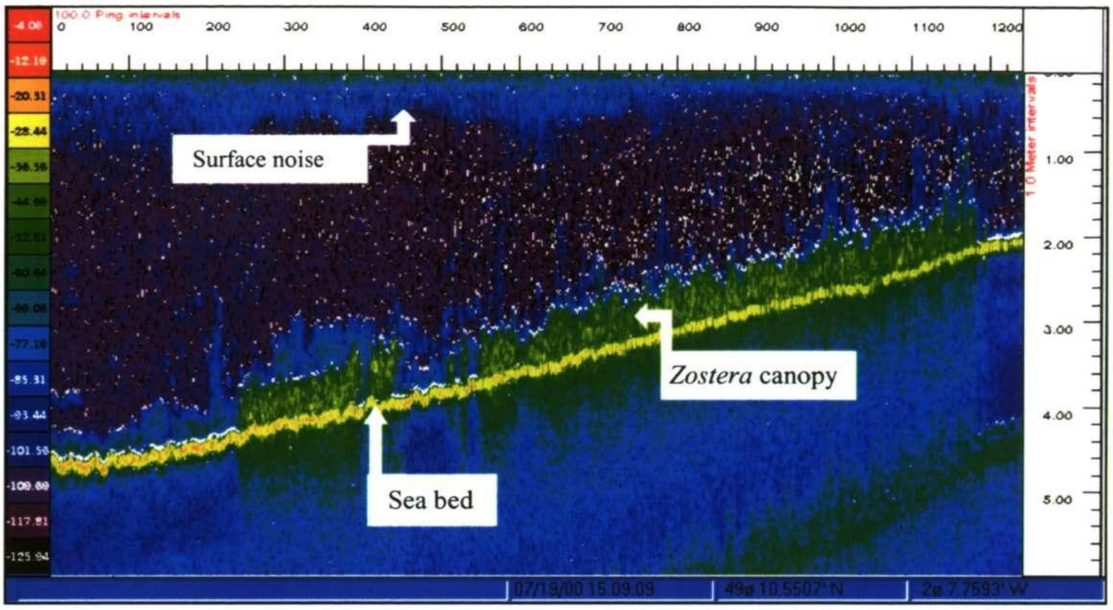


Figure 2.6 Typical Biosonics ™ DT4000 echogram, from the seagrass near to Elizabeth Castle on the south Coast of Jersey. The vertical axis corresponds to depth in metres and the horizontal axis to ping report numbers (equivalent time or distance travelled at a constant speed).

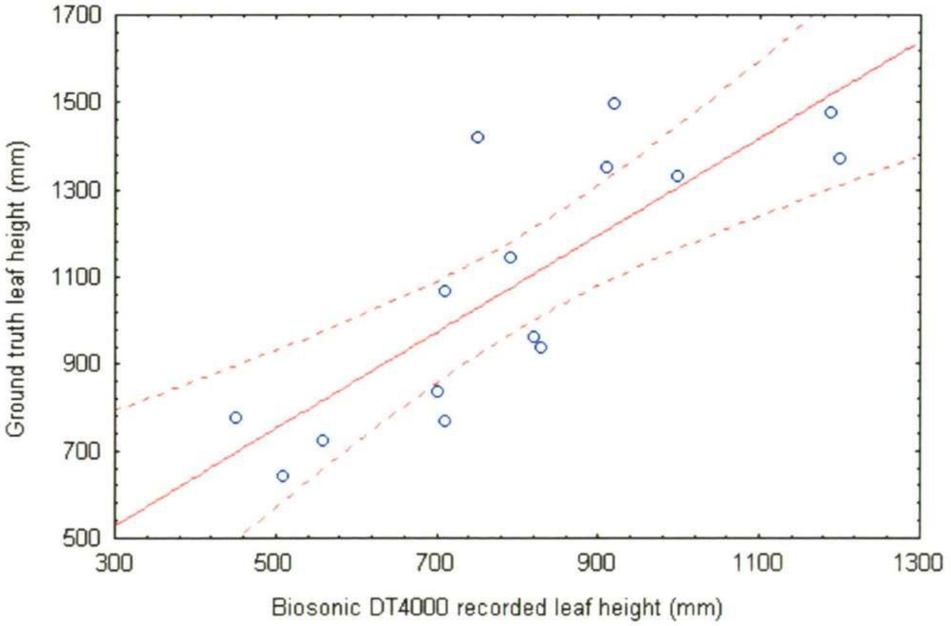


Figure 2.7 Relationship between leaf height (mm) recorded using Biosonics DT4000^{TM} echo-sounder and in situ SCUBA diver measurements. Correlation $r = 0.809$, $p < 0.05$. $y = 193.14 + (1.1127)x$. Dotted red line represents 95% confidence limits.

Pearson's product moment correlation of Biosonics data and *in situ* measurements for leaf height showed a good correlation ($r = 0.81$, $p < 0.05$). But as Figure 2.7 (and the slope of the fitted line) illustrates, the Biosonics appeared to underestimate the length of the seagrass blades.

Seagrass leaf height, measured using the Biosonics DT4000™ echo-sounder, showed significant differences between sites ($F_{(8,68140)} = 126.41$; $p< 0.01$; Figure 2.8b). The highest mean leaf heights were observed at St Catherine Bay (mean height 0.8 m ± 0.35 s.d.) and at near by Ann Port (0.8 m ± 0.34), which did not differ significantly from each other, but were significantly greater than ($p < 0.01$) heights at the other sites (TUKEY HSD unequal N test). The shortest canopy heights, recorded at Flicquet (0.4 m ± 0.31) and Elizabeth Castle (0.5 ± 0.21), were significantly shorter than heights at the remaining sites, which did not differ significantly from each other (range = 0.55 and 0.65m).

In comparison, leaf lengths as measured for those shoots recovered from the above ground sample, showed that the highest mean leaf lengths were at Grande Haise (1.6 m ±0.08), although this was only significantly higher than at Elizabeth Castle (0.7 m ±0.06) and La Coupe (1.0 m ±0.29) (Figure 2.8e). Elizabeth Castle had the shortest leaf lengths as well as canopy height, but the leaf lengths measured at Flicquet (1.4 m ±0.34) were much higher than the canopy heights showed at that site and were not significantly different from mean leaf lengths at St Catherine Bay (1.3 m ±0.18).

Percent seagrass cover, as measured using the Biosonics DT4000™ echo-sounder, appeared only able to determine presence and absence of seagrass cover. At all ground truth points where seagrass was present, the percent cover was 100%, irrespective of the variation in shoot density at each point, and was left out of further analyses.

For *Zostera marina* beds at the study sites around the coast of Jersey, mean shoot density was 390 shoots m^{-2}, and ANOVA indicated significant differences between sites ($F_{(8,18)} = 9.02$; $p<0.001$; Figure 2.8f). Highest mean shoot densities were observed at Grande Haise (597.3 shoots m^{-2} ± 51.43), Icho (560 ± 42.33), Les Elavees (522.7 ± 115.75) and Karame (485.33, ± 33.31). At these sites, shoot densities were significantly higher ($p< 0.05$) than at all other sites except at St Catherine Bay (357.3 ± 143.40) (SNK *post hoc* test). The lowest mean shoot densities were found at La Coupe (241.7 ± 55.62), although there was no significant difference between shoot densities there and at Violet, Elizabeth, St Catherine Bay or Flicquet.

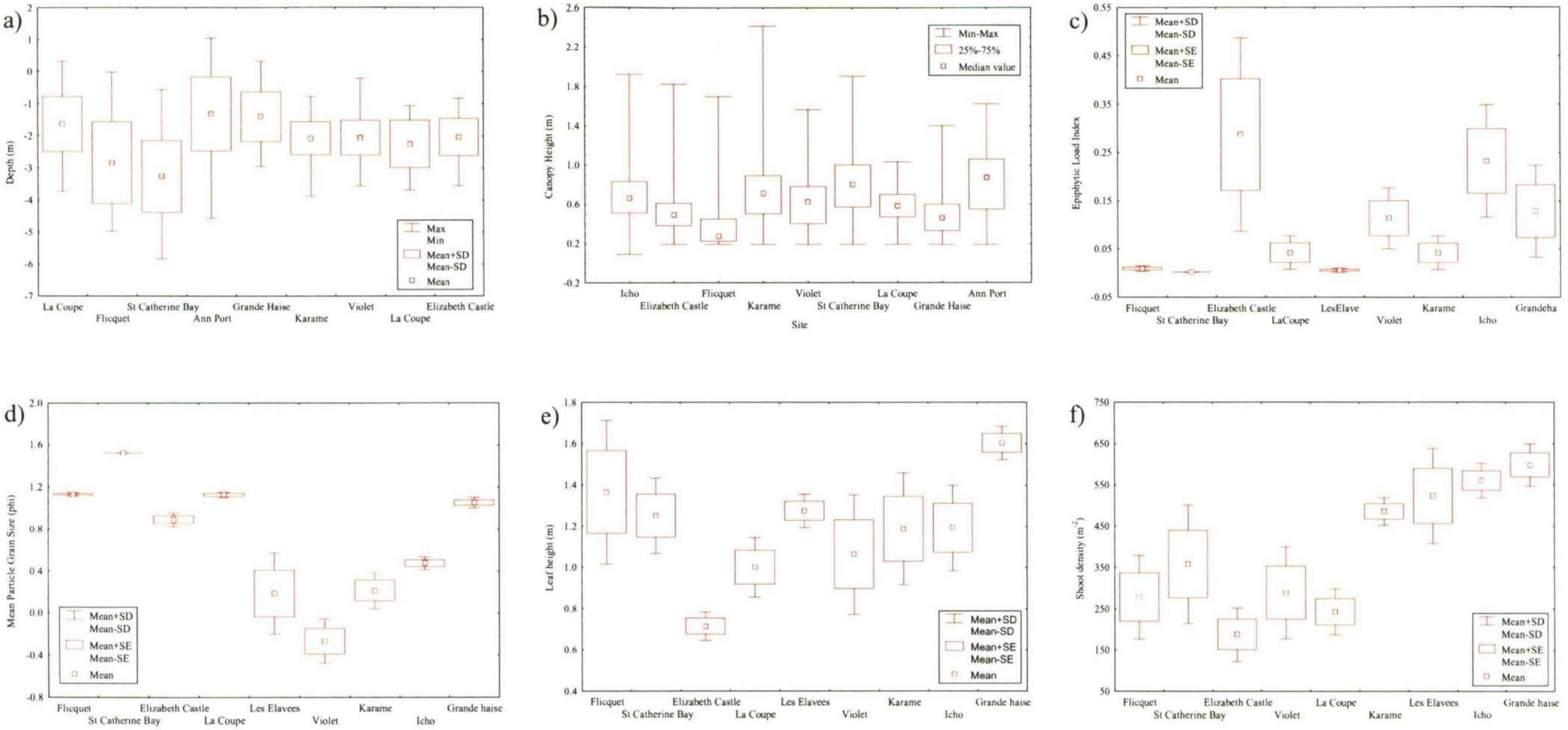


Figure 2.8 Box plots of seagrass plant variables at the different sites around the coast of Jersey. a) Depth and b) Seagrass leaf height as measured using the Biosonics DT4000^{TM} echo sounder system; c) Epiphyte Index; d) Mean Particle Grain Size; e) Leaf height; f) Shoot density, collated from SCUBA diver collections. See Figure 2.4 for locations

ANOVA on the arcsine transformed data showed that there was a significant difference ($p < 0.01$) in the epiphyte index on the seagrass at the different sites around the coast of Jersey ($F_{(8,18)} = 4.012$; $p < 0.01$, see figure 2.8c). At Elizabeth Castle, seagrass showed the highest levels of epiphyte index (mean epiphyte index = 0.35 ± 0.272), significantly higher ($p < 0.05$) than on the seagrass at Ann Port (0.02 ± 0.02), Karame (0.06 ± 0.068) or Flicquet (0.046, ± 0.025); but not significantly higher than Grande Haise (0.138, ± 0.107), Icho (0.334, ± 0.114) or Violet (0.148, ± 0.059) (SNK *post hoc* test). The lowest epiphyte indices were found at St Catherine Bay, Les Elavees and Ann Port, although these sites were only significantly lower ($p < 0.05$) than at Elizabeth Castle and Icho. The dominant epiphyte group at the majority of sites was the crustose coralline, calcium carbonate-depositing red alga of the genus *Fosliella*; however, at Elizabeth Castle, Grande Haise and Icho, the filamentous alga *Polysiphonia lanosa* dominated epiphytes (plants were up to 10cm long in some cases) and at Ann Port the tube-building polychaete *Nicolea zostericola* was the dominant epiphyte.

2.3.4 Environmental setting of seagrass beds

The relative exposure (measured using Relative Exposure Index, REI) at the seagrass bed study sites varied greatly (Figure 2.5a). Mean REI across sites was 10.65 ($x10^6$), ranging from an REI of 19.19 ($x10^6$) at La Coupe (the most exposed site) to St Catherine Bay (the most sheltered site) where REI was only 4.88 ($x10^6$). Seagrass was found only on very slightly sloped sea beds (mean slope across sites was $0.012 m.m^{-1}$). There was a significant difference ($p < 0.01$) in the sea bed slope at the different sites around the coast of Jersey ($F_{(8,33)} = 17.34$; $p < 0.01$). Slope was significantly greater at Flicquet ($0.042\ m.m^{-1}$) than at any other site, which did differ significantly from each other (TUKEY HSD unequal N test).

At the study sites, mean depth of *Zostera marina* was 2.1 m below chart datum (c.d.). Seagrass never exceeded depths of 6m at the beds acoustically surveyed (Figure 2.8a) and were subtidal apart from at Grande Haise, Ann Port and La Coupe, where seagrass was found on the lower intertidal. The upper limit of seagrass was around the mean low water spring tide mark (1.4 m c.d.). One-way ANOVA indicated significant differences in the depth of seagrass between locations ($F_{(1,6591)} = 446.97$; $p < 0.01$). Seagrass beds on the east coast at Flicquet, St Catherine Bay and Ann Port showed the greatest depth ranges (5.0, 5.3 and 5.6 m, respectively; Figure 2.8a). On the south coast at Karame, Violet, Icho and Elizabeth Castle, seagrass exhibited much narrower depth ranges (3.1, 3.3, 2.6 and 2.7 m, respectively; Figure 2.8a). *Post hoc* Tukey's HSD test (for unequal sample sizes) showed no significant difference ($\alpha = 0.01$) between depth of seagrass at Karame, Violet, Icho and Elizabeth Castle. Similarly, depth of seagrass at Ann Port, Grande Haise and La Coupe did not differ significantly between the three sites, but the depths achieved at these sites were significantly less than at the other sites ($\alpha = 0.01$). Depth of seagrass at St Catherine Bay and Flicquet differed significantly ($\alpha = 0.01$), with seagrass reaching greater depths at St Catherine Bay, but at both sites seagrass was found significantly deeper than at any of the other locations (Figure 2.8a).

Zostera marina colonised a variety of sediment types (Figure 2.8b). Mean particle grain size of colonised areas ranged from very fine sand and silt (e.g. St Catherine Bay, $\Phi = 3.56$) to very coarse sand (e.g. Violet, $\Phi = -0.13$). ANOVA revealed significant differences between the mean particle grain size at the different sites ($F_{(8,18)} = 38.66$; $p < 0.001$). SNK *post hoc* tests showed that mean grain size at St Catherine Bay was significantly ($p < 0.001$) finer than at all other sites. At Flicquet and nearby La Coupe, Elizabeth and Grande Haise, sediments had a similar mean particle grain size ($\Phi = 2.086$, 2.077, 1.432 and 1.798, respectively) and were significantly smaller than at all other sites except St Catherine Bay. The mean particle grain size found at Violet was significantly larger than at all other sites.

The percentage of habitat adjacent to the seagrass that was rock was less than 25% at all study sites apart from Icho, where 54.9 % of adjacent habitat was rock (Figure 2.5e). Both Grande Haise and Les Elavees had the lowest percentage of adjacent rock (both < 5% rock).

2.3.5 Relationship between environmental setting and seagrass attributes

Predictions of these seagrass landscape attributes based upon stepwise multiple linear regressions (Table 2.1) indicated that exposure (REI) may have a strong influence on the percentage of core area (as a percentage of landscape), by explaining a large proportion of the variation for this attribute (sr^2 of -0.93; Figure 2.9a). The relationship indicated that, with increasing relative exposure, the percentage of core area decreased. The percentage of adjacent rock and depth also appeared to explain much of the variation (sr^2 of 0.56 and 0.52 respectively; Figure 2.9b and 2.9c), with the amount of core area decreasing with an increase in adjacent rock and increasing with depth of the seagrass landscape. REI also seemed to have a negative relationship with LPI Figure 2.9d. In comparison, REI had no relationship with Edge density, the latter appeared to increase with depth (sr^2 0.70; Figure 2.9e), percentage of adjacent rock (sr^2 0.52) and slope (sr^2 0.64, Figure 2.9f).

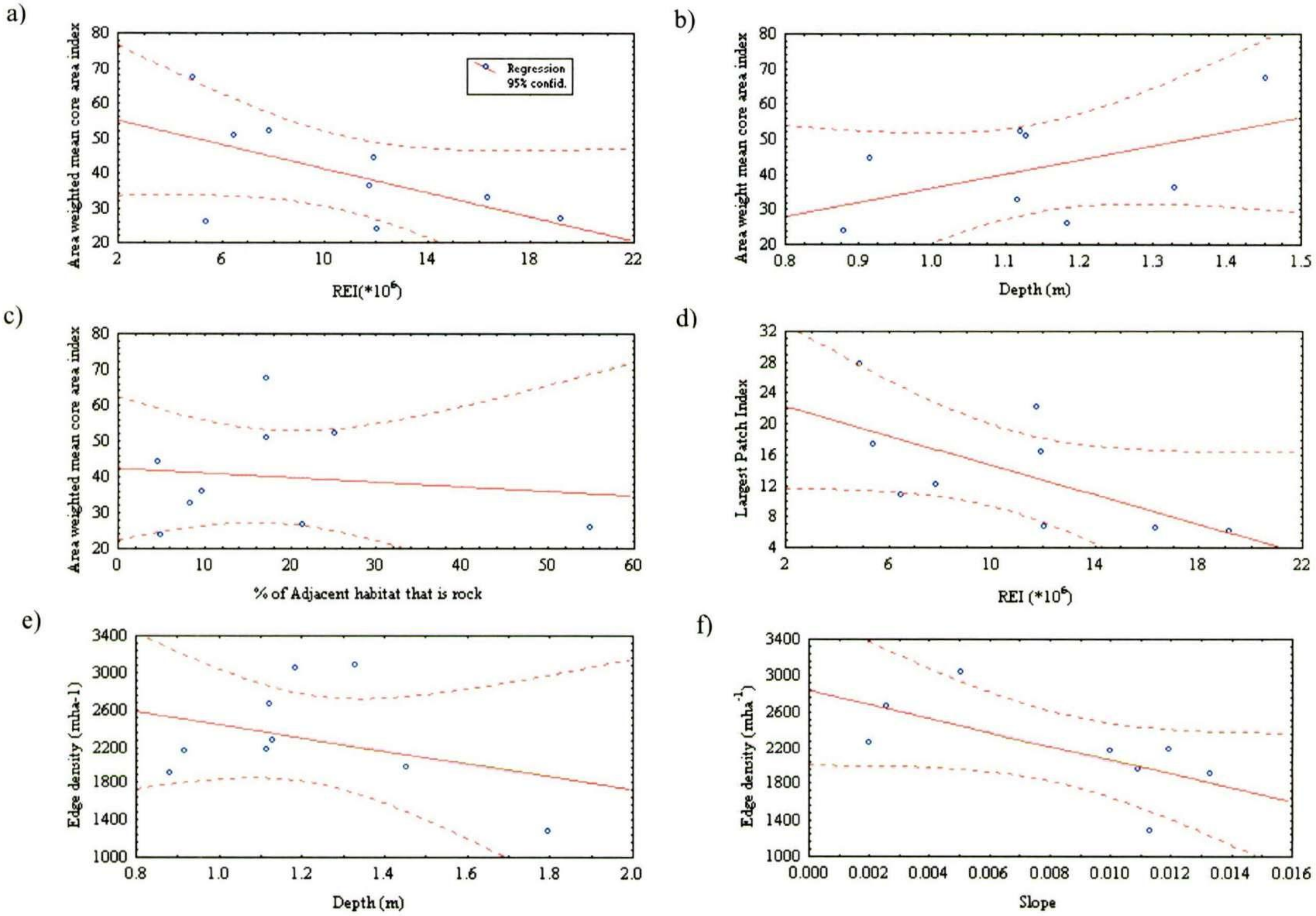


Figure 2.9 Linear regressions and 95% confidence limits for area weighted mean core area index versus (a) Relative Exposure Index (REI), (b) Depth, (c) Percentage of adjacent habitat that is rock; and for (d) Largest Patch Index versus REI; and Edge density versus (e) Depth and (f) Slope.

Table 2.1 Stepwise multiple linear regression of seagrass landscape attributes loaded on REI, Depth (m), % of adjacent habitat that is rock and slope. F to enter was set at $p < 0.10$ and all values are significant at $p < 0.10$. Values shown are the semi partial correlation coefficients (sr^2) and the adjusted r^2 for the model.

Dependent variable	**REI sr^2**	**Depth sr^2**	**% Rock sr^2**	**Slope sr^2**	**Adjusted Model r^2**
CPLAND	-0.931	0.518	-0.563	-	0.817
Largest Patch Index	-0.757	-	-	-	0.556
Edge density (mha^{-1})	-	0.702	0.517	0.644	0.666

Stepwise multiple linear regressions, used to predict these seagrass plant attributes as a function of mean particle grain size, percentage of silt in the sediment and depth, slope and relative exposure index (Table 2.2), indicated that REI may have an influence on shoot density by explaining 57.8% of the variation for this attribute (Figure 2.10a). The relationship indicated that, with increasing relative exposure, shoot density decreased. In comparison, REI had little influence on the leaf lengths which appear to be related mainly to depth (explaining 43.5 % of the variance), with an increase in length following an increase in depth (Figure 2.10b). The epiphyte index showed the opposite trend, decreasing as depth increased (Figure 2.10c). The adjusted r^2 values for these models were low and often most of the variance remained unexplained. In general, seagrass landscape attributes were better predicted by physical setting than the plant attributes (shoot density, leaf length and epiphyte index).

Table 2.2 Stepwise multiple linear regression of seagrass plant attributes loaded on REI, Depth (m), % of silt in sediment, mean particle grain size and slope. F to enter was set at $p < 0.10$ and all values are significant at $p < 0.10$. Values shown are the semi partial correlation coefficients (sr^2) and the adjusted r^2 for the model.

Dependent variable	REI sr^2	Depth sr^2	% Silt sr^2	MPGS sr^2	Slope sr^2	Adjusted Model r^2
Shoot density (m^{-2})	-0.578	-	-0.346	-	-	0.279
Leaf length (m)	-	0.435	-	-	-	0.279
Epiphyte index	-	-0.404	-	-	-	0.116

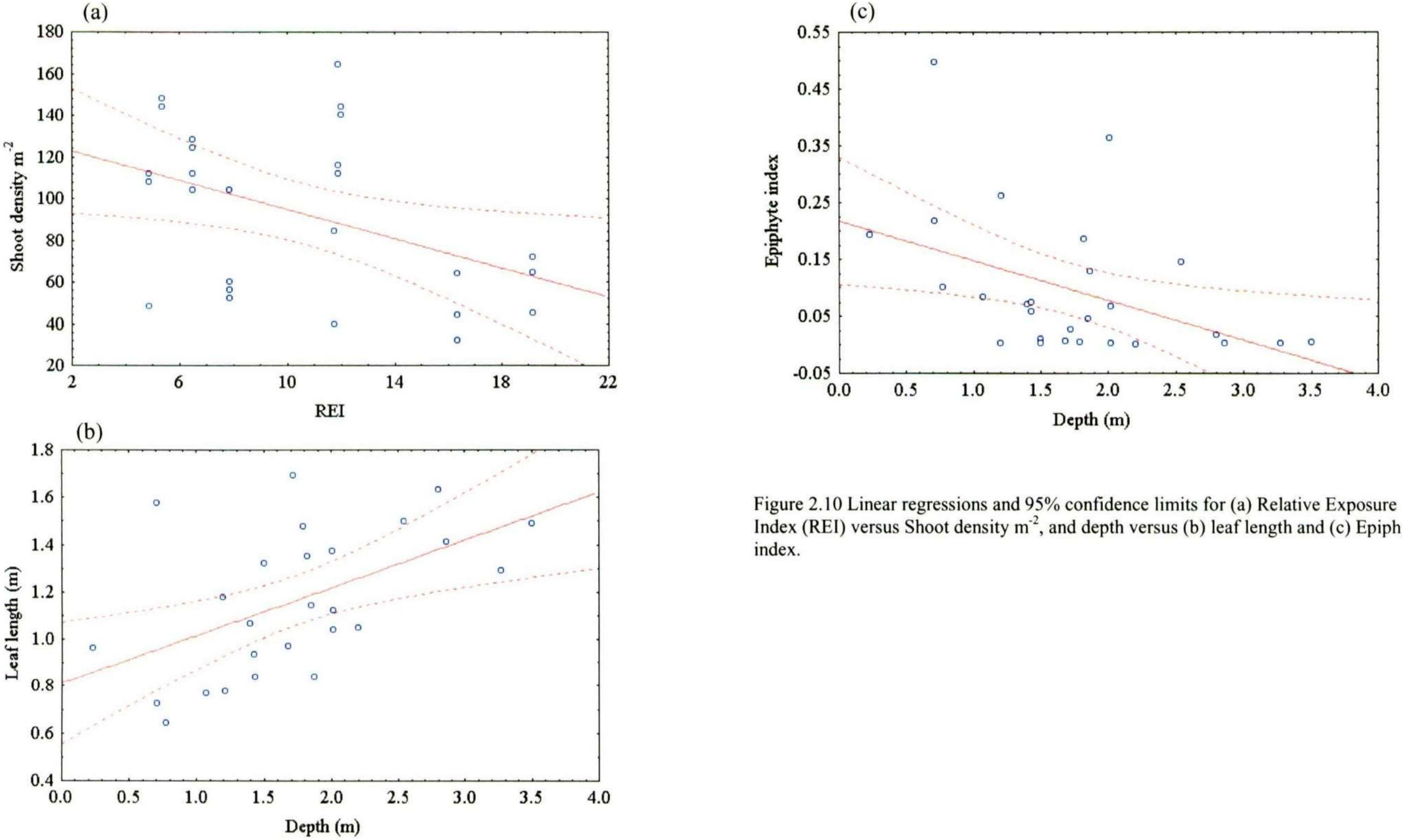


Figure 2.10 Linear regressions and 95% confidence limits for (a) Relative Exposure Index (REI) versus Shoot density m^{-2}, and depth versus (b) leaf length and (c) Epiphyte index.

2.4 Discussion

Three species of *Zostera* have been identified in the shallow coastal regions of the English Channel and other parts of the British Isles (Holmes, 1983; Turks, 1986; Cleator, 1993; Davison, 1997; Webster, *et al.*, 1998). The most common species, and the focus of this study, is *Zostera marina.* Most studies in this region have reported the distribution of *Z. marina* and identified associated fauna, though none has reported specifically fish and decapod associations, commercial species or the role of seagrass as a nursery area, shelter or temporary foraging area (Munro & Nunny, 1998; Irving *et al.*, 1998). With regards to the rest of the southern part of the channel, only the beds at Roscoff, France, seem to have received any major attention (Jacobs, 1979; Hily & Bouteille, 1999), in part as a result of impact assessments of the Amoco Cadiz oil spill (Jacobs, 1980).

To date, no studies have been carried out to map the distribution or assess any ecological roles of *Zostera* in the Channel Islands, although observations of its occurrence and fauna have been made (Crutchley, 1997; Le Sueur, 1967; Sinel, 1906). Personal communications with island residents indicated that there have been severe losses of *Z. marina* in the last 60 years, particularly in the intertidal (Roper, A., pers. comm. 1999; Syvret, A., pers. comm., 1998; Bossy, S.F., pers. comm., 1998). This corroborates observations from other parts of the UK (Davison, 1997; Wilson, 1949) and north-western Europe (Glemarec *et al.*, 1997; Jacobs, 1979; Giesen *et al.*, 1990) where large-scale losses have been attributed to the "wasting disease" which caused a general breakdown of the north-Atlantic populations during the 1930s (Den Hartog, 1987). Losses in the subtidal seagrass beds can often go unnoticed, reinforcing the necessity of mapping these potentially vulnerable habitats.

The success of the use of aerial photography in mapping the distribution of *Zostera marina* around the coast of Jersey (as highlighted by the Kappa statistics, Figure 2.3) is due, in part, to the model conditions (low turbidity, low cloud cover and a particularly low spring tide) under which the photographs were taken. Sun glare caused some masking of areas, but this was minimal and would have been unavoidable even if the photographs had been commissioned specifically to map seagrass. Avoiding sun glare would have required compromising the state of tide (low spring) and the peak-growing season of the seagrass (mid summer), which occur at midday at this latitude. Another factor in the success was the use of an automated image classification system, which removed subjectivity and, in connection with a differential satellite positioning system, improved the spatial accuracy of the final map. Where classification error did occur, it was often due to the similarity between dense seagrass and deep water or macro algae, a commonly encountered problem (Ackleson & Klemas, 1987). Although techniques exist to minimise this problem [for example, water correction algorithms (Bierwith, 1993)], they require detailed information on turbidity and depth that were not available here. In the present study, the problem was limited by masking the deeper area or those known to be macro algae.

The Biosonics DT4000^{TM} echo-sounder system was able to detect clearly the *Zostera marina* blades and the Bioplant software was able to differentiate between seagrass, bare sand and even algal-covered rocks. Leaf height measured *in situ* showed a good correlation with that of the Biosonics ($r = 0.81$, $p < 0.05$) but as Figure 2.7 and the slope of the fitted line illustrate, the Biosonics appeared to underestimate the length of the seagrass blades. Even at slack tide, this may be expected, since the blades of seagrass do not naturally stand straight up. Wave movements, floral epiphyte cover and epiphytic fauna may all influence bending over of the leaf blades. Bending of the seagrass blades may also explain why percent cover, as measured by the Biosonics DT4000, was not a good proxy measure of density as others have suggested (Sabol *et al.*, 1996). It could be argued that the Biosonics' measurements more accurately describe the canopy layer height, as opposed to seagrass blade lengths, and are, therefore, a better measure of the habitat from a faunal perspective. Modification of canopy, via bending of leaves, highlights the indirect effect on habitat structure that epiphytes have, even when the epiphyte is not structurally complex; for example, the crustose coralline algae (genus *Folisella*) dominant at most locations around the coast of Jersey. *Folisella* species have been found to show functional photo-adaptation (Dalla Via *et al.*, 1998), which may explain the decrease in epiphyte index with increase in water depth.

Combining the two methods of mapping (plus ground validation) allowed the structure of the seagrass beds to be characterised at two scales. The Biosonics DT4000^{TM} transects provided detailed, three-dimensional information on canopy height and depth distributions, whilst the maps produced using the aerial photography provided the perspective required to detect larger-scale patterns. Using landscape metrics, widely employed in terrestrial ecology (Turner & Gardner, 1991; Gustafson, 1998) but only recently applied to seagrass landscapes (Fonseca & Bell, 1998; Simenstad & Cordell, 2000; Fonseca *et al.*, 2002), enabled the configuration of the seagrass beds to be quantified and compared, and the factors affecting the distribution of seagrass beds to be assessed.

Factors known to influence seagrass landscape configuration include hydrodynamic (wave action and tidal currents), physical (bottom geology, water depth and its association with light penetration) and chemical setting (salinity, nutrient levels). Seagrass distributions are modified further by sporadic events such as major storms and disease (Den Hartog, 1971; Kelly, 1980; Kirkman & Kuo, 1990; Fonseca & Bell, 1998; Lathrop *et al.*, 2001). The distribution of *Zostera marina* around the coast of Jersey, together with the various patterns of structural attributes observed in this study, confirm the conclusions of previous studies. For example, the overall distribution of seagrass appears to be governed by wind wave exposure [prevailing winds are from the West (Figure 2.1b) and the fetch is unobstructed from across the Atlantic]. The west coast of Jersey is a high-energy environment with very mobile and changeable beach morphology (Gunton, 1997). Severe wave action may result in increased mobility of sediments, dislodging and blanketing seagrass and hence sheltered habitats are more favourable (Den Hartog, 1970; Burrel & Schubel, 1977). On the north coast of Jersey, relative exposure is medium [REI between 10 (x 10^6) and 25 (x 10^6)], but the steep depth profile is likely to limit seagrass growth, which appeared to grow on only very slight slopes (Duarte & Kalff, 1986). In addition, the upper and lower vertical limits of seagrass distribution have been correlated to underwater light attenuation (Dennison & Alberte, 1985; Dalla Via *et al.*, 1998). Essentially, *Zostera marina* is a subtidal species, penetrating the intertidal belt to a limited extent (Phillips & Meñez, 1988) and, in Jersey, the upper limit for most seagrass beds appeared to be the low water spring tide mark. As with other studies, *Z. marina* in Jersey extended down to depths of 6m below chart datum (Phillips & Meñez, 1988), although only in more sheltered locations (for example, at St Catherine Bay). At less sheltered locations, the lower depth limit was around 4m chart datum which compares well to the maximum depths of *Zostera* recorded at nearby Roscoff on the coast of Brittany (France) (Jacobs, 1979). Large tidal ranges result in the outer edges of *Zostera* at St Catherine Bay having up to 17m of water above them some of the time. Observations of some of the shallow water beds to the south east of the island, identified mounding in the seagrass beds [differences in sediment height between seagrass (higher) and unvegetated regions (lower)]. Presumably, this turreted profile was the result of increased deposition and binding of sediment by the rhizomes where there is seagrass, combined with increased, channelled current strength between seagrass patches. Typically, mounding is observed under high current regimes (Fonseca *et al.*, 1983) and wave exposure (Fonseca & Bell, 1998), however, Fonseca *et al.* (1983) suggested it might simply be the result of reduced erosion and increased sediment trapping by the seagrass canopy.

Multiple linear regression indicated some potential influence of depth on the configuration of seagrass landscapes, namely edge density, which increased with increasing depth. Water depth can modulate factors such as exposure and local current speeds, thereby, influencing seagrass landscapes. However, Fonseca and Bell (1998) suggested that there were more pronounced effects of REI when shallow-water waves (depth < half the wave length) can form, which conflicts with the results of this study. Depth may, therefore, have a more direct influence on the *Zostera marina* configuration perhaps relating to light attenuation coefficients (Duarte, 1991).

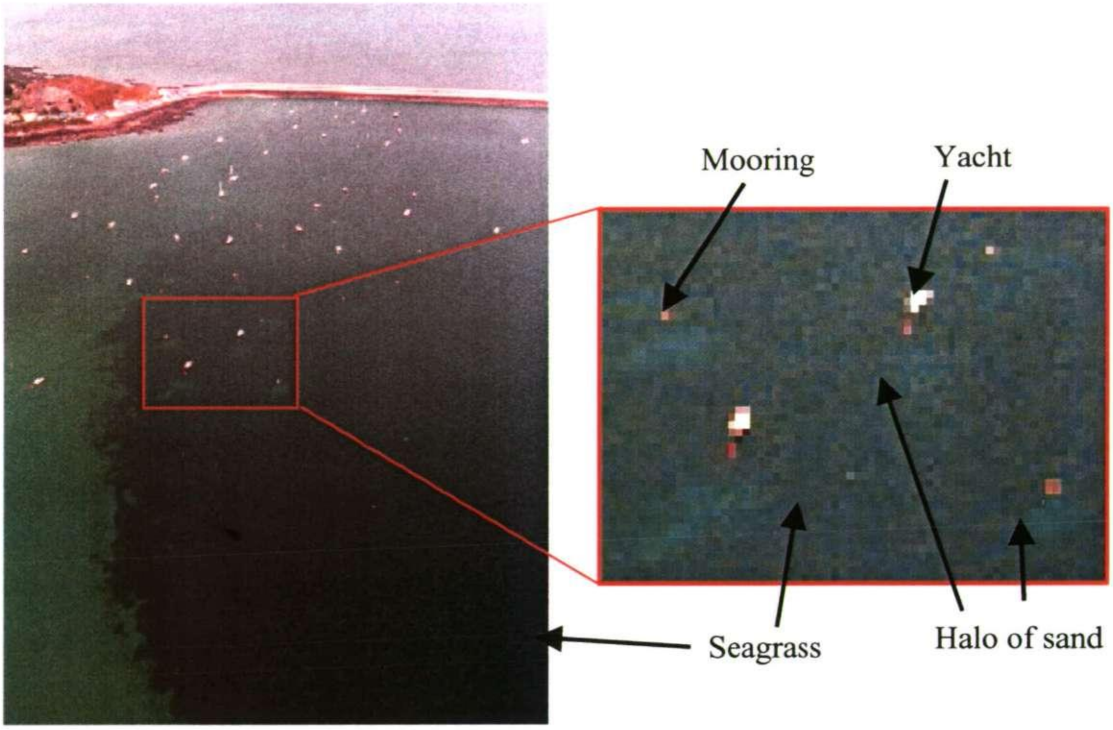


Figure 2.11 Section of the seagrass bed at St Catherine Bay illustrating the unvegetated sand patches caused by dragging mooring chains (taken from a helicopter).

The landscape configurations of the seagrass beds varied significantly with site (Figure 2.5). Most landscapes were mosaics of seagrass, unvegetated sand and macroalgae. St Catherine Bay not only had the highest LPI (27.7%), but showed an above average core area per landscape area (CPLAND; 23.9%) and below average edge density. Combining these measurements indicated a very homogenous seagrass landscape. In fact, as illustrated in Figure 2.11, the halos of bare sand visible in the final maps were a direct result of the dragging of mooring chains. In comparison, the LPI for the seagrass landscape at Violet was relatively low (12.0%) compared with the average, and edge density was very high (2663 mha^{-2}). A similar pattern was observed for Icho (LPI 16.3%; edge density 3044.7

mha^{-2}), however, the percentage of core area per landscape at the two sites differed greatly (Violet 14.9% and Icho 5.52%). This suggests that, whilst both sites, typically, have medium sized patches with highly convoluted edges, the patches at Icho are probably more elongate than those at Violet.

At Flicquet, although the total area of seagrass was relatively small (2.73 ha), this site had the second largest LPI (22.1% of the landscape), suggesting that the seagrass here showed high connectivity. However, Flicquet had relatively low core area of seagrass and very high edge densities, indicating that the bed was fairly complex in shape with highly convoluted edges to its patches. Multiple linear regression indicated that a large part of these landscape configurations could be described by relative exposure, with an increase in REI seeing a decrease in patch size and core area.

Fonseca and Bell (1998) showed that not only were seagrass bed coverage, shape (they used perimeter to area ratio) and sediment composition related to physical setting (in particular exposure and current speed), but even attributes at a sub metre level (for example, flowering and shoot density) showed an association. Although the present study found significant difference in micro-scale plant attributes, explanations for these patterns were not identified readily. Shoot densities (which were comparable with those of studies at similar latitudes; Jacobs, 1979; Poumian-Tapia & Ibarra-Obando, 1999) showed a significant negative relationship with relative exposure (although the model described only a small proportion of the overall variability). Kenworthy *et al.* (1982) suggested that REI may modify shoot density through indirect effects on the depositional environment such as sediment nutrient reserves. Pihl (1986) found a negative correlation between sediment particle size and organic content and exposure index. This may provide explanation for the negative relationship between percentage silt and shoot density.

Other studies have indicated that high exposure may reduce vegetative spreading of seagrass, inhibit seedling colonisation and result in decreased accumulation of fine sediments (Fonseca *et al.*, 1983), with implications for the vulnerability of the seagrass at different locations. For example, it may be hypothesised that the seagrass at St Catherine Bay, where REI was low, may have a better chance of recovering from disturbances (natural or anthropogenic) than, for example, at Les Elavees. At Les Elavees, the REI was higher and the currents were stronger (as indicated by the coarse sand present there), which may exacerbate further the disturbance leading to landscape scale responses such as fragmentation (as proposed by Fonseca & Bell, 1998).

Kelly (1980) described typical seagrass bed landscape patterns and, as studies began to highlight the potentially important relationships between these patterns and ecological functions (Irlandi *et al.*, 1995; Turner *et al.*, 1999; Bell *et al.*, 2001; Hovel & Lipcius, 2001), attempts began to quantify them. With and Crist (1995) suggested that landscape contiguity, and not just the typical microscale seagrass metrics such as biomass, shoot density and canopy height, may be an appropriate measurement of landscape configuration. Landscape patterns may in turn have implications for vegetation persistence and concomitant effects on how organisms perceive and move through the landscape (Kirkman, 1996; Bajjouk, *et al.*, 1996; see also Chapter 5).

The present study and the detailed maps it produced can now be used as a valuable baseline for future monitoring. The maps also allow the present study to focus sampling and the quantitative measures of seagrass structure and configuration can be used to assess influences on the distribution of fauna. An important point highlighted by this Chapter is that the seagrass beds around Jersey extend to depths of 6 m below chart datum, which, in combination with tidal ranges of 11 m, limit the use of standard quantitative methods for sampling the fauna (throw traps and drop nets).

3 Assessment of gear suitability for sampling mobile macro-fauna of subtidal seagrass (*Zostera marina*) beds and adjacent sand

Part of this Chapter was presented:

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S. F. (2000). Seagrass or bare sand: which is more important for English Channel fisheries? September 2000, 4th International Seagrass Biology Workshop, Balagna (Corsica), France. (Oral presentation)

Jackson, E.L., Attrill, M. J, Bossy, S. F., Jones, M. B. and Rowden, A. A., (2000). What to use and when to use it: sampling the large mobile fauna of seagrass (*Zostera marina*) beds. March 2000, 29th Benthic Ecology Meeting, Wilmington (north Carolina), USA. (Oral presentation)

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S.F. (1999) Mapping and sampling seagrass (*Zostera marina*) beds in Jersey, English Channel. December 1999, Linnean Meeting on Remote Sensing of the Littoral Marine Environment, Linnean Society, London, UK. (Poster presentation).

Part of this Chapter was published:

Jackson, E.L., Rowden, A. A., Attrill, M. J., Bossy, S. F. and Jones, M. B. (2002). Comparison of fish and mobile macroinvertebrates associated with seagrass and adjacent sand at St. Catherine Bay Jersey (English Channel): Emphasis on commercial species. *Bulletin of Marine Science*, **71**(3): 1333-1341.

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S. F. (2000). Seagrass or bare sand: which is more important for English Channel fisheries? *Biologia Marina Mediterranea*: Proceedings of the Fourth International seagrass Biology Workshop, 7(2): 381-384.

3.1 Introduction

Numerous techniques exist to sample the mobile macro-fauna of seagrass beds (English *et al.*, 1997; Rosaz & Minello, 1997; Francour, 1999; Petrik & Levin, 2000), including diver observations (Tupper & Boutilier, 1995), poisoning (Weinstein & Brooks, 1983; Bell & Westoby, 1986), beach seining (Gotceitas *et al.*, 1997) and beam trawling (English *et al.*, 1997). However, these methods are often specific to particular habitats, depths, times and may be influenced by other conditions (Lewis & Stoner, 1981; Orth & Moore, 1983; Gray & Bell, 1986; Rozas & Minello, 1997). Attempts to standardise sampling techniques have been made (Phillips & McRoy, 1990) but, because seagrass beds occur under a high variety of environmental conditions, standardisation of methods has proven difficult. For example, seagrass beds deeper than 2m pose particular sampling problems due to the unsuitability of quantitative samplers such as throw traps and drop nets (Zimmerman, *et al.*, 1986; Rosaz & Reed, 1998). Sampling gear/methods more appropriate for deeper water include beam trawls (Leber & Greening, 1986; Mc Neill & Bell, 1992; Kaiser *et al.*, 1994; English *et al.*, 1997), diver observations (Francour, 1997) and more passive capture methods such as traps/pots and gill nets (Hayes, 1989; Millar, 1992). Most of the latter methods are qualitative and acquiring quantitative data for the mobile macro-fauna of relatively deepwater seagrass beds remains a challenge. A further problem relates to the selectivity of individual gear, either for or against a particular size class (for example, due to mesh size), habit (for example, the gear may favour mid water or benthic species) or even species with particular behavioural responses (such as avoidance or attraction to sampling device). Therefore, it may be assumed that without employing a suite of sampling gear, inferences on the species inhabiting subtidal seagrass beds are limited to the selectivity of the gear used.

In addition to gear type, studies have shown that tidal state (Allen, *et al.*, 1992; Peterson & Turner, 1994), time of day (Gray *et al.*, 1998) and the density of macrophyte cover (Miller *et al.*, 1980) may have significant influences on the composition and density estimates of the fauna sampled. This is not always the case, for example, sampling *Zostera marina* at different states of the tide, Sogard *et al.* (1989) found no significant tidal differences between the numbers of epibenthic fishes but did not report a significant difference in the number of water column species. Tides may make alternative habitats with similar benefits as seagrass (such as salt marsh) available to certain species (Rosaz & Minello, 1997). Hettler (1989) illustrated that estuarine-dependent residents and transients moved regularly between flooded salt marsh and adjacent subtidal habitats (including seagrass beds). Thus, if sampled during high tide, seagrass beds may appear temporarily to have fewer more mobile species than at low tide. Conversely, at high tide, shallow subtidal and intertidal seagrass beds may become accessible to foragers (or those seeking refuge) and larger predators may enter these beds without risking avian predation (Peterson & Turner, 1994).

Other diel patterns in species and their densities in seagrass beds are also evident in the literature. Many reports indicating that seagrass habitats support distinct and diverse fish assemblages are based on daytime sampling, even though many estuarine and coastal species of fish display strong diel rhythms of activity (Adams 1976, Greening & Livingston 1982, Sogard *et al.* 1989, Stoner, 1991; Spyker & Van den Berghe, 1995). Studies of diel variation in seagrass beds have reported strong patterns of species composition and density change (Robblee & Zieman 1984, Bauer 1985, Edgar & Shaw 1995a, Rountree & Able 1997, Mattila *et al.* 1999). Summerson and Peterson (1984) suggested that seagrass beds serve as refugia in a manner similar to coral reefs, as their observations indicated that species occupied seagrass as a shelter by day and foraged over sand at night. Hindell *et al.* (2000) looked at spatial, diel and tidal variability in the abundance of piscivorous fish and their prey within an Australian seagrass meadow (*Heterozostera tasmanica*), and reported strong temporal patterns in foraging behaviour. If samples are not taken both during the day and night, and at different tidal states, important temporary residents may be overlooked and the role of the bed inaccurately assessed (Ferrell & Bell 1991). Unfortunately, logistical constraints (e.g. those associated with sampling at night) often prevent the implementation of an ideal sampling programme.

Another factor thought to influence gear efficiency in seagrass beds is the density of plant cover. Pierce *et al.* (1990) identified this as a problem whilst beach seining; the very dense vegetation caused the seine net to roll up from the bottom into a tight coil, allowing benthic fish, in particular, to escape (see also work carried out by Parseley *et al.*, 1989). However, Petrik and Levin (2000), who examined how seagrass habitat structure affected estimates of abundance of two fish species sampled using otter trawls, throw traps and minnow traps, were unable to detect any statistically significant difference in abundance for the three gear types. During sampling with mobile gears, sloughed off seagrass and drift algae may collect in the net. McNeill and Bell (1992) suggested that such build up may clog fine mesh nets and cause water to be pushed ahead of a trawl and increase the net avoidance by larger fish. Size selectivity may be influenced further as the net may catch smaller size classes than a clear one. There are obvious implications of seagrass density on the successful observation of species present exist in the case of dive surveys, with increased density of seagrass obscuring observations of the species living within the canopy. Finally, it has been shown that devices such as traps and pots may attract some fish by acting purely as a "protective" structure, a factor which is potentially less important with increased habitat structure (Petrik & Levin, 2000).

The forgoing account suggests that sampling protocols known to be efficient, for example, on soft sediments during the day, at high tide, cannot be assumed to be transferable to areas with macrophyte cover during the night at low tide. Time of sampling and the type of gear used, therefore, must be considered in any inter-habitat comparisons or in describing the mobile fauna of particular habitats.

An important message to emerge from past sampling studies is that the use of a range of gears, operated together, provides the most accurate representation of the species present in seagrass under most circumstances (Rosaz & Minello, 1997). Rosaz and Minello (1997) also pointed out that gear selection should be based on the specific objectives of the study and not the ease of deployment, historical efforts, or because of limited familiarity in the various gears available. Perhaps a more pragmatic approach is to carry out a pilot study, such as the one described here, to assess the selectivity of all the gear available and determine the appropriate combination of gear to sample the widest range of species and sizes, whilst minimising sampling effort.

3.1.1 Aim

The aim of the study was to assess the relative selectivity of different gears, and their 'cost' of use, for sampling the mobile macro-fauna of subtidal seagrass beds and adjacent sand at different times and tidal states. The results of the study formed the basis of the choice of the combination of gear to be used to sample the widest range of species with the least variation and least person hour cost of the subtidal seagrass beds around Jersey.

3.2 Materials and Methods

3.2.1 Study site

The study was conducted at St. Catherine Bay on the east coast of Jersey, one of the Channel Islands in the Normano-Breton Gulf (49°12'N, 2°01'W) (Figure 3.1). The bay is relatively shallow (less than 10m below chart datum throughout) and accessible at most weather conditions and tides, due partly to its easterly aspect (north-westerly prevailing winds), shelter provided by a large breakwater at its northern limit, and three public boat slip-ways. Other advantages of the site for the present study, included the year-round restrictions on the use of mobile fishing gear, impositions which, to some extent, limit unpredictable events that may give spurious results [termed 'demonic intrusion' by Hurlbert, (1984)]. However, within these restrictions, some recreational line and push net fishing takes place and, due to its shelter, the bay is a popular anchorage for small boats and yachts. Part of St. Catherine Bay is used by the Department of Agriculture and Fisheries for a scallop (*Pecten maximus*) seeding study; that site was known and was avoided.

Prior to the present study taking place, data from remote sensing of the coast of Jersey (Chapter 2) were used to identify areas of continuous seagrass and 'bare' sand within the bay. Divers confirmed the position and boundaries of these areas and sites for carrying out the gear selection study delimited (Figure 3.1). The sampled areas of seagrass bed and sand extend from mean low water mark to approximately 6m below chart datum. Due to macro-tidal conditions, which occur in Jersey's waters, the depth of water above the bed ranged from 0 to 17m.

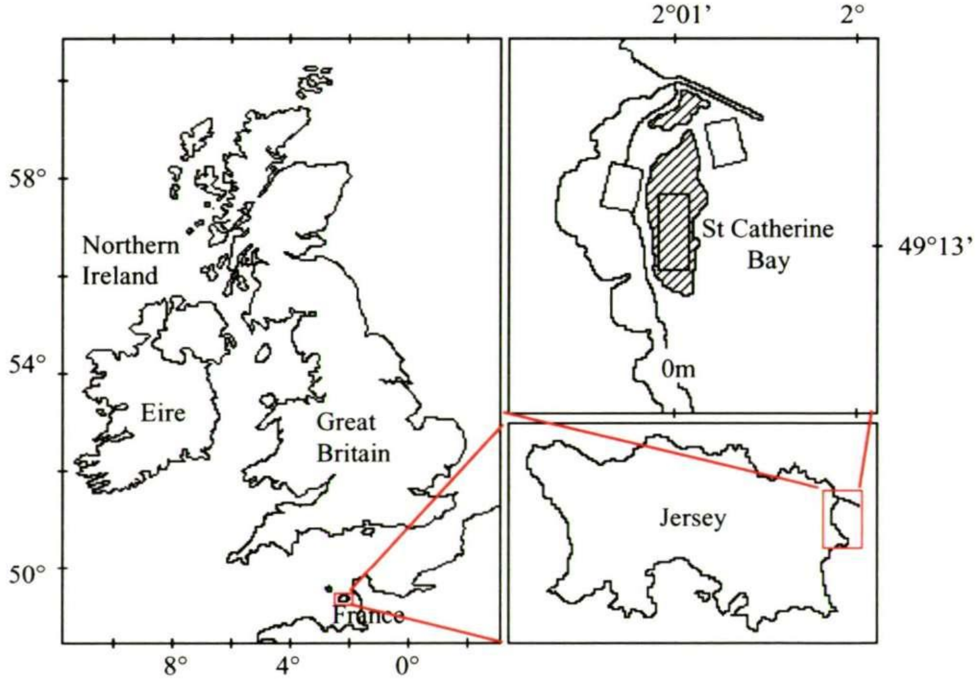


Figure 3.1 Study area on the north-west coast of Jersey (English Channel). Areas of bare sand and seagrass (hatched) delimited within St Catherine Bay.

The target seagrass beds were previously unstudied and information on species to be encountered was limited to some natural history observations made at the beginning of the 20th century (Sinel, 1906) and to lists of local fish species (Le Sueur, 1967). As no previous knowledge existed on which to base gear selection, a pilot study (a precursor to an examination of fishery-seagrass relations), was carried out using five commonly-used methods (trawling, beach seining, push netting, diver survey and potting) of sampling seagrass beds.

3.2.2 Selection of gear for present study

3.2.2.1 Trawling

The major advantage of trawls is their apparent ease of use (English *et al.*, 1997). In addition, recovered samples are usually relatively free of debris, the sample unit can be large and sampling is not limited to shallow depths (Gray & Bell, 1986; Rosaz & Minello, 1997). Beam trawls are preferred to otter trawls (Petrik & Levin, 2000) because the opening is fixed, improving the efficiency (Zimmerman *et al.*, 1986; Kuipers, *et al.*, 1992). With the aid of acoustic equipment, Wathne (1977) found that otter trawls performed erratically, with the wingspread of the trawl fluctuating in up to 25% of the tows. The additional advantages for beam trawls cited by English *et al.* (1997) are that they are highly selective for juvenile prawns and fish (their target species). The main criticism of using beam trawls is that they are difficult to quantify (English, *et al.*, 1997; Rosaz & Minello, 1997), although the fitting of a flow meter and odometers reduce this problem to an extent. Another disadvantage of beam trawls is that catch efficiency varies with the species and size of the targeted animals (Kjelson & Johnson, 1978; English, *et al.*, 1997). Rosaz and Minello (1997) stress that with trawls not only are catch efficiencies low but highly variable (see also Heck & Thoman, 1984; Miller, *et al.*, 1980; Thayer, *et al.*, 1983). High variability means that estimating catch efficiency or standardising the samples, is not only difficult but also prevents the use of a correction value (Allen, *et al.*, 1992).

3.2.2.2 Beach seining

Seining may be considered a more quantitative approach than trawling, since the area sampled can be more easily determined; for example, by marking out the area to be sampled. Catch efficiencies are often higher than trawls but escapes occur due to the timing involved in deployment. Ferrell and Bell (1991) used a seine net (of 6mm stretched mesh) to accurately sample a set area of 25m^2 for small species of fish and juveniles of larger species. Gotceitas *et al.* (1997) used a similar sized seine net to sample juvenile Atlantic cod and assessed the problem of gear avoidance using SCUBA observations to determine the percentage of escaping fish (which they found to be less than 5%).

3.2.2.3 Push netting

Like beach seining, push netting (whether on foot or using a boat) is limited to shallower depths. Again, the area covered can be determined easily and recovering the samples easier than trawling or beach seining. This method also has the advantage that the organisms in the area being sampled are not disturbed prior to collection which, arguably, may occur during trawling as a result of the boat shadow or propeller noise. Push netting is the method used by local fishermen (commercial and recreational) at low water in the seagrass of St Catherine Bay, mainly targeting shrimp and prawns.

3.2.2.4 Diver survey

Visual surveys have been described as the least biased and most precise of survey techniques for assessing the fauna in beds of the seagrass *Posidonia* in the Mediterranean (Francour *et al.*, 1999) and surveying mobile fauna in beds of other seagrass species in this way is well documented (English *et al.*, 1997; Tupper & Boutilier, 1995; Gotceitas *et al.*, 1997). Such studies, however, have highlighted some important limitations of this method. Firstly, there is the problem of observer bias (Thresher & Gunn, 1986). Dive surveys require SCUBA divers to be highly skilled in marine species identification but, even with proficient divers, identification of some organisms to species level (especially when based on a quick glance as they swim away) can be very difficult. Another source of bias is in the counting of abundant species (in particular schooling fish) or in the estimation of size (Francour *et al.*, 1999). Finally, successful diving surveys are highly dependent on low water turbidity, good weather, and diving time and depth, in accordance with safe diver practice. Despite these disadvantages, dive surveys have advantages over other methods, for example, there is the advantage of observing species that may be able to avoid mobile gear (either actively or passively). Dive surveys also allow *in situ* observations of the behavioural habits of some of the species observed (Francour *et al.*, 1999) and are potentially less destructive than many other methods. In addition to improving the possibility of observing species that may be able to avoid mobile gear, diving surveys provide information on the habits of some of the species observed.

3.2.2.5 Potting

The final technique chosen for this comparative study was potting. Rosaz and Minello (1997) suggested that traps such as pots should be categorised as collecting devices rather than sampling gear because they are highly selective in both the species and size of animals they entrap. Whilst their qualitative nature limits their use to relative habitat comparisons (usually based on 'wetting time' or 'catch per unit effort'), pots can be useful for estimating growth. In addition, long-term (e.g. sampling period of 12 h) potting has the potential to capture those species that may avoid mobile gear, either actively or temporally. For example, mobile predators coming into a seagrass bed to forage may do so at times not coincident with sampling by short-term deployment gear.

3.2.3 Sampling design and sample treatment

The ideal design for comparing the 5 methods would require sampling with each of the different gears in the two different habitats (sand and seagrass) at different times (day and night) and at different states of the tide (Green, 1979). Ideally, there should be replication at each level in the design. Unfortunately, with the time period and resources available, such an 'ideal' design was not possible for this study. Instead, the decision was made to sample at only one location and in just one example of each habitat. The basis for this was that whilst the results would not have as much direct application to other sites, the main objectives of the study (that is, a relative comparison of the different gears and an indication of times to sample) would still be met.

Independent night and day sampling periods were defined according to whether the sun was above (day) or below (night) 5° to the horizon. Apart from potting (which had a wetting time of approximately 12 h), sampling was carried out within 1 h either side of low tide (and high tide for trawl samples). For each sampling session, individual sample positions were selected randomly within the set areas of seagrass or sand. The start locations for sampling using mobile gears and divers, and stations for static gear, were allocated, using random numbers, to a $10m^2$ resolution grid covering each site. The direction of travel for trawls, push netting, potting lines and diver transects were decided using randomly generated integers between 1 and 360. For beach seining, the first direction of travel was always perpendicular to the shore. Random numbers were generated using the 'RANDBETWEEN' function in Microsoft Excel©. For all methods, the only stipulation to randomness (in order to ensure independence) was that no sampling paths or stations overlapped. Positions were located in the field with the aid of differential global positioning satellites (DGPS). Typically DGPS has a working error of 2 to 4 m (Green *et al.*, 2000); however, observations from this study indicated a working error of up to 20 m. This increase in error was attributed to interference in the radio transmission correction and 'SA' (Selective Availability, miscalculations programmed into GPS transmissions by the United States Government when the system was first introduced, to limit the accuracy of non-military GPS receivers). Although SA was cancelled in May 2000 and a noticeable improvement in the accuracy of the onboard DGPS was observed (Dana, 2000), the present study was carried out prior to this improvement.

The time taken to deploy and recover the gear used, and the time to sort each sample, was noted. Samples were preserved in 10% formalin and later transferred to 70% ethanol. Macro-faunal individuals were identified to species (Wheeler, 1969; Whitehead *et al.*, 1986; Hayward & Ryland, 1996; Quéro & Vayne 1998). Commercially and recreationally exploited species were identified, and were defined as those landed and recorded by commercial fishermen in the *Normano-Breton* Gulf and species captured by recreational fishermen, including 'peche à pied' (Cohen *et al.*, 1990; Quéro & Vayne 1998; States of Jersey Department of Agriculture and Fisheries, 2000). All decapods, fish and cephalopod molluscs were measured (± 1 mm) using a rule. For most fish the measurement was standard length (total length for Sygnathidae, Cottidae and Anguillidae), carapace width for crabs (carapace length for Majidadae) and carapace length for shrimp and prawns. Definitions of juveniles were based on data from the texts reporting the average size of maturity for the time of year and closest location to the study site (Wheeler, 1969; Whitehead *et al.*, 1986; Hayward & Ryland, 1996; Quéro & Vayne 1998; Froese & Pauly, 2003). Cost was measured in terms of the person hours taken to recover and process a sample in the field (Equation 1).

$$\text{Cost} = (T)^{*}P + B \qquad \text{Equation 1}$$

Where T is the mean time (minutes) taken to collect each sample (deployment, recovery and sorting), P is the minimum number of people required to operate the gear and B is a 60 minute boat penalty added when a boat was used to deploy the gear. The measure of cost was used to assess which gear, or gear combination, gave the widest range of species present (80 percent of all the species found was used as a cut off) for the least cost. Although the absence of detailed distribution maps meant that seagrass density could not be included in the analysis, the amount of vegetation collected in the mobile gears was measured and correlated with the catch. Also, complimentary sampling for each gear was carried out on adjacent sand within the same bay. This not only allowed inferences to be made as to the possible influence of vegetation on the effectiveness of the different gears but also provided information on the diel and tidal movements of certain species between the two habitats.

3.2.4 Methods for specific gears

3.2.4.1 Trawling

Sampling efficiency varies with size of mesh/net and length/speed of trawling, and numerous studies have assessed this variability (Warbutton, 1989; McNeill & Bell, 1992; Kaiser *et al.*, 1994; Wassenberg *et al.*, 1997). Ideally, the optimum number of trawls should be calculated prior to any study to account for the relative efficiency under the particular circumstances of the study. However, due to time constraints, the most commonly used trawling methodology from previous seagrass studies was adopted here (Stoner, 1983; Worthington *et al.*, 1992). The trawl used was a 1.5m beam trawl with a 6m long, fine mesh (10mm stretch) net, with a cod end liner of 6mm knotless mesh, a bobbined foot rope and one light tickler chain (Figure 3.2). The trawl was deployed from a 5.5m open boat with a 40HP 4-stroke petrol engine (Figure 3.3) at a speed of approximately 0.6ms^{-1} for 2 min (to reduce disturbance effects).

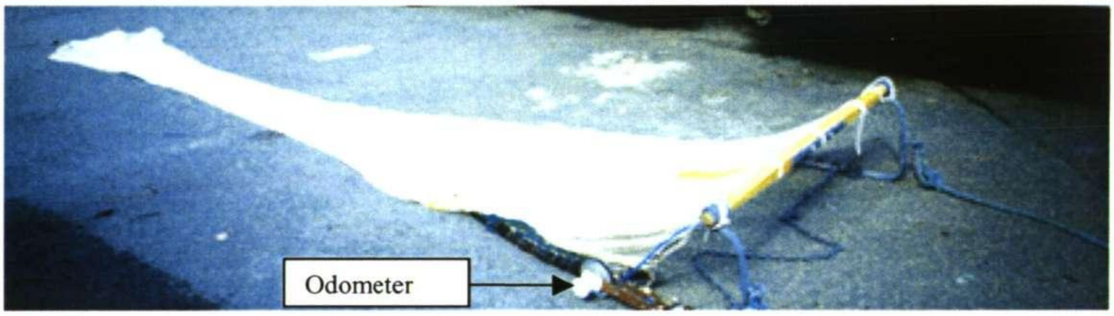


Figure 3.2 The 1.5m beam trawl (10mm mesh and 6mm mesh cod end liner) used in the study. The odometer is visible on the near side shoe.

The distance covered by the trawl (which would vary due to water currents and wind speed) was recorded using an odometer attached to the shoe of the trawl (Figure 3.2). To compensate for the weight of the odometer, an equal weight was attached to the opposite shoe of the trawl. Odometer recordings, in combination with trawl track distance estimated from the DGPS, to allow reasonably accurate determinations of area sampled to be made. Whilst the start locations for each trawl track were allocated randomly beforehand, some adjustments were made in the field due to unmarked objects (yachts, moorings, pot lines).

A few days were allowed to elapse after the sampling by divers surveys for the fauna to recover from the disturbance associated with diving operations. The design of the sampling is illustrated in Figure 3.4. In total, 48 trawl samples were collected during 8 sampling sessions (between 5th and 8th July, and 19th to 22nd July 1999).

Figure 3.3 The small (5.5m) open boat with a 40HP 4-stroke petrol engine used in the deployment of trawl, pots and divers.

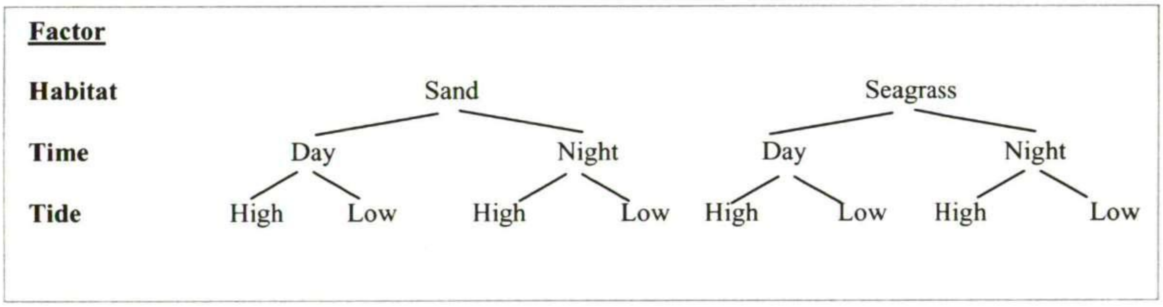


Figure 3.4 Design used to asses the variability in trawl sample composition between habitat, time and tide (all factors are orthogonal and fixed, n = 6).

3.2.4.2 *Beach seining*

A 20 m long beach seine with a 2 m drop and a stretched mesh of 10mm was used to sample an area of approximately 25 m^2. Sampling was restricted to water depths less than 1.5 m and, since the seagrass beds around Jersey are entirely subtidal and tidal ranges reach 11 m, sampling was limited to low water of spring tides (design shown in Figure

3.5). Also, whilst the seagrass bed extended to approximately 7 m (chart datum), only the shallow margins of the delimited area were accessible reducing the choice of possible start positions.

Seining involved placing a pole in a randomly located position from which the net was pulled out 5m parallel to the shore. Both ends of the net were walked 5m towards the shore, keeping 5m apart. Finally, the ends of the net were walked together and the catch was recovered to the shore. In practise, beach seine hauls were separated by at least 5m. Twelve samples were collected in four sessions (14th, 15th, 16th and 17th June 1999).

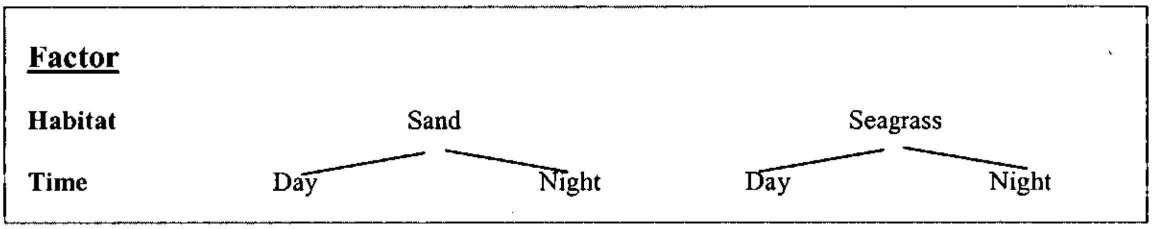


Figure 3.5 Design used to asses the variability in push net, beach seine and diver survey sample composition between habitat, time and tide (all factors are orthogonal and fixed, n = 3).

3.2.4.3 Push netting

The triangular push net was 1m wide, 1m long and 0.5m high, with a 10mm stretched mesh. Sampling was undertaken by pushing the net at an average speed of 0.6ms^{-1} for approximately 25m. Speed was estimated using test runs prior to the sampling proper (Riley, 1971). As with beach seining, push netting could only be undertaken during low spring tides and, again, only within a small proportion of the delimited area (the deeper parts of delimited areas were not possible to sample using this method). Sampling was completed in two sessions (14th and 15th July 1999) and the sampling design is illustrated in Figure 3.5.

3.2.4.4 Diver survey

Diver transects were used to directly survey the mobile macro-fauna inhabiting the sites of seagrass and sand up to 2 m above the seabed (since the average height of seagrass in the bay is 1.5 m). The method used was adapted from Halford and Thompson (1994), Christie *et al.* (1996) and Spyker and Van den Berghe (1995); these references should be referred to for full details of the procedure. At each site, three belt transects 25 m long and 1.5 m wide were surveyed by two divers. One diver made visual observations of species occurring in the water column 2 m above the seabed, whilst the other diver concentrated on those species more directly associated with the benthic habitat under study. During daytime sampling, video-graphic records were also made by the diver recording demersal species. In addition to faunal counts, details of behaviour (flee behaviour, cryptic habits, whether schooling, orientation to the leaf blades) were noted onto a plastic slate and transcribed to data sheets immediately following the survey. The dive survey (design shown in Figure 3.5) was carried out in 6 sessions between the 21st and 24th June 1999.

3.2.4.5 Potting

Two types of pots were utilised in the study (Inkwell and 'D' pots). Inkwell pots had a base diameter of 700 mm, stood 490 mm high and had a single entrance with a diameter of 205 mm. D pots had a base of 660 mm x 460 mm, a height of 400 mm and two 100 mm diameter entrances. Both pot types had a mesh size of 10 mm. Pots were deployed at random stations in a 'quartet' arrangement (2 D traps and 2 inkwells from a buoyed end line of 20m) (Figure 3.6). For each pot type, four different 'baits' were used separately to sample the mobile macro-fauna (a. horse mackerel; b. white tile; c. light stick and d. control), pot type (inkwell or D pot). Sampling by baited pots was replicated four times, requiring eight sampling sessions (between 12th to 15th July, and 26th July to 2nd August 1999).

3.2.5 Data Analysis

3.2.5.1 Effect of habitat, time and tide

For individual gears (except potting), analysis of variance (ANOVA) was used to test the null hypothesis that there was no difference in the species assemblages caught under different states of tide (trawls only) or between day and night (all methods) for seagrass and sand. Fish and macro-invertebrate catch data were separated for analysis, and standardised for area covered by each replicate sample (no. ha^{-2}). Tests were carried out on the number and density of fish, decapod and all exploited species (cephalopod mollusc were not found in sufficient numbers for analysis). The difference in densities of the more abundant species [i.e. species contributing over 10% of the sample composition for that gear as shown by SIMPER analysis (see later) of each gear group] was also investigated.

The ANOVA models used for all tests were fully orthogonal. For analysis of trawl data, there were three fixed factors (Habitat, Tide and Time), each with two levels (Seagrass/ sand, Low/High and Day/Night respectively), replicated six times (Figure 3.4). Push net, beach seine and dive survey data were analysed using a two factor (Habitat and Time) ANOVA each with two levels (Seagrass/Sand and Day/Night respectively), replicated three times (Figure 3.5). The potting data analysis comprised of 4 fixed factors, with factor one (Habitat), factor two (Time) and factor three (Pot type) each having two levels (Seagrass/Sand, Day/Night and D pot/Inkwell, respectively). Factor four (Bait type), had four levels (horse mackerel, white tile, light stick and no bait), all were replicated four times.

For each data set, homogeneity of variance was tested using Cochran's test (Snedecor & Cochran, 1980) and data were transformed using the log (x+1) and arcsine percentage transformation where necessary. In some instances, transformations did not produce homogenous variances, however, since ANOVA is robust to heterogeneous variances when sample size is large and equal, ANOVA was still carried out (Underwood, 1997). When Cochran's test indicated a significant result, the increased likelihood of making a Type I error was compensated for by setting α to 0.01 in such cases (Underwood, 1997). *Post hoc* comparisons were carried out using Student Newman Keuls (SNK) multiple comparison tests. Only the significance of the highest order interactions in which a factor was involved are presented for SNK because lower order interactions or main effects cannot be interpreted (Underwood, 1997). All ANOVA of the effect of habitat, time and tide were performed using the WinGMAV 5 software (Underwood & Chapman, 2000).

3.2.5.2 Species selectivity

Species selectivity of sampling gear was determined by comparing data recovered by push netting, beach seining, trawling and dive surveys (based on low tide conditions for the trawls to remove possible confounding effects of tide, see later section). Due to their qualitative nature, pot collection data were left out of these analyses but species sampled only by this method were noted.

A one-way ANOVA (with unequal sample sizes) was performed to assess differences in the number of individual species related to gear type (push nets, beach seine, trawl and dive surveys). Area-standardised-species-density data were transformed to log (x+1) (Henderson, 1980) where necessary. Rarer species (species absent from two or more gear types) and data showing heterogeneous variance could not be analysed effectively (an

ANOVA with unequal sample sizes being less robust to violations in the assumptions of the test than a fully balanced one; Day & Quinn, 1989; Underwood, 1997) and were excluded. Also, due to the potential hazards in interpreting the results of an unbalanced design, in particular the increased likelihood of Type 1 error (Underwood, 1997), α was set to 0.01 for all tests. *Post hoc* pair-wise comparisons to determine the significant differences between group means in an analysis of variance setting were carried out using the Unequal N HSD test, a modification of the Tukey's HSD test (Day and Quinn, 1989). All univariate analyses of species selectivity were performed using the STATISTICA package (Statsoft Inc., 1998).

Differences in the structure of fish and decapod assemblages caught by different gears at different times were assessed for sand and seagrass samples by multi dimensional scaling and analysis of similarities (Field *et al.*, 1982; Clarke, 1993). Data were transformed to log (x+1) so that each species contributed evenly to each analysis (Clarke & Green, 1988). First, a ranked triangular similarity matrix was generated using the Bray-Curtis similarity measure, after which multidimensional scaling was used to generate two-dimensional ordination plots. Formal significance tests for differences between samples were performed using a two-way crossed analysis of similarities (ANOSIM) permutation test (Clarke & Green, 1988). Factor one was gear (push nets, beach seine, trawl, dive survey) and factor two, time (day/night). Finally, the fauna contributing to the dissimilarities between gears and within gears were investigated using the similarities percentage procedure SIMPER (Clarke, 1993). All multivariate analysis was carried out using the software PRIMER (Plymouth Routines in Marine Ecological Research Version 5; Carr, 1996).

3.2.5.3 Size selectivity

Size selectivity was evaluated only for species caught in relatively high numbers (more than 20 individuals) in more than one of the gears used. Commonly used selectivity indices could not be applied to the data for two main reasons. Firstly, many indices are sensitive to differences in sample size (e.g. Reiger & Robson, 1966) and are normally based on evaluations of size selectivity for similar gears differing in some specific factor such as mesh size, keeping unit effort constant. In the present study, it was not possible to equate the units of effort effectively for all the gears used and, therefore, indices that do not require effort data are needed. The second problem was that many indices require reliable estimates of the size distribution of the population which, in this case, were unknown due to the lack of studies of the population dynamics of the species found at the study location.

Due to the lack of reliable estimates of the size distribution, pooled data from the various gears were used as a population measure against which individual gears were evaluated (Millar, 1992). It was decided to follow the approach of Jackson and Noble (1995) and apply Strauss' (1979) linear index of food selection (L), (Equation 2) which allows a comparison of samples from two or more sources with unknown biases:

$$L = r_i - p_i \qquad \text{Equation 2}$$

Where r_i is the proportion of 'prey' in size class '*i*' captured by a predator (or in this case sampling gear) and p_i is the proportion of 'prey ' of size class '*i*' in the field. The resulting index appears as a value between 1 and –1, with negative values showing under representation of the size class and positive values showing a bias for a particular size class. Values close to zero show no bias or, due to the conditioning against total catch, size classes not represented by any of the sampling devices.

3.3 Results

3.3.1 Effect of habitat, time and tide

3.3.1.1 Trawling

ANOVA of the total number of species in trawl samples showed a significant difference between seagrass and sand (Table 3.1). *Post hoc* SNK tests revealed significantly larger numbers ($p<0.01$) of species in seagrass samples (12 species ± 0.74) compared to sand (6.7 species ± 0.68; Table 3.1). There was also a significant interaction between time and tide ($p<0.05$). Species numbers were significantly higher at low tide during the day (10.5 species ± 1.47) and at high tide during the night (10.3 species ± 1.18) than they were at low tide during the night (6.5 species ± 1.09) (SNK: $p<0.01$).

Total faunal densities of trawl samples also showed significant differences between sampling situations, but this time the interaction was between tide, time and habitat (Table 3.1). For sand, SNK tests showed that total densities in high tide samples were significantly greater than in low tide samples, during the day (HT, 3.02 individuals m^{-2} ± 0.31 > LT, 1.59 ind.m^{-2} ±0.12; $p<0.01$) and at night (HT, 2.25 ind.m^{-2} ± 0.25 > LT, 1.39 ind.m^{-2} ±0.33; $p<0.05$). This pattern was observed also for seagrass samples at night (HT, 2.88 ind.m^{-2} ± 0.46 > LT, 1.32 ind.m^{-2} ±0.15; $p<0.05$) but not during the day, when there was no significant differences between tidal states.

Table 3.1 Analysis of variance results for trawls. Three factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 'time' has 2 levels is orthogonal and is fixed (Day/ Night), factor 3 is tide and has two levels, orthogonal and fixed (Low/High). n = 4. * $P < 0.05$, **, $P < 0.01$, *** $P < 0.001$

		$F_{(1,40)}$						
Variable	**α**	**Habitat0 (Ha)**	**Time (Di)**	**Tide (Ti)**	**Ha x Di**	**Ha x Ti**	**Di x Ti**	**Ha x Di x Ti**
Total species number	0.05	34.89***	4.12	3.41	1.67	0.03	5.67*	2.18
Total density	0.01	0.37	2.6	26.86	0.59	0.19	0.58	4.62*
Fish species number	0.05	50.13***	7.21**	1.12	3.5	0.06	2.39	1.91
Fish densities	0.05	0.05	2.26	14.46***	0.59	1.44	0.44	0.17
Decapod species number	0.05	2.78	0.39	17.39***	2.78	0.04	1.57	0.39
Decapod densities	0.05	0.02	0.68	9.06**	7.14*	0.04	0.28	2.48
Exploited species number	0.05	7.29*	0.54	2.95	2.17	0.24	0.96	7.29*
Exploited species densities	0.05	2.64	1.49	4.41*	0.62	1.39	2.3	4.01

Species number and density of fish, decapods and cephalopods were analysed separately. For the number of fish species, there were significant differences between the two habitats and between day and night samples (Table 3.1). *Post hoc* comparisons showed that the number of fish species was significantly greater in seagrass (6.6 species ± 0.45) than sand samples (2.9 species ± 0.33; $p<0.01$), and daytime samples (5.5 species ± 0.56) contained significantly greater numbers of fish species than night samples (4.08 species ± 0.5; $P< 0.05$). Densities of fish did not differ significantly between day and night or habitat (Table 3.1). However, tidal states did show a significant effect ($p<0.001$), with fish densities significantly greater at high (0.13 ind.m^{-2} ±0.02) than at low tide (0.05 ind.m^{-2} ±0.01).

The number of decapod species also showed significant differences between tidal state (Table 3.1) and SNK tests showed that the high tide decapod species number (1.8 species ± 0.26) was less than ($p<0.01$) at low tide (3.5 species ± .031). In terms of the densities of decapods, a significant interaction between time, tide and habitat was observed (Table 3.1, $p<0.01$). *Post hoc* comparisons showed that highest densities of decapods were observed in seagrass samples taken at high tide during the night (0.15 ind.m^{-2} ±0.05) (Table 3.1). Densities at high tide, night, in seagrass were significantly greater ($p<0.01$) than at low tide, in seagrass during the night (0.01 ind.m^{-2} ±0.003), or at high tide in the seagrass during the day (0.01 ind.m^{-2} ±0.04; $p< 0.01$). During the day, densities of decapods were greater over sand (0.1 ind.m^{-2} ±0.01; $p< 0.05$) than seagrass on the flood tide. Since only two species of cephalopod molluscs were found (*Sepia officinalis* and *Sepiola atlantica*) and total densities were very low, ANOVA was not carried out to analyse differences in species number or densities of this group.

When the exploited species were analysed in terms of number of species, there was a significant interaction between habitat, time and tidal state (Table 3.1). SNK showed that the highest number of exploited species was observed in seagrass at high tide during the night (3.7 species ±0.71). The number of exploited species in these samples was significantly greater ($p<0.05$) than at low tide in seagrass during the night (2 species ±0.26), and higher than those collected at night, high tide over sand (1.5 species ±0.34; $p< 0.01$). Numbers of exploited species at high tide, night in seagrass, were also higher than at high tide during the day in the same habitat (2.17 species ±0.31; $p< 0.05$). Finally, at low tide during the day the number of exploited species was significantly higher ($p< 0.05$) in seagrass (3 species ±0.26) compared to sand (1.5 species ±0.43). There was no significant difference in the densities of exploited species between day and night, tidal state or habitat (Table 3.1).

3.3.1.2 Beach seining

Although ANOVA showed no significant difference between time of sampling or habitat in terms of total densities of beach seine samples, there was a significant interaction between the two factors for total number of species (Table 3.2). *Post hoc* comparisons showed that this difference was due to significantly greater numbers ($p< 0.01$) of species sampled from sand at night (12.3 species ± 1.2) than during the day (6.7 species ± 1.86). However, there were no significant differences in species number between day and night in the beach seine samples taken from seagrass (Table 3.2).

Table 3.2 Analysis of variance results for beach seine. Two factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 'time' has 2 levels is orthogonal and is fixed (Day/ Night). n = 3. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

			$F_{(1,8)}$	
Variable	α set to	Habitat (Ha)	Time (Di)	Ha x Di
Total species number	0.05	0.02	1.89	8.27*
Total density	0.05	2.85	2.16	0.22
Fish species number	0.05	0.03	0.24	2.13
Fish densities	0.01	3.68	1.88	2.28
Decapod species number	0.05	4.08	6.75*	10.08*
Decapod densities	0.01	0.01	3.42	3.67
Number of exploited species	0.05	1.78	1	2.78
Density of exploited species	0.01	0.58	0.64	1.42

Analysing the groups separately showed that there was no significant difference between time or habitat for number or density of fish, cephalopods or exploited species (Table 3.2). Whilst the density of decapods species also did not differ significantly (Table 3.2), the number of decapod species did exhibit diel differences with respect to habitat (Table 3.2). SNK tests showed that there were significantly greater ($p<0.01$) species of decapods sampled during the day in seagrass (5.3 species ± 0.88) than either bare sand during the day (2.3 species ± 0.33) or seagrass at night (2 species ± 0.58).

3.3.1.3 Push netting

There was a significant difference between day and night push net samples, in both the total densities (Table 3.3) and total number of species (Table 3.3), but no difference between habitat. For both total density and species number, *post hoc* SNK tests showed that night samples (9.8 species ± 0.9; 3.6 ind.m^{-2} ± 0.39) were significantly greater ($p< 0.05$) than day (6.8 species ± 0.6; 1.8 ind.m^{-2} ± 0.38).

Table 3.3 Analysis of variance results for push netting. Two factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 'time' has 2 levels is orthogonal and is fixed (Day/ Night). n = 3. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

			$F_{(1,8)}$	
Variable	α set to	Habitat (Ha)	Time (Di)	Ha x Di
Total species number	0.05	4.24	9.53*	1.06
Total density	0.05	3.8	15.07**	2.55
Fish species number	0.05	1.81	6.26*	0.33
Fish densities	0.05	25**	90.55***	43.73***
Decapod species number	0.05	0.89	0.22	0.22
Decapod densities	0.05	0.26	1.13	0.03
Number of exploited species	0.05	1.6	0.4	0.4
Density of exploited species	0.05	0.26	0.21	0.1

Analysing the separate groups showed no significant difference between habitat or time, for decapod, cephalopod or exploited species number or densities (Tables 3.3). However, there was a significant difference ($p< 0.05$; Table 3.3) in the number of fish species with significantly more at night (4.2 species ± 0.65) than the day (2 species ± 0.5; $p< 0.05$). Fish densities showed a significant interaction between time and habitat (Table 3.3). SNK tests showed that the highest densities of fish were found at night in sand samples (2.17 ind.m^{-2} ± 0.13). The latter were significantly greater than either sand during the day (0.61 ind.m^{-2} ± 0.17; $p< 0.01$) or seagrass at night (0.73 ind.m^{-2} ± 0.04; $p< 0.01$).

3.3.1.4 Diver survey

Dive survey results differed from those of the push net and beach seine, in that there was a significant interaction between habitat and time for the total density of species observed ($F_{(1,8)} = 11.94$; $p < 0.01$, Table 3.4). Higher densities were observed at night in seagrass (4.59 ind.m^{-2} ± 1.1) compared to sand (1.93 ind.m^{-2} ± 0.61; $p < 0.05$) and seagrass during the day (0.06 ind.m^{-2} ± 0.01; $p < 0.01$). No interaction was observed for total species number but there was a significant difference between day and night observations ($F_{(1,8)} = 7.81$; $p < 0.05$, Table 3.4), with more species seen at night (4.33 species ± 0.33) than during the day (3 species ± 0.45, $p < 0.05$).

The densities of fish reflected the patterns of total densities, with a significant interaction observed between time and habitat (Table 3.4). SNK tests revealed that the highest densities observed were at night in seagrass (4.49 ind.m^{-2} ± 1.17). There were significantly greater than seen at night over sand (1.57 ind.m^{-2} ± 0.7; $p < 0.05$) or seagrass during the day (0.53 ind.m^{-2} ± 0; $p < 0.01$). In comparison, the number of fish species observed did not differ significantly between habitats or times of day.

Table 3.4 Analysis of variance results for Dive survey. Two factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 'time' has 2 levels is orthogonal and is fixed (Day/ Night). n = 3. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

		$F_{(1,8)}$		
Variable	α set to	Habitat (Ha)	Time (Di)	Ha x Di
Total species number	0.05	0.44	7.11*	4
Total density	0.05	0.12	9.14*	11.94**
Fish species number	0.05	0	1.33	1.33
Fish densities	0.05	0.3	7.02*	12.06**
Decapod species number	0.05	5.33*	12**	5.33*
Decapod densities	0.05	19.94**	25.01**	0.23
Number of exploited species	0.05	0.25	2.25	2.25
Density of exploited species	0.05	2.19	6.08*	0.24

There was a significant interaction between habitat and time (Table 3.4) for species of decapods. SNK tests showed significantly higher numbers of decapod species at night in seagrass (1.7 species ± 0.33; $p < 0.01$) than during the day in seagrass (none was observed), and significantly higher than over sand (1.3 species ± 0.33). Densities of decapods showed significant differences between habitat and time (Table 3.4), with no significant interaction between the two factors. SNK tests showed significantly greater ($p < 0.01$) decapod densities at night (0.22 ind.m^{-2} ± 0.08) than during the day (0.03 ind.m^{-2} ± 0.02), and greater densities over sand (0.21 ind.m^{-2} ± 0.08) compared to seagrass (0.04 ind.m^{-2} ± 0.02; $p < 0.01$). Cephalopod molluscs were observed too infrequently for valid analysis. Of the three that were observed, two were seen during the day and one at night and all three were seen in seagrass.

Finally, for exploited species, a significant difference in density between day and night was found (Table 3.4), with significantly ($p< 0.05$) higher densities observed during the day (0.12 ind.m^{-2} ± 0.03) than at night (0.05 ind.m^{-2} ± 0.01). There was no significant difference between habitat or time for the number of exploited species (Table 3.4).

3.3.1.5 Potting

The total number of species sampled from pots showed significant differences ($p< 0.01$) between day and night sampling (ANOVA, $F_{(1,96)} = 6.92$); significantly more species were sampled at night (2.0 ± 0.20) than during the day (1.4 ± 0.17) (SNK *post hoc* test, $p<0.05$) (Table 3.5). Pot type and bait showed significant interactions with habitat (Table 3.5). The largest number of species was sampled in seagrass using inkwells (2.7 ± 0.3), significantly more ($p<0.05$) than inkwells over sand (1.8 ± 0.27) and 'D' pots in seagrass (1.2 ± 0.24). In seagrass, scad and white tiles sampled significantly more ($p<0.05$) species than no bait (1.2 ± 0.31). Over sand, there were no significant differences in the number of species between pot types or bait used.

ANOVA on log (x+1) transformed total abundances revealed a significant ($p<0.05$) interaction between habitat, time of day and bait type ($F_{(3,96)} = 3.78$). Overall, the greatest total abundances were observed using scad as bait, during the day in seagrass (14, ± 2.5). SNK tests showed this to be significantly greater ($p< 0.01$) than using light sticks under the same conditions. For unvegetated sand samples, total abundances were greatest using scad during the day (14, ± 2.5). SNK *post hoc* means tests showed that, during the day over sand, pots baited with scad sampled significantly more ($p<0.05$) total fauna than any other bait (no bait: 3.88, ± 0.93; light stick: 3.75, ± 1.49; white tile 4.13, ± 1.38). For total abundance, no significant difference was observed between pot types.

Although ANOVA showed a significant difference, ($p< 0.001$) in the number of decapod species sampled between both day and night sampling and bait type, there were significant interactions between these factors and both habitat and pot type (Table 3.5). In general, the highest numbers of decapod species were sampled in seagrass at night, with scad as bait (1.6 species ± 0.32). *Post hoc* means test (SNK) showed this to be significantly ($p<0.05$) higher than samples from seagrass using scad during the day (0.9 ± 0.23) or using light sticks in seagrass at night (0.8 ± 0.31). For seagrass at night 'D' pots (1.3 ±0.23) sampled significantly ($p<0.05$) more species of decapod than inkwells (0.56 ± 0.18).

Table 3.5 Analysis of variance results for potting. Four Factors; factor 1 is habitat has two levels is orthogonal and fixed (sand/ seagrass), factor 2 has 2 levels is orthogonal and is fixed (Day/ Night), factor 3 is Pot type has two levels and is orthogonal and fixed (Inkwell/ D-pot), factor 4 is bait type, which has four levels is orthogonal and is fixed (1=Scad, 2=White tile, 3= Light stick, 4=No Bait). Number of replicates = 4. F values at $_{(1,96)}$ degrees of freedom unless the effect includes the bait type factor ($F_{(3,96)}$).

	Total		Fish		Decapods		Exploited species	
	Species	Density	Species	Density	Species	Density	Species	Density
α set to	0.05	0.05	0.05	0.05	0.05	0.05	0.01	0.05
Habitat (Ha)	2.32	0.19	5.27*	10.99**	1.44	2.02	0.04	6.78*
Time (Di)	6.92**	2.08	0.04	0.02	24.3***	7.88**	0.39	4.04*
Pot (Po)	17.25***	2.12	21.07***	21.38***	0.16	0.88	1.39	1.48
Bait (Ba)	2.69	16.03***	2.1	1.96	13.56***	32.77***	3.56	26.65***
HaXDi	0.02	0.54	0.04	0.04	0.87	0.08	1.08	0.02
HaXPo	6.21*	7.44**	2.34	5.06*	3.99*	3.99*	2.12	1.87
HaXBa	2.72*	1.88	3.9*	3.26*	0.11	0.52	0.35	1.89
DiXPo	1.23	0.01	0.33	0.7	1.44	0.07	1.08	2.04
DiXBa	1.51	2.4	2.38	2.16	1.3	2.59	0.9	0.98
PoXBa	2.01	3.15*	2.24	2.58	0.63	1.06	0.29	1.18
HaXDiXPo	1.23	1.42	0.04	0.5	5.13*	4.69*	0.04	2.95
HaXDiXBa	1.18	3.78*	0.43	1.46	3.14*	4.19**	0.13	6.41***
HaXPoXBa	1.37	1.29	0.49	0.7	3.05*	1.69	0.69	0.71
DiXPoXBa	2.39	1.6	1.6	1	2.1	1.27	0.83	1.31
HaXDiXPoXBa	1.9	1.11	1.7	1.92	1.72	0.28	0.17	0.26

Sampling over unvegetated sand, using inkwells baited with scad, collected significantly more ($p< 0.01$) species of decapod (1.63 ± 0.18) than other baits (white tile 0.75 ±0.25; light stick 0.63, ± 26 or no Bait 0.63, ±0.32). Again, sampling at night, using either pot type, collected significantly ($p<0.01$) more species than during the day. At night on bare sand, there was no significant difference between bait, and no decapods were found in any of the unbaited replicates during the day over sand or seagrass.

ANOVA of decapod abundance showed significant interactions both between habitat time and bait, and habitat, time and pot type (Table 3.5). SNK tests on the first interaction showed that for seagrass sampling at night, scad (10.13 ind. per pot ± 3.60) collected significantly larger ($p<0.01$) numbers of decapods than any of the other baits (WT 2 per pot ± 0.8; LS 1.25 per pot ± 0.56; NB 0.25 per pot ± 0.17). In sand during the day, scad (13.75, ± 2.53) also sampled significantly greater ($p<0.01$) numbers of decapods than other baits (WT 0.25 per pot, ± 0.16; LS 0.25 per pot, ± 0.25, NB none). However, no difference was observed between different baits at night in sand, or between day and night collections in sand.

Pot type was found to be a significant ($p<0.01$) factor in the variability in the number of fish species sampled (Table 3.5). *Post hoc* SNK tests showed that D pots sampled significantly more species of fish (1.28, ± 0.14) than inkwells (0.51, ± 0.1) over all habitats, sampling times and bait types. There was also a significant ($p< 0.05$) interaction between habitat and bait type for the number of fish species (Table 3.5). Pots baited with a white tile caught significantly more fish species in seagrass (1.63, ± 0.14) than those placed on sand (0.5, ± 0.183). On sand, pots baited with light sticks (1.25, ± 0.34) sampled significantly more species of fish than those baited with scad (0.25, ± 0.14). In comparison to the decapod results, time of sampling was not a significant factor in sampling different numbers of fish species.

ANOVA on log (x+1) transformed fish abundances found significant ($p<0.05$) interactions between habitat and both pot type, and the type of bait used (Table 3.5). SNK tests showed that there was no significant difference between baits, pots baited with scad or a white tile sampled significantly more ($p<0.05$ and 0.01 respectively) fish in seagrass (scad: 2.13 ± 0.93; white tile: 2.44 ± 0.43), than over sand (scad: 0.25 ± 0.14; white tile: 0.69 ± 0.27). Similarly, inkwells sampled significantly more fish in seagrass (3.06 ± 0.53) than over sand (1.22 ± 0.28); 'D' pots showed no significant difference.

In terms of the number of exploited species sampled, no significant difference was observed. However, analysis of the abundance of exploited species revealed a significant interaction between habitat, time and bait (Table 3.5). For sand, SNK test showed that significantly higher ($p<0.01$) abundances were caught during the day with scad (13.88 ind. per pot, ± 2.49) compared with other baits (WT 0.25 per pot ± 0.16; LS 0.25 per pot ± 0.16 and NB 0.38 per pot, ± 0.26), or at night using the same bait (7.87 per pot, ± 3.4353; $P< 0.05$). In comparison, for seagrass, significantly higher abundance of exploited species were found with scad as bait, but only when sampling at night (10 per pot, ± 4.74) rather than during the day (3.5 ind. per pot, ± 1.7829). Again, scad as bait sampled significantly more exploited species ($p<0.01$) than the other baits in seagrass at night (WT 2 per pot, ±

0.82; LS 0.25, ± 0.25 and No Bait 0.13, ± 0.13). In seagrass, there was no significant difference in the abundance of exploited species between baits during the day.

3.3.2 Species selectivity

A total of 51 species was sampled during the study (7865 individuals) comprising 33 species of fish, 16 species of decapod crustaceans and two species of cephalopod molluscs. Twenty-five of these are exploited in the Normano-Breton Gulf (Tables 3.6 and 3.7). More species were sampled by trawling (42) than by any other method (beach seine, 28; push net, 23; potting, 19 and dive survey, 18). Overall, more species were found over unvegetated sand (46 species) than from the seagrass habitat (37 species).

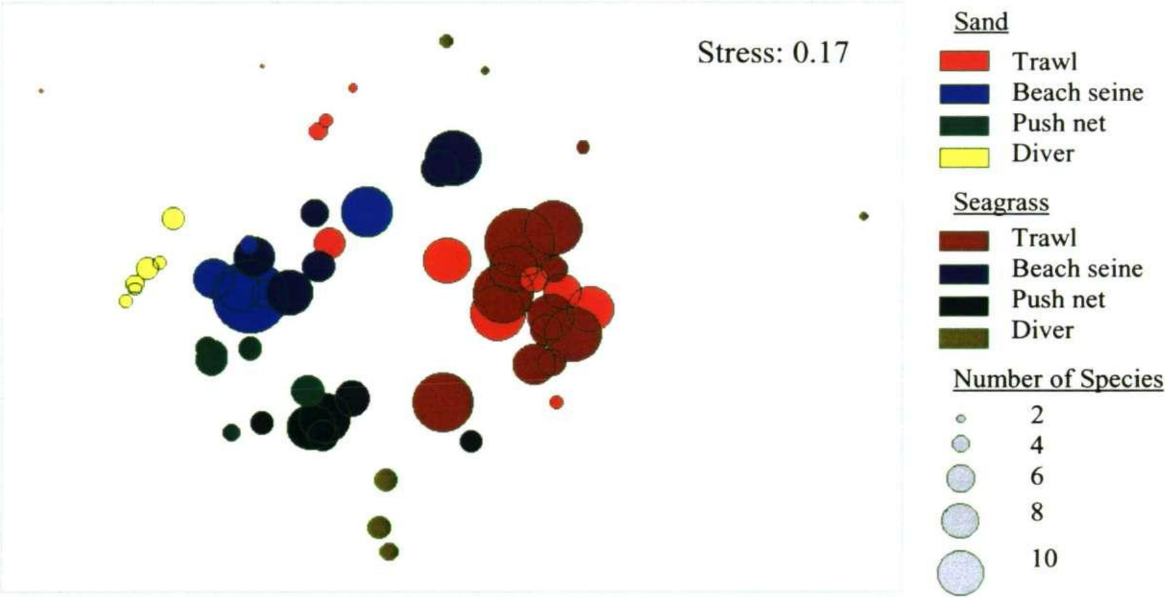


Figure 3.6 MDS ordination computed from the similarities between log (x+1) species densities of different sampling methods over sand and seagrass. (Stress = 0.17). Bubble size is indicative of the number of species sampled.

A two-dimensional ordination plot illustrated a clear separation of samples from different gear types (Figure 3.6). In Figure 3.6, bubble size is indicative of the number of species sampled (condition against the total number of species sampled by all gear types in the specific habitat). In seagrass trawl and push net samples show the strongest clustering. Although trawling may sample different species from other methods, the proportion of species sampled, compared to the other methods (diver survey in particular) was higher. Within gears, there is a clear separation between sand and seagrass. The species selectivity of the gears may therefore, be assessed separately for the two habitats.

3.3.2.1 Species selectivity within seagrass

Table 3.6 shows the distribution of species between the gears for the seagrass bed. Whilst no species was found to be unique to the pot collections, three species (white bream, *Diplodus sargus* and flounder, *Platichthys flexus*) were found only in beach seine samples; four species (the chameleon prawn, *Hippolyte inermis*; common goby, *Pomatoschistus microps* and the pipefish, *Syngnathus rostellatus* and *Entereulus aequoreus*) were found only in trawls; and the worm pipefish, *Nerophis ophidion*, was sampled only using a push net. During the dive surveys only one species, the lesser-spotted dogfish (*Scyliorhinus caniculus*), was seen that other gears had not sampled. The rankings in Table 3.7 indicate that most of these unique species did not represent a substantial proportion of the total number of species sampled by any method type.

Table 3.6 shows pollack (*Pollachius pollachius*) dominated the fish sampled by the beach seine and pouting (*Trisopterus luscus*) the fish sampled by potting. The two spot goby (*Gobiusculus flavescens*) dominated the fish sampled by the other three methods (trawling, push netting and diver surveys). In the trawl and push net samples, dominant decapod crutaceans were the common prawn, *Palaemon serratus*, while the brown shrimp, *Crangon crangon*, dominated beach seine samples and the spider crab, *Maja squinado*, was most frequently sampled by potting. No one decapod species dominated the diver observations.

In terms of cephalopod molluscs, potting and trawling collected the cuttlefish *Sepia officinalis*, whilst beach seining only collected the little cuttle, *Sepiola atlantica*. Divers observed both species although little cuttles were more frequent.

Comparisons of trawling, beach seining, push netting and diver survey (ANOVA) found a significant difference ($p<0.01$) in the total number of species sampled (Table 3.7). Tukey's (unequal N HSD) *post hoc* test showed that, whilst there was no significant difference in total species number between trawling (9.67 species ± 0.64), push netting (7.67 ± 1.02) or beach seining (8.83 ± 0.87), trawling sampled significantly ($p<0.05$) more species than the diver survey. Significant differences were also observed when the decapod, fish and the number of exploited species were analysed separately ($F_{(3,26)} = 6.25$, $p<0.01$; $F_{(3,26)} = 5.51$, $p<0.01$ and $F^{3,26} = 5.83$, $p<0.01$, respectively). *Post hoc* comparisons showed that these significant differences were due mainly to the low number of species observed during diver surveys, with the other three methods not showing significant differences (Table 3.7). There was also a significant difference in the total density of species estimated by these four methods (Table 3.7). Again, this was reflected in significant differences in the densities of both fish and decapods (Table 3.7). This time, however, Tukey's *post hoc* test showed that whilst the highest densities of decapods were sampled using the push net (significantly more, $p<0.05$, than any of the other methods), significantly higher densities of fish were observed using the diver survey than from beach seining, trawling or push netting. Cephalopod molluscs were found in insufficient numbers for analysis.

One-way ANOVA (with unequal sample sizes) of the more common fish species caught by the three mobile gears (trawl, push net and beach seine) showed that only three (*P. pollachius*, *P. minutes* and *G. flavescens*) of the eight most common species exhibited significant differences in densities (Table 3.8). For Pollack and sand goby, Tukey's test (Unequal N HSD test) showed that the number of individuals was significantly greater (at $p<0.05$) in the beach seine samples compared to the trawls and diver survey; for Pollack beach seining sampled significantly more than the push net, although this was not the case for the sand goby (Table 3.7). In comparison, Tukey's tests showed that densities of the two spot goby were significantly greater in the diver survey than either the push net, trawl or beach seine samples. Densities differed significantly for the common prawn (*Palaemon serratus*) ($F^{3,26} = 9.63, p<0.001$), with Tukey's test (Unequal N HSD test) showing that the number of individuals were significantly greater (at $P<0.05$) in the push net samples compared to the beach seines, trawls or diver surveys (Table 3.7).

Table 3.6 Densities (ha^{-1}) of species sampled using the five different methods in seagrass and their rank.

	Potting (n = 64)		**Trawl** (n = 12)		**Beach Seine** (n = 6)		**Push Net** (n = 6)		**Diving survey** (n = 6)	
	Mean number per pot (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank
Fish										
Gobiusculus flavescens	0	-	356.74(175.56)	1	8.33(4.81)	13	2733.33(860.49)	1	2222.2(1124.65)	1
Ctenolabrus rupestris	0	-	69.98(27.62)	2	12.5(11.41)	10	1066.67(682.48)	2	0	-
Spondyliosoma cantharus[a]	0	-	41.53(15.53)	3	0	-	400(206.56)	3	0	-
Syngnathus typhle	0	-	23.82(10.72)	4	25(18.63)	6.5	66.67(66.67)	9.5	44.44(44.44)	15
Labrus bergylta[a]	0.06(0.04)	6.5	19.28(12.17)	5	12.5(11.41)	10	200(136.63)	6.5	0	-
Symphodus melops	0.56(0.12)	2	17.15(5.92)	6	0	-	66.67(66.67)	9.5	0	-
Taurulus bubalis	0.03(0.02)	8	15.77(6.86)	7	0	-	0	-	44.44(44.44)	15
Callionymas lyra	0	-	14.76(7.65)	8	12.5(7.80)	10	333.33(217.05)	4.5	44.44(44.44)	15
Pollachius pollachius[a]	0.06(0.03)	6.5	11.59(6.03)	9	883.33(331.01)	1	66.67(66.67)	9.5	133.33(59.63)	6
Entelurus aequoreus	0	-	9.95(3.57)	10	0	-	0	-	0	-
Pomatoschistus minutes	0	-	9.86(9.86)	11	825(330.09)	2	333.33(217.05)	4.5	0	-
Trisopterus minutes[a]	0.41(0.16)	3	7.02(3.84)	12	0	-	0	-	0	-
Pomatoschistus microps	0	-	5.21(3.56)	13	0	-	0	-	0	-
Syngnathus acus	0	-	4.30(2.90)	14	12.5(5.10)	10	0	-	0	-
Trisopterus luscus[a]	0.63(0.18)	1	3.81(2.58)	15	0	-	0	-	44.44(44.44)	15
Solea solea[a]	0	-	2.21(2.21)	16	25(18.63)	6.5	0	-	0	-
Gobius niger	0.08(0.06)	5	1.73(1.73)	17	0	-	0	-	0	-
Centrolabrus exoletus	0.17(0.06)	4	1.64(1.64)	18.5	12.5(11.41)	10	200(136.63)	6.5	0	-
Syngnathus rostellatus	0	-	1.64(1.64)	18.5	0	-	0	-	0	-
Atherina presbyter[a]	0	-	0	-	154.17(47.66)	4	0	-	44.44(44.44)	15
Diplodus sargus[a]	0	-	0	-	4.17(3.80)	14.5	0	-	0	-
Nerophis ophidion	0	-	0	-	0	-	66.67(66.67)	9.5	0	-
Platichthys flexus[a]	0	-	0	-	29.17(26.63)	5	0	-	0	-
Scyliorhinus caniculus[a]	0	-	0	-	0	-	0	-	44.44(44.44)	15
Pleuronectes platessa[a]	0	-	0	-	162.5(110.2)	3	0	-	44.44(44.44)	15
Raja batis[a]	0	-	0	-	4.17(3.80)	14.5	0	-	44.44(44.44)	15
Density of fish per ha	-		617.99		2183.34		5533.34		2711.07	
Number of fish species	8		19		15		11		10	

Table 3.6 continued.

	Potting		**Trawl**		**Beach Seine**		**Push Net**		**Diving Observations**	
	Mean number per pot (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank	**Mean Density per ha (SE)**	Rank	**Mean Density per ha (SE)**	Rank
Cephalopod Molluscs										
Sepia officinalis[a]	0.03(0.02)	1	5.35(2.82)	1	0	-	0	-	44.44(44.44)	2
Sepiola atlantica	0	-	0	-	75(34.36)	1	0	-	88.89(88.89)	1
Density of molluscs per ha	-		40.98		104.17		133.33		799.99	
Number of mollusc species	3		4		4		1		6	
Decapods										
Palaemon serratus[a]	0.02(0.02)	5	69.22(28.63)	1	437.5(264.10)	2	5333.33(1934.02)	1	133.33(133.33)	2
Macropodia rostrata	0.08(0.05)	4	60.16(18.28)	2	0	-	600.00(322.49)	5.5	0	-
Carcinus maenas[a]	0.11(0.05)	3	50.73(38.97)	3	25(14.43)	3	1600.00(900.37)	4	0	-
Hippolyte varians	0	-	50.10(35.63)	4	4.17(3.80)	5	2200.00(1602.50)	3	0	-
Crangon crangon[a]	0	-	18.59(6.01)	5	983.3(500.89)	1	5266.67(4025.81)	2	0	-
Processa edulis crassipes	0	-	10.14(5.69)	6	0	-	133.33(84.33)	7.5	0	-
Pagurus bernardus	0.72(0.27)	2	2.08(2.08)	7	0	-	600.00(247.66)	5.5	133.33(91.08)	2
Maja squinado[a]	1.94(0.53)	1	2.01(2.01)	8	12.5(7.80)	4	133.33(84.33)	7.5	133.33(91.08)	2
Hippolyte inermis	0	-	2.00(2.00)	9	0	-	0	-	0	-
Density of decapods per ha	-		265.03		1462		15866.66		399.99	
Number of decapod species	6		9		5		8		3	
Density of exploited species	-		220.51		2579.17		13000		711.08	
Number of exploited species	8		9		11		7		8	
Total Density	-		924		3750.01		21533.33		3119.05	
Total species number	19		30		24		20		19	

Table 3.7 Seagrass: Results of a one-way ANOVA ($F^{3,26}$) with unequal sample sizes, (on log (x+1) transformed data where necessary to meet assumptions) for effects of different gear type. Area standardised density data (individuals ha^{-1}) of each species caught at low tide, day/night pooled. Standard error are indicated in parentheses; rare species, species absent from two gear types and data showing heterogeneous variance are excluded from the analysis; [a] exploited species; n.s. not significant, * $p< 0.05$, ** $p<0.01$, *** $p< 0.001$. Also showing the summarised results of *post hoc* means tests where a significant effect of gear was observed.

Species	Beach seine (B) (n = 6)	Trawl (T) (n = 12)	Push net (P) (n = 6)	Dive survey (D) (n=6)	*p (α=0.01)*	Tukey's Unequal N HSD test (*P*< 0.05)
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)		
Fish						
Labrus bergylta [a]	12.5 (11.41)	19.28 (12.17)	200 (136.6)	0	n.s.	-
Syngnathus typhle	25.00 (18.63)	23.82 (10.72)	66.67 (66.67)	44.44(44.44)	n.s.	-
Pomatoschistus minutus	825 (330.09)	9.86 (9.86)	333.33 (217.05)	0	**	P=(B>T=D)
Pollachius pollachius [a]	883.33 (331.01)	11.59 (6.03)	66.67 (66.67)	133.33(59.63)	**	B>T=P=D
Gobiusculus flavescens	8.33 (4.81)	356.74 (175.6)	2733.33 (860.49)	22222.22(11243.65)	**	D>T=P=B
Callionymas lyra	12.5 (7.80)	14.76 (7.65)	333.33 (217.05)	44.44(44.44)	n.s.	-
No. of fish species	5.67 (0.76)	6.25 (0.74)	3.67 (0.92)	2.33(0.21)	**	P=B=(T>D)
Density of fish	2183.33 (82.9)	620.19 (185.91)	5533.33 (1210.69)	22711.11(11208.55)	**	P=(D>B=T)
Decapods						
Palaemon serratus [a]	437.5 (264.10)	69.22 (28.63)	5333.33 (1934)	133.33(133.33)	***	P>B=T=D
Crangon crangon [a]	983.33 (500.89)	18.59 (6.01)	5266.67 (4025.8)	0	n.s.	-
No. of decapod species	2.33 (0.33)	3.17 (0.51)	4 (0.45)	0.83(0.4)	**	B=(P=T>D)
Density of decapods	1462.5 (574.41)	265.03 (86.46)	15266.67 (4297.49)	400(214.62)	***	P>B=T=D
No. of exploited species	5.33 (0.61)	3.5 (0.46)	3.5 (0.62)	1.83(0.31)	**	P=T=(B>D)
Density of exploited species	2733.33 (711.41)	231.32 (55.79)	13000 (4160.45)	622.22163.96)	***	P>B=T=D
Total species number	8.83 (0.87)	9.67 (0.64)	7.67 (1.02)	3.5(0.56)	**	P=(B=T>D)
Total density	3725 (846.34)	890.57 (263.89)	20800 (3981.29)	23244(11378.35)	**	P=B=(D>T)

The two-way crossed ANOSIM confirmed the patterns of the MDS and the univariate ANOVA, in that for the seagrass samples, there was a significant difference in the community structure between gear groups (R = 0.79, $p<0.01$). SIMPER analyses were used to determine which organisms contributed to the similarity/dissimilarity observed. Beach seine, push net and trawl samples showed the highest similarities within groups (32.4%, 30.8% and 28.5% respectively), with dive survey samples showing the lowest similarity within groups (19.02%). The largest dissimilarity between gear groups was between trawl and dive survey samples (96.01%), a difference influenced mostly by the two spot goby (*Gobiusculus flavescens*), which contributed 53.9%. The two spot goby also contributed significantly to the dissimilarities between other gear groups and the dive survey (push net/ dive survey, 31.8%; dive survey/ beach seine, 41.46%). However, the common prawn (*Palaemon serratus*) and the common shrimp (*Crangon crangon*) were the most influential species in the dissimilarity between trawl and push net samples (*P. serratus* contributing 21.34% and *C. crangon* 18.67%), and between beach seine and push net samples (*P. serratus* contributing 18.3% and *C. crangon* 17.5%). At 24.12%, pollack (*Pollachius pollachius*) was the predominant species contributing to the dissimilarity between trawl and beach seine samples due to the higher average abundance of pollack in beach seine samples.

3.3.2.2 Species selectivity on unvegetated sand

Table 3.8 shows the distribution of species between the gears from unvegetated sand. In total, 46 species were collected (nine more than sampling from seagrass). Of these, 29 were fish, 15 were decapod crustaceans and two were cephalopod molluscs. Four species were found to be unique to the pot collections (the four bearded rockling, *Enchelyopus cimbrius*; pouting, *Trisopterus luscus*; the edible crab, *Cancer pagurus* and lobster, *Hommarus gammarus*).

However, with the exception of the edible crab, these species were quite rare to the pot samples [in seagrass, pouting were observed in trawl samples and during the diver survey (Table 3.8)]. Beach seining over sand sampled four species of fish not collected by any other method; they were the eel (*Anguilla anguilla*), the sand smelt (*Atherina presbyter*), flounder (*Platichthys flesus*) and bass (*Dicentrarchus labrax*). Push netting sampled no unique species and the only species unique to the dive surveys was the weever fish (*Echiichthys vipera*).

Table 3.8 Densities (ha^{-1}) of species sampled using the five different methods in sand and their rank.

	Potting (n = 64)		**Trawl (n = 12)**		**Beach Seine (n = 6)**		**Push Net (n = 6)**		**Diving survey (n = 6)**	
	Mean number per pot (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank
Fish										
Pomatoschistus minutus	0	-	637.93(181.39)	1	3258.33(1538.7)	1	10400(4327.89)	1	18355.6(4093.3)	1
Pomatoschistus microps	0	-	48.65(25.09)	2	50(45.18)	6	66.67(66.67)	6.5	0	-
Gobiusculus flavescens	0	-	33.92(15.33)	3	0	-	0	-	0	-
Pleuronectes platessa[a]	0	-	32.06(18.73)	4	333.33(231.81)	2	66.67(66.67)	6.5	44.44(44.44)	5
Pollachius pollachius[a]	0.08(0.04)	5.5	21.71(12.86)	5	279.17(164.75)	3	0	-	44.44(44.44)	5
Solea solea[a]	0	-	16.01(7.91)	6	75(60.55)	5	0	-	88.89(56.22)	3
Ctenolabrus rupestris	0	-	15.79(8.39)	7	0	-	333.33(333.33)	2.5	0	-
Taurulus bubalis	0.02(0.02)	8.5	7.55(4.59)	8	0	-	0	-	0	-
Syngnathus rostellatus	0	-	7.19(3.57)	9	0	-	266.67(197.77)	3	0	-
Spondyliosoma cantharus[a]	0	-	5.27(3.78)	10	0	-	0	-	0	-
Callionymas lyra	0	-	4.965(2.07)	11	8.33(8.33)	8.5	333.33(217.05)	2.5	0	-
Syngnathus acus	0	-	3.355(2.35)	12	0	-	0	-	0	-
Labrus bergylta[a]	0.13(0.04)	3	2.19(1.53)	13	0	-	0	-	0	-
Entelurus aequoreus	0	-	1.66(1.66)	14	0	-	0	-	0	-
Centrolabrus exoletus	0.11(0.05)	4	1.22(1.22)	15.5	4.17(4.17)	11	0	-	0	-
Ciliata mustela[a]	0	-	1.22(1.22)	15.5	0	-	0	-	0	-
Gobius niger	0	-	0.98(0.98)	18.5	0	-	0	-	0	-
Spinachia spinachia	0	-	0.98(0.98)	18.5	0	-	0	-	0	-
Syngnathus typhle	0	-	0.98(0.98)	18.5	0	-	133.33(133.33)	4.5	0	-
Trisopterus minutus[a]	0.08(0.03)	5.5	0.98(0.98)	18.5	0	-	0	-	0	-
Anguilla anguilla[a]	0	-	0	-	4.17(4.17)	11	0	-	0	-
Atherina presbyter[a]	0	-	0	-	266.67(168.78)	4	0	-	0	-
Dicentrachus labrax[a]	0	-	0	-	8.33(5.27)	8.5	0	-	0	-
Echiichthys vipera	0	-	0	-	0	-	0	-	88.89(56.22)	3
Platichthys flesus[a]	0	-	0	-	12.5(8.54)	7	0	-	0	-
Enchelyopus cimbrius[a]	0.03(0.03)	7	0	-	00	0	0	-	0	-
Scyliorhinus caniculus[a]	0.02(0.02)	8.5	0	-	00	0	0	-	88.89(56.22)	3
Symphodus melops	0.31(0.09)	1	0	-	4.17(4.17)	11	133.33(84.33)	4.5	0	-
Trisopterus luscus[a]	0.17(0.07)	2	0	-	0	0	0	-	0	-
Density of fish per ha	-		844.62		4304.17		11733.33		18711.11	
Number of fish species	9		20		12		8		6	

Table 3.8 continued.

	Potting (n = 64)		**Trawl (n = 12)**		**Beach Seine (n = 6)**		**Push Net (n = 6)**		**Diving survey (n = 6)**	
	Mean number per pot (SE)	Rank	Mean Density Per ha (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank	Mean Density per ha (SE)	Rank
Cephalopod Molluscs										
Sepiola atlantica	0	-	16.19(6.73)	1	125(115.29)	1	0	-	0	-
Sepia officinalis[a]	0.02(0.02)	1	1.67(1.67)	2	0	-	0	-	0	-
Density of cephalopods per ha	0.02		17.86		125		0		0	
Number of cephalopod species	1		2		1		0		0	
Decapod Crustaceans										
Crangon crangon[a]	0	-	331.37(127.41)	1	2475(616.58)	1	9800(2985.74)	1	0	-
Macropodia rostrata	0.02(0.02)	8	59.39(19.36)	2	12.5(12.5)	5.5	66.67(66.67)	8	0	-
Palaemon serratus[a]	0.06(0.05)	4	38.26(19.37)	3	170.83(104.96)	2	4066.67(1627.81)	2	0	-
Pagurus bernhardus	0.16(0.07)	3	27.71(20.73)	4	83.33(68.52)	4	800(473.29)	5	0	-
Carcinus maenas[a]	0.05(0.03)	6	23.52(10.27)	5	95.83(34.41)	3	1733.33(1267.72)	3	0	-
Hippolyte varians	0	-	21.16(8.53)	6	12.5(8.54)	5.5	1466.67(1176.06)	4	0	-
Pisidia longicornis	0	-	11.79(8.71)	7	0	-	0	-	0	-
Processa edulis crassipes	0	-	9.77(8.80)	8	0	-	400(400)	6	0	-
Maja squinado[a]	3.20(0.77)	1	6.91(3.53)	9	8.33(5.27)	7.5	0	-	844.44261.43	1
Thoralus cranchi	0	-	3.66(3.66)	10	0	-	0	-	0	-
Eualus occultus	0	-	1.30(1.30)	11.5	0	-	0	-	0	-
Palaemon longicornis	0	-	1.30(1.30)	11.5	0	-	133.33(133.33)	7	0	-
Necora puber[a]	0.05(0.03)	6	0.99(0.99)	13	8.33(8.33)	7.5	0	-	0	-
Cancer pagurus[a]	0.25(0.09)	2	0	-	0	-	0	-	0	-
Homarus gammarus[a]	0.05(0.03)	6	0	-	0	-	0	-	0	-
Density of decapods per ha	-		537.13		2866.67		18466.67		844.44	
Number of decapod species	8		13		8		8		1	
Density of exploited species	-		460.46		3458.33		15666.67		1066.67	
Number of exploited species	12		12		8		4		5	
Total Density	-		1399.62		7295.83		30200		19555.56	
Total species number	17		33		20		16		7	

As Table 3.8 illustrates, trawling sampled the most unique species from sand (seven species of fish and three species of decapods), most notably the two spot goby (*Gobiusculus flavescens*), black bream (*Spondyliosoma cantharus*) and the pipefish *Entelurus aequoreus* and *Syngnathus acus*. Corkwing wrasse (*Symphodus melops*) dominated the fish sampled by potting, but all remaining methods were dominated by the sand goby (*Pomatoschistus minutus*) (Table 3.8). The dominant decapod crutacean in the trawl, push net and beach seine samples was the brown shrimp, *Crangon crangon*. As with the seagrass samples, *Maja squinado* dominated potting collections, and diver observations from sand habitats. Divers observed neither of the two cuttlefish species over sand.

Comparisons of the four semi-quantitative methods (trawling, beach seining, push netting and dive survey) using a one-way ANOVA (with unequal sample sizes) found no significant difference in either the number of fish species, number of decapod species or the total number of species (Table 3.9). Cephalopod molluscs were found in numbers to small to analyse. However, there was a significant ($p<0.01$) difference in the total density of species, and this was reflected in both the density of fish and the density of decapods (Table 3.9). Tukey's (unequal N HSD) *post hoc* means tests showed that push netting (30200 ind.ha^{-1} ± 594.25) and diving (19555.56 ind.ha^{-1} ± 402.07) sampled significantly more individuals than beach seining (7295.83 ind.ha^{-1} ± 251.04) (Table 3.9). However, as with push netting and diver survey, beach seining sampled significantly more ($p<0.05$) individuals than trawling (1399.62 ind.ha^{-1} ± 49.50). Although there was no significant difference in the densities of fish and decapods between beach seining, push netting and diving, they all sampled significantly more ($p< 0.05$) than trawling (see Table 3.9).

ANOVA of the more common species of fish and decapods sampled by the four gears showed three species (*P. minutus*, *P. serratus* and *C. crangon*) exhibited significant differences (at $\alpha= 0.01$) in densities between sampling methods (Table 3.9). For sand gobies Tukey's test showed that the densities using beach seining (3258 ind.ha^{-1} ± 231.81), push netting (10400 ind.ha^{-1} ± 4327.89) and dive surveys (18355 ind.ha^{-1} ± 4093.3) were significantly higher than those using the trawl (637.9 ind.ha^{-1} ± 181.39). Highest densities of the common prawn, however, were found using push netting; the latter were significantly ($p<0.05$) greater than those found with either beach seining (170.8 ind.ha^{-1} ± 104.9), trawl (38.2 ind.ha^{-1} ± 19.37) or dive survey (no individuals), with no significant difference between the three. Finally, both push netting and beach seining collected significantly higher ($p<0.05$) numbers of brown shrimp (9800 ind.ha^{-1} ± 2985.74 and 2475 ind.ha^{-1} ± 616.58, respectively) than either the dive survey (no individuals) or trawling (331.37 ind.ha^{-1} ± 127.41).

The test for differences in the species composition between gear groups used on sand (two-way crossed ANOSIM) was significant (R=0.52, $p<0.01$). Pair-wise tests illustrated significant differences in the species composition between trawl and push net samples (R = 0.58, $p< 0.01$), trawl samples and diver survey (R = 0.58, $p< 0.01$). However, there was no significant difference between beach seine and either trawling or push net samples (R = 0.47, R = 0.48), or between diver survey and either push net or beach seine samples (R = 0.78, R = 0.65).

SIMPER analysis revealed that beach seine, push net and diver survey showed the highest similarities within groups (37.4%, 36.8% and 59.1% respectively). For the diver survey, this was due to the almost complete dominance by sand gobies. Unlike the samples collected in seagrass, trawled samples showed the lowest similarity within groups (17.24%). However, as with the seagrass samples, the largest dissimilarity between gear groups was between trawls and dive survey samples (97.94%), a difference influenced mostly by the sand goby, which contributed 79.9%. Along with the brown shrimp, the sand goby also contributed significantly to the dissimilarities between other gear groups and the dive survey (push net/ dive survey, 73.48%; dive survey/ beach seine, 79.94%; beach seine/ trawl, 91.96%; push net/ beach seine, 77.46%).

Table 3.9 Sand: Results of a one-way ANOVA ($F_{(3,26)}$) with unequal sample sizes, (on log (x+1) transformed data where necessary to meet assumptions) for effects of different gear type. Area standardised density data (individuals ha^{-1}) of each species caught at low tide, day/night pooled. Standard error are indicated in parentheses; rare species, species absent from two gear types and data showing heterogeneous variance are excluded from the analysis; [a] exploited species; n.s. not significant, * $p< 0.05$, ** $p<0.01$, *** $p< 0.001$. Also showing the summarised results of *post hoc* means tests where a significant effect of gear was observed.

Species	Beach seine (B) (n = 6)		Trawl (T) (n = 12)		Push net (P) (n = 6)		Dive survey (D) (n=6)		*p (α=0.01)*	Tukey's Unequal N HSD test ($p< 0.05$)
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)		
Fish										
Pleuronectes platessa [a]	333.33	(231.81)	32.06	(18.73)	66.67	(66.67)	44.44	(44.44)	n.s.	-
Pomatoschistus minutus	3258.33	(1538.70)	637.93	(181.39)	10400.00	(4327.89)	18355.60	(4093.3)	***	B=P=D>T
Pollachius pollachius [a]	279.17	(164.75)	21.71	(12.86)	0	0	44.44	(44.44)	n.s.	-
No. of fish species	5.00	(0.82)	2.75	(0.59)	2.33	(0.56)	2.33	(0.21)	n.s	-
Density of fish per ha	4304.17	(266.05)	844.62	(80.99)	11733.33	(943.74)	18711.11	(649.62)	***	B=P=D>T
Decapods										
Palaemon serratus [a]	170.83	(104.96)	38.26	(19.37)	4066.67	(1627.81)	0	0	**	P>T=D=B
Crangon crangon [a]	2475.00	(616.58)	331.37	(127.41)	9800.00	(2985.74)	0	0	***	P=B>D=T
No. of decapod species	3.83	(0.79)	2.67	(0.62)	3.33	(0.42)	1.50	(0.22)	n.s	-
Density of decapods	2866.67	(94.83)	537.13	(63.45)	18466.67	(197.11)	844.44	(125.88)	***	B=P=D>T
No. of exploited species	5.83	(1.33)	1.58	(0.48)	2.67	(0.21)	1.67	(0.21)	***	B>T=P=D
Density of exploited species	3458.33	(852.10)	460.46	(313)	15666.67	(3015.37)	1066.67	(291.11)	***	P>T=D=B
Total species number	9.17	(1.70)	5.58	(1.10)	5.67	(0.49)	3.83	(0.40)	n.s	-
Total density	7295.83	(251.04)	1399.62	(49.50)	30200	(594.25)	19555.56	402.07	***	P=D>B>T

3.3.3 Size selectivity

Small individuals (< 150mm) and juveniles of larger species dominated the catches from all gears. Eight species of fish were sampled in sufficient quantities in several gears to allow analysis of potential size selectivity. They were black bream (*Spondyliosoma cantharus*), pollack (*Pollachius pollachius*), the wrasses (*Labrus bergylta*, *Ctenolabrus rupestris* and *Symphodus melops*), the gobies (*Gobiusculus flavescens* and *Pomatoschistus minutus*) and two species of the genus *Trisopterus* (*T. luscus* and *T. minutus*). Data from the two species of *Trisopterus* were pooled to provide a sufficiently large data set, which was deemed valid due to the similarities in growth rates and habit of these two species (Cohen *et al.,* 1990).

Figure 3.7a shows that for ballan wrasse (*Labrus bergylta*), gear showed some selectivity for fish below 60 mm standard length (SL), with trawl and push net index values being positive, but pot and beach seine samples showing negative values (indicative of negative bias). Above 60 mm SL, there was a switch in bias for the pairs of gear type, to some extent. For beach seining, this held only until 160 mm, but potting continued to show bias with increasingly larger fish. After 60 mm, push netting and trawling showed no size selectivity. Not enough Ballan Wrasse were collected from unvegetated sand to allow a between habitat comparison in the selectivity of the gear.

The pattern of selectivity was somewhat different for Pollack (*Pollachius pollachius*). Below 40 mm, there was no observable bias by any of the gears. However, in contrast to the Ballan Wrasse, smaller Pollack (40 to 70 mm) were not sampled effectively by the trawl (mainly negative values in this size range, Figure 3.7b), although potting once again under sampled these smaller fish. Both trawling and potting appeared to more effectively sample pollack between 80 and 110 mm than the other gears, although for trawling this was more evident in seagrass compared to sand. Beach seining appeared to sample all size ranges of pollack effectively (near zero index values, Figure3.7b).

Only trawl and push net samples from seagrass contained sufficient numbers for an analysis of size selectivity for black bream (*Spondyliosoma cantharus*). Trawling appeared to sample most size classes of black bream (all of which were juveniles) and push netting showed a bias for and against particular size classes but with no clear threshold (Figure3.7c).

In sand samples, beach seining, trawling and push netting showed no bias for a particular size class of sand goby (*Pomatoschistus minutus*) (Figure 3.7d). However, in seagrass, trawling showed positive selection for smaller (< 30 mm) sand gobies and underestimated sizes between 30 and 40 mm (although above 40 mm no bias was observed). Push netting did not effectively sample sand gobies between 20 and 30 mm in length and was biased toward gobies of the size class of around 40 mm. Above 40 mm, none of the three gears showed any size selectivity.

In seagrass, trawling showed no bias for any size class of two spot goby (Figure 3.7e). However, push netting on seagrass, and trawling over sand, under sampled smaller size classes (up to 20 mm), and showed a positive bias for two spot gobies between the 30 and 40 mm size class. Above 40 mm there was no bias.

Push netting in seagrass showed a bias for the smallest size classes (< 40 mm) of goldsinny (*Ctenolabrus bergylta*); for larger size classes, this method was either not effective (50 mm) or showed no bias (>80 mm). Trawling in seagrass appeared to under sample the smaller size classes of goldsinny, with some indication of selection for the smallest goldsinnies (<20 mm). Above 50 mm, push netting and trawling in seagrass showed no bias, Trawling sand showed Trawling over sand under sampled size classes of goldsinny between 30 and 50 mm, and some selection for medium sized fish 60 to 70 mm and the largest fish 120 mm (Figure 3.7f).

Despite showing strong selectivity for most species, potting (sand and seagrass) showed no selectivity for Cork Wing Wrasse (*Symphodus melops*), in any size class. Trawling seagrass showed a slight bias for the smaller classes (<50mm) of *S. melops*. For the 60 to 80 mm size classes of this fish, beach seining was selective, but under selected individuals over 90 mm; for this size grouping other methods showed no bias (Figure 3.7g).

As with many species, potting underestimated and trawling overestimated smaller size classes (<90mm) of *Trisopterus* species. Over sand, even fish up to 120 mm were under sampled with the potting method, although above this size *Trisopterus* species were positively selected for by potting on sand (Figure 3.7h)

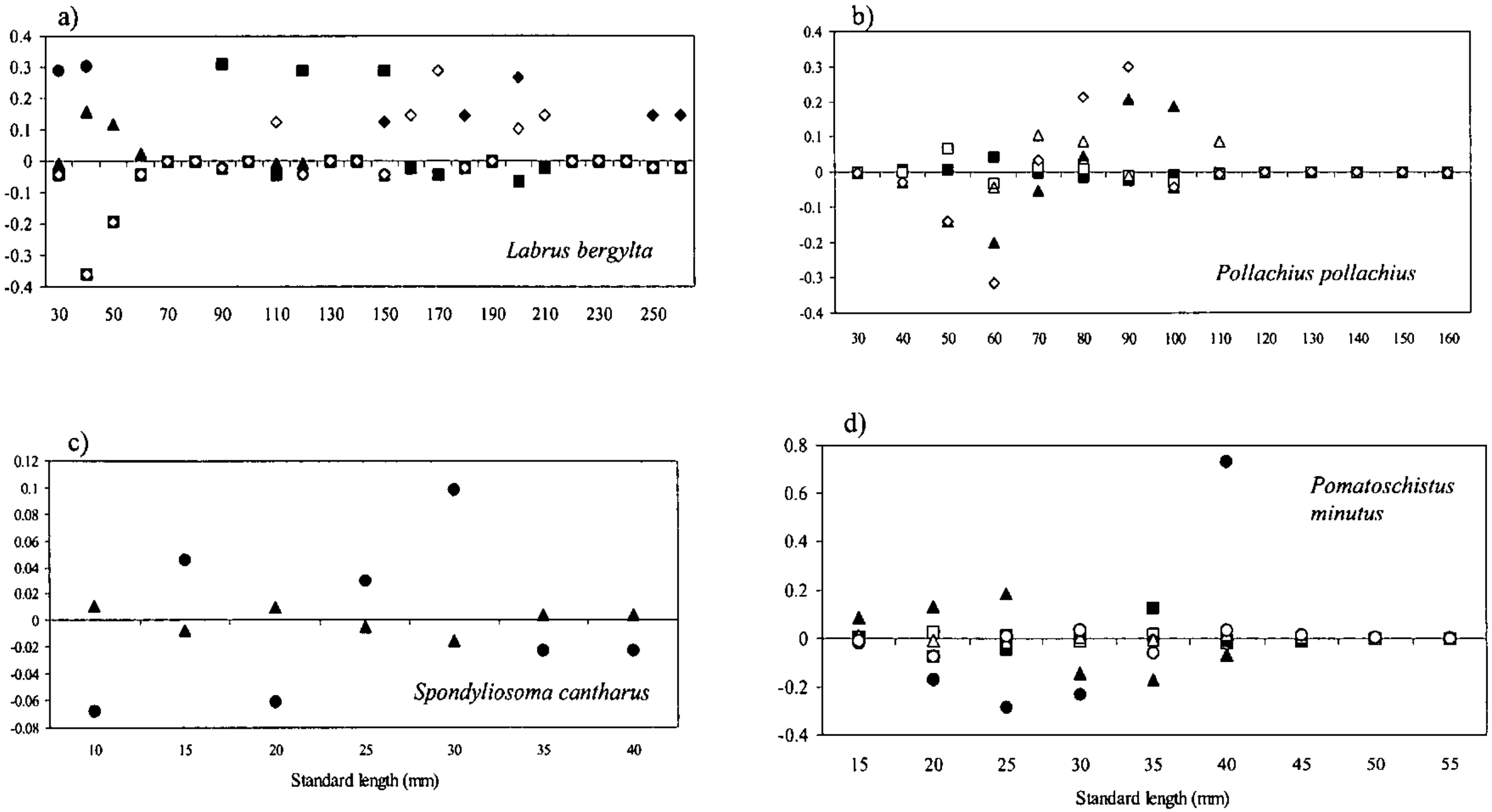


Figure 3.7 Plotted Strauss indices for various size classes of different species of fish sampled by different gears in seagrass and sand habitats conditioned against total catch from all gears. Values > 0 indicate selection for the specific size class, < 0 against and 0 no bias. ■ seagrass beach seining; □ sand beach seining; ○ sand push netting; ● seagrass push netting; Δ sand trawl; ▲ seagrass trawl; ◆ seagrass potting; ◊ sand potting

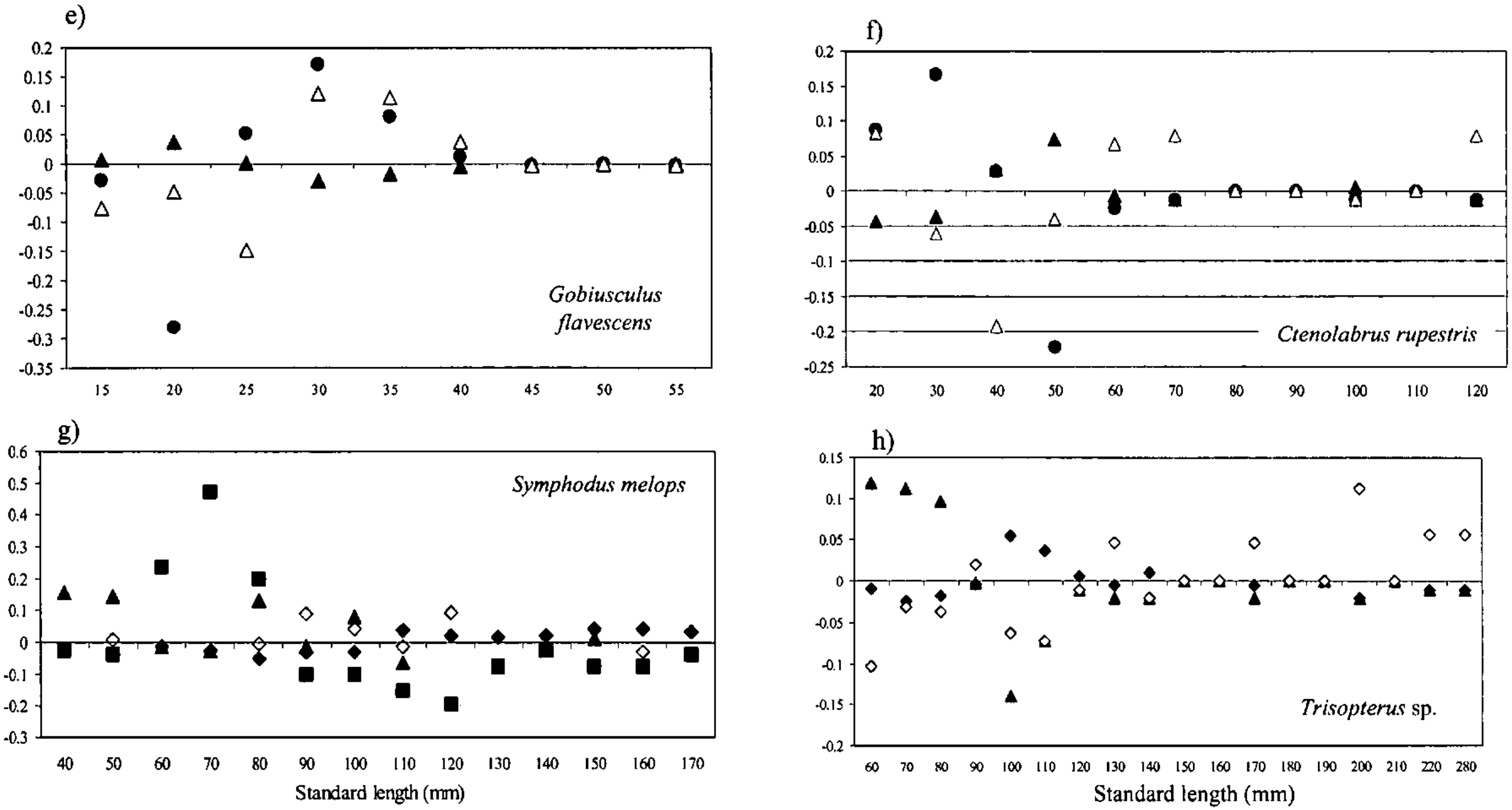


Figure 3.7 continued Plotted Strauss indices for various size classes of different species of fish sampled by different gears in seagrass and sand habitats conditioned against total catch from all gears. Values > 0 indicate selection for the specific size class, < 0 against and 0 no bias. ■ seagrass beach seining; □ sand beach seining; O sand push netting; ● seagrass push netting; Δ sand trawl; ▲ seagrass trawl; ◆ seagrass potting; ◊ sand potting

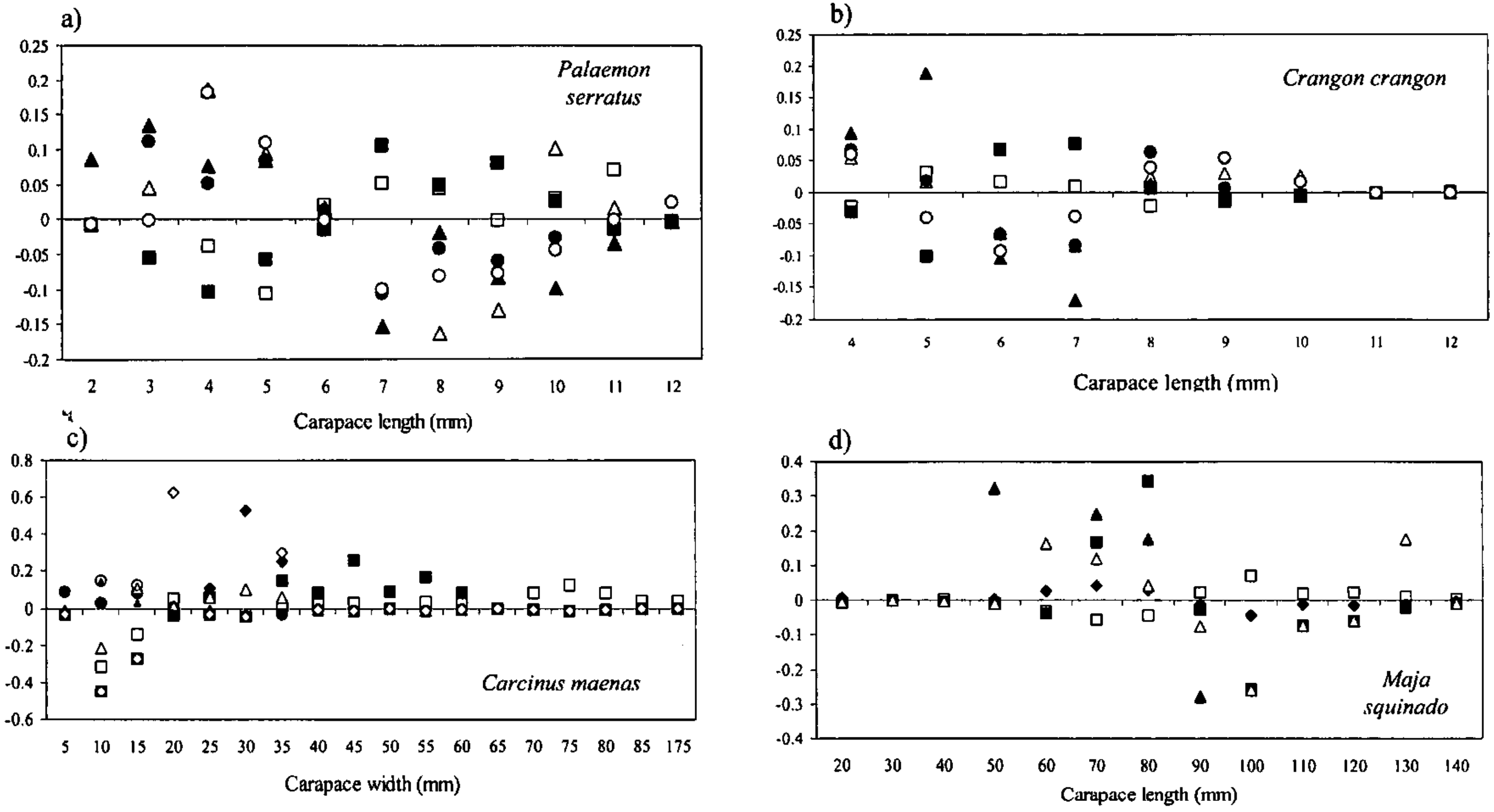


Figure 3.8 Plotted Strauss indices for various size classes of different species of decapod sampled by different gears in seagrass and sand habitats conditioned against total catch from all gears. Values > 0 indicate selection for the specific size class, < 0 against and 0 no bias. ■ seagrass beach seining; □ sand beach seining; O sand push netting; ● seagrass push netting; Δ sand trawl; ▲ seagrass trawl; ◆ seagrass potting; ◊ sand potting.

Up to a carapace length of 6 mm, push netting and trawling were more effective at sampling the common prawn (*Palaemon serratus*) than beach seining (Figure 3.8a). However, above 6mm there is a changeover, with beach seining showing a positive bias for larger prawns, and push netting and trawling under sampling. Above a carapace length of 9 mm, a similar pattern of gear bias was observed for the Brown Shrimp (*Crangon crangon*) (Figure 3.8b). Beach seining (along with potting) under sampled smaller size classes of the Shore Crab (*Carcinus maenas*). Shore crabs between 20 and 35 mm were positively selected for by beach seining and potting (Figure 3.8c).

Finally, none of the methods showed bias for the smaller size classes (<40 mm) of the Spider Crab (*Maja squinado*). Between carapace lengths of 50 and 80 mm, trawling and beach seining (in seagrass) showed some positive selection; however, above 80 mm these methods under selected, whilst beach seines from sand selected for larger crabs (Figure 3.8d).

3.3.4 Cost

The most costly method, based upon the formula used, was the diver survey (55 minutes per sample), which required up to four people and the use of a boat. The cost per sample of push netting, of only eight minutes, was the least expensive and did not require the use of a boat. However, the total number of species sampled was relatively low for each of these methods compared to the others (Table 3.6 and 3.7). Pairwise combinations of gears sampled between 60 and 95% of species (conditioned against total collected from all gears). Figure 3.9 indicates that whilst a combination of push netting and beach seine is the cheapest in person hours (21 minutes), these two methods capture less than 75% of species caught by all methods. A combination of beach seine and trawling captured the greatest percentage (95%) of species with an added cost of 18 minutes per sample.

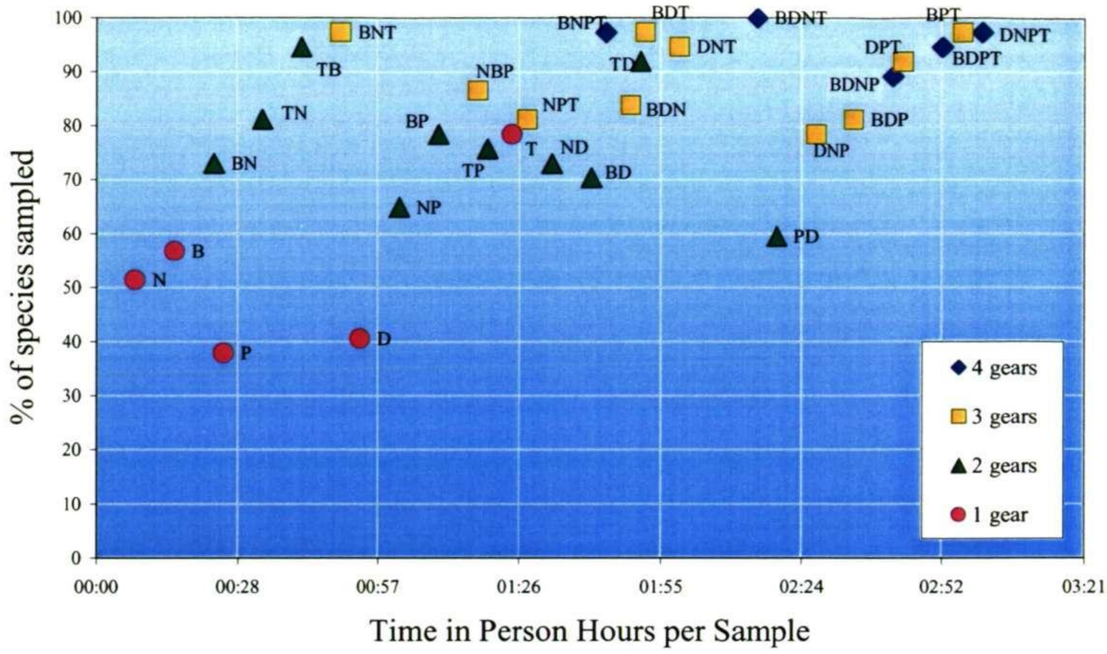


Figure 3.9 Combinations of gear and the percentage of species sampled in seagrass (conditioned against catch from all gears) versus cost in person hours. Potting (P), beach seining (B), trawling (T), Diver survey (D) and push netting (N).

3.4 Discussion

As the large mobile fauna of seagrass beds in Jersey had not been sampled previously, it was important to use a range of techniques to determine the most appropriate sampling method or methods to capture the widest range of species. As this study has shown, only 7% of species were shared by all five methods, indicating the bias of the different gears needs to be assessed, as it has significant implications to future studies of these seagrass beds. The seagrass bed under study supports a diverse fauna, including species exploited within the Normano-Breton Gulf (Table 3.6 and 3.7) and species at the limit of their distribution (*Diplodus sargus*, White Bream, first British record; Wheeler, A., pers. comm., 2001). Beach seining and trawling caught the greatest number of exploited species (11) and trawling caught the greatest total number of species (42 out of 51).

Despite the inclusion of potting in the trials in an attempt to capture species that may avoid mobile gears, no species was unique to this method when used in seagrass. Pots appeared to be highly selective for large decapod crustaceans (in particular *Maja squinado*, the Spider Crab). The smaller size classes of fish, which dominated other methods, were significantly underestimated by potting and were probably able to escape through the entrance to, or mesh of, the traps. Pots also collect fauna from an area or volume of water, which is poorly defined and variable, depending, for example, on the distance from which a species is attracted to the pot, which can change with time of day and water currents. This method was therefore deemed unsuitable for assessing the relative habitat value of seagrass beds. However, pot samples provide a useful complimentary method for species such as *Maja squinado*, as catch rates are high, providing large samples on which to base length frequency or dietary analysis.

Although the other methods have a more easily definable sample area, making density estimates easier, with any method an uncertainty always exists as to whether all species in the area will be captured and retained by the gear. All the methods showed some degree of selectivity (species selectivity and size selectivity). An important aspect of species selectivity can be attributed to the behaviour and distribution of fauna. With diver observations the physical appearance of the species can influence the results. Divers recorded two species (scallop and lesser spotted dogfish) not caught by any other method, but neither of these species was dominant in their observations. Many species found in the seagrass bed during the trials were small individuals (for example gobies, sticklebacks, common prawns), or juveniles of larger species (*Spondyliosoma cantharus*), many had a cryptic appearance (Syngnathidae, scorpion fish, chameleon prawn, *Hippolyte varians*) and were difficult for divers to see. In addition, the disturbance created by the divers may have caused larger mobile fish to flee before they could be observed or identified. All these features contribute to a bias of the diver surveys (Jansson *et al.*, 1985) towards larger individuals (for example *Maja squinado* and *Pollachius pollachius*) and species with distinctive colouration (for example *Gobiusculus flavescens*).

Diving surveys for assessing the fauna of seagrass beds are favoured in the Mediterranean *Posidonia* beds (Francour, 1999) due to the legal protection of the meadows, the structural complexity of the root 'matte' and good diving conditions. The good diving conditions in the Mediterranean include the lack of tides and low turbidity and, whilst the conditions for diving during the present trials were good, they could not be guaranteed in future sampling. Also, despite having the advantage of being non-destructive, diver observations do not allow accurate information on lengths or weights (but see Gotceitas *et al.*, 1997) and the identification of rare or fast swimming species is sometimes not possible. An advantage of diver surveys is that they provide information on behaviour and habit, which can be used to explain the selectivity identified by cluster analysis and ANOVA between the active gears.

Previous studies have shown that species may avoid capture either passively or actively (Alverson & Pereyra, 1969; Gulland, 1980; Rosaz & Minello, 1997). Passive avoidance can be related to the habit of the species, escaping capture by being so close to the sea bed that the net or tickler chains roll over them. The diver surveys observed that in addition to scallop (*Pecten maximus*) and slipper limpets (*Crepidula fornicata*), which lay close to the sea bed, many spider crabs (*Maja squinado*) kept close to the sea bed and some were observed to grip the *Zostera* root system. Such habits and behaviours may have aided evasion of the mobile gears. Alternatively, species may fail to be captured by being further from the seabed than the height of the head rope or beam (Alverson & Pereyra, 1969). The floated head rope of the beach seine was designed to sample the entire water column. Pierce *et al.* (1990) identified a major source of bias in beach seines was related to physical obstructions such as rocks and macrophytes (including seagrasses) which interfere with the seine and prevent it from passing through the entire water column. Process of snagging and un-snagging from obstructions can provide an escape route for enclosed fish. These authors also observed that dense seagrass growth caused the seine to roll up from the bottom in a tight coil which may allow benthic fish to escape more easily than fish higher up in the water column (Pierce *et al.*, 1990). These problems have been recognised previously (Parsely *et al.*, 1989) and species-specific correction factors have been proposed. However, variability in habitat and fish community factors results in widely varying degrees of sampling bias and existing corrections are not sensitive to this variation. During the present gear trials, the beach seine was not observed to roll up nor did it become snagged. Species such as the sand smelts (*Atherina presbyter*) and pollack (*Pollachius pollachius*), which the diver surveys observed swimming above the seagrass canopy (perhaps disproportionately to those in the canopy itself), were caught in significantly higher densities with the beach seine compared with the trawl and push net samples.

In terms of active avoidance, behavioural characteristics such as the species response to a net or disturbance may also be responsible for their evasion of capture and should be taken into account when interpreting data. Some species, for example, the two spot goby (*Gobiusculus flavescens*) and common prawn (*Palaemon serratus*), were observed to retreat into the seagrass canopy upon disturbance. Others (for example the pipefish, *Syngnathus typhle*) are often orientated to the seagrass blades within the canopy. Selectivity for these species would be expected to be similar but, whilst each was caught by all three mobile gears, the catch rates showed significant differences. In contrast, species such as Pollack and Sand Smelt were seen to swim away from the 'disturbance' and, therefore, due to the 'herding' action of beach seine may be more susceptible to this method of capture than to the trawl or push net. Another observation of the divers was that whilst larger wrasse swam away, smaller juvenile wrasse darted into the canopy to avoid 'predation'. This may explain partly the variability in catch rates between gears, which for Ballan Wrasse at least was not significant, but may also explain the size selectivity between gears for this group.

Fish size is often proportional to their power and swimming speed (Bone *et al.*, 1996). Larger fish may be able to out-swim the trawl and push net but find themselves trapped by the encircling beach seine. This may explain the greater proportion of larger wrasse in the beach seine catches. Size selectivity is not only related to active avoidance but also is a result of the ability of a gear to retain captured individuals. In past studies, retention has been correlated to a number of factors including tow duration and speed, time to recover and mesh size (Kjelson & Colby, 1977; Warburton, 1989; Kirkman, 1990; Misund *et al.*, 1999). These factors were not investigated in this trial, and choice of mesh and tow speed were based on previous studies (Gray & Bell, 1986; Kirkman, 1990; English *et al.*; 1997). However, the findings of previous studies may help explain some of the present data. For example, mesh size was kept constant (10mm) during the trials with the exception of the cod end of the trawl (6mm), chosen because of the extra strain on this region, especially when the gear is retrieved. It would be expected, therefore, that the trawl would retain smaller size classes than the beach seine and push net. This was observed for *Labrus bergylta*, *Symphodus melops*, *Trisopterus* species, and gobies but not for Pollack or Goldsinny. In addition to the reasons already suggested for this selectivity, another possible explanation, given by McNeill and Bell (1992), is that, in seagrass beds, finer meshes may become clogged, which causes water to be pushed ahead of the trawl and increases net avoidance by larger fish. An important observation here was that, despite the size selectivity of the different gears, where the trawl underestimated a size class (indicated by their negative index values) beach seining over estimated and vice versa, suggesting that a combination of the two would provide a good representation of the range of size classes.

In terms of cost, whilst push netting was the cheapest method of sampling (diving being the highest), the disadvantages of this gear, in terms of selectivity, out-weighed the cost advantage. In addition, it is important to consider the variance, which was an order of magnitude higher (both for decapod and fish density separately and total density) in push netting compared with beach seines or trawls. Since variance is inversely proportional to the number of samples, the number of push netting replicates would, undoubtedly, have to be increased to be able to detect a significant difference in densities in future sampling and hence the cost of this method would increase.

The question of when to carry out sampling remains. The results of temporal sampling in this trial support those of past studies, showing significant differences in catches between night and day and, for some species, tidal situation. As with previous studies, explanations for these differences in catch rates include both differences in a species' susceptibility to avoidance and the availability of different species under the different conditions (day/ night, high/low tide).

'Susceptibility', which has also been linked to temporal shifts in catch rates, describes species which do not migrate out of the seagrass bed but show vertical migration or increased activity at a certain time; both behaviours may increase or decrease an individuals chance of capture by different methods. For example, if a species of fish migrates vertically upwards at night, it may avoid capture by the trawl, but because the beach seine samples the entire water column, such differences may not be apparent, explaining the pattern seen in this study. Also, many decapod crustaceans are more active at night than day and densities are often much higher at this time (Gray & Bell, 1986); significant differences were observed for both gears.

'Availability' describes the process whereby species migrate out of or in to the seagrass bed and, thereby, become available to or avoid the gear. Studies have shown that this movement may be initiated by the ebb and flood of the tide, making intertidal habitats either available or inaccessible due to aerial exposure (Peterson & Turner, 1994; Rosaz & Minello, 1998). Although no differences from tidal effects were observed for fish species or density, there were significant interactions between tide and day/night for both decapod species number and decapod density. During the day, some species may move into the seagrass bed to avoid predation and may move out of it at night to forage (Summerson & Peterson, 1984). Such differences may be observed for both gears in a similar pattern and may be reflected in temporal differences in species number, although such movements are species specific.

3.4.1 Conclusions

Only 7% of species were shared by all five methods, indicating a high degree of species selectivity. Beach seining and trawling caught the greatest number of exploited species (11) and trawling caught the greatest total number of species (30 out of 43). Pots were highly selective for large decapod crustaceans and underestimated smaller size classes of fish, which dominated other methods. Diver surveys were expensive in terms of time and showed a bias toward larger and sessile individuals. Trawling showed positive size selectivity for small fish and decapod crustaceans, and under sampled larger more mobile species. Beach seining showed an opposite size bias, and sampled species from the entire water column, which may have included species not strongly associated with the seagrass habitat.

Based on these results, two types of fishing gear (trawl and beach seine) were selected to sample the range of target species within the identified seagrass habitats in the proceeding studies. However, due to the depth limits of the beach seine and the difficulty in accessing some of the seagrass beds from the shore, trawling was the main sampling method. Both methods showed significant variability in fauna sampled with different sampling times. For the trawling, significant differences in the density of fish and number of decapod species were observed for the two tidal states. Also the number of exploited species were highest at night high tide. Although this suggests that tidal state should be incorporated into future sampling programmes, Chapter 2 showed that the seagrass beds around Jersey vary considerably in their depth ranges. Tidal state would therefore be difficult to incorporate into future studies, instead it is suggested that the potential influence be recognised and controlled for by limiting future sampling to low tide. For both beach seining and trawling, diel differences in fauna sampled were strong, with some species only being sampled during the day or night. Numbers of exploited species were highest at night but overall species numbers were highest during the day. Previous studies investigating the patterns of fauna in seagrass habitats were undertaken only during the day. At night it is hypothesised that many of these patterns may change, as species move out of the seagrass patches to forage, become less susceptible to predation or become more active at night. In order to make these comparisons both day and night-time sampling should be carried out in future.

4 Spatial and temporal variability of large mobile fauna in seagrass beds (Jersey, English Channel)

Parts of this Chapter have been presented:

Jackson, E.L., Rowden, A. A., Attrill, M. J., Jones, M. B. and Bossy, S. F. (2001). *Variability of large mobile fauna in seagrass beds (Jersey, English Channel): which scale is most important?* March 2001, 30th Benthic Ecology Meeting, Durham (New Hampshire), USA. (Oral presentation). April 2002 MBA Postgraduate Workshop, Plymouth (Oral Presentation).

4.1 Introduction

The spatial and temporal scales used in ecological studies can strongly influence the interpretation of results (Wiens, 1989; Paiva, 2001). As a result, ecologists are increasingly employing hierarchical spatial and temporal scales in sampling designs which not only enhance interpretation, but may also aid assessments of system functioning or anthropogenic change (Underwood, 1992). Studies examining the mobile fauna associated with seagrass beds are no exception (Ferrell *et al.*, 1993). In fact, the variability in structure of these habitats (see Chapter 2), together with their roles as temporary nursery, foraging and protective habitats (see Chapter 1), makes the inclusion of different levels of temporal and spatial scale in seagrass studies a necessity. Many studies do not include small-scale temporal variability in sampling (for example, sampling to include potential spawning periods), therefore, there is potential to miss species that utilise the seagrass beds for only a short portion of their life histories. In addition, there has been little research carried out on the variable functioning of seagrass beds at different spatial scales in British waters.

In Chapter 1, some of the spatial and temporal scales that influence the organisation of the faunal assemblages associated with seagrass beds were identified (Figures 1.1, 1.2) and the studies that have assessed these patterns were reviewed (Sections 1.6.1 and 1.6.2). For example, geographic location and latitudinal position determine differences in day lengths, tidal amplitude, climate and the level of seasonal environmental change, all of which influence patterns of faunal densities and species composition of seagrass systems (Young, 1981; Anderson, 1989; Nelson, 1997). Species-specific spawning times, larval dispersal patterns and ontogenetic shifts all influence seasonal patterns of seagrass bed fauna density and species composition within the year (Rooker & Dennis, 1991). Such seasonal patterns are further complicated by the incorporation of monthly weather events and tidal patterns that may produce favourable current conditions for larval transport (Joyeux, 1999). In addition, many reports of seagrass habitats supporting different, and more diverse, fish assemblages are based on daytime sampling programmes, even though many estuarine and coastal species of fish display strong diel rhythms of activity (Adams, 1976; Greening & Livingston, 1982; Sogard *et al.*, 1989; Stoner, 1991). For those studies that have assessed diel variation in seagrass beds, similar strong differences in faunal densities and species composition are evident (Chapter 3; Robblee & Zieman, 1984; Bauer, 1985; Edgar & Shaw, 1995a; Mattila *et al.*, 1999; Hindell *et al.*, 2000). If samples are not taken during both day and night, and at different tidal states, important temporary residents may be missed and the ecological role of the bed inaccurately assessed (Ferrell & Bell, 1991).

Following Kikuchi's (1974) division of the mobile fauna of seagrass beds into four categories (permanent residents, seasonal residents, temporary visitors that forage in a wider area than the seagrass bed, and occasional migrants), Kikuchi and Pérès (1977) reviewed the faunal communities of seagrass beds world-wide. They identified a noteworthy amount of parallelism in community structure (Kikuchi & Pérès, 1977, see also Bell & Pollard, 1989), showing that, in most seagrass systems, there was dominance by small or cryptic species, and utilisation as temporary nursery areas or as occasional foraging grounds for larger species. Incorporating some level of temporal scale into sampling, therefore, not only strengthens the certainty of collecting all the species that only inhabit the seagrass bed temporarily, but also identifies the temporal extent that these species utilise the seagrass habitat. Although in this current study, time was limited due to restricted available resources, sampling from early summer to early autumn enabled the inclusion of spawning times and the recruitment periods of species suggested by the previous study to be utilising the seagrass beds around Jersey (see Chapter 3).

In terms of spatial scale, previous studies have suggested that variability in the species composition of mobile seagrass fauna is linked to seagrass density, biomass and bed heterogeneity at a local scale (Sogard *et al.*, 1987; Loneragan *et al.*, 1998), whilst at larger scales, hydrography plays a greater role, for example, in larval supply and habitat structuring (Olney & Boehlert, 1988; Jenkins *et al.*, 1997b; Hannan & Williams, 1998; Valle *et al.*, 1999). Bell & Westoby (1987) were amongst the first to identify that patterns in fish assemblages associated with small-scale seagrass bed characteristics weakened when studies moved from local to larger geographical scales. For example, the importance of seagrass beds to economically valued fish and shellfish may vary with latitude (Heck *et al.*, 1989; Sogard & Able, 1991). Sogard *et al.* (1987) questioned the assumption that seagrass (*Zostera*) meadows were important nursery grounds for warm temperate to tropical species and further proposed that the proportion of permanent residents in a seagrass bed would increase with decreasing latitude as the extent of winter migrations outside the bed declined. Such regional differences in functional relationships and inter-specific interactions emphasise both the importance of local studies and the need for caution in comparing seagrass beds from different regions.

At regional scales (ones within the scope of most studies and of most immediate value to local environmental managers), coastal location of a seagrass bed and its particular position within a bay, lagoon or estuary influence its value as a refuge, foraging site or nursery ground (Livingston, 1984; Sogard *et al.*, 1987; Bell *et al.*, 1988; Sogard, 1989; Worthington *et al.*, 1995; Hannan & Williams, 1998; Valle *et al.*, 1999). Bell *et al.* (1988)

suggested that the location of a seagrass bed within an estuary may affect the distribution and abundance of recently-settled fish and decapods, and hypothesised that this "location effect" was related to the settlement competency of larvae of different species in different parts of an estuary. The authors proposed that these distributions were the result not only of the site of spawning and behavioural mechanisms to aid colonisation, but also the temperature and salinity tolerances of the eggs and larvae (Bell *et al.*, 1988). This hypothesis was supported by Hannan and Williams (1998) who found the number of ocean-spawned fish settling within seagrass (*Z. capricorni*) habitats decreased with distance from the mouth of a New South Wales lagoon. Monthly length-frequency data gathered over the course of the study season indicated that progressively larger juveniles were found at the distant sites (Hannan & Williams, 1998). Valle *et al.* (1999) observed an analogous pattern in Alamitos Bay, California (USA) and reported that although community composition was similar between sites, the abundance of juveniles of the barred sand bass and California halibut decreased with increasing distance from the mouth of the bay. The consideration of which areas of seagrass would be the first to be met by ocean-dispersed fry and larvae is, therefore, extremely important in any study, particularly when sites are located in lagoons or estuaries with poor circulation. The present study is one of the first to examine whether similar predictable patterns of spatial distribution of recruits are observed in seagrass beds located in different parts of the coast of a small island which, whilst not as enclosed as an estuary or lagoon, has a strong tidal current surrounding it. This strong tidal gyre, which forms seasonally around Jersey (see Chapter 2, Figure 2.1), is thought to have important implications for larval supply and transport around its coast (Pingree & Mardell, 1987).

4.1.1 Aims

The aim of the present study was to to assess which species of fish, decapod crustaceans and cephalopod molluscs (with particular emphasis on exploited species) inhabit the seagrass habitats around Jersey? And of these species, which are permanent residents and which use the seagrass beds on a temporary basis (nursery ground, temporary foraging grounds or temporary protection from predators)? A local-scale, temporal and spatial levelled design was used to test the following null hypotheses: Firstly it was hypothesised that the seagrass beds around the island of Jersey would not differ significantly in terms of faunal species composition, richness and density between individual beds or at a larger scale of coastal location. Secondly it was hypothesised that the faunal species composition, richness and density, particularly with resepct to the apparent roles of the seagrass beds, would not show consitent patterns over time.

Finally, due to the lack of studies of the mobile fauna of subtidal seagrass beds in this part of north-western Europe, the present study aimed to put Jersey seagrass beds in the context of other seagrass beds from other parts of the globe. The way in which the composition of large mobile fauna in Jersey seagrass beds compared to the parallels made by Kikuchi and Pérès (1977) and others (Ledoyer, 1969; Bell & Pollard, 1989) was discussed.

4.2 Materials and Methods

4.2.1 Study location

Although the largest and southernmost of the English Channel Islands, Jersey has a relatively small area (116 km^2). The island is situated in the Normano-Breton Gulf (49°12'N 2°01'W), approximately 70km from Mont Saint-Michel Bay, France (Chapter 2, Figure 2.1a) and, like the world famous bay, has a semi-diurnal macrotidal system with the some of the highest tidal ranges in Europe (averaging 10 to 11m). These large tidal amplitudes generate intense tidal currents in the Normano-Breton Gulf, with residual eulerian velocities (the long-term average velocity of currents at a fixed point, 20 to 30 cm.s^{-1}) indicating an intensified anticlockwise flow, which exceeds wind-driven components in the region (Orbi & Salomon, 1988). Strong tidal gyres sustain a front that develops between Jersey and adjacent islands, and the flow around Jersey appears essentially closed (Pingree *et al.*, 1974; Pingree & Mardell, 1987), which intensifies the contrast of water properties across the frontal zone and has important implications for larval transport (Pingree & Mardell, 1987). In addition, calculated residual eulerian velocities and tracks of current markers released at different points in the Normano-Breton Gulf indicate that tidal exchange between the Gulf and adjacent parts of the English Channel are limited except under certain wind conditions (Orbi & Salomon, 1988). This reduced water exchange may increase the importance of potential seagrass nursery grounds to local faunal populations, due to the potential for retaining planktonic larvae spawned in Jersey's inshore waters.

Historical and anecdotal reports indicate that large areas of intertidal *Zostera marina* were once common around the 70km of Jersey coastline (Sinel, 1906; Bossy, S.F., pers. comm., 1998; Roper, A., pers. comm., 1999; Syvret, A., pers. comm, 1999). Today, all that remains are subtidal meadows, exposed at their fringes for a short time only on the lowest spring tides (intertidal areas of the dwarf eelgrass, *Zostera noltii,* occur in sheltered bays on the south and eastcoasts, but were not included in the present study). *Zostera marina* is estimated to cover 130 ha of the shallow subtidal around the coast of Jersey (see Chapter 2). Colonisation is predominantly on the north-east, south-east and south coasts of the island, although some small (less than 0.5 ha) isolated patches occur on the north coast, restricted to easterly facing bays and rocky gullies (Chapter 2, Figure 2.6). The largest expanses of seagrass occur at St Catherine Bay (571379, 54452242 UTM), between rock out crops at Les Elavees (572852, 5444496 UTM) and within the Violet Channel (572000, 5443845 UTM), at estimated coverage of 27.39, 13.42 and 11.54 ha respectively.

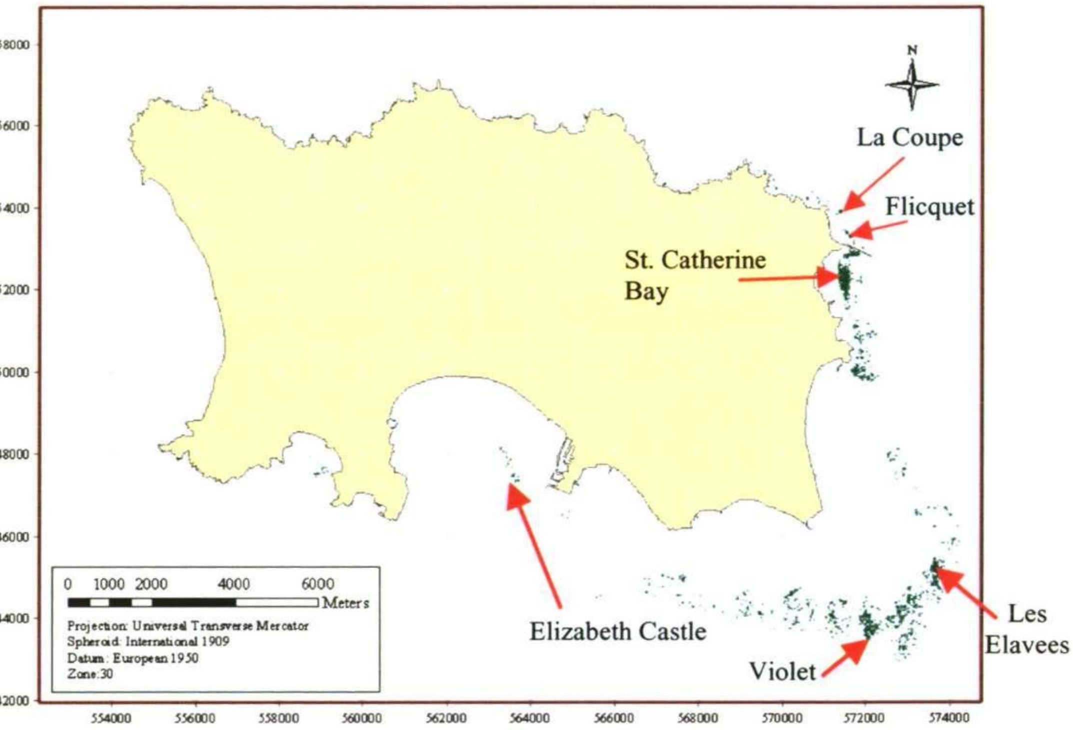


Figure 4.1 Distribution of seagrass (dark green) around Jersey and locations of the sites sampled in the present study.

Using distribution maps of the seagrass, a subset of seagrass beds was chosen at random from all the isolated seagrass beds around the coast. Figure 4.1 illustrates the cover of seagrass at the sites used in the present study (the site names on Figure 4.1 are used throughout the text to reference particular seagrass beds). As highlighted in Chapter 2, the sites differed in both physical setting and various seagrass plant characteristics; however, the seagrass beds used were chosen at random (by assigning them numbers) from all isolated seagrass beds to test larger scale temporal and spatial patterns.

4.2.2 Sampling method

The method used for sampling was the same as that described for trawling in Chapter 3. More details of the trawl and rationale for the choice of both this method and time of sampling can be found in Chapter 3. In brief, fish, decapod crustaceans and cephalopod mollusc samples were collected using a 1.5 m beam trawl with a 6m long, 10 mm stretch mesh net (6 mm knotless mesh cod end liner) (Figure 3.2). Four replicate trawls (randomly located within each seagrass bed) were carried out for each sampling situation.

Macro-faunal individuals (those retained by a 1mm mesh sieve) were identified to species and measured to the nearest 0.1 mm (Wheeler, 1969; Whitehead *et al.*, 1986; Hayward & Ryland, 1998; Quéro & Vayne 1998). Commercially and recreationally exploited species (termed exploited species) were identified for specific analyses, and were defined as those landed and recorded by commercial fishermen in the Normano-Breton Gulf and species captured by recreational fishermen, including 'peche à pied' (Cohen *et al.*, 1990; Quéro & Vayne 1998; States of Jersey Department of Agriculture and Fisheries, 2001). For most fish, the measurement was standard length (total length for Sygnathidae, Cottidae and Anguillidae), carapace width for crabs (carapace length for Majidadae) and carapace length for shrimp and prawns. Definitions of juveniles were based on data for the average size of maturity for the time of year and closest location to the study site (Wheeler, 1969; Whitehead *et al.*, 1986; Hayward & Ryland, 1998; Quéro & Vayne 1998; Froese & Pauly, 2003).

In the absence of previous information on what might be the most appropriate spatial scales for the present study's location, the local variation in abundance and composition of fish, decapod crustaceans and cephalopod molluscs was described at two spatial levels. The largest scale (location) was stratified into the north-east and south coasts of the island (the two prominent areas of seagrass growth). In each location, three seagrass beds were selected randomly (sites, at a scale of individual beds within each location) and, at each site, four replicate trawls were taken at night and four during the day, all at low tide. Sampling was carried out between the 18th and 22nd September 2000.

To assess small-scale temporal variability in species residing in the seagrass beds around Jersey, three seagrass beds were sampled. The seagrass beds were chosen at random from sites on the north east of the island so that potential larger scale location effects did not confound results. Whilst useful additional information could have been gained regarding the permanent residents of the seagrass beds, sampling was not possible in winter due to difficult and dangerous sampling conditions. Samples were collected at the beginning, middle and end of the summer spawning seasons of species previously identified as inhabiting the beds, during 3 sampling sessions (months) May (22nd and 23rd), end of July (26th and 27th) and September (18th and 22nd September). At each of the three seagrass sites, four replicate trawl samples were collected during the day and four at night, all at low tide.

4.2.2.1 Data Analysis

To examine whether parallels in faunal assemblage structure existed between sites and whether these were consistent over different months, the similarities between fish and decapod assemblages among locations and sites, and among months and sites, were assessed using multivariate analysis. For each site, day and night samples were pooled. All species of fish, decapod crustacean and cephalopod were included and data were transformed to log (x+1) so that each species contributed more evenly to analyses (Clarke & Green, 1988). First, a ranked triangular similarity matrix was generated using the Bray-Curtis similarity measure, after which multidimensional scaling (MDS) was used to generate two-dimensional ordination plots (Field *et al.*, 1982; Clarke, 1993). Formal significance tests for differences between samples were performed using an analysis of similarities (ANOSIM) permutation test (Clarke & Green, 1988). All multivariate analyses were carried out using the software PRIMER (Plymouth Routines in Marine Ecological Research Version 5; Carr, 1996).

ANOVA was used to test the null hypothesis that there was no significant difference in the assemblages of large mobile fauna (fish, decapod and cephalopod) associated with *Zostera marina* at the different locations and times within the design. The ANOVA model used to assess spatial variability in mobile seagrass fauna had 3 factors, with the factor Site nested within Location (two fixed locations, each with 3 random sites) and both these factors orthogonal to Time (fixed day/night). Temporal data were analysed with a three-factor ANOVA. Factor one (Month) was fixed and had three levels (May, July and September). Factor two (Site) again fixed, was orthogonal to Month and had three levels (St Catherine Bay, Flicquet and La Coupe). Finally, factor three, Time (fixed, day/night), was orthogonal to factors one and two.

For both designs, the variables analysed were total fish, decapod and cephalopod species number and density, with an emphasis on exploited species. ANOVA was also carried out on the densities of common species (those species representing more than 1% of the total). Some common species did not occur in all months, locations or were purely nocturnal. Therefore, when less than 5 % of the total abundance of a species was recorded in a particular month, location or time (day/night), that level of the factor was not analysed and the degree of freedom for the test was reduced appropriately. For the spatial variability study, additional analyses were carried out on only the ocean-spawned species, which have previously been identified as showing the greatest degree of similarity between sites within location. Finally, ANOVA was carried out using variables relating to the ecological grouping of the fish individuals (adapted from Kikuchi, 1974) to identify patterns in the use of different seagrass beds at different times. These variables were the proportion of fish that were:

- juveniles of species that move out of the seagrass bed at a later life stage (temporary residents using the seagrass bed as a nursery, **Temporary juveniles**)
- juveniles of permanent residents in the seagrass habitat (**Permanent juveniles**)
- mature permanent residents which are less than 100mm in size (**Small permanents**)
- permanent residents of cryptic morphology (**Cryptic permanents**)
- permanent residents but measured greater than 100mm (**Large permanents**)
- temporary residents that are not juvenile (perhaps using the seagrass bed as a foraging ground, as protection from predation or for spawning, **Temporary mature**)

Prior to analysis, any data shown by Cochran's C test (Winer, 1971) to be non-normal, were log (x+1) transformed (apart from proportional data, which were transformed using the arcsin% transformation), where necessary. Where the data remained non-normal following transformations, α was set to 0.01 (Underwood, 1981). When ANOVA indicated significant differences among means, the Student Newman Keul's (SNK) test was used to distinguish between them. All parametric ANOVAs were carried out using GMAV5 for Windows (Underwood and Chapman, 1997). Finally, a Kruskal Wallis ANOVA was used to test for significant variations in species' body length between the main factors of each study (that is Location, Site and Time for spatial comparisons and Month, Site and time for temporal ones), using the software package STATISTICA (Statsoft Inc., 1998).

4.3 Results

4.3.1 Spatial patterns of distributions

A total of 1519 fish (30 species) and 3924 decapods (35 species), was collected by the 48 trawl samples from the six *Zostera marina* beds for this study (Table 4.1). In total, 24 of the species caught were classified as exploited species (highlighted in Table 4.1). In terms of the species of fish sampled, just five species made up about 90% of the total numbers. *Gobiusculus flavescens* (the two spot goby) was the most abundant species of fish, constituting 73.12% of the total fish sampled, followed by the corkwing wrasse (*Symphodus melops*) and ballan wrasse (*Labrus bergylta*) representing 5% and 4.7% respectively. Dragonets (*Callionymus lyra*), and the economically valuable black bream (*Spondyliosoma cantharus*) also made up a significant proportion of the total catch (3.93% and 3.75%, respectively, see Table 4.1).

As Table 4.1 illustrates, the two spot goby dominated at all sites except at Flicquet were black bream was found in the greatest numbers. For decapods, *Hippolyte varians* (the chameleon prawn) dominated (54.17% of total decapods sampled) at each of the six sites. Other caridean prawns, *Processa edulis crassipes* (Nouvel & Holthuis, 1957) and the economically valuable, *Palaemon serratus* were also numerically abundant (15.11% and 10.88%, respectively). Only twelve cephalopod individuals were sampled during the study; represented by just two species, the cuttlefish *Sepia officinalis* (79.7%) and the European squid *Loligo vulgaris* (20.3%). Only five species of fish (*Pomatoschistus pictus*, *Lepadogaster microcephalus*, *L. bergylta*, *S. cantharus* and *G. flavescens*) were found at all six sites and similarly only six species of decapod (*Hippolyte inermis*, *Macropodia rostrata*, *Macropodia deflexa*, *Pisidia longicornis*, *H. varians* and *P. serratus*).

Of the 1519 fish collected from the six seagrass beds, about 9% were identified as juveniles utilizing the seagrass bed as a temporary nursery area. All of these temporary juveniles were recognised as exploited species (seasonal residents, Kikuchi, 1974), for example pollack (*Pollachius pollachius*) and black bream (*Spondyliosoma cantharus*). A further 13.63% were also juvenile, but of species which reside in the seagrass habitat throughout their lives (permanent residents). The largest proportion (74.7%) of all the fish sampled were also identified as permanent residents but which, although small (<100mm), were mature individuals (see Figure 4.2). These were mainly comprised of the gobies (Gobiidae) and clingfish (Gobiesocidae).

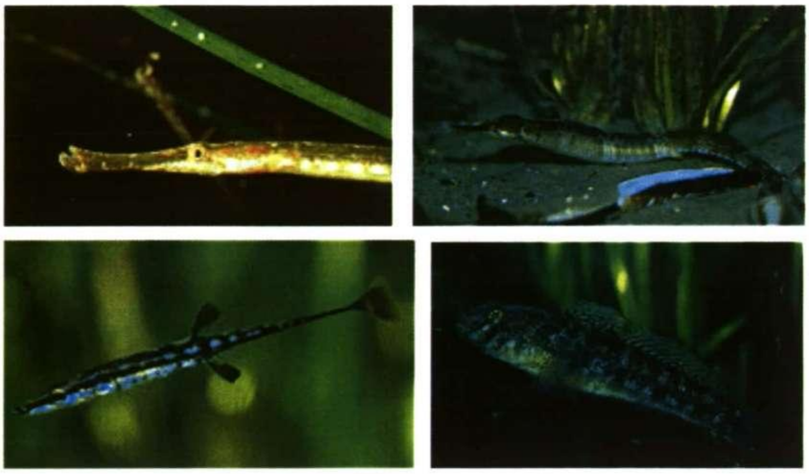
Table 4.1 Mean densities (100m^{-2}) of fish, decapod crustaceans and cephalopod molluscs at three north-eastern and three southern sites of seagrass. Standard errors of the mean are given in parentheses. Exploited species are highlighted with '*'.

	North East						South					
Species	**La Coupe**		**St Catherine**		**Flicquet**		**Violet**		**Les Elavees**		**Elizabeth**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Fish												
Gobiusculus flavescens	159.95	(96.32	54.58	(20.92	0.92	(0.92)	19.57	(11.02	22.33	(6.12)	15.40	(8.10)
Pomatoscistus pictus	6.83	(3.06)	0.20	(0.2)	12.23	(6.85)	1.23	(0.89)	0.76	(0.76)	1.89	(1.05)
*Symphodus melops**	5.47	(1.84)	0.49	(0.32)	0.39	(0.26)	1.71	(0.93)	4.60	(2.17)	5.99	(3.28)
Callionymas lyra	5.01	(3.00)	-		3.35	(3.35)	0.65	(0.43)	0.76	(0.76)	4.88	(2.43)
*Spondyliosoma cantharus**	0.36	(0.24)	0.25	(0.25)	4.73	(1.96)	1.46	(0.95)	4.07	(2.33)	3.14	(1.22)
*Labrus bergylta**	1.46	(1.24)	3.44	(1.60)	1.27	(0.96)	5.70	(1.84)	4.43	(2.33)	1.22	(1.22)
Pomatoschistus microps	0.62	(0.62)	0.20	(0.20)	1.44	(1.44)	-		-		0.79	(0.79)
Ctenolabrus rupestris	0.16	(0.16)	0.21	(0.21)	-		2.32	(1.21)	-		0.66	(0.66)
*Labrus mixtus**	0.57	(0.57)	0.46	(0.46)	-		-		0.68	(0.68)	0.98	(0.48)
Lepadogaster microcephalus	1.69	(0.92)	1.05	(0.53)	2.03	(1.22)	1.00	(0.49)	0.33	(0.33)	0.60	(0.39)
*Solea solea**	-		-		-		-		-		0.34	(0.34)
Gobius gasteveni	-		-		0.21	(0.21)	-		-		-	
*Raja undulate**	-		0.25	(0.25)	-		-		-		-	
*Gobius niger**	-		0.24	(0.24)	-		-		-		-	
*Mullus sermuletus**	-		-		0.62	(0.62)	-		-		-	
*Raja clavata**	0.16	(0.16)	-		-		-		-		-	
*Ciliata mustela**	0.25	(0.25)	-		-		0.32	(0.32)	-		-	
Pomatoschistus paganellus	-		0.25	(0.25)	0.97	(0.49)	-		-		-	
*Cyclopterus lumpus**	-		-		-		0.32	(0.32)	-		-	
Lepadogaster lepadogaster	0.17	(0.17)	-		0.64	(0.64)	0.29	(0.29)	-		-	
Syngnathus acus	-		0.95	(0.50)	0.15	(0.15)	-		-		-	
*Trisopterus minutes**	-		0.20	(0.20)	-		0.32	(0.32)	-		-	
Centrolabrus exoletus	0.35	(0.23)	0.76	(0.52)	0.31	(0.31)	-		-		-	
Syngnathus typhle	-		0.72	(0.50)	0.48	(0.48)	-		-		-	
*Trisopterus luscus**	-		-		1.23	(0.70)	-		-		-	
Entelurus aequoreus	0.68	(0.50)	-		-		0.64	(0.42)	0.52	(0.34)	-	
Taurulus bubalis	0.25	(0.25)	1.32	(0.55)	-		0.32	(0.32)	0.38	(0.38)	-	
*Pollachius pollachius**	-		0.68	(0.49)	-		-		0.33	(0.33)	-	
*Zeus faber**	-		-		-		-				0.34	(0.34)
Spinachia spinachia	-		0.71	(0.50)	-		0.52	(0.52)	2.48	(1.03)	-	

Table 4.1 continued from previous page.

Species	La Coupe		St Catherine		Flicquet		Violet		Les Elavees		Elizabeth	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Decapod												
Hippolyte varians	129.42	(41.94)	196.91	(74.43)	91.60	(24.46)	51.84	(17.78)	41.26	(24.42)	59.70	(21.49)
Processa edulis crassipes	90.15	(56.94)	36.38	(14.42)	31.04	(15.06)	-		0.63	(0.41)	1.02	(1.02)
*Palaemon serratus**	28.35	(20.78)	80.51	(34.9)	0.72	(0.50)	1.21	(0.80)	0.30	(0.3)	3.52	(3.14)
Pisidia longicornis	0.25	(0.25)	1.42	(0.58)	5.03	(2.43)	19.08	(19.08)	0.60	(0.6)	0.65	(0.65)
Liocarcinus arcuatus	3.54	(2.66)	21.15	(7.48)	3.79	(3.01)	-		-		-	
Macropodia deflexa	2.80	(1.28)	13.10	(11)	3.34	(2.21)	0.58	(0.58)	0.93	(0.65)	0.28	(0.28)
Macropodia rostrata	0.57	(0.57)	10.96	(5.5)	7.39	(3.13)	0.26	(0.26)	0.64	(0.42)	0.40	(0.4)
Hippolyte inermis	5.63	(3.31)	5.49	(2.66)	0.39	(0.26)	0.62	(0.41)	0.30	(0.3)	3.22	(1.58)
Athanas nitescens	-		6.27	(5.46)	3.19	(2.02)	1.64	(1.27)	-		-	
Macropodia linearesi	1.69	(0.75)	2.71	(1.88)	5.19	(2.60)	0.36	(0.36)	-		0.33	(0.33)
Thoralus cranchii	-		3.17	(1.7)	4.94	(3.75)	0.64	(0.64)	0.30	(0.3)	0.32	(0.32)
*Maja squinado**	0.92	(0.48)	-		3.28	(1.87)	0.66	(0.43)	0.33	(0.33)	0.40	(0.4)
Pisa tetraodon	1.62	(1.08)	1.65	(0.76)	0.69	(0.49)	0.26	(0.26)	0.33	(0.33)	0.66	(0.66)
*Carcinus maenas**	-		3.68	(3.68)	-		-		-		-	
Pisa armata	0.90	(0.73)	0.72	(0.72)	1.63	(0.95)	0.69	(0.69)	-		-	
*Crangon crangon**	0.19	(0.19)	2.19	(1.94)	0.48	(0.48)	-		-		0.34	(0.34)
Palaemon elegans	0.66	(0.66)	0.21	(0.21)	2.49	(1.48)	-		-		-	
*Palaemon adserpus**	1.23	(1.23)	1.47	(1.47)	-		-		-		-	
Philocheras trispinosus	-		-		2.06	(2.06)	-		-		-	
Inachus phalangium	0.16	(0.16)	0.24	(0.24)	1.65	(1.20)	-		-		-	
Pagurus bernhardus	0.16	(0.16)	0.25	(0.25)	1.02	(0.53)	-		0.3	(0.3)	0.34	(0.34)
Pirimela denticulate	0.49	(0.49)	-		0.81	(0.54)	-		-		-	
Hippolyte longiostris	0.16	(0.16)	1.01	(1.01)	-		-		-		-	
Pilumnus hirtellus	-		0.25	(0.25)	0.24	(0.24)	0.64	(0.64)	-		-	
Liocarcinus pusillus	-		-		0.47	(0.31)	-		0.33	(0.33)	-	
Catapagurus timidus	0.37	(0.37)	-		-		-		-		0.32	(0.32)
Galathea squamifera	-		0.21	(0.21)	0.15	(0.15)	0.32	(0.32)	-		-	
Liocarcinus holstas	0.25	(0.25)	0.25	(0.25)	-		-		-		-	
*Necora puber**	0.25	(0.25)	0.24	(0.24)	-		-		-		-	
Pagurus prideauxi	-		-		0.48	(0.48)	-		-		-	
Percilimenes sagittifer	0.16	(0.16)	0.28	(0.28)	-		-		-		-	
Pagurus cuanensi	-		-		-		-		0.33	(0.33)	-	
Achaeus cranchii	-		-		0.31	(0.31)	-		-		-	
Eualus occultus	-		-		-		-		-		0.3	(0.3)
Palaemonetes varians	-		0.24	(0.24)			-		-		-	
Cephalopod Molluscs												
*Loligo vulgaris**	0.63	(0.63)	-		-		-		-		-	
*Sepia officinalis**	0.38	(0.38)	-		1.71	(1.05)	0.36	(0.36)				

Another small but significant proportion (1.8%) of the species sampled were permanent residents that showed some level of cryptic morphology, for example the pipefish (Syngnathidae) and sea stickleback, (*Spinachia spinachia*) (Figure 4.2). Finally, only a very small proportion of the fish sampled were larger than 100 mm, with 0.12% of those identified as temporary residents (perhaps spawning in the seagrass beds or foraging in a wider area) and 0.65% as permanent residents. Large fish were mainly composed of different species of wrasse (Labridae) and the occasional foraging ray (Rajidae).



Syngnathus typhle
(Broad nosed pipefish)

Syngnathus acus
(Greater pipefish)

Spinachia spinachia
(Sea stickle back)

Pomatoschistus microps
(Common goby)

Figure 4.2 Common small and cryptic fish, identified as permanent residents within the seagrass beds. Clockwise from top left: *Syngnathus typhle* (from Froese & Pauly, 2003 with permission from C.L. Hernández-González). *Syngnathus acus* (from Froese & Pauly, 2003 with permission from J. Jensen), *Spinachia spinachia* (from Froese & Pauly, 2003 with permission from J. Jensen) and *Pomatoschistus microps* (Froese & Pauly, 2003).

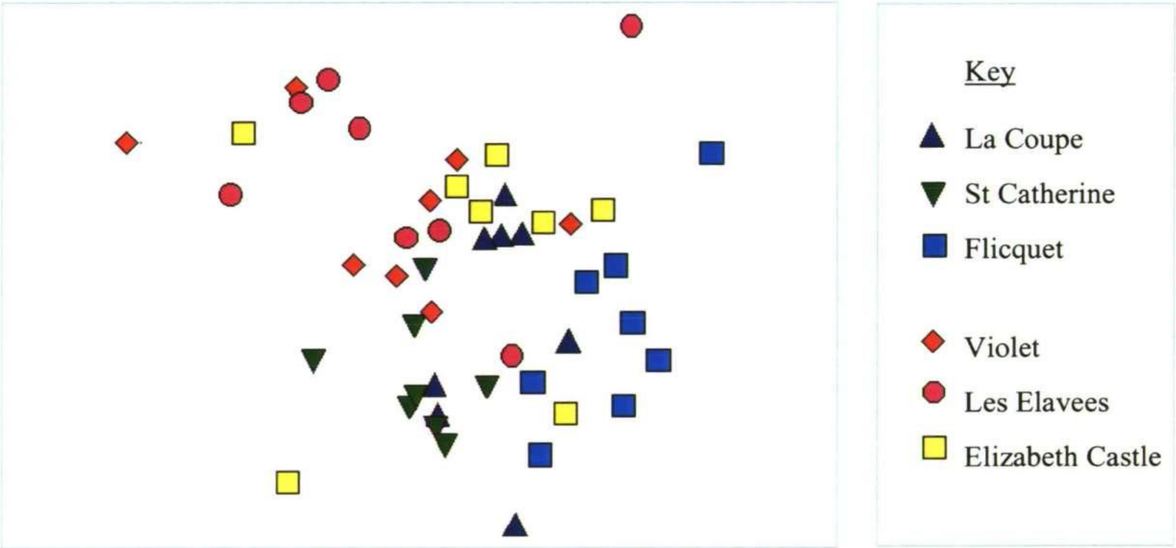


Figure 4.3 MDS ordination computed from the similarities between log (x+1) species densities at different seagrass sites on the north-east (La Coupe, St Catherine Bay and Flicquet) and south coasts (Violet, Les Elavees and Elizabeth Castle) of Jersey, English Channel Islands. (Stress = 0.15).

The multi dimensional scaling plot suggests that whilst some grouping of sites occurs and there is even some degree of dissimilarity between north and south locations, a great deal of overlap is apparent in the assemblage structure of the different seagrass beds (Figure 4.3). Two way nested ANOSIM (Site nested in Location) showed no significant differences between Site groups (averaged across all Location groups) (Global R 0.017, p

= 0.591) or between Location groups (using Site groups as sample) (Global R 0.407, p = 0.10).

4.3.1.1 Univariate spatial analysis

4.3.1.1.1 Variation in mean total species number and total densities

Total numbers of species showed a significant difference between the north and south locations (ANOVA, $F_{(1,4)} = 62.93$, $p < 0.01$), but this could not be interpreted directly due to a significant interaction between the three factors ($F_{(4,36)} = 3.61$, $p < 0.05$). For most of the sites, the number of species was higher in the north than in the south of the island (Figure 4.4). However, SNK tests showed that at night in the north, species numbers were significantly ($p < 0.05$) lower at La Coupe (9.8 species ± 3.12), than at St Catherine (16.3, ± 2.36) or Flicquet (16.8, ± 1.6). At Flicquet the night samples also contained significantly ($p < 0.01$) more species than found during the day at that site (9.5, ± 1.3). South sites showed no significant differences between site either during the day or at night (Figure 4.4).

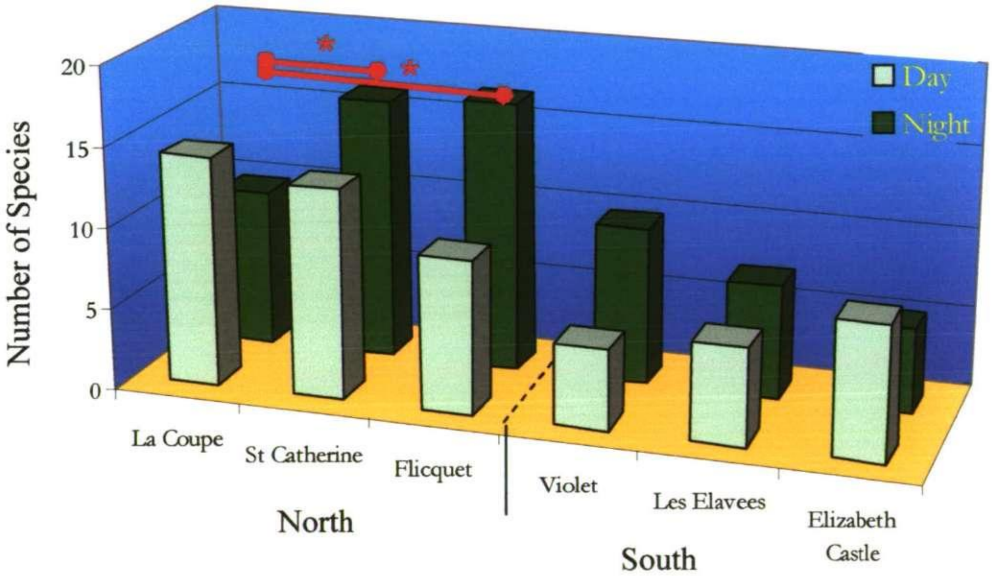


Figure 4.4 Spatial patterns in total species numbers for north and south seagrass beds on the coast of Jersey, English Channel Islands during the day and at night. Bars represents a significant difference (* = P <0.05, ** = P <0.01).

ANOVA found no significant difference in the total densities of species either between site and day or night (at $\alpha = 0.01$). However, after the interaction between day/night and site nested in location was pooled there was a significant difference in the interaction between location and day/night ($F_{(1, 40)} = 7.84$, $p < 0.01$). SNK tests revealed that during the day there were no significant differences in total densities between the north and south sites. In comparison, during the night, total densities in the south were significantly less than those in the north ($p < 0.01$) (Figure 4.5).

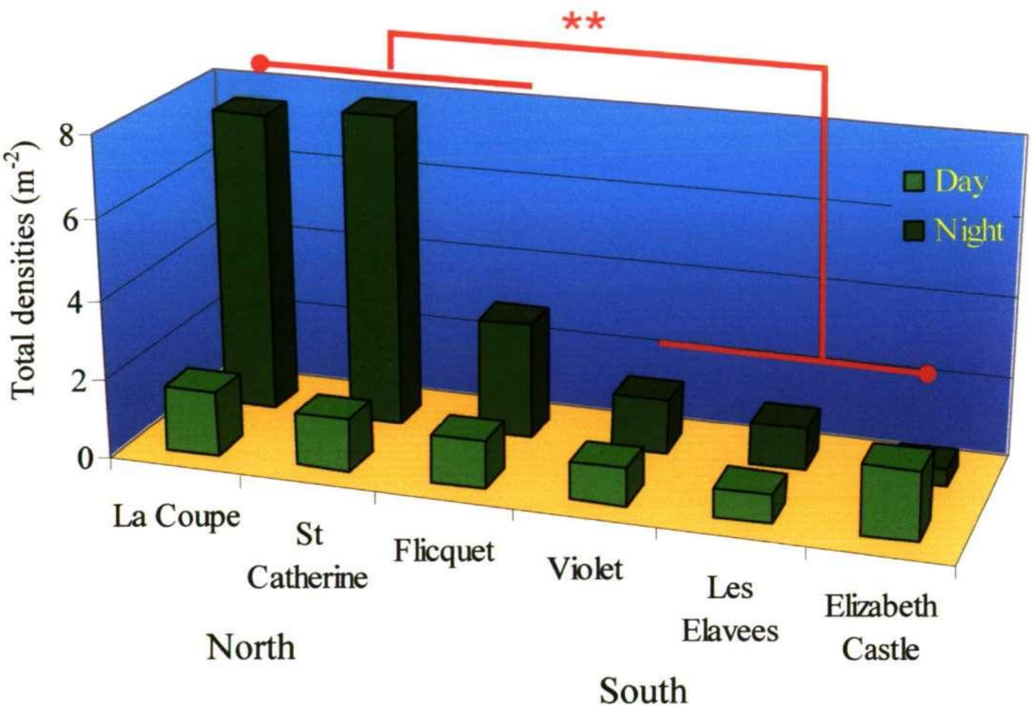


Figure 4.5 Spatial patterns in total densities for north and south seagrass beds on the coast of Jersey, English Channel Islands during the day and at night. Bars represents a significant difference (* = P <0.05, ** = P <0.01).

4.3.1.1.2 Variation in mean number of fish species and densities

Fish species number also showed a significant interaction between the three factors ($F_{(4,36)} = 5.59$, $p < 0.01$). SNK tests showed that in the north, during the day there was a significantly ($p < 0.05$) greater number of fish species at La Coupe (6.75 species, ± 0.48) than at Flicquet (3.25, ± 0.25), but did not differ significantly from fish species numbers at St Catherine Bay (5.5 species, ± 1.32). During the night at Violet on the south coast there were significantly ($p < 0.01$) more species of fish (6, ± 1) than at Elizabeth Castle, but not significantly more than at Les Elavees (3.75, ± 0.95)(Figure 4.6).

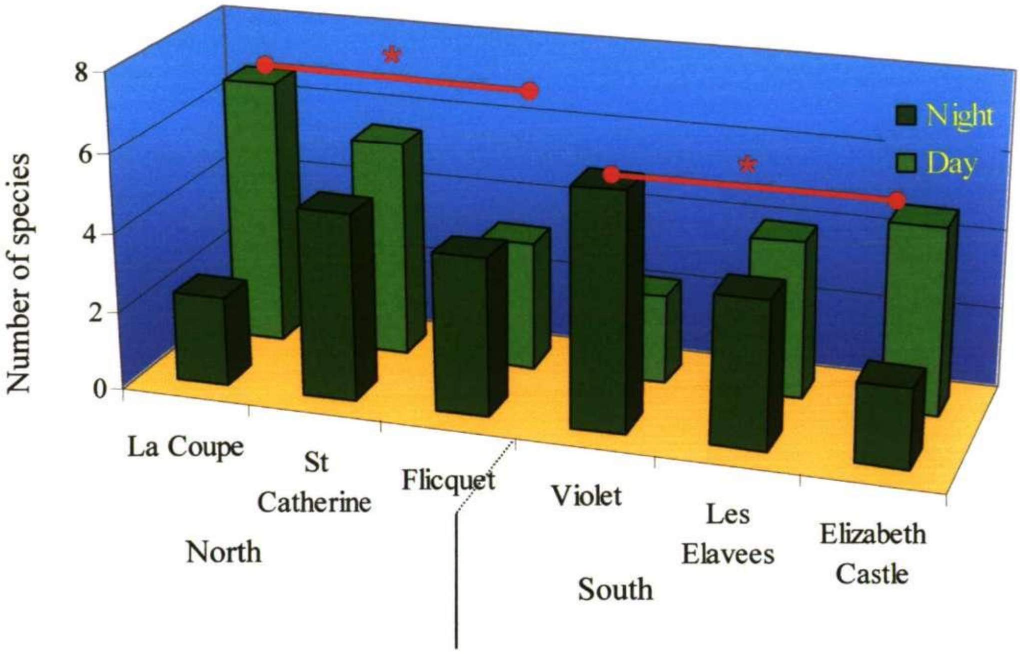


Figure 4.6 Spatial patterns in fish species numbers for north and south seagrass beds on the coast of Jersey, English Channel Islands during the day and at night. Bars represents a significant difference (* = P <0.05, ** = P <0.01).

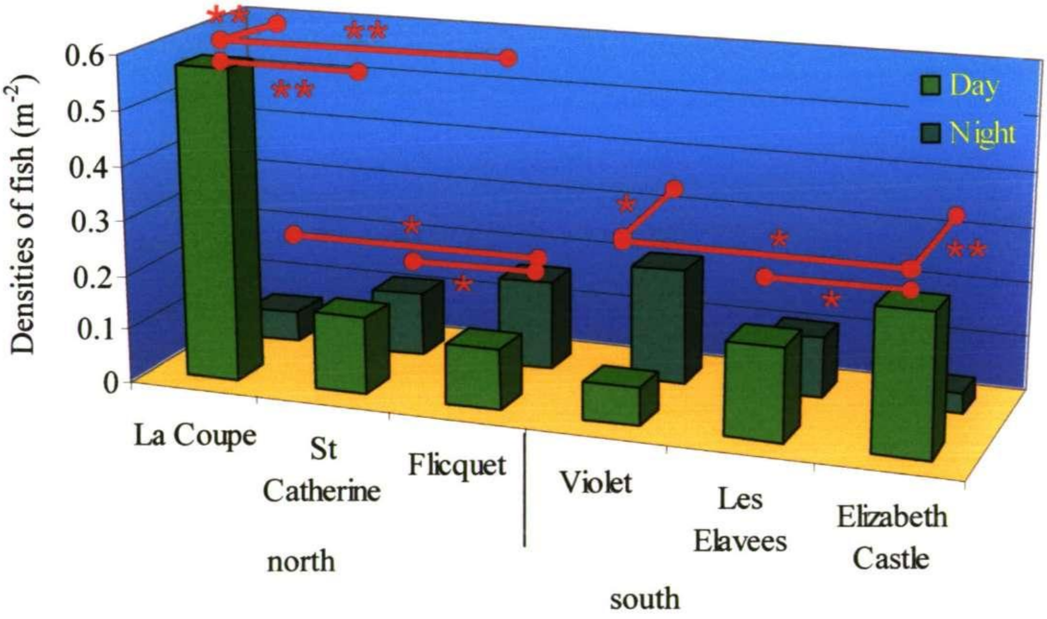


Figure 4.7 Spatial patterns in fish densities (minus *Gobiusculus flavescens*) for north and south seagrass beds on the coast of Jersey, English Channel Islands during the day and at night. Bars represents a significant difference (* = P <0.05, ** = P <0.01).

There was no significant difference in the total density of fish between sites (nested in location) or between day and night. When the total density was analysed removing the most common fish (the two spot goby, *Gobiusculus flavescens*), there was a significant interaction between the three factors ($F_{(4,36)} = 16.04$, $p < 0.01$). SNK examination of this interaction, revealed highest fish densities during the day at La Coupe (0.57 individuals m^{-2}, ± 0.06 SE), where densities were significantly ($p < 0.01$) greater than during the night at that site (0.06, ± 0.03) or during the day at the two other north coast sites (St Catherine Bay, 0.14, ± 0.04; Flicquet, 0.11, ± 0.05)(Figure 4.7).

4.3.1.1.3 Variation in mean number of decapod species and densities

The number of decapod species showed a significant difference between the location of the seagrass sites ($F_{(1,4)} = 58.49$, $p < 0.01$), which SNK revealed to be a significantly greater number of decapod species in samples from the northern seagrass beds (8.6, ± 0.79) than those of the south (3.0 ± 0.47). In comparison there was no significant difference in the density of decapods between coastal location (at $\alpha = 0.01$). If *Hippolyte varians,* the most common decapod species, and therefore the species which may be responsible for the most of the variation, is removed and the interaction term pooled, there is a significant interaction between Location and day/night ($F_{(1, 40)} = 11.88$, $p < 0.01$). SNK showed that at night north samples have significantly greater decapod densities than south and north during the day ($P < 0.01$). There was no difference in decapod densities between day and night in the south.

4.3.1.1.4 Variation in mean densities of selected dominant species

ANOVA on the most numerically abundant species of fish and decapods (those that each constitute >1% of the total individuals sampled) are illustrated in Table 4.2. Although only one of the species analysed (the chameleon prawn, *Hippolyte varians*) showed any significant variation between north and south directly ($F_{(1,4)} = 26.74$, $P < 0.01$; north > south), it is interesting to note that where significant differences between sites occurred, the variability was between sites in the north. In the south, no significant differences were observed between sites or between day and night, with the exception of *Labrus bergylta* (ballan wrasse).

For three of the most abundant species of fish, *Gobiusculus flavescens*, *Symphodus melops* and *Spondyliosoma cantharus,* there was a significant difference between site (nested in location) ($F_{(4,36)} = 5.61$, $p < 0.01$; $F_{(4,36)} = 6.06$, $p < 0.01$ and $F_{(4,36)} = 2.73$, $p < 0.05$). SNK tests showed that for all three of these species there were no significant differences between sites in the south. *Symphodus melops* densities were significantly higher at La Coupe (1.53, ± 0.39) than at St Catherine Bay (0.21, ± 0.14) or Flicquet (0.2, ± 0.13). For *Gobiusculus flavescens*, whilst densities were also significantly higher ($p < 0.01$) at La Coupe (3.31, ± 0.81) than at Flicquet (0.27, ± 0.27), they did not differ significantly from those at St Catherine Bay (where densities were highest for this species; 3.37, ± 0.48). In comparison, densities of the economically valued *Spondyliosoma cantharus* (which appear to utilise the seagrass beds as a nursery area) were significantly higher ($p < 0.05$) at Flicquet (0.05, ± 0.02) than at either of the other two northern sites (St Catherine 0.002, ± 0.002; La Coupe 0.01, ± 0.01).

Table 4.2 ANOVA on dominant fish and decapod species (> 1% of total catch). Three factor mixed model ANOVA, Factor 1, Location (Lo, fixed, 2 levels; north, south), Factor 2, Site [random, nested in location, Si(Lo)], Factor 3 is time of sampling (Ti), fixed and orthogonal, with 2 levels (n = 4). * = P < 0.05, ** = P < 0.01, n.s. = not significant. Location codes: LC = La Coupe, StC = St Catherine Bay, F= Flicquet, V = Violet, LE = Les Elavees, EC = Elizabeth Castle. Species underlined: less than 5 % of the total abundance of a species recorded in southern locations.

Variable	**Significant factors**	**F-ratio**	**SNK**
Fish species			
Gobiusculus flavescens	Si(Lo)	$F_{(4,36)} = 5.61$**	north: (LC = StC) > F
Symphodus melops	Si(Lo)	$F_{(4,36)} = 6.60$**	north: LC > (StC = F)
Labrus bergylta	Ti x Si(Lo)	$F_{(4,36)} = 4.17$**	south, Night: V > (LE =EC)
Callionymus lyra	Ti x Si(Lo)	$F_{(4,36)} = 4.96$**	north, Day: LC > (StC = F)
Spondyliosoma cantharus	Si(Lo)	$F_{(4,36)} = 2.73$*	north: F > (StC = LC)
Pomatoschistus pictus	n.s	-	-
Decapod species			
Hippolyte varians	Lo	$F_{(1,4)} = 26.74$**	north> south
<u>*Palaemon serratus*</u>	Si x Ti	$F_{(2,18)} = 6.42$**	Night: StC > LC > F
<u>*Liocarcinus arcuatus*</u>	Si	$F_{(2,18)} = 4.93$**	StC > (F = LC)
<u>*Processa edulis crassipes*</u>	n.s.	-	-
Pisidia longicornis	n.s.	-	-
Macropodia deflexa	n.s.	-	-

ANOVA for the abundant fish species *Labrus bergylta* and *Callionymus lyra*, showed a significant interaction between Site (nested in Location) and Time ($F_{(4,36)} = 4.17$, $P < 0.01$ and $F_{(4,36)} = 4.96$, $p < 0.01$ respectively). SNK test showed that densities of *Labrus bergylta* did not differ significantly between sites in the north during the day or at night, or between sites in the south during the day. At night in the south, however, densities were significantly higher ($p < 0.01$) at Violet (0.08, ± 0.004) than at Les Elavees (0.01, ± 0.01) or Elizabeth Castle, where no *L. bergylta* were observed. *Callionymas lyra* densities did not show any significant variations between Site or day/night in the south, but in the day at

La Coupe (0.1942, ± 0.02) in the north, densities were significantly higher ($p < 0.01$) than at St Catherine or Flicquet (where no *C. lyra* were found).

Less than 5 % of the total abundances of common prawn (*Palaemon serratus*), arch-fronted swimming crab (*Liocarcinus arcuatus*) and *Processa edulis crassipes* were recorded from sites in the south, therefore the Location factor was not analysed and the degrees of freedom for these tests reduced appropriately. For the common prawn, ANOVA showed significant differences between Site and Time of sampling ($F_{(2,18)} = 6.42$, $p < 0.01$). SNK tests revealed that whilst there were no significant differences between sites in the south (day or night), or in the north during the day, at night in the north densities of *P. serratus* at St Catherine Bay (1.59, ± 0.43) were significantly greater ($p < 0.01$) than at La Coupe (0.5836, ± 0.37). At both sites densities of *P. serratus* were significantly greater than at Flicquet (0.012, ± 0.007). The arch-fronted swimming crab (*Liocarcinus arcuatus*) also showed greatest variability in the north sites ($F_{(4,36)} = 4.83$, $p < 0.01$). SNK tests showed that, like *P. serratus*, densities of this species were significantly higher at St Catherine Bay (0.22, ± 0.07) than at Flicquet (0.03, ± 0.02) or La Coupe (0.05, ± 0.04).

4.3.1.1.5 Variation in the proportion of fish residency groups

ANOVA was also performed on different goups of fish according to their residency within the seagrass habitats. ANOVA for the proportion of fish which were permanent residents of the seagrass beds and exhibited cryptic morphology, showed significant ($p < 0.05$) differences between sites (nested in Location, $F_{(4,36)} = 2.83$, $p < 0.05$). Highest proportions of cryptic fish in the north, were found at Flicquet (12.63%, ± 4.4), significantly greater than at La Coupe (1.57, ± 0.11) although not significantly different from the proportion found at St Catherine (4.95, ± 3.774). In the south there were no significant differences between sites either during the day or at night (Table 4.3).

The proportion of fish that were juveniles of species permanently residing in the seagrass beds, did not differ significantly between Location, Site (nested in Location) or day/night, nor did the proportion of permanent fish residents greater than 100 mm in standard length (SL). As already stated, most of the species sampled were permanent residents that were less than 100 mm SL; for this group ANOVA found a significant difference in the number of individuals between Site nested in Location ($F_{(4,36)} = 2.64$m $P < 0.05$). SNK tests showed that on average, La Coupe and Flicquet samples (0.57, ± 0.14 and 0.69, ± 0.08) had significantly more ($p < 0.05$) small permanent residents than St Catherine (0.24, ±

0.09) (see Table 4.3). As for the proportion of cryptic species, no significant differences were observed between sites or day and night in the south.

Table 4.3 ANOVA on proportions of fish resident groups. Three factor mixed model ANOVA, Factor 1, Location (Lo) is fixed, with 2 levels (north, south), Factor 2, Site is random and nested in Location [Si(Lo)], Factor 3 is Time of sampling (Ti), fixed and orthogonal, with 2 levels (n = 4). * = $P < 0.05$, ** = $P < 0.01$, n.s. = not significant. Location codes: LC = La Coupe, StC = St Catherine Bay, F= Flicquet.

Variable	Significant factors	F	SNK
Permanent			
Cryptic	Si(Lo)	$F_{(4,36)} = 2.83$*	north: (F > LC) = StC
Large	n.s.		
Small	Si(Lo)	$F_{(4,36)} = 2.64$*	north: F > (LC = StC)
Juvenile	n.s.		
Temporary			
Juvenile	Ti x Si(Lo)	$F_{(4,36)} = 4.02$	north, night: StC > (LC = F)

Temporary residents mainly comprised the juveniles of exploited species, but there was the occasional large predatory mature fish (for example rays (Rajidae) and a John Dory, *Zeus faber*). The latter were observed in numbers too small for valid analysis; however, one consistent pattern was that they were only collected in night samples. ANOVA for temporary juveniles, however, showed a significant interaction between Time and Site (nested in Location, $F_{(4,36)} = 4.02$, $p < 0.01$). During the day in the north, there were no significant differences in the proportion of temporary juveniles (SNK test). At night, the proportion of temporary juveniles was significantly ($p < 0.01$) greater at St Catherine (3.88 ± 0.84) than at Flicquet (1.13 ± 0.41) or La Coupe (0.07 ± 0.07). Once again, in the south, no significant differences were observed in the proportion of temporary juveniles either between sites or between day and night.

ANOVA for offshore ocean-spawned juveniles, brought by currents to the seagrass beds, showed a significant interaction between Time and Site (nested in Location) ($F_{(4,36)} = 14.88$, $p < 0.01$). SNK tests illustrated that, on average, in the north during the day, significantly more ocean spawned juvenile fish were sampled at La Coupe (10.35 ± 4.89) than at Flicquet (1.23 ± 0.79) or St Catherine (none). This is in contrast with northern sites during the night, when significantly greater ($p < 0.01$) numbers of ocean spawned juvenile fish were found at St Catherine Bay (9.17 ± 5.94) than at Flicquet (0.95 ± 0.96) or La Coupe (0.49 ± 0.49). Significant differences in the densities of ocean spawned species were also evident between southern sites and day/night. SNK tests showed that during the day, densities were significantly higher ($p < 0.01$) at Elizabeth Castle (11.97 ± 3.97) than at Violet (2.19 ± 2.19) or Les Elavees (none), but at night, densities were highest at Violet (5.02 ± 0.83).

4.3.1.1.6 Spatial patterns of size distributions

For those species that were identified as permanent residents of seagrass but were not small or cryptic when mature (for example *Labrus bergylta, Symphodus melops and Callionymus lyra*), small juveniles dominated (Figure 4.8 a,b, and c), with the occasional larger mature individuals (for example 250 mm standard length *Labus bergylta* specimen observed at La Coupe). The majority of *Labrus bergylta* (ballan wrasse) individuals were between 30 and 80 mm standard length (SL) (Figure 4.8a) with no significant difference between sites (Kruskal Wallis, $H_{(5,68)} = 3.43$, not significant). Larger adult *Symphodus melops* were also found at La Coupe (three > 120mm), but also at St Catherine Bay (Figure 4.8b) and, once again, there was no significant difference in SL between sites ($H_{(5,72)} = 4.22$, not significant). *Callionymus lyra* (Dragonets), however, did show some differences (at $p < 0.1$) in SL between north and south ($H_{(1,52)} = 2.96$, $P = 0.08$), with significantly larger fish observed in the southern sites (Figure 4.8c).

Black bream, which utilise the seagrass bed as a nursery area, showed no significant difference in median standard length between north and south, Site or day/night (Kruskal Wallis). Maximum body lengths observed for this species were approximately 67 mm and the smallest individual was just over 8 mm (sampled from La Coupe), although at the other sites, minimum size was greater than 30 mm.

Finally, standard lengths of the two spot gobies showed significant differences between Site, within and between Location ($H_{(5,1020)} = 262.99$, $p < 0.01$, Figure 4.8e). Kolmogorov-Smirnov paired tests showed that length distributions differed significantly between St Catherine and La Coupe, median lengths of two spot gobies being larger at St Catherine than at La Coupe or any of the south coast sites (too few individuals were observed at Flicquet for robust comparisons). Most of the fish sampled were over 24 mm SL (with the exception of a 14 mm individual at Flicquet) and reached a maximum of 40 mm SL at Violet. In the south, fish were significantly smaller at the Elizabeth Castle seagrass bed (median standard length, 31 mm) than at Violet (35 mm) or Les Elavees (35mm).

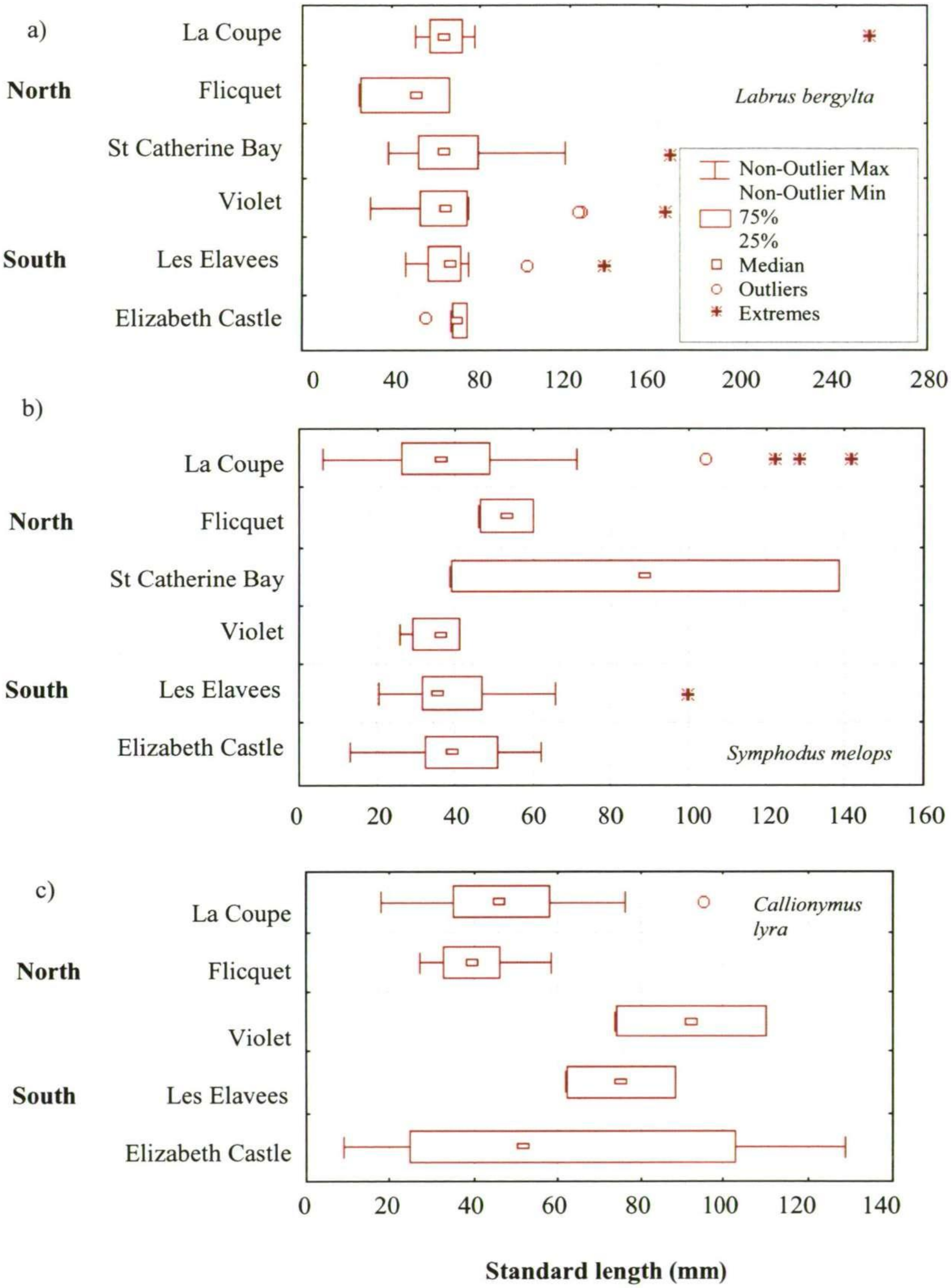


Figure 4.8 Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for fish a) *Labrus bergylta*, b) *Symphodus melops*, c) *Callionymus lyra* sampled from six seagrass on the north East and south coast of Jersey, during September 2000.

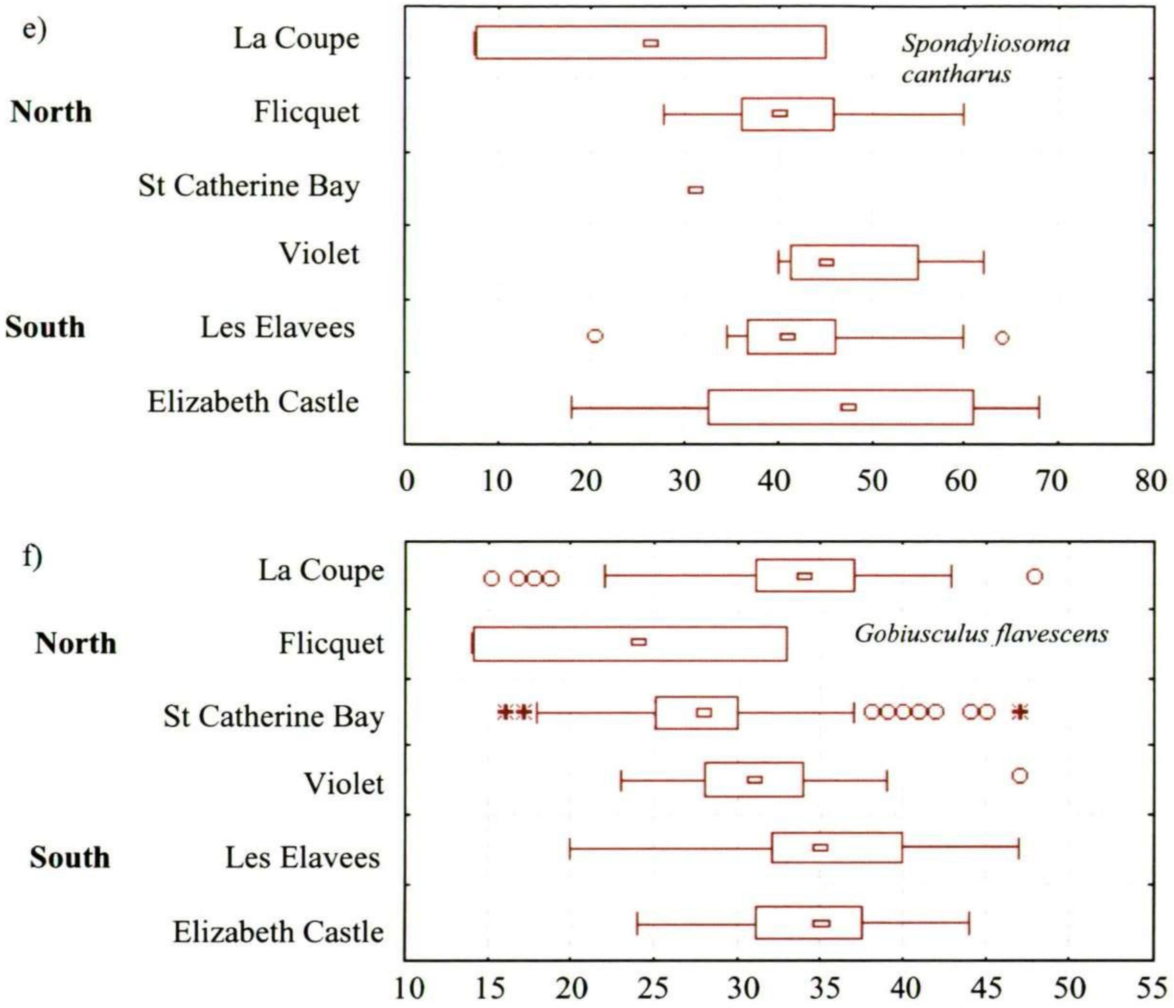


Figure 4.8 continued. Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for d) *Spondyliosoma cantharus*, e) *Gobiusculus flavescens*.

North and South comparisons of length distributions were not possible for decapods, due to absence (*Processa edulis crassipes*, *Liocarcinus arcuatus*) or very low numbers (*Palaemon serratus*) at the southern sites. Highest median carapace length for *Palaemon serratus* (the economically valued common prawn) was observed at St Catherine Bay (maximum carapace length of 19 mm). As illustrated in Figure 4.9, many of the larger individuals were extremes and outliers from the main distribution, which at St Catherine Bay, La Coupe and Violet were ovigerous females. Despite these extremes, and the low numbers of *Palaemon serratus* in the south, there was no significant difference between sites (or day and night).

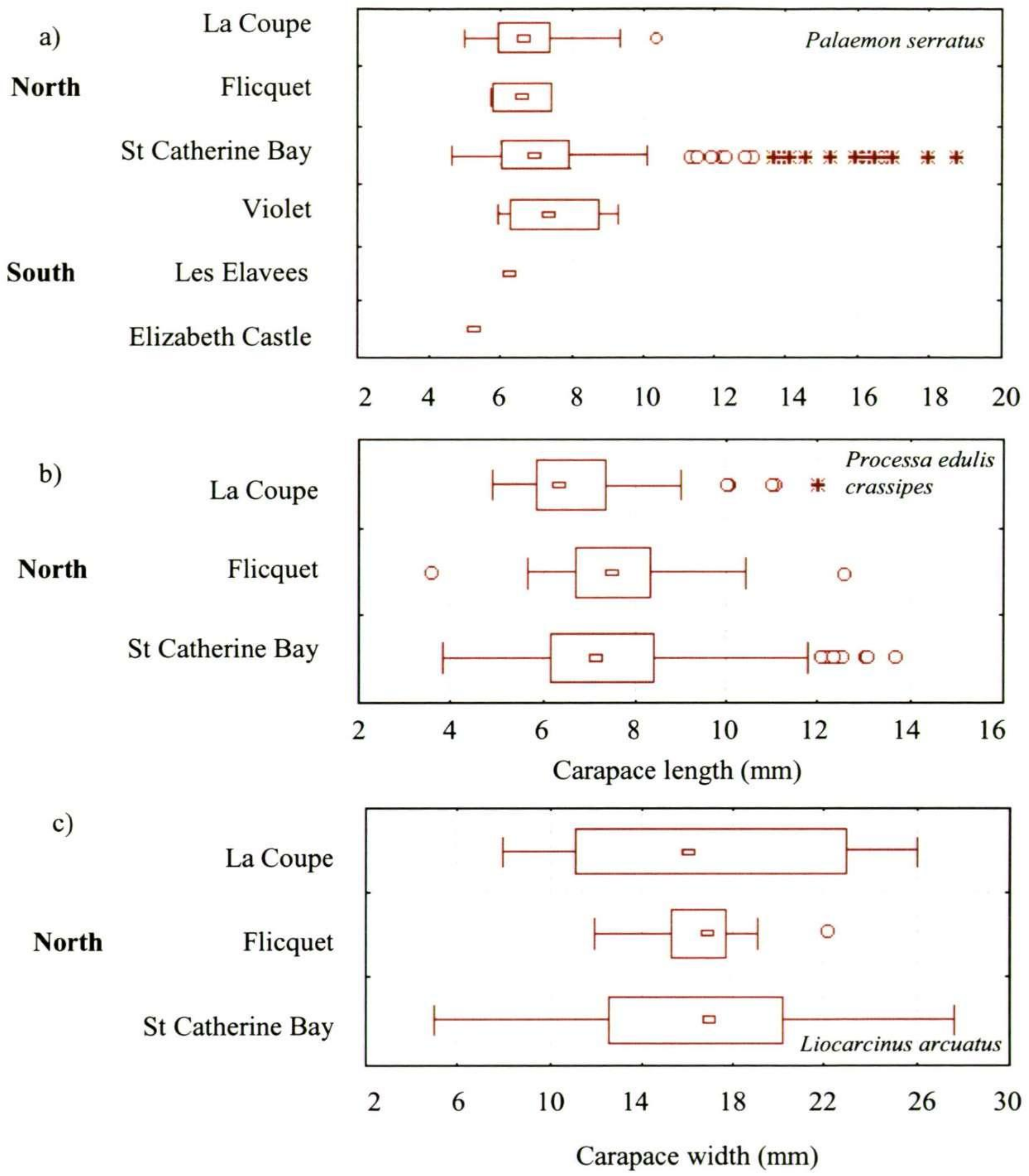


Figure 4.9 Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for decapods a) *Palaemon serratus*, b) *Processa edulis crassipes*, c) *Liocarcinus arcuatus* sampled from six seagrass on the north East and south coast of Jersey, during September 2000.

4.3.2 Temporal patterns of distribution

The 68 trawls collected a total of 1766 fish (33 species) and 5517 decapods (36 species) from the three *Zostera marina* sites (Flicquet, St Catherine and La Coupe) at different times during the summer period (Table 4.4). In total, 27 of the species sampled were classified as exploited species.

Table 4.4 Monthly mean densities ($100m^{-2}$) of cephalopod molluscs, fish, decapod crustaceans from three north eastern isolated seagrass beds. Standard errors of the mean are given in parentheses. Exploited species are highlighted with '*'.

	May		July		September	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
Fish						
Nerophis ophidon	0.31	(0.17)	-		-	
*Cyclopterus lumpus**	0.27	(0.15)	0.52	(0.25)	-	
*Labrus bergylta**	3.32	(2.05)	4.76	(2.58)	2.06	(0.74)
Pomatoscistus pictus	0.11	(0.11)	0.74	(0.39)	6.42	(2.60)
Symphodus melops	0.64	(0.27)	4.31	(1.84)	2.12	(0.78)
Callionymas lyra	1.51	(0.54)	0.15	(0.15)	2.79	(1.50)
*Pollachius pollachius**	1.94	(0.68)	2.45	(0.56)	0.23	(0.17)
Taurulus bubalis	0.70	(0.34)	1.46	(0.50)	0.52	(0.23)
*Spondyliosoma cantharus**	0.15	(0.15)	0.40	(0.21)	1.78	(0.77)
Entelurus aequoreus	1.56	(0.43)	0.70	(0.24)	0.23	(0.17)
*Trisopterus luscus**	0.16	(0.16)	0.78	(0.35)	0.41	(0.25)
Syngnathus typhle	0.28	(0.15)	0.32	(0.15)	0.40	(0.23)
Syngnathus acus	0.21	(0.15)	0.08	(0.08)	0.37	(0.19)
Lepadogaster lepadogaster	0.09	(0.09)	0.16	(0.11)	0.27	(0.22)
Gobiusculus flavescens	-		32.02	(9.11)	71.82	(34.28)
*Ciliata mustela**	-		1.57	(1.21)	0.08	(0.08)
Lepadogaster microcephalus	-		0.08	(0.08)	1.59	(0.52)
Pomatoschistus microps	-		0.58	(0.30)	0.75	(0.51)
Spinachia spinachia	-		1.14	(0.39)	0.24	(0.17)
*Labrus mixtus**	-		0.43	(0.43)	0.34	(0.24)
*Raja clavata**	-		0.10	(0.10)	0.05	(0.05)
*Trisopterus minutus**	-		0.66	(0.38)	0.07	(0.07)
*Mullus sermuletus**	-		-		0.21	(0.21)
Centrolabrus exoletus	-		-		0.47	(0.21)
Pomatoschistus paganellus	-		-		0.40	(0.20)
*Raja undulata**	-		-		0.08	(0.08)
*Gobius niger**	-		-		0.08	(0.08)
Gobius gasteveni	-		-		0.07	(0.07)
Ctenolabrus rupestris	0.16	(0.16)	-		0.12	(0.08)
Lepadogaster candelloni	-		0.16	(0.16)	-	
Pomatoscistus minutus	-		9.61	(3.33)	-	
*Solea solea**	-		0.09	(0.09)	-	
Ammodytidae sp.	-		0.08	(0.08)	-	

Table 4.4 continued.

	May		**July**		**September**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
Decapod crustaceans						
Liocarcinus depurator	0.13	(0.13)	-		-	
Pontophilus fasciatus	1.11	(0.53)	3.83	(2.56)	-	
Hippolyte varians	43.88	(8.63)	93.50	(24.00)	139.31	(29.73)
Processa edulis crassipes	7.41	(4.15)	12.92	(5.87)	52.52	(20.10)
*Palaemon serratus**	1.04	(0.55)	3.26	(1.00)	36.53	(14.66)
Liocarcinus arcuatus	0.83	(0.33)	5.16	(2.44)	9.49	(3.21)
Macropodia deflexa	1.63	(0.45)	3.63	(0.90)	6.41	(3.73)
Macropodia linearesi	3.38	(1.04)	3.80	(2.70)	3.20	(1.09)
Macropodia rostrata	0.78	(0.63)	0.90	(0.35)	6.31	(2.21)
*Crangon crangon**	0.44	(0.32)	6.22	(2.43)	0.95	(0.67)
Pisidia longicornis	0.18	(0.12)	0.68	(0.30)	2.23	(0.90)
*Maja squinado**	1.14	(0.44)	0.41	(0.19)	1.40	(0.68)
Pisa tetraodon	0.08	(0.08)	1.12	(0.44)	1.32	(0.46)
Pisa armata	0.09	(0.09)	1.25	(0.47)	1.08	(0.45)
Pirimela denticulata	0.41	(0.23)	1.30	(0.67)	0.44	(0.24)
Palaemon elegans	0.12	(0.12)	0.71	(0.33)	1.12	(0.56)
Pagurus bernhardus	0.08	(0.08)	0.41	(0.23)	0.48	(0.21)
Hippolyte inermis	2.27	(0.60)	0.47	(0.26)	3.84	(1.45)
Thoralus cranchii	2.42	(1.19)	0.29	(0.16)	2.70	(1.38)
*Carcinus maenas**	0.11	(0.11)	3.88	(1.22)	1.23	(1.23)
Catapagurus timidus	0.19	(0.19)	0.24	(0.13)	0.12	(0.12)
Liocarcinus pusillus	0.10	(0.10)	0.10	(0.10)	0.16	(0.11)
*Necora puber**	-		0.09	(0.09)	0.16	(0.11)
Palaemon adserpus	-		0.33	(0.33)	0.90	(0.62)
Liocarcinus holstas	-		0.51	(0.31)	0.16	(0.11)
Galathea squamifera	-		0.35	(0.20)	0.12	(0.08)
Athanas nitescens	-		-		3.15	(1.93)
Philocheras trispinosus	-		-		0.69	(0.69)
Inachus phalangium	-		-		0.68	(0.42)
Hippolyte longiostris	-		-		0.39	(0.34)
Pagurus prideauxi	-		-		0.16	(0.16)
Pilumnus hirtellus	-		-		0.16	(0.11)
Percilimenes sagittifer	-		-		0.15	(0.11)
Achaeus cranchii	-		-		0.10	(0.10)
Palaemonetes varians	-		-		0.08	(0.08)
Pontophilus trispinosus	-		6.44	(4.37)	-	
Cephalopod molluscs						
*Alloteuthis subulata**	-		0.08	(0.08)	-	
*Sepia officinalis**	0.16	(0.16)	0.26	(0.18)	0.70	(0.39)
Sepiola atlantica	0.12	(0.12)	0.15	(0.11)	-	
*Loligo vulgaris**	-		-		0.21	(0.21)

Similar to the spatial study, the fish fauna was dominated by few species (nine species represented 90% of the total fish sampled). The two spot goby was the most abundant species of fish, constituting 61.5% of the total fish sampled, followed by the ballan wrasse (6%) and the painted and sand gobies (4.3% and 5.7% respectively). Decapods also showed a similar hierarchy of species dominance to the spatial orientated study, with the chameleon prawn comprising 55.6% of total decapods sampled, followed by *Processa edulis crassipes* (14.7%) and the economically valuable *Palaemon serratus* (8.2%). During this part of the study, four species of cephalopod mollusc were sampled (16 individuals);

the cuttlefish *Sepia officinalis* (62.6%), little cuttle *Sepiola atlantica* (19.6%) and the two species of squid *Loligo vulgaris* (14.6%) and *Alloteuthis subulata* (5.6%).

Of the 1766 fish sampled from the three seagrass sites over the six study periods, 9.3% were juveniles utilising the seagrass bed as a temporary nursery area. All these juveniles were exploited species (seasonal residents, Kikuchi, 1974). A further 12.5% were also juvenile, but of species which appeared to reside in the seagrass habitat throughout their lives (permanent residents). The largest proportion (60.2%) of all the fish sampled were permanent residents, which, although small (<100 mm), were mature individuals. These comprised mainly of the Gobiidae (2.8% of mature, small individuals, see Figure 4.2). Another significant proportion (2.2%) of the species sampled were permanent residents, which showed some level of cryptic morphology, including the pipefish (Syngnathidae, Figure 4.2) and sea sticklebacks (*Spinachia spinachia*). Finally, a very small proportion of the fish sampled were larger than 100 mm, with 0.2% of those species identified as mature temporary residents (perhaps spawning in the seagrass beds or foraging in a wider area) and 0.6% as permanent residents. The latter were composed mainly of different species of wrasse (Labridae) and the occasional foraging ray (Rajidae).

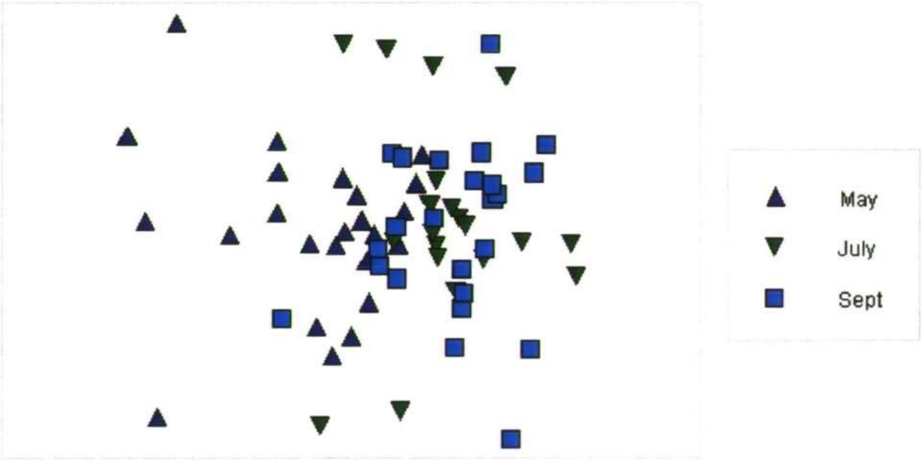


Figure 4.10 MDS ordination computed from the similarities between log (x+1) species densities at three different seagrass beds during May, July and September 2000. (Stress = 0.18).

The MDS ordination plot for all species (Figure 4.10) indicated some separation of samples between the three sampling times (May, July and September). The significance of this separation was confirmed using an ANOSIM test (global $R = 0.38$, $p < 0.001$). Pairwise ANOSIM tests showed significant ($p < 0.001$) differences between each combination of months.

4.3.2.1 Univarite analysis of temporal patterns

4.3.2.1.1 Temporal variation in mean total species number and total densities

ANOVA on untransformed data for total species numbers identified significant interactions ($p < 0.05$) between Month and Site ($F_{(4,54)} = 2.71$), and between Time and Site ($F_{(2,54)} = 4.32$). *Post hoc* comparisons of means (SNK) showed that at St Catherine and Flicquet, mean species numbers were greater at night than during the day (Figure 4.11), although this difference was only significant ($p < 0.01$) at Flicquet (day, 6.92 species ± 1.09 and night, 11.83 ± 1.98). At La Coupe, mean species numbers were higher, though not significantly, during the day than at night, highlighting a lack of consistency between sites for diel patterns.

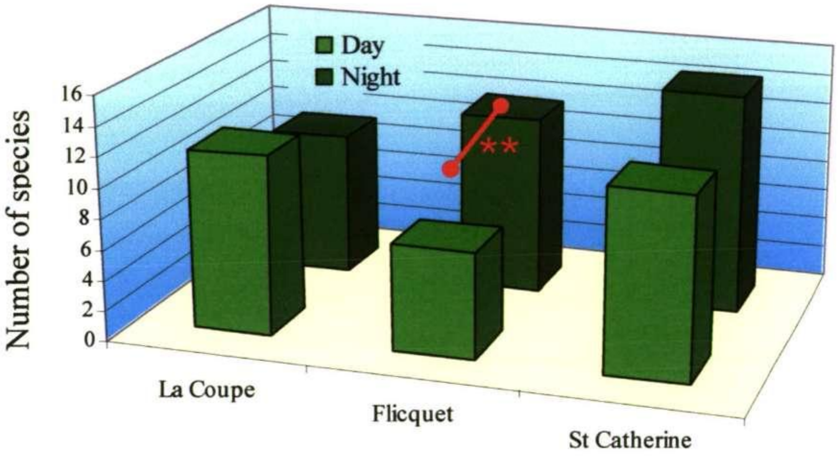


Figure 4.11 Diel patterns in total species numbers for seagrass beds at La Coupe, Flicquet and St Catherine Bay, on the north east coast of Jersey, English Channel Islands. Bar represents a significant difference (** = $p < 0.01$).

The SNK tests also showed that at all sites, species numbers, lowest in May (Figure 4.12). All three sites had significantly fewer species in May than in September (St Catherine and Flicquet, $p < 0.05$; La Coupe $p < 0.01$). For St Catherine and La Coupe, May samples, on average, had significantly ($p < 0.01$) less species than in July, when at both sites, species numbers were at their highest (but not significantly higher than in September).

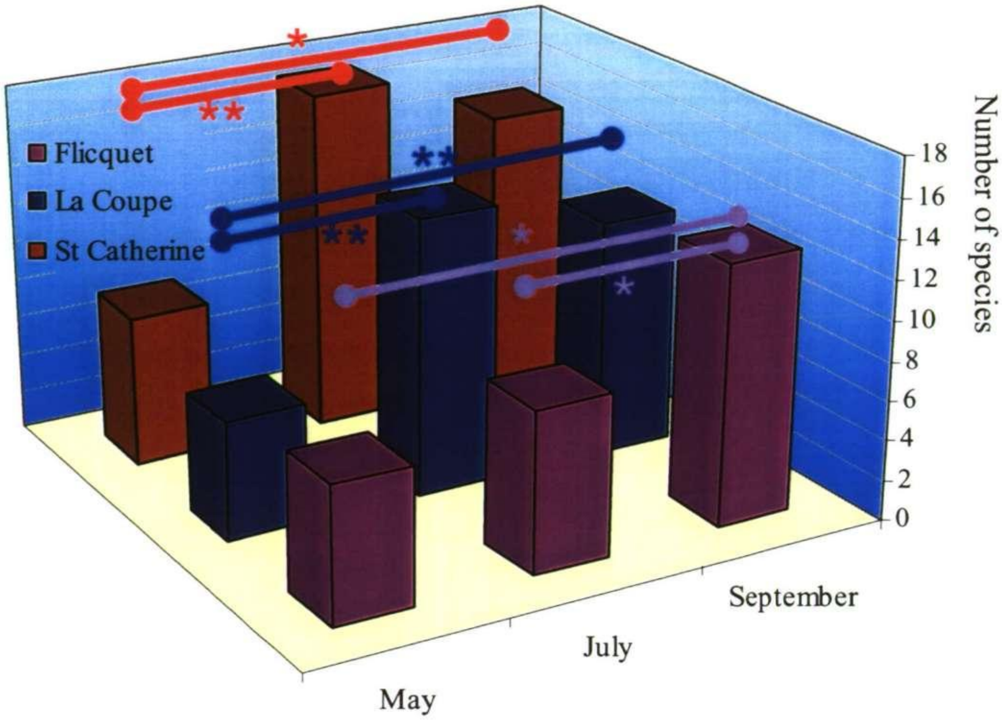


Figure 4.12 Monthly total species numbers for seagrass beds at La Coupe, Flicquet and St Catherine Bay. Bars represent significant differences (* = $p < 0.05$; ** = $p < 0.01$).

At Flicquet, although fewer species were observed in May compared to July, this difference was not significant. There were, however, significant ($p < 0.05$) differences in mean species numbers between September and July at this site (September greater than July).

For total densities, ANOVA showed a significant interaction ($p < 0.01$) between Month and time of sampling (day or night) ($F_{(2,54)} = 6.9$), with patterns consistent between sites (main factor Site and interactions with Site were not significant). The patterns observed are illustrated in Figure 4.13. SNK tests showed that, whilst there were no significant differences in total densities between the three month periods when only daytime samples were considered, night time sampling showed a different pattern. At night, densities increased over the time period with highest densities during September (6.1 ± 1.35 individuals m^{-2}), significantly higher ($p < 0.01$) densities than in May (1.05 ± 0.2) or July (2.7 ± 1.3). For all months across all sites, night time total densities were significantly higher than day time ones, although this difference was only significant for September (Day 1.35 ± 0.54; Night 6.10 ± 0.19).

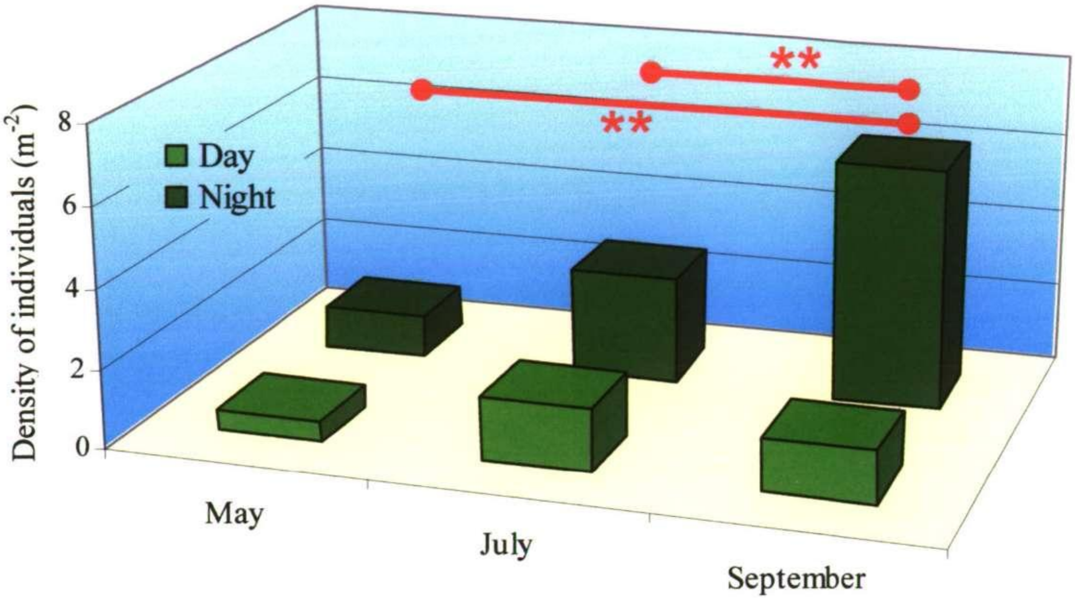


Figure 4.13 Monthly total densities (m^{-2}) for day and night samples from all three seagrass beds (La Coupe, Flicquet and St Catherine Bay, on the north east coast of Jersey, English Channel Islands). Bars represent significant differences (** = $p < 0.01$).

4.3.2.1.2 *Temporal variation in mean number of fish species and densities*

Temporal patterns in the number of fish species were not consistent between sites, with ANOVA revealing a significant ($p < 0.01$) interaction between both Time (day/night) and Site, and Month and Site ($F_{(2,54)}=5.23$ and $F_{(4,54)}= 3.84$, respectively).

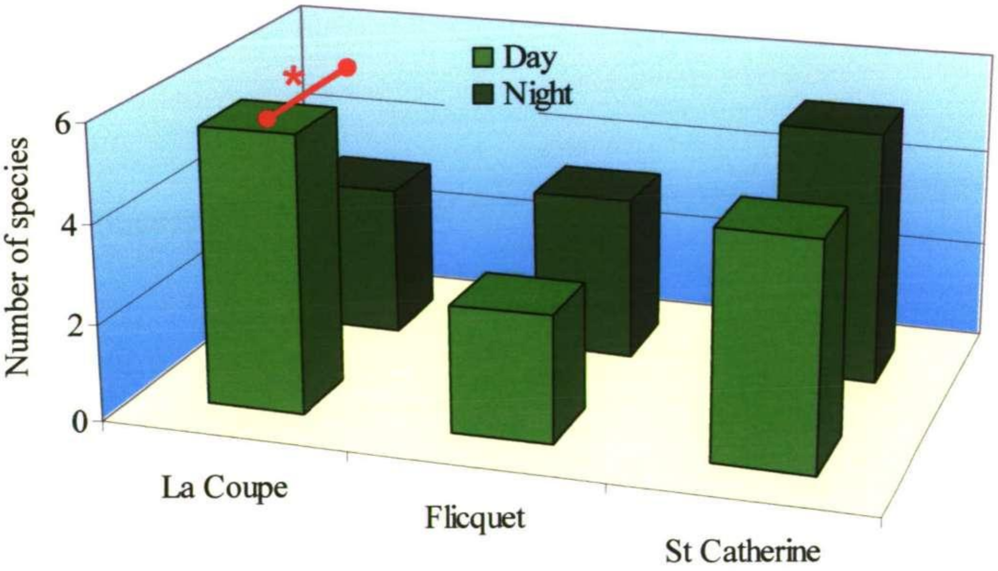


Figure 4.14 Diel variation in total species of fish for seagrass beds at La Coupe, Flicquet and St Catherine Bay, on the north east coast of Jersey, English Channel Islands. Bars represent significant differences (* = $P < 0.05$; ** = $P < 0.01$).

SNK *post hoc* means tests indicated that, although there was no significant difference in the number of fish species between day and night at either Flicquet or St Catherine Bay, at La Coupe there were significantly ($p < 0.01$) more species of fish during the day (3.08 ± 0.65 species) than at night (5.67 ± 0.92) (Figure 4.14).

SNK tests also showed that at La Coupe and St Catherine, the highest number of fish species was observed in July (La Coupe 6.13 ± 0.83; St Catherine 6.75 ± 0.77, Figure 4.15). These numbers of fish species were significantly ($p < 0.01$) more than in May (La Coupe 1.88 ± 0.48; St Catherine 2.75 ± 0.70). At Flicquet there was no significant difference in fish species numbers between months.

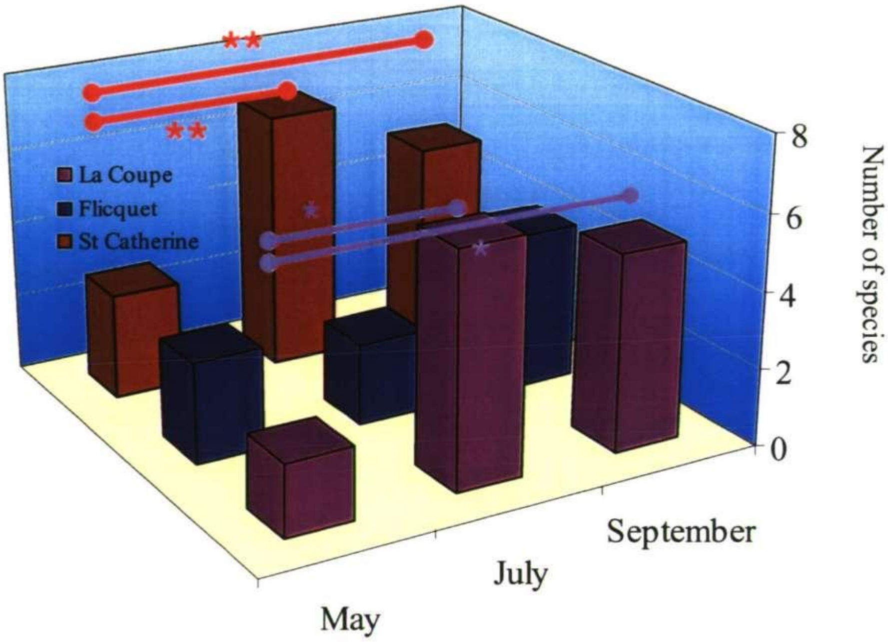


Figure 4.15 Monthly variations in total number of fish species for seagrass beds at La Coupe, Flicquet and St Catherine Bay. Bars represent significant differences (* = $p < 0.05$; ** = $p < 0.01$).

Significant differences were found in densities of fish for the factors Month and Site ($F_{(2,54)}= 5.63$, $p < 0.01$ and $F_{(2,54)}= 8.07$, $p < 0.01$, respectively). No significant difference was found for time of sampling (day/ night). SNK tests showed significantly higher ($p < 0.01$) densities of fish at La Coupe (1.35 ± 0.41) than at St Catherine Bay (0.48 ± 0.10) (Figure 4.16a). Fish densities were highest in July (1.05 ± 0.28), although July fish densities were not significantly higher than in September (0.88 ± 0.34). Densities during both these months were significantly higher ($p < 0.01$) than in May (0.11 ± 0.02) (Figure 4.16b).

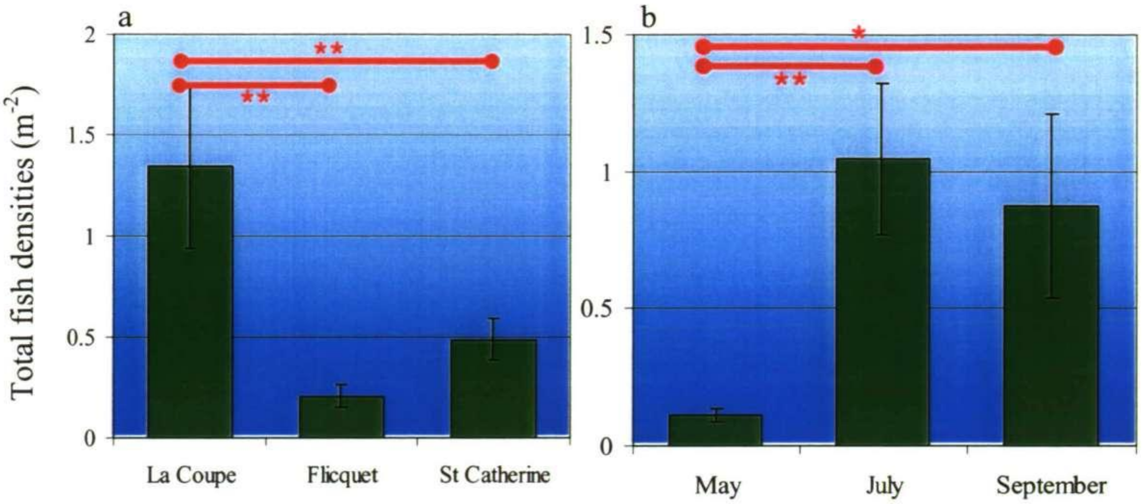


Figure 4.16 a) Variations in total fish densities between the seagrass beds at La Coupe, Flicquet and St Catherine Bay. b) Monthly variations in total fish densities between the seagrass beds. Bars represent significant differences (* = $p < 0.05$; ** = $p < 0.01$).

4.3.2.1.3 Temporal variation in mean number of decapod species and densities

The number of species of decapod showed significant differences ($p < 0.01$) in all the main factors (Month, $F_{(2,54)} = 10.77$; Time $F_{(1,54)} = 8$; Site $F_{(2,54)} = 4.69$) indicating that temporal patterns were maintained across sites. As illustrated in Figure 4.17a, the number of species of decapod was significantly lower in May (4.33 ± 0.49) than in July (7.58 ± 0.84) or September (8.17 ± 0.8), although there was no significant difference between the latter two months. The number of decapod species was significantly greater at St Catherine Bay (8.25 ± 0.77) than at La Coupe or Flicquet (5.71 ± 0.87), but there was no significant difference between the latter two sites (Figure 4.17b). Finally, the number of decapod species was significantly greater ($p < 0.01$) at night (7.72 ± 0.72) than during the day (5.67 ± 0.52) across sites and months (Figure 4.17c).

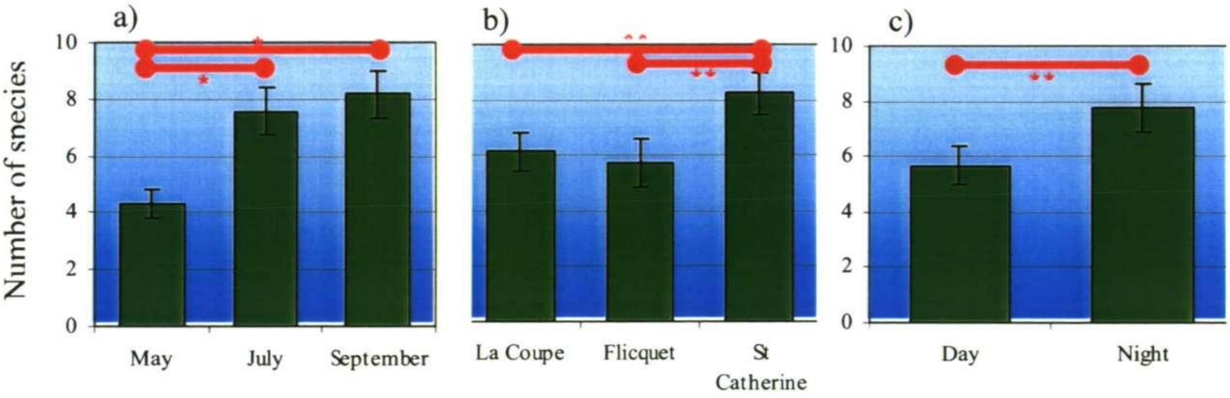


Figure 4.17 Variations in number of decapod species between a) months, b) sites and c) day/night. Bars represent significant differences (* = $p < 0.05$; ** = $p < 0.01$).

ANOVA for the densities of decapods from the three seagrass beds showed a significant interaction between Month and Time ($F_{(2,54)}$= 8.68, $p < 0.01$). Lack of significance for the factor Site suggested that these patterns were consistent over all three seagrass beds. As illustrated in Figure 4.18, during the day no significant differences were observed between months; however, at night, densities of decapods were significantly higher in September (0.89 ± 0.26) than in May (0.12 ± 0.04) or July (0.38 ± 0.1). Whilst densities of decapods were higher at night than during the day, across months these differences were not significant, except in September (Night, 4.69 ± 0.88 > Day, 0.99 ± 0.18, $p < 0.01$).

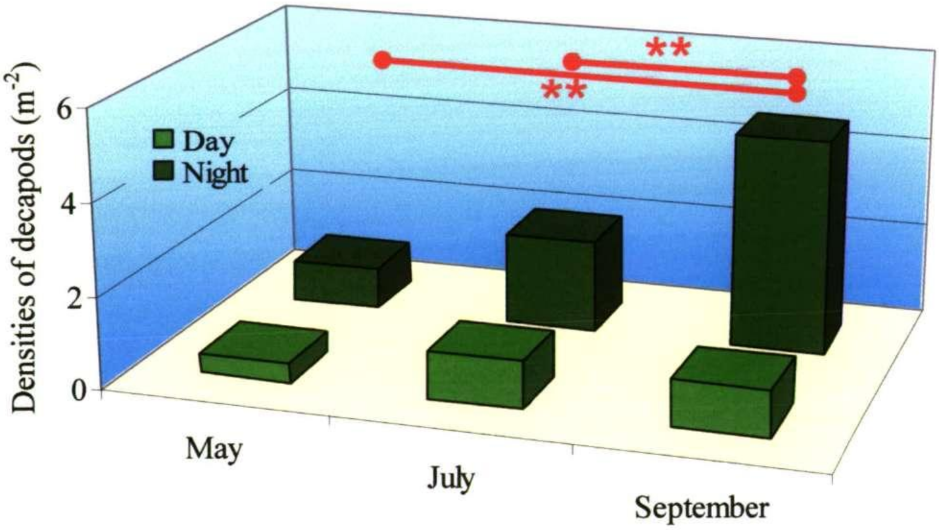


Figure 4.18 Monthly and diel variations in total decapod densities across all seagrass beds (La Coupe, Flicquet and St Catherine Bay) Bars represent significant differences (** = P <0.01).

4.3.2.1.4 Temporal variation in mean densities of selected dominant species

Table 4.5 illustrates the results of ANOVA on the densities of the most numerically abundant fish and decapod species. Two species of wrasse (*Labrus bergylta* and *Symphodus melops*) did not show any significant differences between Month, Site or Time of sampling. *P. pollachius*, *S. spinachia*, *E. aequorues* and *P. pictus* showed significant variability between months (see Table 4.5) with each species showing different peaks in density between the three months sampled. *P. pictus* densities were significantly higher in September (6.42 ± 2) than in either July (0.74 ± 0.39) or May (0.11 ± 0.11); for *P.*

pollachius, densities in September (0.11 ± 0.08) were significantly lower ($p < 0.01$) than in either July (0.89 ± 0.18) or May (0.66 ± 0.18). Sea stickleback (*S. spinachia*) densities were highest in July (1.14 ± 0.39), significantly higher ($p < 0.01$) than in September (0.24 ± 0.17) and none was found in May. In comparison, densities of *E. aequoreus* were significantly higher in May (1.56 ± 0.42) than in July (0.7 ± 0.24) or September (0.23 ± 0.17).

Table 4.5 ANOVA on dominant fish and decapod species (> 1% of total catch). Three factor, orthogonal ANOVA, Factor 1, Month (Mo, fixed, 3 levels; May, July and September), Factor 2, Time of sampling (Ti, fixed, two levels day/night), and Factor 3 is site (fixed with 3 levels) (n = 4). * = P < 0.05, ** = P < 0.01, n.s. = not significant. Location codes: LC = La Coupe, StC = St Catherine Bay, F= Flicquet.

Variable	Significant factors	F	SNK
Fish species			
Gobiusculus flavescens	Mo	$F_{(2,54)} = 3.75^*$	July = (Sept > May)
	Si	$F_{(2,54)} = 3.46^*$	StC = (LC > F)
Pomatoschistus pictus	Mo	$F_{(2,54)} = 5.60^{**}$	Sept > (May = July)
Pollachius pollachius	Mo	$F_{(2,54)} = 8.19^{**}$	(May = July) > Sept
Spinachia spinachia	Mo	$F_{(2,54)} = 6.58^{**}$	July > (May = Sept)
Entelurus aequoreus	Mo	$F_{(2,54)} = 4.72^{**}$	May > (July = Sept)
Spondyliosoma cantharus	Mo x Si	$F_{(4,54)} = 5.06^{**}$	Sept: F > (LC = StC) F= Sept > (May = July)
Pomatoschistus minutus	Mo x Ti x Si	$F_{(4,54)} = 3.88^{**}$	LC, day: July > (May = Sept) Day, July : LC > (F = StC) Night, July : (F > StC) = LC
Symphodus melops	n.s.	-	-
Labrus bergylta	n.s.	-	-
Decapod species			
Hippolyte varians	Mo	$F_{(2,54)} = 5.44^{**}$	Sept> (July = May)
	Ti	$F_{(1,54)} = 7.48^{**}$	Night > Day
	Si	$F_{(2,54)} = 6.3^{**}$	StC > F < LC
Palaemon serratus	Mo x Si x Ti	$F_{(4,54)} = 4.85^{**}$	Night, LC: Sept > (July = May) Night, StC: Sept > (July = May) Sept, all sites: Night> Day
Liocarcinus arcuatus	Ti	$F_{(1,54)} = 12.09^{**}$	Night > Day
	Mo x Si	$F_{(4,54)} = 2.68^*$	StC: May < (July = Sept)
Processa edulis crassipes	Mo x Ti	$F_{(2,54)} = 5.72^{**}$	Night: Sept > (May = July) Sept: Night > Day
Pisidia longicornis	Ti x Si	$F_{(2,54)} = 6.62^{**}$	F: Night > Day
	Mo x Si	$F_{(4,54)} = 2.83^*$	StC: Day > Night F: May < July < Sept
Macropodia deflexa	Si	$F_{(2,54)} = 4.69^*$	StC> (LC = F)
Macropodia rostrata	Mo x Ti	$F_{(2,54)} = 5.8$	Night: Sept > (May = July)
Macropodia linaresi	n.s.	-	-

Two spot gobies (*Gobiusculus flavescens*), the most abundant species of fish found during the study, showed significant differences between Month and Site. SNK tests showed that over all sites and times (day/night), densities were highest in September (0.71 ± 0.34), significantly more than in May (none) but not significantly more than in July (0.32 ± 0.09). *Post hoc* tests also showed that densities were significantly higher at La Coupe (0.71 ± 0.34) than Flicquet (0.02 ± 0.01), although they were not significantly different from those at St Catherine Bay (0.3 ± 0.09).

ANOVA for sand gobies (*Pomatoschistus minutus*) revealed significant interactions between all three factors ($F_{(4,54)} = 3.88$, $p < 0.01$). SNK tests illustrated that the highest mean density of sand gobies was found at La Coupe during the day in July, and this was significantly greater ($p < 0.01$) than at Flicquet or St Catherine Bay at this time (July, day), or at night at La Coupe. At night, only in July were sand gobies were found at all three sites.

Finally, the economically valued black bream (*Spondyliosoma cantharus*), which was found only temporarily in the seagrass beds as juveniles, showed a significant interaction between Site and Month. At La Coupe, black bream were observed in September but not in May or July. At St Catherine Bay, black bream were observed in July, whilst at Flicquet, they were found in May and September but were absent in July. The only significant differences occurred at Flicquet, where densities in September (4.73 ± 1.96) were significantly higher than in July (none) or May (0.46 ± 0.46). In September, densities black bream at Flicquet were significantly higher than at La Coupe (0.36 ± 0.24) and St Catherine Bay (0.25 ± 0.25).

The dominant species of decapod also showed strong temporal patterns; however, for the majority of species, differences between Site and Month were only observed in night samples (Table 4.5). For example, densities of the economically valued common prawn, *Palaemon serratus*, with a significant interaction between all three factors ($F_{(4,54)} = 4.85$, $p < 0.01$) due to a significant interaction between Site and Month only occurring at night. SNK tests showed that densities of *P. serratus* at all three sites were highest in September (although only significantly higher at La Coupe and St Catherine) with no significant differences in densities between July and May. Highest overall densities of *P. serratus* were found at St Catherine Bay at night in September.

The most abundant species, the chameleon prawn (*Hippolyte varians*), showed significant variation in each of the three main factors (Table 4.5). Lack of significant interactions illustrates that, for this species, temporal patterns were consistent across sites. SNK tests showed that densities of *H. varians* were significantly higher ($p < 0.01$) in September (1.39

± 0.29) than in July (0.93 ± 0.24) or May (0.43 ± 0.09), and were significantly higher at night (1.26 ± 0.22) than during the day (0.58 ± 0.14). SNK tests on the differences between sites identified significantly higher densities of *H. varians* at St Catherine Bay (1.36 ± 0.32) and at La Coupe (0.82 ± 0.81) than at Flicquet (0.57 ± 0.16). Like *H. varians*, *Liocarcinus arcuatus* (arch-fronted swimming crab) showed significant day/ night differences in density (SNK: night greater than day) and densities were significantly highest at St Catherine Bay, although this was only in July and September (Site x Month interation, Table 4.5); monthly patterns were not consistent over all sites.

The three species of *Macropodia* had different patterns of densities between sites and months. *Macropodia linaresi* showed no significant differences in density between Time, Month or Site, but *Macropodia deflexa* showed significant differences between site (Table 4.5), with significantly higher densities at St Catherine Bay (0.76 ± 0.37) than at La Coupe (0.19 ± 0.06) or Flicquet (0.22 ± 0.83). In comparison, *Macropodia rostrata* densities showed a significant interaction between Time and Month, with significant differences between months only at night (Table 4.5). *Pisidia longicornis* (Long clawed porcelain crab) was the only decapod with significantly higher densities during the day (1.21, ± 0.39) than at night (0.33, ± 0.33) although this was only at St Catherine Bay (Table 4.5). Monthly patterns in the densities of *P. longicornis* were not consistent across sites (Month x Site interaction, Table 4.5). Only densities at Flicquet showed significant differences ($p < 0.01$) between months, with densities showing a significant increase with each consecutive month.

Finally, densities of the caridean prawn, *Processa edulis crassipes,* showed differences between months, which were only significant at night (Month x Time interaction, Table 4.5). SNK tests illustrated that nocturnal densities of this species were significantly higher ($p < 0.01$) in September (1.04 ± 0.35) than in May (0.15 ± 0.08) or July (0.23 ± 0.11).

4.3.2.1.5 Temporal variation in the proportion of fish residency groups

Analyses showed that the proportion of fish which resided permanently in seagrass beds, but had cryptic morphologies (examples in Figure 4.2), showed significant differences between months ($F_{(2,54)} = 4.88$, $p < 0.05$) and sites ($F_{(2,54)} = 4.72$, $p < 0.05$). SNK tests showed that the proportion of cryptic fish was significantly greater ($p < 0.05$) at St Catherine Bay (16.47% ± 4.98) than at Flicquet (4.1 ± 2.28) and this surpassed Month or

Time of sampling. It was also observed that the proportion of cryptic fish species was significantly higher ($p < 0.05$) in May (16.59 ± 5.22) than either July (4.44 ± 2.22) or September (4.03 ± 1.74).

The proportion of small permanent residents also exhibited significant differences between months and between sites (but no interaction; $F_{(2,54)} = 23.2$, $p < 0.01$ and $F_{(2,54)} = 3.4$, $p < 0.05$). The proportion of small permanent residents was significantly higher ($p < 0.01$) in July (49.57 ± 7.36) and September (50.06 ± 6.94) than in May (2.08 ± 1.53). Large permanent residents showed no significant variation between Month, Site and Time of sampling. There were significant interactions for the proportion of juveniles of permanent residents between both Time and Site ($F_{(2,54)} = 3.27$, $p < 0.05$), and Month and Site ($F_{(4,54)} = 0.03$, $p < 0.05$). At Flicquet, SNK tests showed that the proportion of permanent juveniles was significantly higher during the day than at night and significantly increased ($p < 0.05$) in September (37.65 ± 8.49) compared to July (4.69 ± 3.28). No significant differences between day and night or months were observed at any other site.

Finally, the proportions of temporary juveniles showed significant differences with Month ($F_{(2,54)} = 3.27$, $p < 0.05$). SNK tests identified significantly greater ($p < 0.05$) proportions in May (32.29 ± 6.72) than in July (14.57 ± 4.97) or September (16.31, ± 4.93).

4.3.2.1.6 Temporal patterns of size distributions

Overall, the size of fish utilising seagrass sites during the summer months sampled ranged from about 10 mm to 240 mm standard length (SL), with the vast majority of individuals (25 to 75% range) being less than 100 mm in SL (Figure 4.19). Juveniles of the larger, economically valued species (such as black bream and pollack) showed significant ($p < 0.01$) variability in SL between months ($H_{(2,25)} = 10.68$ and $H_{(2,36)} = 10.68$, respectively). During May and July, black bream had very patchy distributions and individuals were only between 10 and 20 mm in SL (see Figure 4.19b). In September, median SL was greater than 50 mm, reaching a maximum of 60 mm. Kruskal Wallis ANOVA showed significant ($p < 0.01$) differences in SL of black bream between sites, with median SL longer at St Catherine Bay than at Flicquet or La Coupe ($H_{(2,25)} = 10.38$).

In May, juvenile pollack had median SL between 20 and 40 mm (Figure 4.19c). In July, there were fewer pollack at Flicquet and La Coupe compared to St Catherine Bay, but median SL were higher than in May. SL distributions increased significantly in September and July compared with May ($p < 0.01$, Kolmogorov-Smirnov). In general, maximum

St Catherine Bay in July, one individual was significantly larger (280 mm; see Figure 4.19) than the size distribution of the other fish (an extreme).

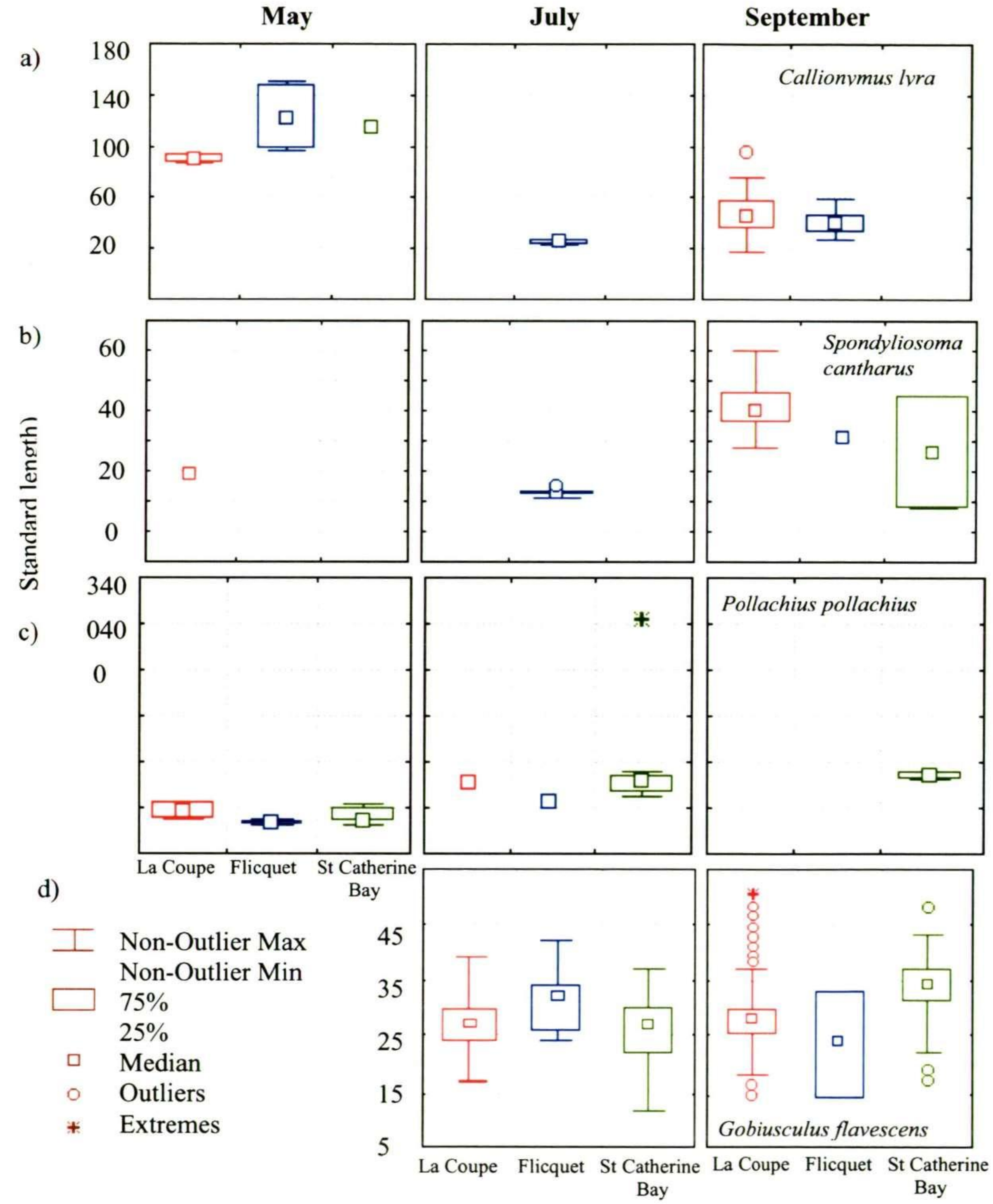


Figure 4.19 Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for fish a) *Callionymus lyra*, b) *Spondyliosoma cantharus*, c) *Pollachius pollachius* d) *Gobiusculus flavescens* sampled from three seagrass on the north east coast of Jersey, during May, July and September 2000.

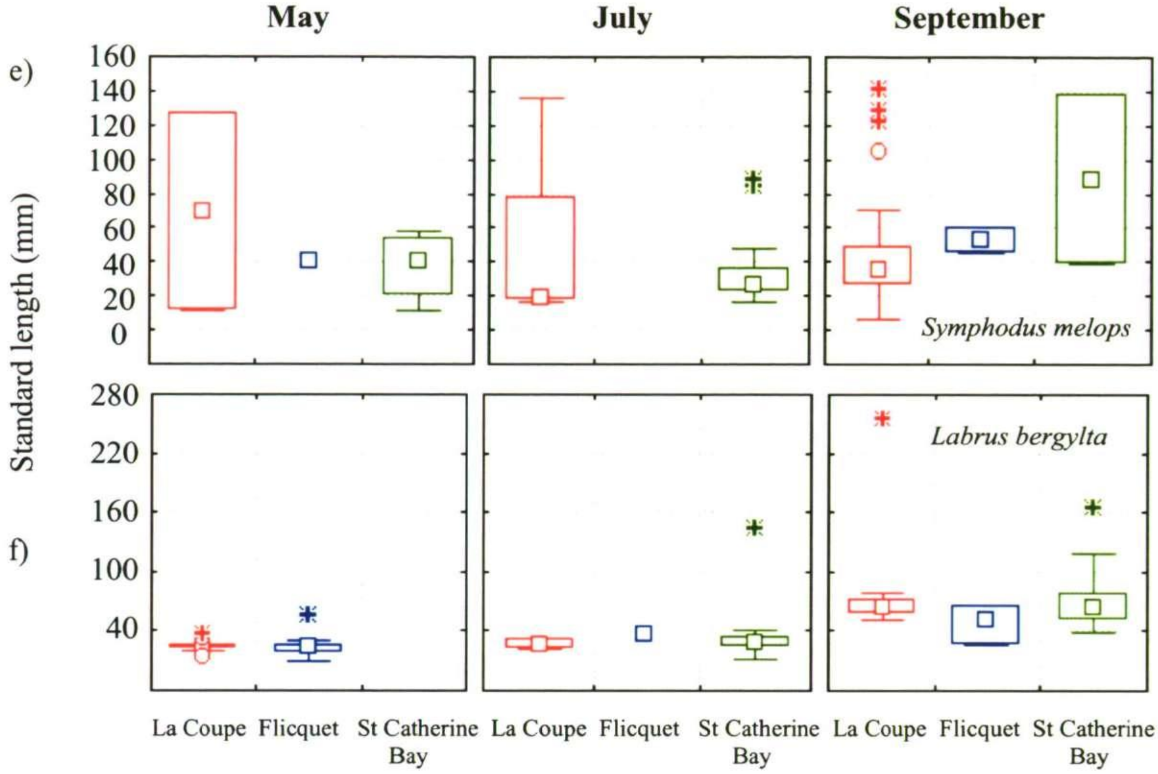


Figure 4.19 continued

Corkwing wrasse (*Symphodus melops*) showed no significant differences in standard length between months or sites (Figure 4.19e). At Flicquet, few individuals were observed and the maximum SL was the lowest over all months (though not significantly lower). At La Coupe, corkwing wrasse showed the greatest size ranges (10 to 140 mm). The majority of ballan wrasse were classified as juveniles, although a few larger individuals (occasional mature) were visible as extreme points on the plots (Figure 4.19f) at St Catherine Bay and La Coupe.

The median SL of juvenile ballan wrasse appeared to increase gradually over the months sampled and achieved a maximum of 80 mm SL. These monthly differences in median SL were significant ($H_{(2,84)} = 50.46$, $p < 0.01$) with the SL in September being larger than in July or May (there was no significant difference in SL distributions between the latter two months, Kolmogorov-Smirnov). Kruskal-Wallis ANOVA showed that, over the entire sampling period, SL at Flicquet were significantly lower than at St Catherine or La Coupe

(Figure 4.19f). The common dragonets (*Callionymus lyra*) also showed differences in SL between months ($H_{(2,42)} = 19.53$, $p < 0.001$). For this species, however, standard lengths in May were greater than in July or September (Figure 4.19a). In May, SL of dragonets was between 80 and 150 mm, whereas in July numbers were very low and individuals ranged from 20 to 30 mm SL.

Finally, two spot gobies were absent from the May samples, however, comparisons between July and September showed a significant difference in median SL ($H_{(1,1135)} = 34.46$, $p < 0.001$), with SL being greater in September. There was no significant difference in median SL between sites and the maximum SL observed for the two spot goby was 60 mm (at St Catherine Bay and La Coupe, Figure 4.19d).

The arch fronted swimming crab showed significant differences in carapace width (CW) between months ($H_{(2,149)} = 50.04$, $p < 0.001$). Paired Kolmogorov-Smirnov tests showed that CW was significantly lower in July, than either September or May. In July, CWs ranged from 6 to 12 mm with one exception at St Catherine Bay (CW of about 23 mm). Maximum CWs (28 mm) were observed at St Catherine Bay in May for this species. In September, median CWs did not differ significantly between sites, although size ranges at Flicquet were smaller (12 to 18 mm) than at La Coupe (8 to 26 mm) or St Catherine Bay (6 to 27 mm CW) (Figure 4.20a).

Processa edulis crassipes showed a significant difference in carapace length (CL) between months ($H_{(2,347)} = 13.64$, $p < 0.01$). Paired Kolmogorov-Smirnov tests showed that the CL of individuals was significantly smaller in September than in July or May although, as Figure 4.20b illustrates, larger individuals (> 10 mm CL) were observed at all three sites in September.

Finally, *P. serratus* showed significant differences in CL between months ($H_{(2,307)} = 14.71$, $P < 0.001$); the median CLs were significantly larger in September than in May, but smaller in July (when few of individuals were observed at St Catherine Bay, Figure, 4.20c). In September, although the majority of individuals had a CL of between 6 and 8mm, at St Catherine Bay, there were many larger individuals (extremes and outliers) which, as mentioned previously, were ovigerous females.

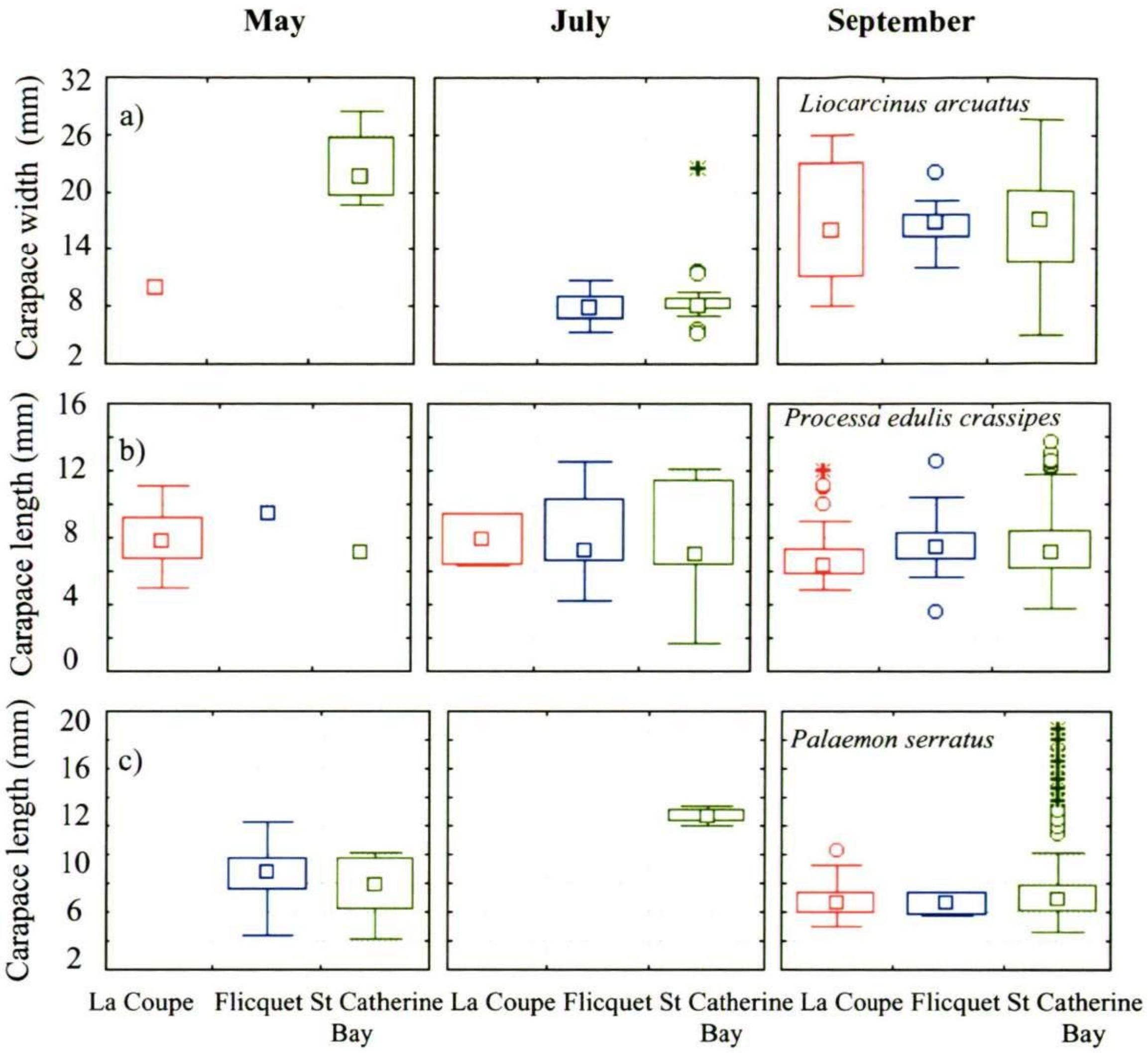


Figure 4.20 Medians, 25 and 75% ranges, maximum /minimum and extreme and outlier sizes (Standard length) for decapods a) *Palaemon serratus*, b) *Processa edulis crassipes*, c) *Liocarcinus arcuatus* sampled from 3 seagrass on the north East coast of Jersey, during May, July and September 2000.

4.4 Discussion

At first, it would appear from the data that there is a high degree of similarity in species composition and relative abundance between seagrass bed sites and locations in Jersey; however, only five species of fish and six species of decapods were common to all sites. This, together with significant differences at the site level in species number, but not total densities, suggests that the similarities between sites are due to a few dominant common species, rather than subsets of the same fauna found in different degrees of relative abundance.

Although species densities and composition of specific seagrass beds differed between sites, certain characteristics of the fish, decapod and cephalopod assemblages could be considered fundamental features not only of Jersey seagrass beds, but of the mobile fauna of seagrass beds throughout the world (Kikuchi & Pérès, 1977; Pollard, 1984; Bell & Pollard, 1989; Guidetti & Bussotti, 2000). Taxonomic similarities in the species of fish are often limited by the species pool present in the zoogeographic province where the seagrass occurs. Some taxonomic similarities can, however, be made between the species found in the present study and Pollard's (1984) comparison of fish assemblages from 25 seagrass beds world-wide (done using dominance ranking of families, incorporating number of species per family and their relative abundances). For example, the Syngnathidae and Gobidae were recorded in 24 of the 25 studies reviewed by Pollard (1984), and were usually among the ten most dominant families as observed in this study (Gobidae: *Gobiusculus flavescens* and *Pomatoschistus pictus*; Syngnathidae: *Enterlurus aequoreus*, *Syngnathus typhle* and *Nerophis ophidion*). The Syngnathidae is one of the few families of fish that have members that mimic seagrass (Figure 4.2), both morphologically and behaviourally. Families Sparidae, Labridae and Cottidae dominated both the present study sites and at many other localities (Pollard, 1984; Guidetti, 2000). Such basic similarities in composition, despite biogeographical differences, increase the validity of making ecological comparisons with studies in other parts of the world. However, at a family level present data suggest that the fish fauna of Jersey seagrass beds compare more closely with the Mediterranean (Francour, 1997; Guidetti & Bussotti, 2000) and the Atlantic coast of Portugal (Costa *et al.*, 1994) than with seagrass beds on the Atlantic coast of the United States of America (Heck & Thoman, 1984; Adams, 1976).

Many studies have identified that the fish in seagrass beds comprise mainly small species and/or those with a cryptic habit (for example, the Gobidae and Syngnathidae), juveniles of larger species and occasional adults of larger mobile species (Bell & Pollard, 1989; Costa *et al.*, 1994). Kikuchi's (1974) groupings ('permanent residents', 'seasonal residents', 'temporary visitors that forage in a wider area than the seagrass bed' and 'occasional migrants') have been adopted and adapted by other authors (Bell & Harmelin-Vivien, 1982; Middleton *et al.*, 1984). One of the most common adaptations, and one adopted here, was to identify species as 'temporary residents' (rather than seasonal); for example, juveniles of larger species which utilise the seagrass bed only up to a critical point in their life history, or those individuals that do not appear in the seagrass beds as juveniles but as adults may forage in the seagrass beds for short periods or seek shelter there during the day.

Decapod crustaceans are also a conspicuous component of the macrofauna of seagrass beds (Young, 1981; Gray, 1991a,b) and caridean prawns in particular are thought to play an integral role in determining the structure and dynamics of seagrass faunal assemblages. As seen in the present study, they often occur in great densities (Gray, 1991), are predators on other seagrass macrofauna and meiofauna (Chessa *et al.*, 1989; Gore *et al.*, 1981), and are themselves important prey items for larger prawns and fish (Adams, 1976; Bell & Harmelin-Vivien, 1982; Primavera, 1997).

Although cephalopod molluscs were not present in sufficient numbers for valid statistical analysis, some general patterns were observed for the European squid, *Loligo vulgaris*, and the cuttlefish, *Sepia officinalis*. Observations during this and previous studies (Blanc & Daguzan 1998; Sea Fish Industry Authority, 1996) revealed that the economically valued cuttlefish, with its zebra-like cryptic coloration, utilised certain seagrass beds as spawning grounds, attaching their egg cases to the seagrass shoots.

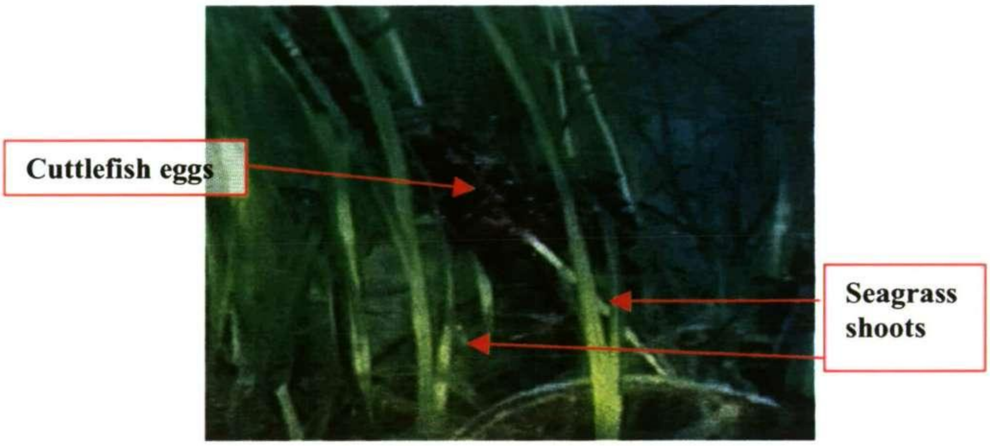


Figure 4.21 Cuttlefish (*Sepia officinalis*) eggs attached a seagrass shoot in St Catherine Bay on the north East Coast of Jersey, English Channel.

No adult spawning cuttlefish was caught during the present study, despite their appearance in potting samples during the 1999 sampling (see Chapter 3) and observations of the egg cases attached to seagrass blades at St Catherine Bay (pers. obs. 2000, Figure 4.21). Length measurements of *S. officinalis* caught in the present study, however, indicated recently hatched individuals (10 to 20mm, newly-hatched individuals being between 6 and 9 mm, Arkley *et al.*, 1996) at Flicquet in May and La Coupe in September. Larger returning juveniles were observed in seagrass beds at Violet, Elizabeth Castle and Flicquet in September. Cuttlefish migrations have been well documented (Pawson, 1995; Quéro & Vayne, 1998, Arkley *et al.*, 1996) and are related mainly to spawning and over wintering.

Autumnal concentrations of cuttlefish have been identified to the west of Jersey and one of the main spawning grounds is in the Baie du Mont St. Michel (Arkley *et al.*, 1996). The present study suggests that the seagrass beds of Jersey represent another previously unidentified spawning ground for this species within the English Channel. Finally, whilst the seagrass bed may offer some protection to the juvenile cuttlefish, their primary predation avoidance mechanism is to burrow into the sediment during which they are very prone to damaging themselves if the sediment is too coarse. Sediment properties may, therefore, influence the survival of the juveniles as much as the cover of seagrass (Paulij *et al.*, 1991).

ANOVA tests showed larger total numbers of species at the north-eastern sites, but also the highest variability between sites, which was not observed in the southern sites. There was also a significant difference for total species number between day-night, which were not consistent over site or location. Total densities were significantly different bewteen the north-east and south, but only at night when densities were significantly higher in the north. Separating the analysis into decapods and fish showed that total density location patterns were primarily driven by the distribution of decapods, which did appear to differ at this larger scale of Location, with decapod species numbers and densities higher in the north. Fauna of the seagrass bed at St Catherine Bay showed the greatest richness of species for all months, particularly in terms of decapods (La Coupe showing the greatest species richness in terms of fish overall).

For decapods, larger-scale (north-east/south location) differences were also apparent at a species level. The most abundant species, *Hippolyte varians,* was common at both north-eastern and southern locations, but in significantly higher densities in the north. *Palaemon serratus* (a species collected by low water recreational fishermen), *L. arcuatus* and *Processa edulis crassipes* were absent or in low numbers in the south coast seagrass beds sampled. Most studies have attributed differences in densities of caridean prawns to qualitative and quantitative differences in the seagrass plant/bed structure (Lewis, 1984; Bell & Westoby, 1986b; Halliday, 1995; Walsh & Mitchell, 1998). Species specific density variability may be due to factors extrinsic to the sites themselves, including depth (Baden & Pihl, 1984; Young 1981; Gray, 1991). Gray (1991) hypothesised that the *Macrobrachium* spp. moved away from seagrass into deeper water in winter (caught down to depths of 35m) and, during late winter/ early spring, some individuals, mainly recruiting juveniles and a few of the largest sized prawns, re-colonise the seagrass. Similar patterns of seasonal depth migrations and over wintering in deeper waters have been reported for other estuarine/near shore palaemonid prawns (Nixon & Oviatt, 1973; Baden & Pihl, 1984;

Guerao & Ribera, 2000; Walsh & Mitchell, 1998). There are, however, few reported seasonal movements of seagrass-associated caridean prawns (Kikuchi, 1974; Emmerson, 1986; Gray, 1991), presumably as most are resident species. In the present study, it is proposed that seasonal migrations account for not only the bimonthly variability during the summer but also the coastal location scale variability of the common prawn *Palaemon serratus*, which occurs down to depths of 40m. As Figure 4.1 shows, sites on the north-eastern coast of Jersey lie much closer to the 20m isobath than those in the south. This difference may mean that for recruiting juveniles, and returning adults, which re-colonise shallow-water habitats in late winter/ early spring from deep water, the seagrass beds on the north coast may be the first suitable habitat they contact. In comparison, seagrass beds on the south coast are located at a much greater distance from deeper water. There are also other habitats (for example, shallow sandbanks, algal-covered rocky reefs and channels containing *Sargassum*), potentially inhabitable by the prawns (which like many of the species found in this study are seagrass associated but not obligate residents) closer to the deeper water than the seagrass beds studied. These habitats may "intercept" the migrating prawns before they arrive at the seagrass beds.

Compared with decapod patterns, coastal location differences were not as evident for number of fish species and there were no consistent diel patterns. Instead, differences in fish species number occurred at the smaller spatial scale (between sites within location), although once again variability in species number between sites was high in the north but not in the south. There are several possible explanations for this site level variability. Firstly, local recruitment failure (Bell & Westoby, 1986a; Bell *et al.*, 1988; Olney & Bohlert, 1988; Ferrell & Bell, 1991) or recruitment to a restricted part of the available habitat. Contrary to the theory that ocean-spawned species would show greatest variability between locations and greatest similarity between sites within location (Bell *et al.*, 1988; Hannan & Williams, 1998), no coastal location effect was observed in this study for the distribution of ocean-spawned individuals with pelagic larvae.

In the present study, few of the species spawned offshore and the majority spawned within the seagrass beds as either brooders (Sygnathidae and most decapods) or benthic spawners (*Gobiusculus flavescens* and cephalopods) with benthic or pelagic larvae. It would appear that the use of seagrass beds as a site of reproduction is confined largely to the permanent residents which often have short life spans (the average life span of a two spot goby is about 1 year; Wheeler, 1969), necessitating continually successful recruitment. Few temporary fish residents identified in this study reproduced within the seagrass; rather, they spawned away from seagrass beds, often offshore (Wheeler, 1969; Whitehead *et al.*, 1986;

Pawson, 1995). Sogard *et al.* (1987) observed that resident fish of seagrass meadows had reproductive strategies that minimised planktonic dispersal (attached eggs, parental brooding or the complete elimination of a pelagic stage) and suggested that this behaviour increased chances of recruitment to seagrass beds where the adults were able to live and spawn successfully. Spatial inconsistencies in temporal patterns of species density (which were observed in this study) could, therefore, be influenced considerably by the way fish utilise the habitat. If the adult population is resident and spawning occurs within the seagrass bed, then fluctuations in total numbers caused by recruitment will be smaller (Ferrell *et al.*, 1993), as was observed here for the proportion of permanent juveniles, which showed no significant site to site variability. The prevalence of this strategy is thought to increase with latitude in a response to dealing with unreliable seasonality of plankton productivity (Longhurst, 1999). The present results suggest that only when seagrass beds are dominated by non-locally spawning species, will patterns in seagrass fauna reflect larval supply.

With larvae being released within the seagrass bed itself, recruitment becomes heavily dependent on local-scale hydrography (tidal currents, Jenkins & Black, 1994; wind forcing, Farrell *et al.*, 1991; fronts and convergencies, Shanks & Wright, 1987, Clancy & Cobb, 1997, meso scale current eddies, Hare & Cowen, 1996; Jenkins *et al.*, 1999). Local-scale hydrography may account for the lack of clear differences in fish fauna between zones of greater mixing (La Coupe and Flicquet seagrass fish faunal assemblages more similar to each other than to St Catherine Bay, and Les Elavees and Violet than to Elizabeth Castle). In an estuarine or embayment system, where the direction of larval movement is more predictable, patterns relating to seagrass bed location are easier to explain (Bell *et al.*, 1988; Hannan & Williams, 1998).

In addition to the spawning behaviour of adults, temperature and salinity tolerances of eggs (Hempel, 1979), duration of the planktonic phase (Brothers & Thresher, 1985) and larval behaviour (Holt, *et al.*, 1983), the behaviour of juvenile fish may influence the amount of temporal variation found in seagrass beds. Young fish may settle initially in one habitat and later move into the *Zostera* beds [Middleton *et al.* (1984) observed this for many fish in *Posidonia australis* beds]. Distinct settlement episodes, and more-or-less synchronised departures of individuals at a certain life stage, may result in alternating periods of presence and absence of a species, which is not always consistent between beds at the temporal and spatial scales assessed.

As many recent studies have demonstrated, initial settlement patterns may not persist and may be rapidly modified by physical processes and behaviour of the settled fish, so whilst larval supply may explain short-term recruitment variability, over larger time frames such patterns break down (Hamer & Jenkins, 1997). There is also the influence of differential post-settlement processes on fish distribution patterns (predation, food reserves, and choice of spawning area by benthic spawners); because the physical complexity of seagrass habitats can mediate predation on juvenile fish and decapods this may cause selection. Some of the larger piscivorous fish (John Dory, *Zeus faber,* and adult pollack and wrasse) were observed in the seagrass beds only sporadically, but at night, contradicting suggestions that piscivorous predators in seagrass beds are primarily diurnal (Greening & Livingstone, 1982). Physical complexity of the seagrass bed at a landscape level may account for greater diversity of species (for example, fish species richness being highest at La Coupe). In a more patchy seagrass habitat, the trawl may travel over areas of different habitat type that make up the defined seagrass bed (patch of sand or algae), thus collecting different species related to these other habitats (Jenkins *et al.*, 1997b; Jackson *et al.*, 2002). There is also the increased likelihood of sampling those species that may use unvegetated areas as long as refuge is available nearby, therefore preferring edge regions of the seagrass bed (Summerson & Peterson 1984).

Clear patterns in the temporal variability of species numbers and densities of fauna of the *Zostera marina* beds were observed. Total species numbers (and the numbers of fish and decapod species separately) were significantly lower in May than in July or September, due possibly to reduced numbers of temporary residents (for example, juveniles) at the beginning of summer. Reduced numbers of temporary residents may also explain the peak in fish and decapod densities in July; numbers fell again in September, perhaps as juveniles reached critical sizes or ontogenetic shifts in diets or behaviour resulted in migrations out of the beds. It is proposed here that the adjacent habitat type (algae, rocks, un-vegetated sand) may influence the stage or level at which these migrations occur.

Diel changes in the density of many species of fish varied as much between site within location, as between locations. In some cases, this variation may have been due to small-scale (within location) spatial patchiness in abundance of individual species and the patchy (for example, schooling species) distributions of some species. Another explanation could be the natural small-scale variations in the physical characteristics (for example, density and height) of each *Zostera* bed (Bell & Westoby, 1986b), or even localised variations in the activity/behaviour (for example, foraging) affecting the presence or catch rates of individuals. Notably, the activity patterns of individuals may vary within site as well as from site to site [for example, depending on tidal phase and turbidity of the water (Sogard *et al.*, 1989; Stoner, 1991)]. Quantification of the behaviour and movements of individuals may be required to further understand diel changes in behaviour of fishes in these habitats.

Sogard *et al.* (1987) proposed that the proportion of permanent residents in a seagrass bed increased with decreasing latitude as the extent of winter migrations outside the bed declined. The majority of individuals found in the present study were identified as permanent residents. This was due, however, to the numerical dominance of permanent residents such as the gobies. Almost half (44 %) of the fish species were temporary inhabitants of the seagrass bed which, in comparison to other lower latitude studies (Burchmore *et al.*, 1984; Middleton *et al.*, 1984), supports Sogard *et al.*'s (1987) proposal. It is further suggested that many of the species reported as permanent residents may in fact move amongst habitats and further research on adjacent habitats is need to assess this.

As predicted by other studies, juvenile fish, of both permanent and temporary (moving out of the seagrass bed at a particular size) residents, made up a significant proportion of the total individuals. However, as observed by Ferrell and Bell (1991), these rarely outnumbered adults. Several hypotheses have been proposed to explain the high abundance of juvenile fish in seagrass beds, including avoidance of predators, abundance of food and the interception of fish larvae. It must be emphasised that many studies describing the nursery function of seagrass beds are based on qualitative observations (Costa *et al.*, 1994) with no distinction between abundances of juveniles and adult fish, and no quantitative data on fish size as given here.

None of the permanent fish residents of the Jersey seagrass beds were exploited, either recreationally or commercially. However, some of the temporary juveniles were exploited valued in the region; the most common were pollack (*Pollachius pollachius*) and black sea bream (*Spondyliosoma cantharus*). In 2000, black bream represented 27% of the total weight of wet fish (83195 kg) caught by the Jersey fleet and pollack 4% (11603 kg; States of Jersey Department of Agriculture and Fisheries, 2000).

Black bream are relatively common in northern European waters, although it is only a summer migrant north of the English Channel (Bauchot & Hureau, 1990; Rogers *et al.*, 1998). Costa *et al.* (1994), using gear similar to that used in this study (1.5m beam trawl, with a 10 mm mesh), found black sea bream at densities of about 0.02m^{-2} in *Zostera marina* beds in the Mira estuary and defined the beds as a nursery ground for this species. Densities in this study ranged from 0.0015 to 0.05m^{-2} depending on the time and place sampled. In the English Channel, concentrations of spawning black sea bream (offshore benthic spawners) are observed around the Channel Islands in April and the Isle of Wight in May (Rogers *et al.*, 1998; Pawson, 1995). Previous observations of juveniles in inshore areas of the Channel Islands and Isle of Wight suggest that the pelagic larvae of black sea bream do not travel far from their spawning grounds (Pawson, 1995). In the present study, all the black sea bream were less than 70 mm and previous studies on this species have shown that juveniles remain in the inshore areas for 2-3 years before recruiting to the adult stock at a length of approximately 200 mm (Pawson, 1995). It is proposed therefore that this species moves from seagrass beds to other inshore habitats in the two to three years prior to its recruitment to offshore adult stocks. The utilisation of inshore regions, and particularly seagrass only as juveniles, contrasts with the situation in the Mediterranean where both juveniles and adults of this species are found typically over seagrass beds (Bauchot & Hureau, 1990; Bell & Harmelin-Vivien, 1982). It is suggested that the recruitment of pelagic larvae from offshore to inshore nursery grounds may make distributions of this species both temporally and spatially more 'patchy' than in the Mediterranean, where the spawning population also inhabits the seagrass beds, and may explain local recruitment failure.

Finally, it was suggested in the previous chapter (Chapter 3) that, like a number of other fish inhabiting seagrass beds, black sea bream occupy the water column above the canopy during the day (thus avoiding the trawl) and shelter in the seagrass bed at night (see references in Bell & Pollard, 1989). In the present study, however, whilst showing significant differences in density between month and site nested in location no significant diel patterns were observed for this species.

Pollack were observed as small young-of-year at all sites in May; in July, a significant increase in size was observed but also significantly less individuals were collected. A number of explanations for this decline in numbers may be hypothesised. For example, the fish may be migrating to deeper regions or to other inshore habitats at a certain size threshold or ontogenetic stage. It may also be that the individuals move up into the water column or a change in behaviour was such that they avoided capture by the trawl. Observations along the coast of France and England suggest that young Pollack are abundant in the coastal zone before moving to deeper inshore waters when 150 to 200 mm in length (Pawson, 1995). In this study, pollack were observed only up to the standard length of about 100 mm (with the exception of one individual of about 240 mm) supporting previous observations.

Analysis of the length frequencies of some of the other fish inhabiting the seagrass beds helped to suggest possible reasons for their distributions. Several authors have reported that when fish become too large for optimal protection by the seagrass blades, they migrate to other nearby habitats or deeper regions (Weinstein & Heck, 1979; Middleton *et al.*, 1984; Rooker & Dennis, 1991; Nagelkerken *et al.*, 2000). With different seagrass bed complexities, species may migrate or be preyed upon at different levels and at different times (Nelson & Bonsdorff, 1990), which may account for not only the different maximum size limits observed but also densities and temporal variation between sites. For the juvenile black sea bream examined at different sites, this size threshold appeared to be below 70 mm; for pollack, the size limit appeared to be about 80 mm. For pollack, this threshold appeared to be lower for La Coupe and Flicquet (compared to St Catherine Bay) since pollack were absent in September at these sites despite showing similar distributions in May and July. A similar threshold was observed for ballan wrasse juveniles.

Size distributions of *Symphodus melops*, *Callionymus lyra* and *Gobiusculus flavescens* confirmed their classification as permanent residents within seagrass in Jersey (full size range of individuals). *Gobiusculus flavescens*, the most dominant species, did not exceed 50 mm in length. These fish, whilst dominant at all sites in September, were not collected in May. A possible explanation for this is that individuals may have been too small to be captured by the trawl rather than not having arrived in the seagrass beds (see Chapter 3). The eggs of *G. flavescens* adhere to seagrass or weed and pelagic larvae hatch out at about 2.5 mm in length (Muus & Nielsen, 1999). It is unlikely that the hatched fish would drift far from the seagrass, but again this would depend on the local hydrography of each particular site.

The different monthly patterns of density observed by different species at different sites (different peaks in recruitment for the same species) may have been due to the inability of the present study to determine exact timings of events. A peak in recruitment at one site a few days before sampling and a few days after would have given peaks apparently two months apart). Changes in abundance at shorter intervals have been well documented for decapods (Gray, 1991; Worthington *et al.*, 1995).

In this study, densities of decapod crustaceans showed significant temporal patterns, the most significant of which were diel fluctuations in number of species and densities. As described in Chapter 3, many decapod species are more active at night and hence are more easily captured by the trawl (Gray and Bell, 1986), which may account for the significantly higher densities and number of decapod species found at night. Analysis of night samples, when many decapod species are at their most active, indicated a significant difference in decapod densities between north and south. These nocturnal patterns were not consistent with location (densities being so low in the south that the patterns were not detected) but in the north they were consistent between sites and across the months sampled (Figure 4.17 a,b and c).

Seasonal variability is a common feature of seagrass-associated decapods (Young & Carpenter, 1977; Vance *et al.*, 1985; Worthington *et al.*, 1995). In their six-year study, Vance *et al.* (1985) saw the abundance of the paneaid prawn *Panaeus semisulcata* change over time at three temporal scales: short term on the scale of bi-weekly, seasonally at a scale of months and annually. Annual patterns, bi-weekly and seasonal patterns of decapod abundance require further study in Jersey seagrass beds. Together with the locally and temporally variable distribution of larvae ready to settle (as proposed for fish), the reasons proposed again relate to post-settlement mortality and migration (critical size, ontogenetic habitat shifts) (Worthington *et al.*, 1995). Vance *et al.* (1985) proposed further that the primary cause for migration in juvenile prawns is related to the complexity of the seagrass (Loneragan *et al.*, 1998; Kenyon *et al.*, 1997). This, together with the proximity to deep water over wintering regions may be another reason for the spatial and temporal patterns shown by *Palaemon serratus,* with inconsistent monthly patterns of occurrence and size distributions with site. In the English Channel, *P. serratus* spawns twice between winter and spring (Quéro & Vayne, 1998), resulting in two periods of hatching (once in spring and once in summer), although older specimens also lay eggs during August to September [similar observations for other palaemonid prawns (Bauer, 1985)]. The temporal differences in densities and carapace length distributions, observed over the course of the present three sampling periods, reflect this pattern. *Processa edulis crassipes* avoids predation by being nocturnal and burying into the sediment during the day (Smaldon, 1993), which explains the absence of this species in diurnal samples and may explain greater consistencies between site within location for this species. A study on consumers in *Posidonia* beds of northwest Sardinia (Chessa *et al.*, 1989) identified *P. edulis crassipes* as an important food item in the diet of another palaemonid prawn (*Palaemon xiphias*), but little information was available on its importance as a prey item for fish. For *P. edulis crassipes*, prey availability and sediment properties may have a greater influence on the distribution of post settlement individuals than predation.

4.4.1 Summary

This study provides detailed information on changes in abundance of fish and decapods associated with the previously unstudied *Zostera marina* beds around the coast of Jersey, English Channel. In addition, the findings contribute to our understanding of the spatial and temporal associations of fish and decapods with seagrass habitats in the following ways. Firstly, they provide further evidence that, for some species, distributions and densities at larger spatial scales are not under the primary control of the physical complexity of seagrass (Bell & Westoby, 1987). Secondly, this is one of the first studies to illustrate this important point in the context of a coastal location around a small island. Jersey is not under the influence of gradients of salinity and temperature which underpin the findings of previous studies of the implications of seagrass bed location on resident fauna in estuarine or enclosed bay systems (Olney & Boehlert, 1988; Jenkins *et al.*, 1997b; Hannan & Williams, 1998). Thirdly, this study is one of the first British studies to investigate patterns in abundance and species composition of large mobile fauna of seagrass beds (*Zostera marina*) and ask questions about the roles of seagrass beds in this region, thus contributing to latitudinal and larger geographic knowledge of these habitats.

5 Habitat characteristics and spatial arrangement affecting fish and decapod assemblages of seagrass (*Zostera marina*) beds around the coast of Jersey (English Channel)

Part of this Chapter was presented:

Jackson, E.L. (2002). Habitat characteristics affecting fish assemblages of seagrass (*Zostera marina*) beds around the coast of Jersey. July 2002, Fisheries Society of the British Isles, Annual Symposium, Hull, UK. (Poster presentation).

Jackson, E.L. (2002). Habitat characteristics affecting fish and decapod assemblages of seagrass (*Zostera marina*) beds around the coast of Jersey. March 2002, 31st Benthic Ecology Meeting, Florida. (Oral presentation)

5.1 Introduction

Seagrass beds are presumed to have a fundamental role in maintaining populations of commercially exploited fish and invertebrate species. This role is achieved by providing one or more of the following: a permanent habitat, allowing completion of the full life cycle; a temporary nursery area for the successful development of the juvenile stages and/or a feeding area for various life stages or a refuge from predation (see Chapter 1). The evidence supporting the contribution of seagrass to these processes is such that the taxation benefits of seagrass restoration have been assessed favourably by economists (Anderson, 1989) and fishery agencies in many countries are commissioning research and development plans to further investigate seagrass-fishery links (Butler & Jernakoff, 1999). Seagrass beds have also been highlighted as important habitats due to the higher faunal diversity they often support (Lewis & Stoner, 1983; Sogard & Able, 1991; Orth, 1992).

There is some argument as to the relative 'value' of seagrass beds in these respects compared to other structural marine habitats, such as macro-algae stands (Sogard & Able, 1991; Borg *et al.* 1997; Heck *et al.*, 2003). However, the fact that seagrass colonises soft sediments, where algae cannot, may increase their habitat value in such areas. Seagrass beds are also identified as being highly vulnerable to various natural and anthropogenic disturbances, whether direct (for example dredging, boat anchoring) or indirect (for example eutrophication) (Walker *et al.*, 1989; Duarte & Sand-Jensen, 1990; Fortes, 1991; Orth, 2000). A global atlas of seagrasses estimates that seagrass beds have declined in area by 15% over the past decade (Green & Short, 2003). Not surprisingly, seagrass beds (*Zostera* sp.) are already one of the focal biotopes for Marine Habitat Action Plans (part of the UK Biodiversity Action Plan) and are a named component of '*Lagoons and Shallow Sandbanks*' within the EU Habitats directive (92/43/EEC). Despite this statutory recognition, few studies have assessed the functional value of different seagrass beds for fish and mobile macroinvertebrates in north western Europe (but see Pihl Baden & Pihl, 1984; Costa, *et al.*, 1994). Instead, studies have concentrated on estuaries (Elliott *et al.*, 1990), shallow sandy bays (Gibson, 1994) and salt marshes (Lafaille *et al.*, 1998). This bias may be due to potential latitudinal differences in the ecosystem functioning of seagrass beds (Heck *et al.*, 1989, 2003) or an apparently less extensive distribution of seagrasses in north western Europe. Seagrass beds have only been locally mapped in this region (e.g. Glémarec *et al.*, 1996; Frost *et al.*, 1999; Chapter 2).

In addition to latitude, the habitat 'value' of seagrass beds has been shown to vary with coastal location, depth, proximity to other habitats and position within a bay, lagoon or estuary (Figure 1.1). At the level of individual beds, the degree of spatial heterogeneity (or 'patchiness'), and other meso-scale variables, appear to have effects, as do micro-scale variables such as shoot density (Figure 1.1 in Jackson *et al.,* 2001). Seagrass beds exist naturally as vegetational units of various shapes and sizes, or have unvegetated or macroalgal regions interspersed among more homogenous seagrass areas (Robbins & Bell, 1994; Turner *et al.,* 1999). These patterns are not necessarily the result of human perturbations, and are attributable to a host of factors including water current (Fonseca *et al.,* 1983), wave exposure (Fonseca & Bell, 1998), changes in underlying sediment type (see Chapter 2), and non-human bioturbations (Townsend & Fonseca, 1998). Factors relating to the configuration of seagrass landscape are likely to influence significantly the value of meadows as fisheries habitats (Kirkman, 1996; Bajjouk, *et al.,* 1996). In Chapter 4, it was proposed that, whilst many decapod species showed variability in abundance at a coastal location level, species diversity (decapods and fish) and the densities of many fish species showed variability at the scale of individual beds. Also, in some cases, lack of significant differences between seagrass beds may have been due to the high variation between individual trawls. Results from Chapter 4 indicated that further investigation was required to assess the possible influences of seagrass bed landscapes and environment on fish and decapod distributions in Jersey.

A number of different models have been proposed in the past to describe the relationships between seagrass habitat characteristics and large mobile fauna. Figure 5.1 summarises some of the different models suggested from key studies, at both the landscape level (Figure 5.1a) and plant level characteristics (Figure 5.1b). This Chapter addresses whether or not the patterns observed in Jersey seagrass beds support such models. At the landscape level, due to the management implications and results of terrestrial studies, investigations have concentrated on the effects of seagrass habitat fragmentation. There also appears to be an increasing move toward the characterisation of natural seagrass meadows at scales of hectares using the concept of landscape ecology (Robbins & Bell, 1994; Kendrick *et al.,* 1999; Hovel & Lipcius, 2001; Salita *et al.,* 2003), with landscape defined by the predominant mosaic and patchiness of different habitats. At its simplest, fragmentation is observed as a reduction in the area of seagrass cover, decrease in patch size and an increase in the distance of between patches (decreased connectivity).

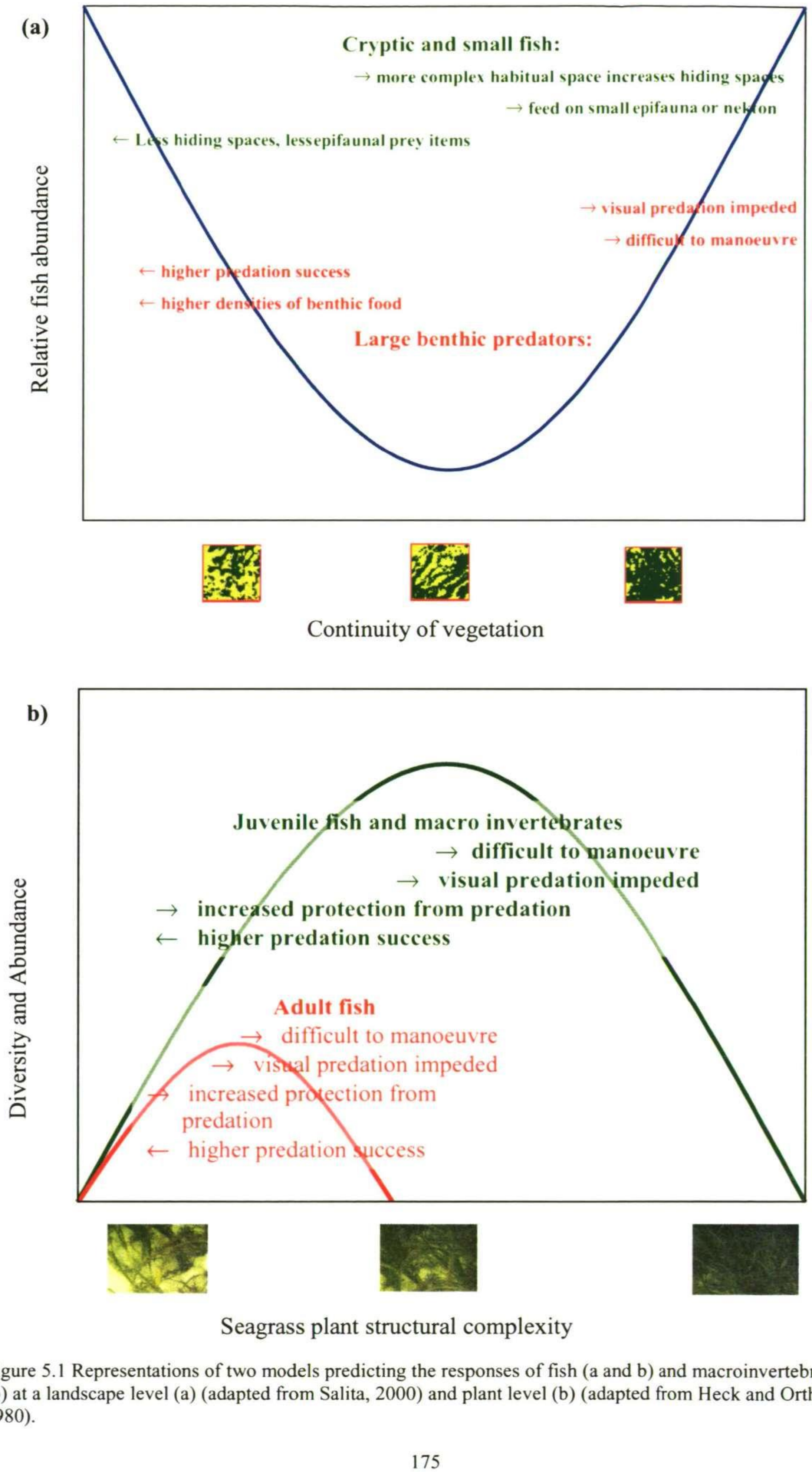


Figure 5.1 Representations of two models predicting the responses of fish (a and b) and macroinvertebrates (b) at a landscape level (a) (adapted from Salita, 2000) and plant level (b) (adapted from Heck and Orth, 1980).

The predominant concern is that loss of seagrass may result in a reduction of species diversity. One of the main reasons put forward for this prediction is based upon the general principle that species diversity is higher in seagrass compared with adjacent bare sand habitats (e.g. Arrivillaga & Baltz, 1999; but see Hanekom & Baird, 1984; Jackson *et al.*, 2002). This difference is often attributed to increase protection from predation and food availability in seagrass beds, together with the overall stability of the environment. Alternatively, patchy seagrass beds would provide a more diverse habitat, particularly if the seagrass landscape was a mosaic of sand, seagrass and algal habitats. This would attract fish with both preferences for vegetation and bare substrata, which follows Leopold's (1933) theory of increased habitat diversity leading to increased faunal diversity.

However, as with the fragmentation of any habitat, ecologists have recognised increasingly that small changes in 'patchiness' of seagrass habitat can cause significant shifts in the distribution of species. The commonly-proposed mechanisms behind these changes relate to immigration and extinction rates [but see Hart & Horwitz (1991) for a summary of other explanations]. For example, it is proposed that fragmentation can modify water flow and available habitat edge and, thereby, alter larval settlement (immigration rates). Bowden *et al.* (2001) looking at the influence of seagrass patch size on the infauna, argued that the greater number of taxa found in larger patches may be due to greater immigration via dispersive larvae. Such a theory may be true for the larger mobile epifauna of the seagrass bed which have dispersive larvae. In contrast, other studies of seagrass systems suggest that many small patches may increase the overall probability of larvae, or other immigrants encountering seagrass, increasing overall colonisation of the smaller patches compared to larger patches (McNeill & Fairweather, 1993; Sogard, 1989). Of course, a greater number of species then depend on post-settlement processes such as emigration and extinction. Recently, the 'terrestrial debate' as to whether a single large patch will contain more or less species than several small patches (single large or several small, SLOSS) has been experimentally tested using seagrasses, but with ambiguous results (McNeill and Fairweather, 1993; Eggleston *et al.*, 1998), warranting further investigation.

Fragmentation may also result in modifications of foraging behaviour, predator distribution (and success), and the overall environmental stability of the habitat (McNeill & Fairweather, 1993; Eggleston *et al.*, 1998; Bowden *et al.*, 2000). For macroinvertebrates, increase in seagrass patchiness has been demonstrated to increase mortality rates due to increased predation intensity (Irlandi *et al.*, 1995), although growth increased with fragmentation of the seagrass habitats. Conversely, Hovel and Lipcius (2001) found that as seagrass patch area increased, juvenile crab survival decreased. They suggested that although predators may not avoid patchy areas, foraging efficiency may be reduced, since the search for appropriate feeding patches takes longer in fragmented seagrass (Hovel & Lipcius, 2001). Similarly Eggleston *et al.* (1998) found higher densities of grass shrimp at small seagrass patch sizes, and Loneragan *et al.* (1998) found lower numbers of juvenile fish and prawns with increasing seagrass cover. Many of these studies sampled only within the seagrass beds and were not concerned with the overall habitat value of the landscape mosaic.

Similar studies with fish communities are less frequent. McNeill and Fairweather (1993) reported that two small beds of *Zostera* and *Posidonia* supported significantly greater species diversity than a single large bed. If patchiness facilitates foraging (Irlandi, 1994), it may lead to a higher proportion of active foraging species to be found on patchy beds. Assessing relative fish abundance in seagrass landscapes in the Philippines, Salita *et al.* (2000, 2003) found an inverse parabolic response to increasing continuity of seagrass (Figure 5.1a). Their explanation was that in very fragmented seagrass habitats there were high numbers of large benthic feeders (Salita *et al.*, 2003). However, in more continuous seagrass beds, these were replaced by high numbers of small, juvenile or cryptic species feeding on small epifauna or nekton where protection from visual predators was afforded and the movements of larger species impeded (Salita *et al.*, 2003).

Of course other scales may also be important. Since the 1980s, seagrass research has focused on the role of small-scale structural complexity (such as biomass, density, canopy height and percentage cover) in determining faunal species richness and density. Natural seagrass beds can be highly heterogeneous in terms of, for example, leaf density and height within the bed. Increased abundance and diversity of fishes and decapods associated with seagrass meadows have frequently been positively linked to the complexity of the seagrass canopy (Heck & Orth 1980; Bell & Westoby 1986b; Ansari *et al.* 1991), although the models proposed do differ. Jenkins and Sutherland (1997) saw an increase in the number of juvenile and cryptic species as seagrass complexity increased, but there was no change in the overall species diversity. Worthington *et al.* (1992b) found that the number of fish and decapod individuals increased with increasing leaf density, but like others, found that the relationship was not a simple linear one (Nelson, 1979; Heck & Thoman, 1981; Lipcius *et al.*, 1998).

These authors showed that at a certain level of seagrass 'complexity' a threshold was reached, possibly where protection from predators was significantly greater above a particular plant density (see also Chapter 1 section 1.3.2). Heck and Orth (1980) proposed the model that seagrass canopy protects juvenile fish and mobile invertebrates from predation (providing increased hiding places, Sebens, 1991) and so their survival and density increases as canopy complexity increases, up to a point where the seagrass impedes movement. A similar pattern was suggested for adult fish but at a lower canopy complexity level (Figure 5.1b). This theoretical model was supported by the work carried out by Salita *et al.* (2000).

Not surprisingly, the relationships between seagrass bed and plant characteristics and large mobile fauna are often found to be species specific due to factors such as the size, behaviour, mobility and the dispersal ability of the organism and its perception of patchiness (Eggleston *et al.*, 1998). When evaluating the relative importance, or predicting the carrying capacity of different seagrass habitats, it is important to consider, *a priori*, whether the complexity measures employed are directly relevant to the group of organisms under investigation (Attrill *et al.*, 2000). Attrill *et al.* (2000) advocated the construction of complexity perception windows for different sized organisms (see Attrill *et al.*, 2000; Figure 2; see also Kotliar & Wiens, 1990), which for megafauna (> 20mm) were at the scale of leaf length and bed size/patchiness. These authors make the point that there may be a cascade effect, whereby, due to predation or food resources, smaller scale attributes affecting smaller sized organisms, may indirectly affect the distributions of larger organisms (Attrill *et al.*, 2000) and drive the higher level processes of population dynamics and community structure. The target species in the present study were classed as megafauna (> 20mm) and macrofauna (1mm to 20mm). With two size ranges of target species it was decided *a priori* to look at both the plant and landscape level structure of the seagrass.

In addition to the structure of the seagrass beds at the landscape and plant level, several studies have highlighted the importance of the depth of the seagrass bed (irrespective of the structural aspects) (see Chapter 1 section 1.6.1). Bell *et al.* (1992) examined differences in fish assemblages in deep and shallow margins of the seagrass *Posidonia australis* and reported significantly more fishes in deep seagrass than shallow. In French *P. oceanica* beds, however, Francour (1997) identified lower fish densities in deeper meadows when compared with shallow beds. Coles *et al.* (1993) found a similar situation for juvenile prawns. In shallow seagrass beds, the refuge status may be related to both the complexity of the seagrass and the depth of the bed. Not only is the vulnerability of larger piscivores to avian predation thought to be greater in shallow waters, but also these larger fishes may have difficulty moving and foraging and must tolerate higher fluctuations in temperature and oxygen (Ruiz *et al.* 1993, Pardieck *et al.* 1999). Similarly, Bell & Harmelin-Vivien

(1982) found that juveniles of many species were more abundant in shallow sublittoral rocky reefs than *Posidonia* beds at depths of 15 to 20m. They suggested that this difference was due to pelagic larvae being driven to the shore by currents and settling on the most readily available shelter.

5.2 Aims and Objectives

The aims of this study were to measure the configuration and composition of subtidal seagrass landscapes around Jersey and to understand their influence on the distribution of large mobile fauna. Based on the common findings of the models described, some key patterns were hypothesised for the fauna inhabiting seagrass beds in Jersey. Firstly, it was hypothesised that an increase in the diversity of the habitat mosaic would result in an increase in overall species diversity. As fragmentation of the seagrass landscape increased, it was proposed that species diversity, the density of decapod crustaceans and the number of large benthic predators would increase, but the number of small and cryptic species of fish would decrease. At a smaller scale, cryptic species of fish, juveniles and mobile decapod crustaceans would increase with seagrass structural complexity (canopy height, epiphytal load and homogeneity of seagrass) as large adult fish decrease. Increasing depth, it was expected, would be associated with an increase in larger predatory fish and a decrease in juvenile fish, prawns, and total fish densities.

Finally, the majority of studies investigating the patterns described here were undertaken only during the day. At night it is hypothesised that many of these patterns may change, as species move out of the seagrass patches to forage, become less susceptible to predation or become more active at night (Chapter 3). In order to make these comparisons both day and night-time sampling were carried out in the present study and the patterns compared separately with predictions.

These data are valuable in distinguishing and understanding potentially important processes, and can be used by local fishery agencies to predict the relative importance of seagrass beds (to aid conservation designation) or the consequences of different perturbation scenarios.

5.3 Materials and Methods

5.3.1 Study location and site selection

All fieldwork was carried out around the coast of Jersey, which, although with a total area of only 116 km^2, is one of the larger islands in the Normano-Breton Gulf (English Channel, 49° 15 N, 02° 10 W; see Chapter 2 Figure 2.1a). Seagrass (*Zostera marina*) is not distributed evenly around the coast of Jersey (see Chapter 2) and the absence of seagrass on the north and west-facing coasts has been attributed to a steeply shelving seabed and high wave exposure. Sites of seagrass studied were, therefore, restricted to the north-eastern, eastern, south-eastern and southern coast of the island. Chapter 2 illustrated how, due to Jersey's unique physical setting and varied coastline, the distribution and landscape patterns of the *Zostera marina* habitats found there are diverse.

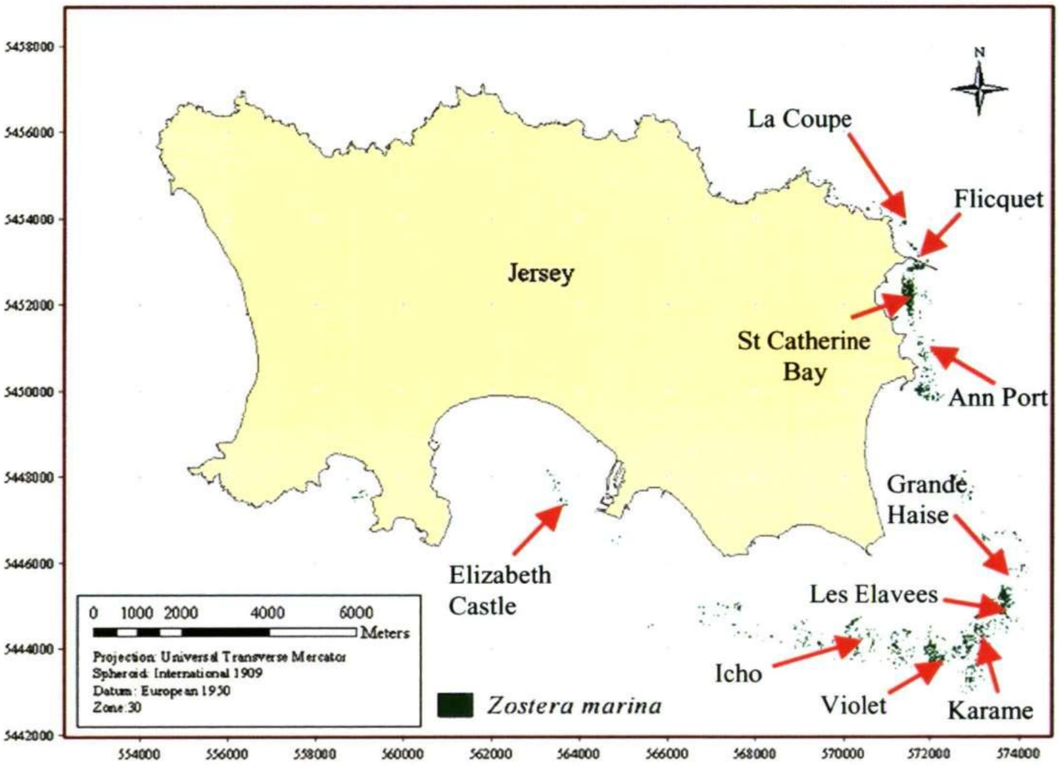


Figure 5.2 Distribution of seagrass around Jersey and the locations of the sites sampled in the present study.

Seagrass beds around the island differ significantly in size, density, landscape pattern and adjacent habitat, all attributes that have been shown previously to influence their functions as habitats to large mobile fauna (Figure 1.1). Despite these differences, the relatively small size of the island means that the seagrass beds are geographically close, sharing larger scale influences such as tidal factors, water currents, climatic conditions and species biogeography. The combination of which potentially makes Jersey a good location in North-Western Europe to investigate some of the seagrass habitat characteristic- faunal links.

In this study, a seagrass bed was defined as a separate bed where the shortest distance from the edge of the seagrass bed to another patch of seagrass was greater than the greatest distance from the epicentre of the bed to an edge. Of the seagrass beds defined in this way, ten were selected at random (each bed was given a number and random numbers were generated using the 'RANDBETWEEN' function in Microsoft Excel©). Figure 5.2 shows the location of the selected beds in relation to each other and the coastline.

5.3.2 Estimation of habitat variables

5.3.2.1 Measurement of physical variables

Although between site differences in salinity and water temperature were considered to be negligible because of the close proximity of the sites and the strong tidal mixing (Pingree, & Maddock, 1979), seawater temperature and salinity (refractometer) were measured on each sampling occasion. Surface water temperatures recorded around Jersey during the study ranged from 16.8 to 18.4° C, with salinity fully marine at all study sites (> 32 p.s.u.). ANOVA showed no significant difference in salinity and temperature (all less $p > 0.05$) between sampling time or location, and these variables were not used in further analysis.

The mean depth of each trawl replicate was calculated using ArcInfo™ version 8, by overlaying the trawl paths onto the Biosonics DT4000™ derived, bathymetric maps (see Chapter 2, Section 2.2.3.2; example shown in Figure 5.3). Although the trawls were all carried out during low spring tides at slack water, tidal heights would vary between sampling occasions and the time of each trawl was used to determine the height above chart datum.

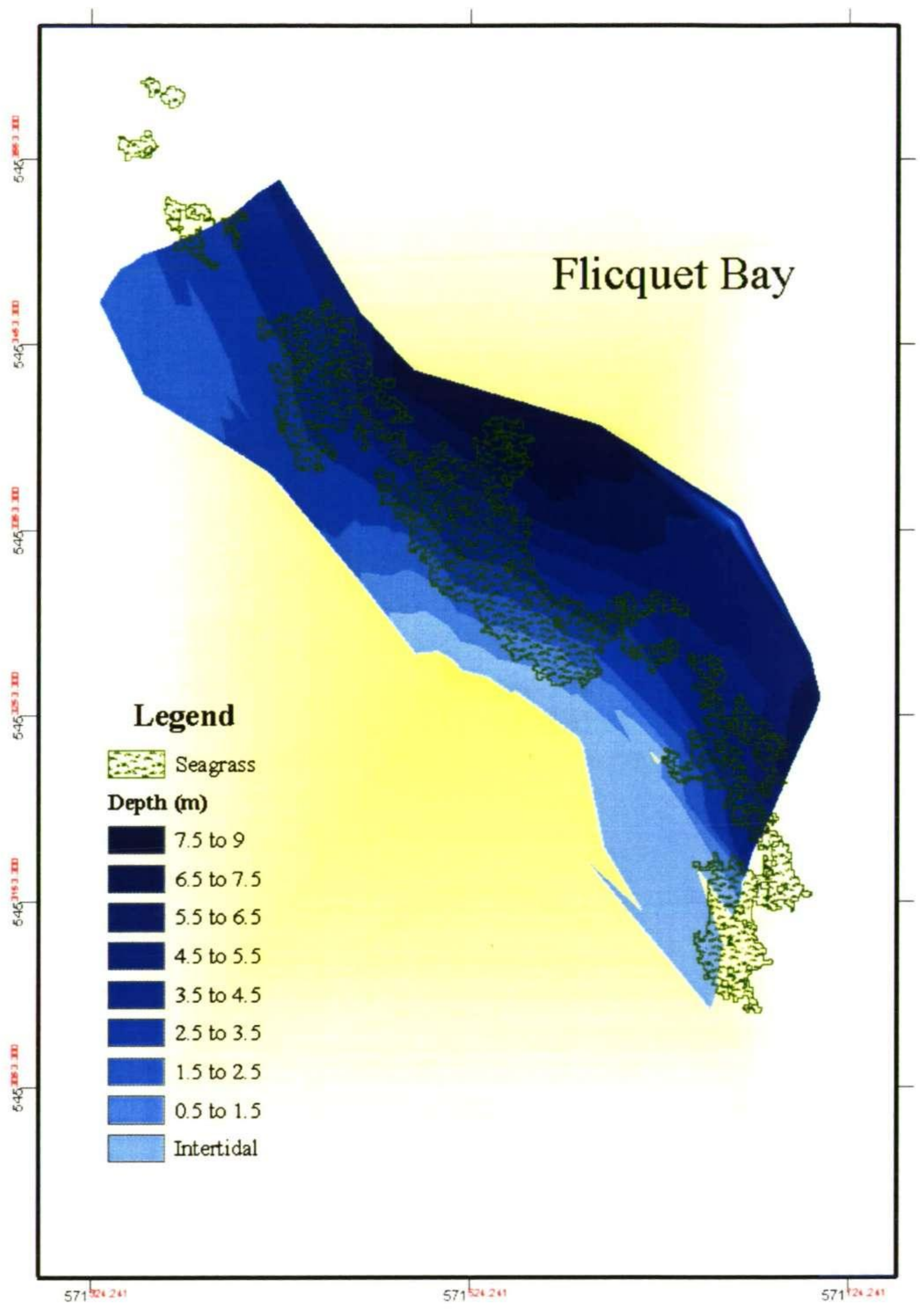


Figure 5.3 Example of a Biosonics DT4000^{TM} derived, bathymetric map with seagrass bed overlaid at Flicquet Bay on the north East coast of Jersey

5.3.2.2 Measurement of trawl-specific variables

Many previous fauna seagrass relationship studies measured seagrass leaf length as a variable (Bell & Westoby, 1986b; Irlandi *et al.*, 1995; Salita, 2000). However, as shown in Chapter 2, even at slack tide blades of seagrass do not naturally stand straight up. Wave movements, epiphyte cover and epiphytic fauna, all contribute to the leaf blades bending. It is argued that canopy layer height, as opposed to seagrass blade lengths, is a better measure of the habitat from a faunal perspective. Therefore, for the present study, canopy height was used. For each trawl, the mean seagrass canopy height was estimated using ArcInfo™, by overlaying the trawl paths onto the Biosonics DT4000™ derived maps of leaf height within the seagrass beds (see Chapter 2, section 2.2.3). Shoot density was measured *in situ* using a team of two SCUBA divers. The minimum distance from each trawl to the outer edge of the seagrass was also measured using the tools within ArcInfo once the trawl path coverage had been overlain onto thematic maps of the seagrass coverage (Table 5.1).

A measure of transect heterogeneity was calculated as a fractal dimension for each trawl (Burrough, 1983; Manzanera & Romero, 2000). Using ArcInfo, an intersect-overlay was used to combine the coverage of the trawl transect and the corresponding area from the thematic habitat layer. Along each section, the position of each seagrass to unvegetated sand or algae transition was recorded as the distance (to the nearest metre) to the transect origin. Next, for each section, the length of seagrass (L) was measured at increasing levels of resolution [(R): 1 m, 2 m, 4 m and 8 m]. The slope of the line obtained by regressing log(L) on log(R) gave the fractal dimension (Burrough, 1986). Using this method, a dimension of zero implies strict spatial dependence (homogeneity) and as the value increases towards one, reflects an increase in heterogeneity. Whilst this measure gives an indication of the patchiness of the seagrass in the trawl swept area, it does not differentiate between non-seagrass habitats. Therefore, to compliment the measure of transect heterogeneity, the percent of trawl swept area that was algae, was calculated.

5.3.2.3 Measurement of seagrass bed-specific variables

Seagrass samples collected in the field from each seagrass bed were used to assess the epiphytic load (full methodology can be found in Chapter 2). In the laboratory, seagrass samples were first rinsed with distilled water to remove the salt. Vegetative shoots were separated into leaf blades and sheaves, and any remaining root rhizomes were removed. Each leaf blade was scraped with a razor blade to remove epiphytes; the latter were identified to genus (Kentula & McIntire, 1986; Novak, 1984) and weighed separately.

Each sub sample was blotted with absorbent paper before wet weighting and dried to constant weight at a temp of 100 °C. The index of epiphytic load was calculated as the weight of epiphytes divided by the sum of mean leaf length, width and number.

Table 5.1 Trawl specific, seagrass landscape specific and physical variables used to explain distributions of fish and decapod assemblages. † entered as an independent variable into multiple regression models.

Variable	Units	Method of measurement	Level
Physical			
Mean water temperature	° C	Temperature gauges	Location/ Date
Mean salinity	‰	Refractometer	Site/ Date
Mean depth of trawl (chart datum) †	M	Biosonics DT4000	Replicate
Trawl specific variables			
Estimated Mean seagrass canopy height †	M	Biosonics DT4000/ SCUBA	Replicate
Distance to seagrass bed edge †	M	Aerial photographs/ GIS	Replicate
Transect heterogeneity †	Index	Aerial photographs/ Biosonics DT4000/ GIS	Replicate
Percent algae in trawl swept area †	%	Aerial photographs/ Biosonics DT4000/ GIS	Replicate
Seagrass landscape specific variables			
Epiphytic load index †	Index	SCUBA collections	Site
Contrast weighted edge density	$m.ha^{-1}$	Aerial photographs/ GIS	Site
Area weighted mean perimeter area ratio	Ratio	Aerial photographs/ GIS	Site
Landscape shape index	Index	Aerial photographs/ GIS	Site
Area weighted mean core area	Ha	Aerial photographs/ GIS	Site
Contagion Index	Index	Aerial photographs/ GIS	Site
Area weighted mean core area	Ha	Aerial photographs/ GIS	Site

Previous studies suggest that landscape contiguity, and not just the typical seagrass metrics such as biomass, shoot density and leaf length, may be an appropriate measure of the landscape arrangement and may have associated effects on how organisms perceive and move through the landscape (*sensu* With & Crist, 1995, in Fonseca & Bell, 1998; Irlandi *et al.,* 1995). In the present study, the characteristics of the spatial configuration of each seagrass landscape mosaic (seagrass, unvegetated sand and algae) were quantified from the thematic images (see Chapter 2, Section 2.2), using a number of landscape metrics. Calculations of the metrics were carried out using the spatial statistical software FRAGSTATS version 3.3 (McGarigal *et al.*, 2002). The metrics were calculated both at a landscape level (extent determined here by a 100m buffer around each defined seagrass bed) and at the seagrass component level within each landscape. All metrics were selected *a priori* as the most appropriate measures of the characteristics under study (continuity, fragmentation, amount of edge and core areas, habitat diversity). To allow comparisons between different sized landscapes, the metrics calculated were chosen on the basis that they were size independent (Jaeger, 2000).

The level of fragmentation of each seagrass landscape was measured using a combination of five complimentary metrics. Firstly, as a measure of complexity of seagrass patch shape, the perimeter to area ratio (PARA) was calculated. PARA is equal to the ratio of the perimeter of the seagrass patch (m) to the area (m^2), summed across the entire seagrass class. To allow comparisons between different sized landscapes (area weighting, AW), this metric was multiplied by the proportional abundance of the patch [that is patch area (m^2) divided by the sum of patch areas].

The PARA metric does not give a good indication of patch shape. For example, if shape is constant, increasing patch size is inversely proportional to the PARA (McGarigal *et al.*, 2002). To overcome this limitation, McGarigal and Marks (1995) suggested using the shape index proposed by Patton (1975), a diversity index based on shape for quantifying habitat edge for wildlife species as a means for comparing alternative habitat improvement efforts (for example, landscape clearings). The Landscape Shape Index (LSI) equals the total length of seagrass edge divided by the minimum length of seagrass edge possible for a maximally aggregated class [that is, if all the patches were amalgamated into a single compact patch (almost square)]. An LSI of 1, therefore, denotes a single compact patch of seagrass and the LSI increases (without limit) as the seagrass becomes more disaggregated.

LSI, whilst a good indicator of the aggregation of seagrass patches, does not give any indication of the degree to which a patch may be broken up (subdivided) into separate patches (fragments). Therefore, as a measure of 'graininess' of the landscape (many small patches or fewer larger patches (McNeil & Fairweather, 1993), the Contagion index was calculated. This index describes how interspersed and disaggregated habitats are within the landscape and increases (0 to 100) as a landscape is dominated by a few large patches of seagrass and decreases in value with increasing subdivision and interspersion of patch types.

Further quantification of fragmentation is necessary with regards to its effect on the amount of core area in the landscape. Core area is the area of each patch deemed to be unaffected by the edges of the patch, where predation and foraging success and disturbance may be greater. The area-weighted mean core area was calculated, as the mean of all the core area (m^2), based on a specified edge depth of 1m of patches within a landscape. Once again, each core area was multiplied by its proportional abundance in the landscape, to standardise for differences in landscape area. Core area metric integrates patch size, shape and edge effect distance (smaller patches with greater shape complexity have less core area).

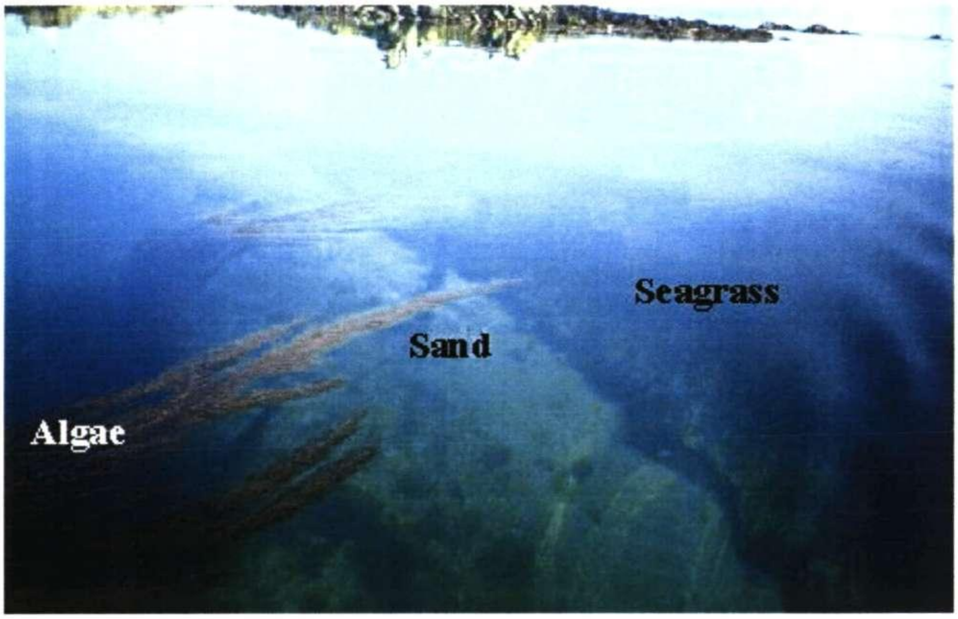


Figure 5.4 A close up image of the sort of habitat edges encountered

Finally, as a measure of the relative amount of seagrass edge found in the seagrass landscape, the edge density was measured at the seagrass component level. Although this measure was used as an indication of the areas susceptible to erosion and re-growth in Chapter 2, here the edge density was more an indication of sites of habitat change as perceived by the organisms being studied. It is unlikely, however, that organisms exhibited a binary response to habitats (patch types such as seagrass) but rather use the habitats proportionate to the fitness they confer to the organism. Movement along suitable habitat patches is usually a function of the character of the intervening habitats (Micheli & Peterson, 1999). For these reasons, contrast weighted edge density was used, which in addition to standardising edge to a per unit area basis, reduces the length of each edge segment proportionate to a predetermined degree of contrast. Seagrass to unvegetated sand is assumed to have a greater contrast to that of seagrass to macroalgal stands (Figure 5.4).

5.3.3 Sampling the fauna

Based on the results of Chapter 3, two types of fishing gear (trawl and beach seine) were selected to sample the range of target species within the identified seagrass habitats. However, due to the depth limits of the beach seine and the difficulty in accessing some of the randomly-selected seagrass beds from the shore, trawling was the main sampling method. The beach seine was deployed at only four sites to identify any larger species which trawling may have missed (Chapter 3 showed that the latter method was biased towards smaller size ranges of fish and decapods).

Results of the temporal variation study (Chapter 4) showed significant differences in the time of sampling during the summer. Since sampling all these situations at this level was beyond the resources available, sampling was carried out from the 28th July to the 30th August to coincide with what appeared to be a peak in the densities and diversity of species inhabiting the beds. Results from Chapters 3 and 4 identified significant day/night differences for many species which, in some instances, were attributed to movements in and out of the seagrass beds; therefore, day and night-time sampling was carried out. Trawls were replicated 4 times in the day and four at night. Independent night and day sampling periods were defined according to whether the sun was above (day) or below (night) 5° to the horizon; sampling was carried out within 1h either side of low tide (choice based on the results of the gear trial). For each sampling session, individual sample positions were randomly selected within the seagrass bed. For all methods, the only stipulation to randomness (in order to ensure independence) was that no sampling paths or stations overlapped. Positions were located in the field using differential global positioning systems (DGPS). Usually, DGPS is found to have a working error of 2 to 4m (Green *et al.*, 2000) although observations during previous studies found larger discrepancies than this (error of up to 20m). More details on gear deployment are presented in Chapters 3 and 4.

The distance covered by the trawl (which varied due to water currents and wind speed) was recorded using an odometer, attached to the shoe of the trawl (see above). Odometer recordings, in combination with trawl track distance estimated from the DGPS, allow for reasonably accurate determinations of the area sampled. Whilst the start locations for each trawl track were allocated randomly beforehand, some adjustments were made in the field due to unmarked objects (yachts, moorings, pot lines). Initial plans to carry out Biosonics transects concurrent with trawls was deemed impractical. Therefore, each replicate sample transect was built into a coverage in ArcInfo™ and overlaid on the contour maps of seagrass coverage, leaf canopy height and depth, the corresponding cross section taken and the mean of each of these variables estimated for each replicate transect.

For the beach seining, a 20 m-long seine with a 2 m drop and a stretched mesh of 10 mm was used to sample an area of approximately 25 m^2. Sampling was restricted to water depths less than 1.5 m and, since the seagrass beds around Jersey are entirely subtidal and tidal ranges reach 11 m, sampling was limited to low water of spring tides. Also, whilst the seagrass bed extended to approximately 7 m (chart datum), only the shallow margins of the delimited area were accessible, which reduced the choice of possible start positions. More details of how the beach seine was deployed and the sample recovered are given in Chapter 3 (Section 3.3.4.2.). Beach seine samples were collected during the day and at night (three replicates during each) at four locations (St Catherine Bay, Ann Port, Grande Haise and Les Elavees).

Samples were preserved in 10% formalin and later transferred to 70% ethanol. Macro-faunal individuals were identified to species (Hayward & Ryland, 1996; Quéro & Vayne 1998; Whitehead *et al.,* 1986; Wheeler, 1969). Commercially and recreationally exploited species (i.e. those landed and recorded by the Jersey fleet from Jersey territorial waters by commercial fishermen in the Normano Breton Gulf and species captured by recreational fishermen, including 'peche a pied') were identified for specific analyses (States of Jersey Department of Agriculture and Fisheries, 2001, Quéro, 1997, Cohen *et al.,* 1990, Froese & Pauly, 2003). All decapods, fish and cephalopod molluscs were measured (± 1 mm) using a rule to standard length for most fish (total length for Sygnathidae, Cottidae and Anguillidae), carapace width for crabs (carapace length for Majidadae), and carapace length for shrimp and prawns. Definitions of juveniles were based on data from the texts on the average size of maturity for the time of year and closest location to the study site (Hayward & Ryland, 1996; Quéro, 1997; Quéro & Vayne, 1998; Whitehead *et al.,* 1986; Wheeler, 1969; Froese & Pauly, 2003). Following the definitions given in Chapter 4, all fish were classified into an ecological grouping of the fish individuals (adapted from Kikuchi, 1974) based on size and habit (temporary juveniles; temporary mature; permanent juveniles; small permanents; large permanents; cryptic permanents).

5.3.4 Statistical analysis

In all analyses, day and night faunal samples were separated to identify any expected differences in observed patterns. A two-factor ANOVA was carried out on trawl-specific variables to verify that there were no significant differences between day and night samples for the independent variables. Factor one (time) was fixed and had two levels (day and night). Factor two (site) again fixed, was orthogonal to time and had eight levels (St Catherine Bay, Flicquet, La Coupe, Les Elavees, Violet, Karame, Icho and Elizabeth Castle).

Faunal samples were first analysed using modules of the software PRIMER (Plymouth Routines in Marine Ecological Research Version 5; Carr, 1996). Multidimensional scaling (MDS) was carried out on fish and decapod assemblages to distinguish potential similarities between different seagrass bed sites in 2-dimensional space. The Bray Curtis similarity index was used in all analyses, following log (x+1) transformations, which minimised the stress of the MDS plots and stabilised the variance of the abundance data (down weighted the influence of dominant species). Regression analysis was used to explore potential influences of habitat characteristics on this variability (see explanation of regression method below).

Using several landscape metrics to measure similar phenomena can result in a high degree of multicolinearity among variables (Li and Reynolds, 1995), which can cause difficulties in later interpretation. Pearson product moment correlation coefficients were carried out and relationships were detected for the landscape level variables. However, since the chosen metrics measured different aspects of the seagrass landscape configuration, composition and context, and were meaningful to the questions being asked, they were not considered to be redundant. To overcome these problems, a Principal Components Analysis (PCA) was carried out (Johnson & Cage, 1997). The PCA was based upon a correlation analysis. Only PCs with eigen values greater than 1.0 were considered and significant component weights were evaluated as > 0.40. PCA linearly transformed the original variables into a new set of uncorrelated principal components (Table 1a) against which ensemble variables (total densities, species numbers, diversity and ecological fish groups) and densities (log x+1 transformed) of the most frequently occurring individuals (see Table 1b) were regressed. Target species were selected using the following criteria: only fish and decapod species with greater than 10% contribution to the total abundance were selected for individual analysis and those species where ANOVA produced very low F values ($p > 0.9$) were omitted due to extreme variability in catch due to patchy distribution and gear selectivity (based on the results of Chapter 3). Some species were omitted because they were ubiquitous amongst all habitats in the area (which diluted between-station differences in species composition), precedence was given to exploited species.

Prior to regression analyses, the Kolmogorov-Smirnov test of normality was computed for each variable (dependent and independent). Where the statistic was significant, the hypothesis that the respective distribution is normal was rejected. Species densities better described by a log-normal than by a normal distribution were log (x+1) transformed. Any variables that still gave significant statistics were left out of further analyses (which assumed normal distribution). For these dependent variables, non-parametric correlation coefficients were carried out. Due to the high number of ties expected (due to zero abundance) the Gamma correlation statistic was used instead of the more commonplace Kendall *tau* (difference between the probability that the two variables are in the same rank order, minus the probability that order differs, divided by 1 and minus the probability of ties, Statsoft, 2003). Analyses were carried out using the STATISTICA package (Statsoft, 2003). For those dependent variables conforming to normality, the contributions of habitat variables as predictors were evaluated using stepwise multiple linear regression models ($F_{(1,32)}$ to enter had a criteria of $p < 0.05$). Pearson product moment correlation coefficient was used to produce a correlation matrix of all independent variables to check for co-linearity and bivariate plots were displayed to check that the relationships were linear. For some ensemble variables and species, values peaked at intermediate levels of independent variables and, in such cases, second degree polynomial regressions were run in addition to the linear model. Residuals were plotted against the independent variables and examined for patterns, outliers or heteroscedasticity, which would violate the assumptions of the regression.

5.4 Results

5.4.1 General description of assemblages

A total of 64 trawls and 21 beach seines sampled 10 seagrass landscapes around the island of Jersey. From these, 10 935 decapod crustaceans (32 species from 11 families), 4942 fish

(43 species from 20 families) and 41 cephalopod molluscs (3 species) were collected (see Tables 5.2, 5.3 and 5.4). Of the 43 species of fish, 19 had direct economic value, as did five of the species of decapod and two of the species of cephalopod mollusc.

Table 5.2 List of fish species collected during beach seining and trawling with information on their total abundance, frequency of occurrence in samples and range of total lengths. * = exploited species.

Family	**Species**	**Abundance**		**Frequency**		**Range of total length (mm)**
		Day	**Night**	**Day**	**Night**	
Gobiidae	*Pomatoschistus minutus*	1466	1069	44	20	13 to 57
	Gobiusculus flavescens	527	413	67	35	12 to 45
	Pomatoschistus pictus	59	65	36	17	5 to 43
	Pomatoschistus microps	8	71	17	10	12 to 47
	Gobius paganellus	8	4	4	2	15 to 46
	Gobius niger	2	5	4	3	14 to 110
Labridae	*Labrus bergylta**	89	157	42	24	9 to 195
	*Symphodus melops**	99	55	56	26	8 to 152
	Ctenolabrus rupestris	10	12	12	6	12 to 100
	*Labrus mixtus**	2	5	2	1	20 to 92
	Centrolabrus exoletus	5	0	3	0	21 to 148
	Symphodus bailloni	4	1	4	1	20 to 142
	Labrus bimaculata	1	0	1	0	142
Gadidae	*Pollachius pollachius**	38	197	31	16	46 to 285
	*Trisopterus minutus**	9	20	12	6	56 to 92
	*Trisopterus luscus**	3	24	10	8	52 to 109
	Gaidropsarus mediterraneus	1	0	1	0	32
Callionymidae	*Callionymas lyra*	79	22	20	9	11 to 162
Atherinidae	*Atherina presbyter**	12	70	9	6	20 to 155
Sparidae	*Spondyliosoma cantharus**	53	27	28	10	10 to 100
	*Diplodus sargus**	0	4	2	2	16 to 121
Cottidae	*Taurulus bubalis*	5	32	19	14	32 to 109
Gasterosteidae	*Spinachia spinachia*	18	16	21	10	52 to 103
Lotidae	*Ciliata mustella**	3	23	6	4	25 to 117
Syngnathidae	*Syngnathus acus*	11	12	7	2	28 to 453
	Entelureus aequoreus	8	7	14	7	223 to 443
	Syngnathus typhle	8	6	10	3	34 to 388
	Nerophis opidion	2	7	5	3	33 to 127
Pleuronectidae	*Pleuronectes platessa**	21	4	5	1	11 to 77
Soleidae	*Solea solea**	6	8	8	4	31 to 241
Serranidae	*Dicentrachus labrax**	10	1	4	1	29 to 481
Cyclopteridae	*Cyclopterus lumpus**	1	4	5	4	18 to 30
Gobiesocidae	*Lepadogaster candelloni*	5	9	8	5	6 to 49
	Lepadogaster lepadogaster	2	1	3	1	5 to 6
	Apletodon microcephalus	2	1	3	1	7 to 12
Rajidae	*Raja clavata**	0	3	3	3	246 to 286
Ammodytidae	*Ammodytes tobianus**	1	1	2	1	24 to 81
	*Hyperoplus lanceolatus**	1	1	2	1	83 to 104
Anguillidae	*Anguilla anguilla**	0	2	1	1	385 to 679
Liparidae	*Liparis montagui*	2	0	1	0	29 to 33
	Chelon labrosus	1	0	1	0	336
Zeidae	*Zeus faber**	0	1	1	1	140

Fish from two families, the gobies (Gobiidae) and the wrasse (Labridae), dominated both trawl and beach seine samples. The gadoid *Pollachius pollachius* was also numerically abundant and occurred frequently in the beach seine samples. Overall, the most abundant fish was the sand goby (*Pomatoschistus minutus*); however, this schooling species was collected in fewer instances than one of the next most dominant (also schooling) species, the two-spot goby (*Gobiusculus flavescens*), which dominated the trawl samples. Small and cryptic fish species (for example, the fifteen-spined stickleback, *Spinachia spinachia*, and pipefish such as the broad-nosed pipefish, *Syngnathus typhle*) made up a large proportion of samples. Populations of many larger fish species were dominated by young of year and juvenile life-history stages (for example, *Symphodus melops*, *Labrus bergylta* and *Callionymas lyra*) and, whilst the total length ranges of the fish collected ranged widely, the majority of individuals were under 100 mm in total length (Figure 5.5 and 5.6) with significantly ($p<0.01$) larger sizes found during night sampling (Kolmogorov-Smirnov test).

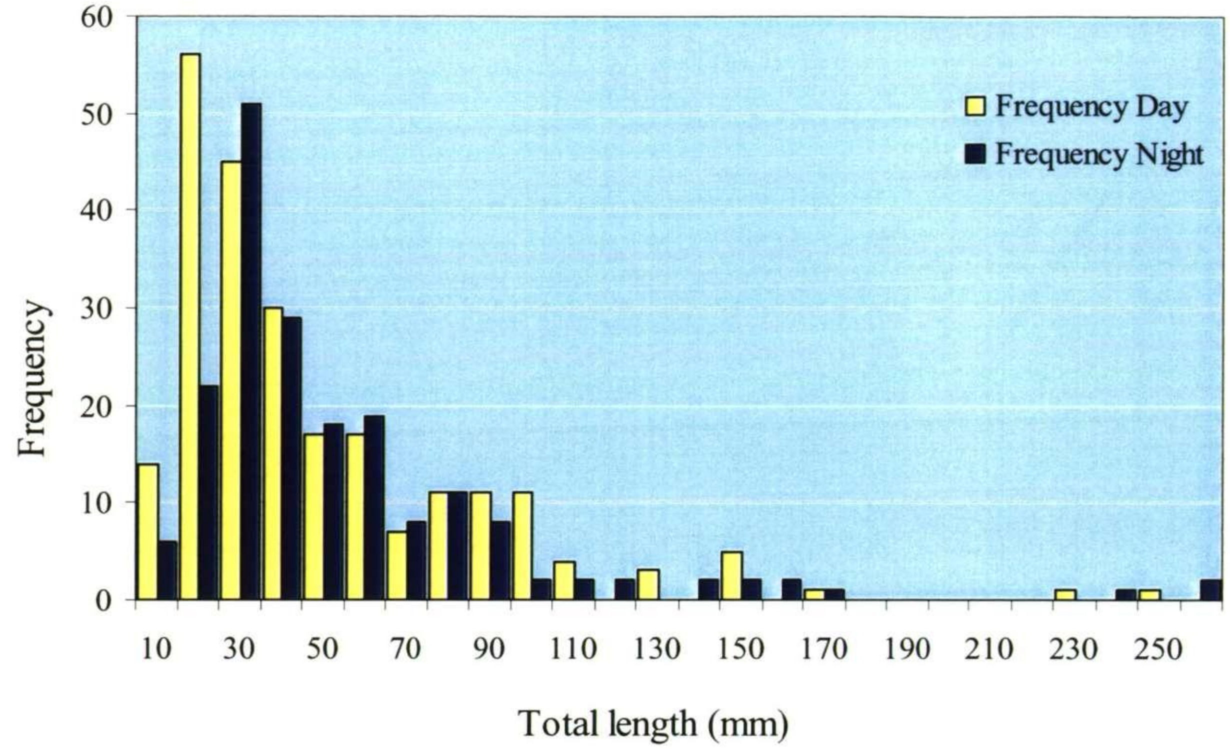


Figure 5.5 Length-frequency distribution of fish (minus Gobidae or Syngnathidae) sampled using trawls during the day and night.

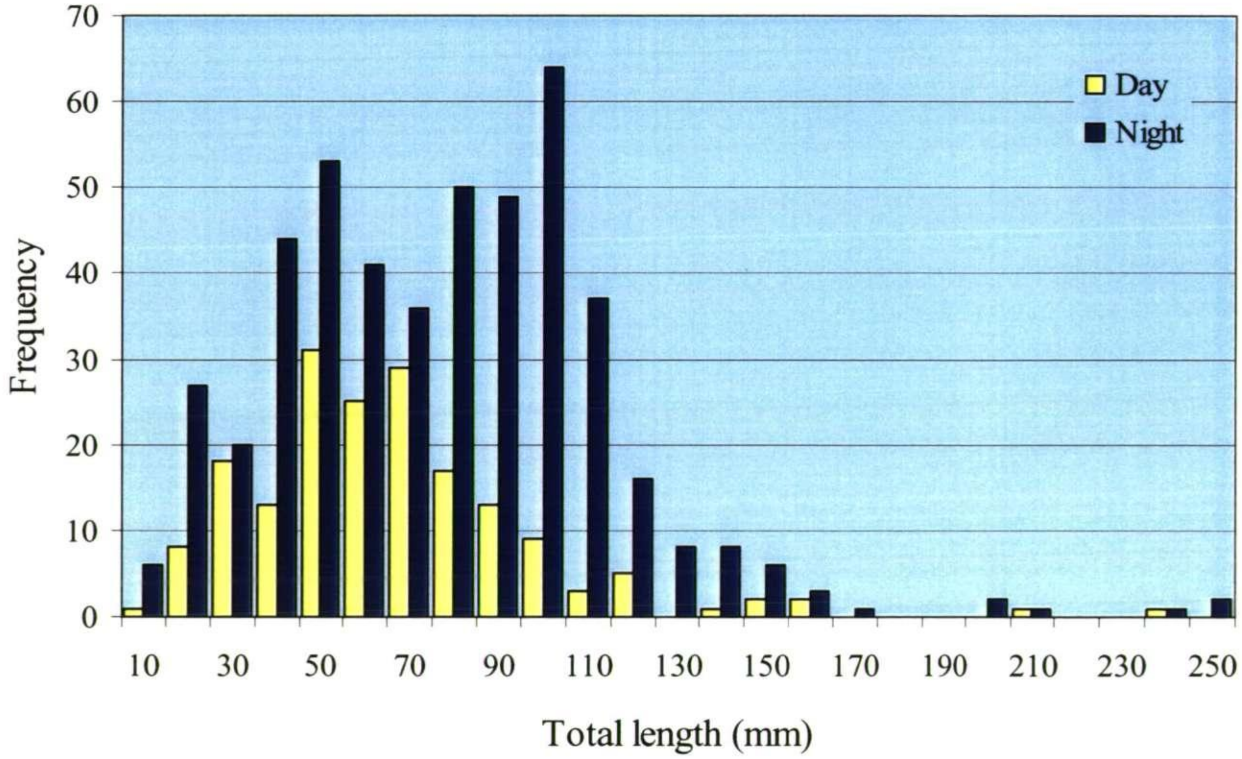


Figure 5.6 Length-frequency distribution of fish (minus Gobidae or Syngnathidae) sampled using beach seine during the day and night.

Table 5.3 List of decapod species collected during beach seining and trawling with information on their total abundance, frequency of occurrence in samples and range of total lengths. * = exploited species.

Family	**Species**	**Abundance**		**Frequency**	
		Day	**Night**	**Day**	**Night**
Crangonidae	*Crangon crangon**	1989	702	10	12
	Pontophilus fasciatus	6	40	5	6
	Pontophilus trispinosus	2	67	2	3
Hippolytidae	*Hippolyte varians*	2096	2378	40	42
	Hippolyte inermis	8	4	5	3
	Thoralus cranchii	6	17	7	7
Palaemonidae	*Palaemon serratus**	774	904	21	19
	Palaemon elegans	68	62	9	9
	Palaemon adserpus	13	13	1	2
Portunidae	*Carcinus maenas**	533	430	9	17
	Liocarcinus arcuatus	20	82	9	13
	Pirimela denticulata	12	23	11	10
	Liocarcinus holstas	10	10	2	6
	Liocarcinus depurator	7	0	0	1
	Liocarcinus pusillus	0	1	0	1
	*Necora puber**	0	3	1	2
Majidae	*Macropodia linearesi*	50	75	12	22
	Macropodia deflexa	44	45	14	12
	Macropodia rostrata	17	17	4	10
	Pisa tetraodon	15	14	13	12
	Pisa armata	11	24	6	8
	*Maja squinado**	3	19	3	11
Paguridae	*Catapagurus timidus*	22	7	9	5
	Pagurus bernhardus	10	11	7	8
	Pagurus varians	4	0	1	0
	Anapagurus chiroacanthus	1	0	1	0
	Pagurus prideauxi	1	0	1	0
	Pagurus cuanensis	0	3	0	1
Processidae	*Processa edulis crassipes*	21	185	12	23
Porcellanidae	*Pisidia longicornis*	19	26	12	12
Xanthidae	*Pilumnus hirtellus*	1	2	2	2
Galatheidae	*Galathea squamifera*	1	4	1	4
Alpheidae	*Athanas nitescens*	1	2	0	2

Table 5.4 List of cephalopod mollusc species collected during beach seining and trawling with information on their total abundance, frequency of occurrence in samples and range of total lengths. * exploited species.

Family	Species	**Abundance**		**Frequency**		Range of mantle length (mm)
		Day	Night	Day	Night	
Loliginidae	*Alloteuthis subulata**	1	1	1	1	83 to 84
Sepiidae	*Sepia officinalis**	5	6	5	5	8 to 152
	Sepiola atlantica	7	21	6	5	18 to 25

In terms of exploited species of fish, juvenile black bream (*Spondyliosoma cantharus*, mean total length 19 mm) occurred in high numbers as did juvenile pollack (*P. pollachius*, mean total length 71 mm) and ballan wrasse (*Labrus bergylta*, mean total length 53 mm), but these were not recorded frequently, indicating that they occurred in groups or at particular sites (Table 5.2). Other exploited species, the *Trisopterus* species (bib and pouting) were also relatively abundant but in markedly higher numbers during the night, when they were found in fewer instances. Again, juveniles dominated catches for *Trisopterus* species (mean total length 70 mm). Other exploited species were collected, but infrequently and in low numbers; for example, bass (*Dicentrachus labrax*). The ten bass sampled during the day in the seagrass beds were all juveniles (less than 40 mm total length) and the one bass sampled during the night was an adult (481 mm total length). All five occurrences of this species were from St Catherine Bay and Ann Port. Also found at these sites were four juveniles of the economically valuable annular bream (*Diplodus sargus*), the first British record of this warm water Mediterranean species (Wheeler, A., pers. comm, 2001).

In terms of dominant decapod crustaceans in the samples, four species represented approximately 90 percent of the total decapods sampled. They were the brown shrimp (*Crangon crangon*), the chameleon prawn (*Hippolyte varians*), the common prawn (*Palaemon serratus*) and green crab (*Carcinus maenas*) (Table 5.3). Only the chameleon and common prawn were represented frequently in samples, with the brown shrimp and green crab dominating beach seine samples and only at a few sites. All these species have some economic value, except the chameleon prawn. Also with relatively high abundance and present in over half the samples collected were species of the genus *Macropodia* (Majiidae) (Table 5.3). Many decapod species showed greater overall abundance in night than day samples (for example, *H. varians*, *P. serratus* and *Processa edulis crassipes*).

Finally, 41 cephalopod molluscs were sampled (Table 5.4). The most abundant species was the little cuttlefish (*Sepiola atlantica*) which, whilst numerically more abundant in night samples, showed little difference in the frequency it was caught in day or night samples. The common cuttlefish (*Sepia officinalis*) and the squid (*Alloteuthus subulata*) both have economic value in the region. All, but one, of the *S. officinalis* sampled were juveniles (less than 60 mm in mantle length, Pawson, 1995).

5.4.2 Comparison of trawl and beach seine samples

In addition to the length-frequency distributions of fish, comparison of beach seine and trawl at the same seagrass sites using non metric multidimensional scaling (MDS) showed significant separation in the species assemblages from trawl and beach seine samples (ANOSIM R=0.371, $p<0.001$; Figure 5.7). SIMPER analysis showed an average dissimilarity between same site trawl and beach seine samples to be 83.19%. This high dissimilarity was due mainly to the higher densities of many species sampled using the beach seine compared to the trawl. *Palaemon serratus* (average density in trawls, 0.04 m^{-2} and beach seine 3.73 m^{-2}) contributed to 29.3% of the dissimilarity, followed by *Hippolyte varians* (20.7%), *Carcinus maenas* (13.6%), *Pomatoschistus minutus* (6.7%) and *Gobiusculus flavescens* (5.8%).

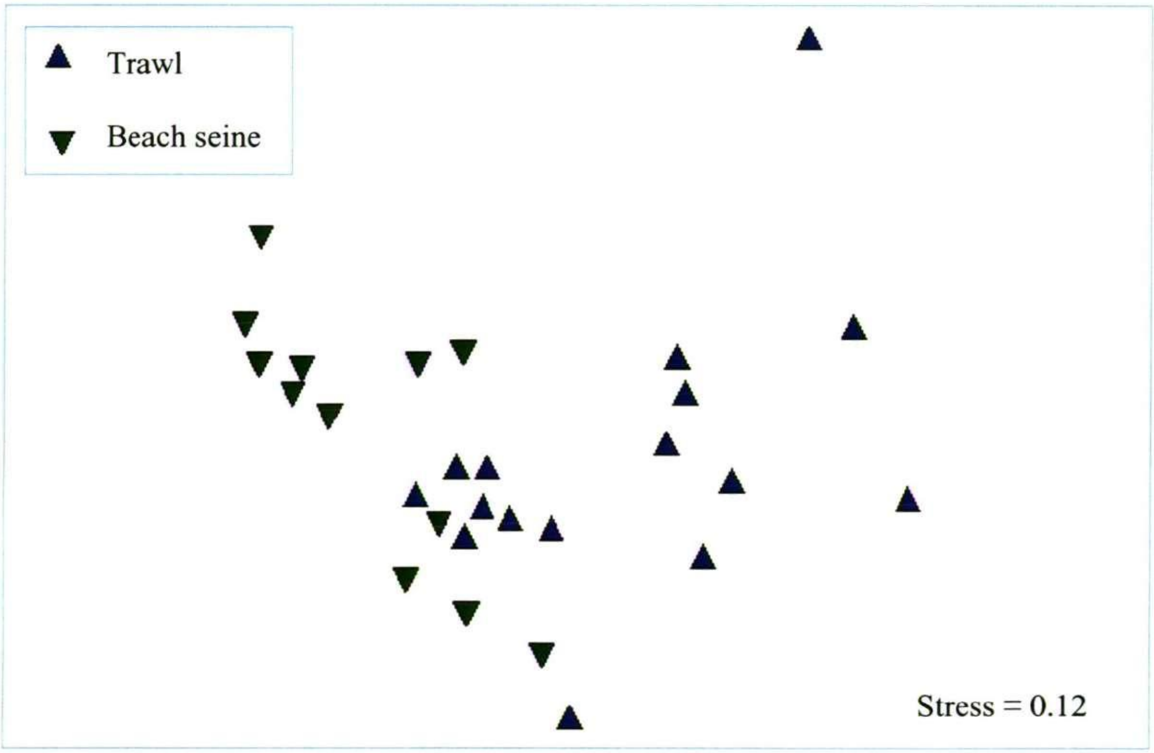


Figure 5.7 Multidimensional scaling plot of trawl and beach seine samples from Les Elavees and St Catherine Bay seagrass beds. MDS is based on Bray-Curtis similarity matrix of log (x+1) transformed density data.

Comparison of trawl and beach seine samples at the same sites indicated 22 species were sampled only using the beach seines. Of these, half were sampled using trawls at other sites (Table 5.5). Those that were not included were species that are more pelagic such as sand smelt (*Atherina presbyter*) and species that are more common to unvegtated habitats (sole, *Solea solea*; plaice, *Pleuronectes platessa;* sand eel *Hyperoplus lanceolatus* and the common goby *Pomatoschistus microps*). It is important to note that in the case of the bass

(*Dicentrachus labrax*), only juveniles were caught in other trawl samples whereas one adult bass was sampled using the beach seine.

Table 5.5 Species absent from trawl samples but present in beach seines at same sites. Table shows the frequency of occurrence of the species in beach seine samples (out of n = 12) and whether or not the species was sampled at other sites using the trawl.

Species	**Frequency of occurrence**	**Present in trawl samples from different sites**
Callionymas lyra	6	Yes
Pagurus bernhardus	6	Yes
Pomatoschistus microps	4	Yes
Nerophis ophidon	3	Yes
Gobius paganellus	3	Yes
Gobius niger	3	Yes
Ctenolabrus rupestris	3	Yes
*Sepia officinalis**	3	Yes
*Dicentrachus labrax**	2	Yes (juveniles)
Athanas nitescens	2	Yes
Cyclopterus lumpus	1	Yes
*Pleuronectes platessa**	1	No
Symphodus bailloni	1	No
*Solea solea**	1	No
Mugil cephalus	1	No
Hyperoplus lanceolatus	1	No
Gaidropsarus mediterraneus	1	No
Diplodus sargus	1	No
Palaemonetes varians	1	No
*Atherina presbyter**	3	No
Anapagurus chiroacanthus	1	No
Liocarcinus depurator	1	No

5.4.3 Faunal assemblage variability in trawl sampled seagrass landscapes

Non metric Multidimensional scaling (MDS) was also carried out on faunal assemblages sampled by the trawls during the day and night (Figures 5.8 and 5.9) to distinguish potential similarities between different seagrass bed sites. Although some site to site clustering may be occurring, differences between replicates appear to be at a smaller scale than site. Both during the day and night, the fauna sampled at Flicquet showed the greatest variability. Regression analysis was used to explore potential influences of habitat characteristics on this variability.

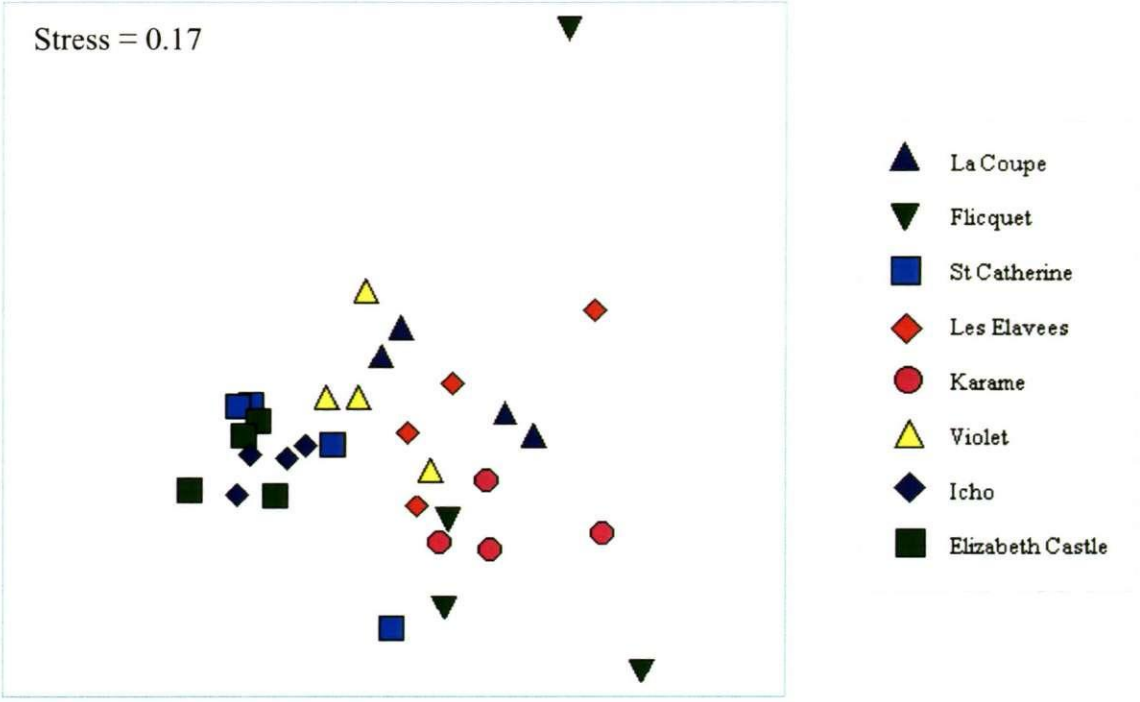


Figure 5.8 Multidimensional scaling plot of day-time trawl samples from eight seagrass landscapes around Jersey. MDS is based on Bray-Curtis similarity matrix of log (x+1) transformed density data.

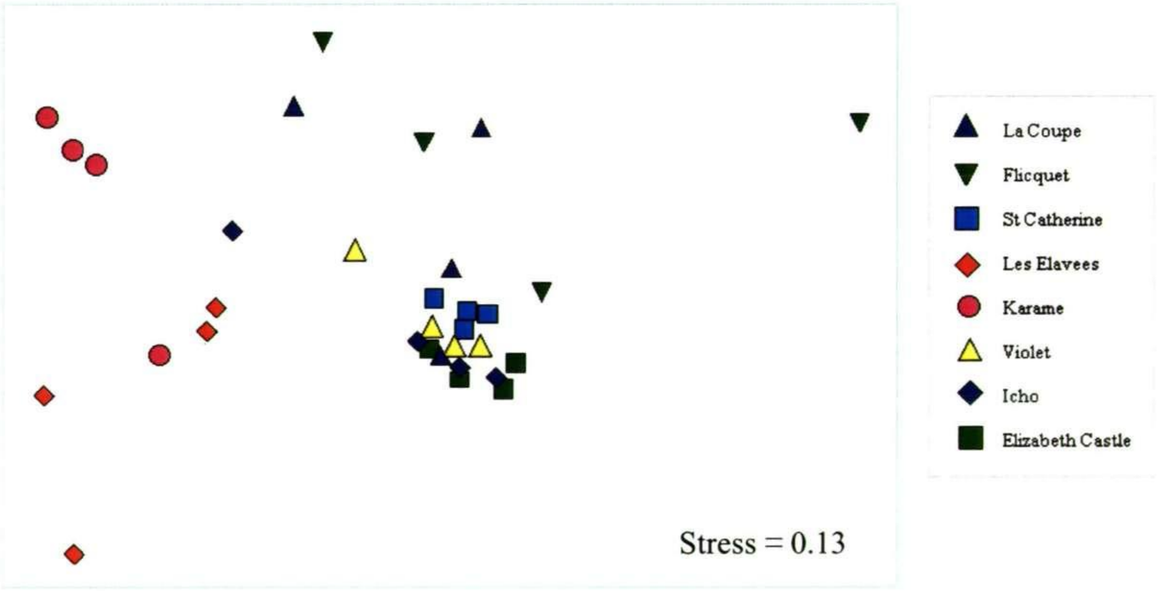


Figure 5.9 Multidimensional scaling plot of night-time trawl samples from eight seagrass landscapes around Jersey, English Channel. MDS is based on Bray-Curtis similarity matrix of log (x+1) transformed density data.

5.4.4 Determination of similar seagrass habitats

In the Principal Component Analysis (PCA) of 7 seagrass habitat attributes (dependent variables), two PCAs had eigenvalues greater than 1.0 and together accounted for 83.3% of the standardised variance (Table 5.6). The first principal component (PC1) had an eigenvalue of 3.67 and contributed to 52.5% of the variation of the whole matrix. It was dominated by weights of area weighted mean patch area, perimeter area ratio, landscape shape index and core area. This suggests that this axis is representative of the actual amount of seagrass in the landscape and its configuration, based on the definitions given in the introduction; this principal component was useful as a description of fragmentation of the seagrass bed. The representation is, however, inverse, with an increase in PC1 representing a decrease in the size of patches and with it core area and aggregation (LSI), whilst at the same time the ratio of perimeter to area of seagrass increases.

Table 5.6 Principal component analysis evaluations from seagrass bed landscape variables and Coefficients in the linear combination of variables making up Principal components. Highest variable weights area given in red. † entered as an independent variable into multiple regression models.

Eigenvalues			
Principal component	**PC1 †**	**PC2 †**	**PC3 †**
Eigenvalues	3.67	2.16	0.7
%Variation	52.5	30.8	10
Cumulative % variation	52.5	83.3	93.3
Variable weights			
Distance to the 10m isobath	-0.269	0.276	0.89
Landscape shape index (LSI)	-0.481	-0.051	-0.164
Area weighted mean patch area	-0.489	-0.165	-0.23
Area weighted mean perimeter area ratio (PARA)	0.45	0.012	-0.093
Area weighted mean core area	-0.485	-0.194	-0.089
Contrast weighted edge density	-0.096	0.655	-0.241
Contagion	0.103	-0.654	0.229
Principal Component Scores			
La Coupe	2.537	-1.433	-0.37
Flicquet	0.81	-1.002	-1.002
St Catherine	-3.358	-0.509	-0.196
Les Elavees	-1.454	-1.638	0.781
Karame	0.081	1.677	1.437
Violet	-1.41	0.29	-0.486
Icho	0.379	2.79	-0.894
Elizabeth Castle	2.416	-0.177	0.731

Edge density and contagion loaded heaviest for the second principal component (PC2), which accounted for an additional 30.8% of the variance and had an eigenvalue of 2.16. PC2 was therefore identified as being representative of habitat heterogeneity of the landscape, with interspersion of habitat types and disaggregation of seagrass increasing with an increase in the value of PC2 (as contagion decreases and edge density increases). This principal component was not correlated (r = 0.01), with PC1, showing that the information provided by these metrics was independent. Finally, the third PC (eigenvalue 0.7), which was not correlated with either of the other principal components, was dominated by the distance of the seagrass beds to the 10m isobath.

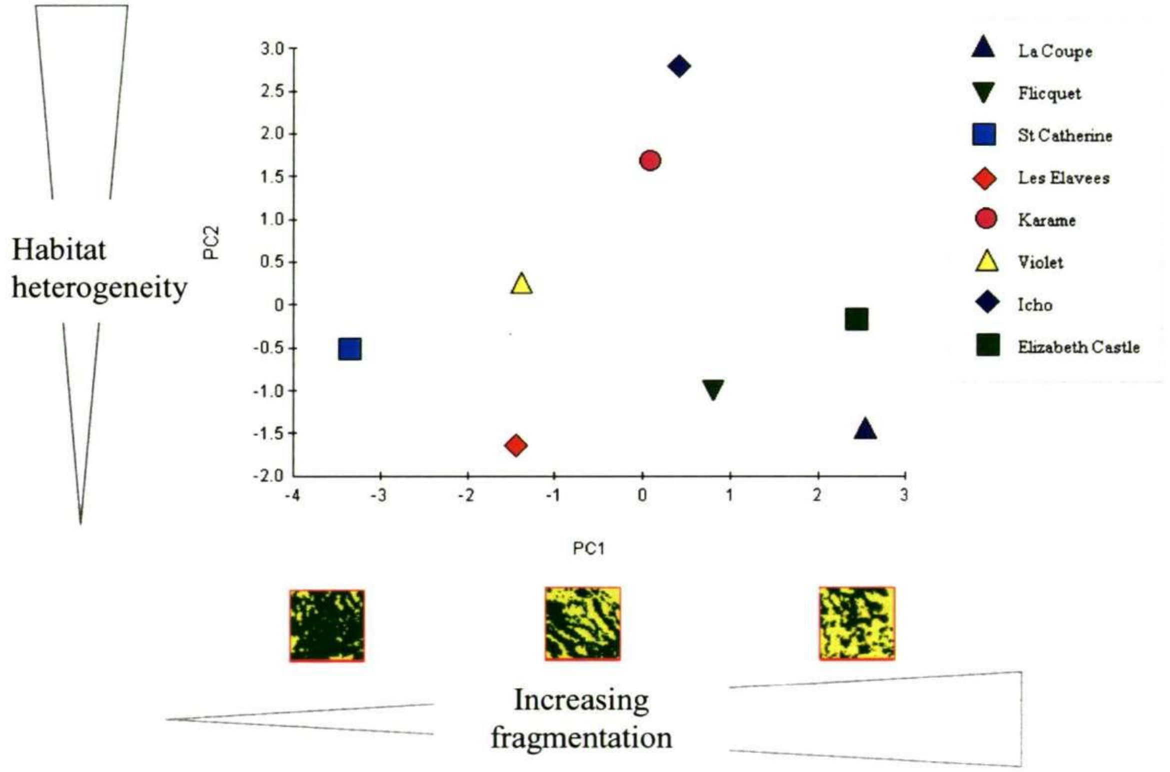


Figure 5.10 The distribution of the eight seagrass beds sampled using the trawls, against the first two principal component axes in Table 5.6. PC1 represents fragmentation of the seagrass bed as illustrated by the example areas from the binary thematic images *green is seagrass, yellow is unvegetated sand.

Figure 5.10 illustrates the distribution of the seagrass landscapes against the first two principal components. The spread along PC1 axis (representative of the continuity and fragmentation of the seagrass bed landscapes) separates out the seagrass at St Catherine

Bay (most homogenous, continuous seagrass landscape) from those at the other extreme, the more fragmented landscapes for example at Icho (Figure 5.10).

ANOVA on trawl-specific seagrass variables showed no significant differences in the measurements between night and day sampling (Table 5.7) but did show significant differences at the site level ($p < 0.001$ for all variables) (Table 5.7).

Table 5.7 Results of the two-factor ANOVA carried out on trawl-specific variables Factor one (Time) was fixed and had two levels (day and night). Factor two (Site) again fixed, was orthogonal to Time and had eight levels (St Catherine Bay, Flicquet, La Coupe, Les Elavees, Violet, Karame, Icho and Elizabeth Castle).

Variable	**Factors**			
	Day/Night		**Site**	
	$F_{(1,63)}$	p	$F_{(7,63)}$	p
Distance from trawl to outer sg edge (m)	0.1248	n.s.	11.85	**
Estimated Mean leaf height per trawl	0.30	n.s.	4.30	**
Mean depth of trawl at cd (m)	1.12	n.s.	41.93	**
Transect heterogeneity	0.00	n.s.	10.4	**
Percentage algae in trawl	0.28	n.s.	3.39	**

** = $p <$ 0.001, n.s. = not significantly different

5.4.5 Multiple regression models of the effects of habitat variables

Tables 5.8 and 5.9 show the results of stepwise multiple regression models of seven independent habitat variables on ensemble variables of fish and decapod assemblages. Observations of bivariate plots showed no strong non-linear relationships and only linear first-order terms are presented in this section; however, more general models are considered in the discussion. The night-time densities of temporary juvenile fish and the day-time densities of permanent juvenile, large permanent and temporary mature fish could not be transformed to give a normal distribution and therefore could not be analysed using multiple linear regression techniques. Although percentage of algae in the trawl swept area and the distance from the trawl area to the outer seagrass edge were used as variables in the multiple linear regression, these variables did not meet the criteria ($p < 0.05$) for entry into any of the models, so are not included in the tables.

The measured habitat variables described more variability in the distribution of fauna (ensemble faunal variables) during the day than at night, as seen by the higher overall adjusted R^2 values (Tables 5.8 and 5.9). During the day, mean depth explained significant proportions of the variability seen in the number of species (total and when divided into decapod and fish species) and their densities (except for the density of decapods and small permanent fish residents of the seagrass bed) (Figure 5.11). In all cases, increase in depth was associated with an increase in species number or density. Controlling for depth, other variables were also substantially important in explaining the variation. Total species number showed a negative relation to PC1 (fragmentation), indicating that as seagrass landscapes became more fragmented (increase in perimeter to area ratio and a decrease in core area), the number of species decreased. Total species number was also related positively to PC3 (distance to the 10m isobath). The patterns observed for total species number may be attributed to the number of fish species, which were explained by the same independent variables. The diversity of fish increased with estimated canopy height of the seagrass, which may have been due to an increase in cryptic species of fish with this variable.

Total density was most strongly associated with the epiphytal load index and PC2 (habitat heterogeneity and continuity), increasing with the amount of epiphytal load and decreasing as the landscape became more heterogeneous between habitat types and seagrass patches became more disaggregated. Observing similar relationships for total decapod density suggests that this was the group driving patterns for total density. In comparison, the total density of fish was inversely associated with the heterogeneity of the trawl swept area (transect heterogeneity), with fish densities decreasing as the trawl area became less homogenous in terms of the seagrass habitat it covered. Transect heterogeneity also showed inverse relationships with total diversity, the number of decapod species and diversity and the number of small permanent fish. Of the groups of fish identified, only the density of temporary juveniles, small permanent residents and cryptic species showed any relationship to the chosen habitat variables (Table 5.8). In addition to transect heterogeneity, small permanent fish residents showed a strong positive relationship with seagrass fragmentation (PC1). In comparison, temporary juveniles were inversely proportional to fragmentation of the seagrass landscape and increased as distance to the 10m isobath increased.

Table 5.8 Results of stepwise multiple regression of habitat variables on ensemble variables of fish and decapod assemblages from daytime trawl samples (n = 32). Values given are the squared semi-partial correlation coefficients (sr^2, the correlation between the unadjusted dependent variable with the respective variable after controlling for all independent variables in the equation). Only those variables entered into the final equation are listed, all others did not meet a criteria of $p = 0.05$ for entry. Those dependent variables marked with a '*' indicate variables which could not be transformed to give a normal distribution and were therefore not analysed using multiple linear regression. All Multiple R-values of final equations were significant at $p < 0.01$. Negative signs indicate a negative relationship.

DAY	sr^2								
	Independent variables								
Dependent variables	Transect heterogeneity	Epiphytal load index	Mean depth (m)	Estimated canopy height (m)	BED_PC1	BED_PC2	BED_PC3	Multiple R	Adjusted R^2
Total species number			0.72		-0.37		0.48	0.74	0.49
Total density		0.59	0.30			-0.31		0.67	0.39
Total diversity	-0.47		0.51					0.68	0.42
Fish species number			0.71		-0.3		0.69	0.76	0.53
Fish density	-0.42		0.42					0.59	0.3
Fish diversity			0.61	0.35			0.65	0.76	0.53
Decapod species number	-0.37		0.49					0.61	0.33
Decapod density		0.59				-0.38		0.59	0.30
Decapod diversity	-0.40		0.60					0.71	0.47
Fish Groups									
Temporary juveniles			0.69		-0.34		0.45	0.70	0.43
Permanent juveniles*									
Small permanents	-0.57				0.50			0.60	0.32
Cryptic permanents			0.33	0.46				0.57	0.28
Large permanents*									
Temporary mature*									

Table 5.9 Results of stepwise multiple regression of habitat variables on ensemble variables of fish and decapod assemblages from night-time trawl samples ($n = 32$). Values given are the squared semi-partial correlation coefficients (sr^2, the correlation between the unadjusted dependent variable with the respective variable after controlling for all independent variables in the equation). Only those variables entered into the final equation are listed, all others did not meet a criteria of $p = 0.05$ for entry. Those dependent variables marked with a '*' indicate variables which could not be transformed to give a normal distribution and were therefore not analysed using multiple linear regression. All Multiple R-values of final equations were significant at $p < 0.01$. Negative signs indicate a negative relationship.

Night	sr^2 **Independent variables**								
Dependent variables	Transect heterogeneity	Epiphytal load index	Mean depth (m)	Estimated canopy height (m)	BED_PC1	BED_PC2	BED_PC3	Multiple R	Adjusted R^2
Total species number							0.35	0.35	0.09
Total density		0.34					0.27	0.68	0.42
Total diversity		-0.45						0.45	0.18
Fish species number							0.53	0.53	0.26
Fish density								-	-
Fish diversity		0.35	0.61				0.65	0.60	0.34
Decapod species number								-	-
Decapod density		0.64						0.64	0.39
Decapod diversity		-0.48						0.48	0.20
Fish Groups									
Temporary juveniles*								-	-
Permanent juveniles*								-	-
Small permanents					0.63	-0.29		0.48	0.21
Cryptic permanents				0.48				0.48	0.21
Large permanents			-0.57					0.57	0.30
Temporary mature*								-	-

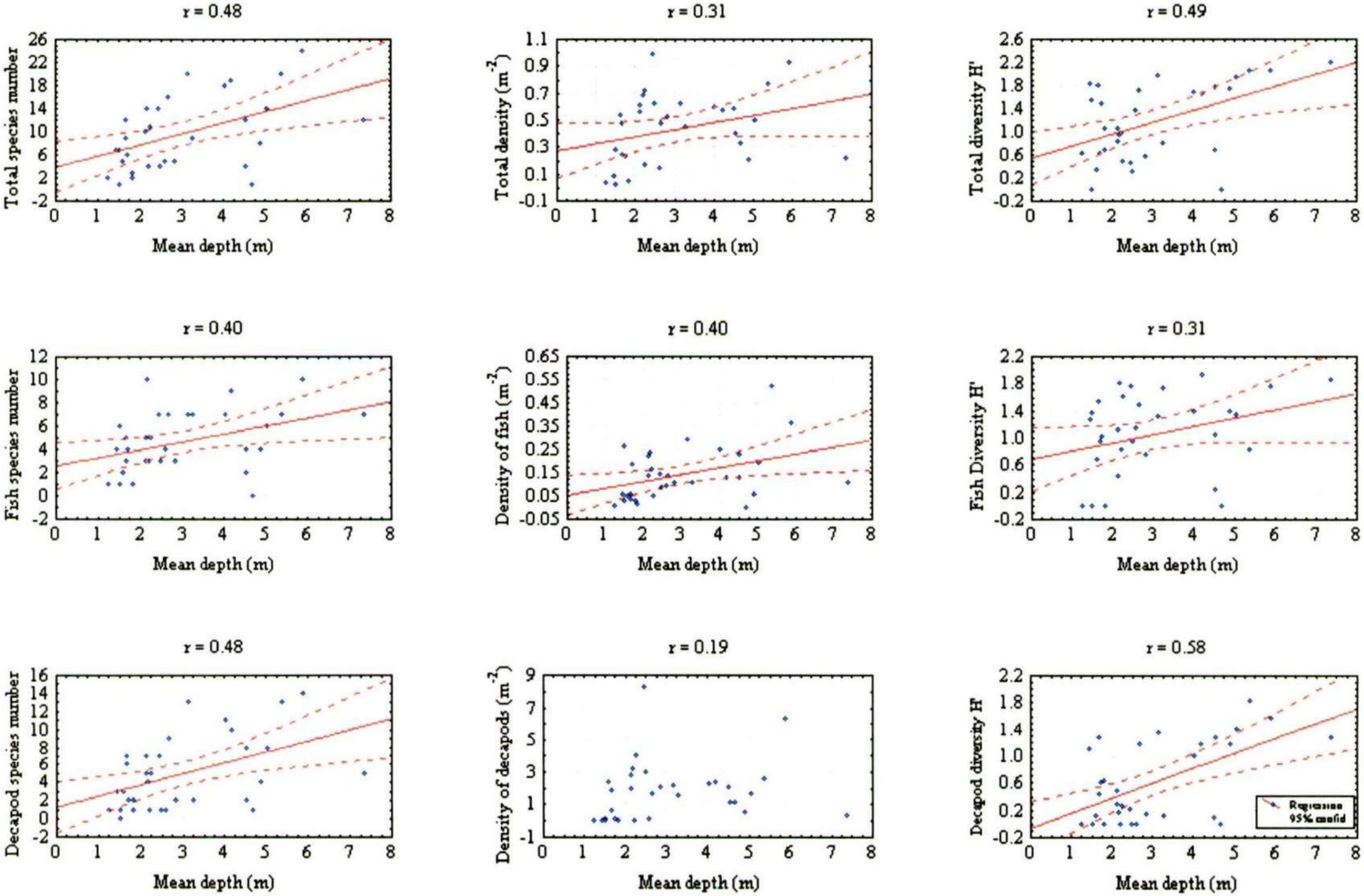


Figure 5.11 Linear regressions and 95% confidence limits for depth versus daytime (a) total species number, (b) total density (m^{-2}), (c) total diversity (H'), (d) fish species number, (e) density of fish (m^{-2}), (f) fish diversity (H'), (g) decapod species number, (h) density of decapods (m^{-2}), (i) decapod diversity (H').

Additional non-parametric correlations (Gamma) were carried out for large permanent residents, temporary mature residents and juvenile residents. The ranks of large permanent resident densities showed agreement with those of distance to the seagrass outer edge (45% probability), estimated canopy height (40% probability) and PC2 (44% probability). Mature fish, which enter the seagrass landscape temporarily, showed a strong probability of agreement in order with transect heterogeneity and the index of epiphytal load.

At night, fewer patterns could be explained by the independent variables in the model (Table 5.9). Transect heterogeneity and fragmentation (PC1) were less important variables than in the day, as was depth. Distance to the 10m isobath still explained some of the variation for total species number, fish species number and diversity, but was also weakly associated with total density. For night-time samples, mean depth only showed a strong relationship with fish diversity (positive) and density of large permanent residents (negative). Cryptic fish densities showed a similar positive relationship to canopy height at night as they did during the day.

For ensemble variables that could not be transformed to meet assumptions of normality (temporary juvenile fish residents, permanent juvenile fish residents and temporary mature residents) non-parametric correlations (Gamma) were carried out (Table 5.10). Again, fewer significant agreements with any of the independent variables were observed at night than during the day. Juveniles of permanent residents showed no agreements, but both the densities of temporary juveniles and temporary mature residents showed an agreement in rank order with mean depth (36% and 48% respectively).

Table 5.10 Results of non-parametric correlations (Gamma coefficient) between fish resident groups and the independent variables. Only Gamma significant at $p < 0.05$ are shown.

	Significant Gamma ($p < 0.05$)							
	Independent variables							
Dependent variables (fish resident groups)	Distance to seagrass outer edge	Transect heterogeneity	Epiphytal load index	Mean depth	Estimated canopy height	PC1	PC2	PC3
Day								
Large permanent	0.45				0.40		0.44	
Temporary mature		0.80	0.89					
Permanent juvenile								0.51
Night								
Temporary juvenile				0.36				
Permanent juvenile								
Temporary mature				0.48				

Table 5.11 Results of stepwise multiple regression of habitat variables on ensemble variables of fish and decapod assemblages from night and daytime trawl samples ($n = 32$). Values given are the squared semi-partial correlation coefficients (sr^2, the correlation between the unadjusted dependent variable with the respective variable after controlling for all independent variables in the equation). Only those variables entered into the final equation are listed, all others did not meet a criteria of $p = 0.05$ for entry. Those dependent variables marked with a '*' indicate variables which could not be transformed to give a normal distribution and were therefore not analysed using multiple linear regression. All Multiple R-values of final equations were significant at $p < 0.01$. Negative signs indicate a negative relationship.

	sr^2								
	Independent variables								
Dependent variables	Transect heterogeneity	Epiphytal load index	Mean depth	Estimated canopy height	PC1	PC2	PC3	Multiple R	Adjusted R^2
Day									
Spondyliosoma cantharus				0.60				0.6	0.34
Symphodus melops							0.49	0.49	0.21
Labrus bergylta								-	-
Gobiusculus flavescens	-0.55				0.46			0.59	0.30
Pomatoschistus minutus					0.57	-0.30		0.64	0.37
Spinachia spinachia				0.61				0.61	0.35
Callionymas lyra					0.39		0.66	0.77	0.56
Hippolyte varians	-0.28	0.75						0.74	0.53
Carcinus maenas			0.36		0.88			0.50	0.20
Night									
*Spondyliosoma cantharus**									
Symphodus melops							0.47	0.47	0.20
Labrus bergylta									
Spinachia spinachia				0.44		-0.32		0.58	0.29
Gobiusculus flavescens				0.38				0.38	0.12
Hippolyte varians		0.67				-0.31		0.68	0.42
Carcinus maenas			0.4					0.40	0.14
Crangon crangon			0.62					0.62	0.37
Processa edulis crassipes			0.43					0.43	0.16

Table 5.11 illustrates the results of multiple linear regression carried out on dominant individual fish and decapod species. As for assemblage parameters, models of daytime sampling were able to explain more of the variation in faunal densities than at night. During the day, *S. cantharus* (black bream) showed a positive relationship with increasing canopy height of the seagrass bed. This variable also explained much of the variability in the cryptic fish *S. spinachia* (fifteen-spined stickleback) density during the day and night. PC1 (fragmentation/ contiguity of the seagrass) showed positive relationship with many of the individual species densities, including the gobies (*G. flavescens* and *P. minutus*), dragonet (*C. lyra*) and the green crab (*C. maenas*), but was not influential at night. For chameleon prawns (*H. varians*), it appeared that epiphytal load continued to influence densities during the day and at night.

5.5 Discussion

The aims of this study were to measure the configuration and composition of subtidal seagrass landscapes around Jersey and to understand their influence on the distribution of large mobile fauna. Although landscape approaches are now being applied increasingly to the study of seagrass beds (Robbins & Bell, 1994; Kendrick *et al.*, 1999; Bell *et al.*, 2001; Hovel & Lipcius, 2001; Salita *et al.*, 2000, 2003), the present study differs from these in a number of ways. Firstly, many previous studies have focused on the fauna inhabiting seagrass patches (Eggleston *et al.*, 1998; Hovel & Lipcius, 2001; but see Salita, 2000), whereas this study sampled the seagrass landscape as it exists is a mosaic of habitats, dominated by seagrass. Also, previous studies have focused on just one scale of habitat characterisation (McNeill & Fairweather, 1993; Bell *et al.*, 2001 and references within) and on the more sedentary species and infauna (Irlandi *et al.*, 1995; Bowden *et al.*, 2001). Finally, there is a concentration in previous studies on shallow water seagrass beds, presumably because of the difficulty in mapping and sampling deeper subtidal beds. The methods used in the current study for the detailed mapping of seagrass around Jersey are reported in Chapter 2 with the various sampling methods assessed in Chapter 3.

Results from Chapter 3 suggested that, of the methods studied, beach seining and trawling captured the largest proportion of species and the largest range of size classes. However, beach seining was limited to the shallow fringes of the seagrass beds and, therefore, may add another source of bias if used to assess generic habitat effects. To identify the sampling inadequacies of the trawls, beach seining was carried out during the day and night at two sites and results were compared with the trawls. These comparisons confirmed the results of Chapter 3, in that the beach seine sampled larger size classes of fish (Figures 5.4 and 5.5), and higher densities of common fish and decapods than the trawls. Finally, of the species caught only in beach seine samples, over half were species that were sampled by trawling at other sites, and the remainder occurred very infrequently in the beach seine samples (Table 5.5). These limitations of trawling were taken into account during the interpretation of results, but the advantage of the trawl, in that it was able to sample all parts of the seagrass landscape, made it the most appropriate method for this study. However, further work is needed to devise a method that is able to sample effectively the larger more mobile species of fish in both the shallow and deeper subtidal beds.

5.5.1 Influence of habitat variables on daytime fauna

Multiple linear regression results identified several plant and landscape variables that may influence faunal distributions in seagrass beds around Jersey. However, the differential importance of the different independent variables to the fish groups identified may indicate that the fish were discriminating amongst different structural, landscape and location aspects of the seagrass bed.

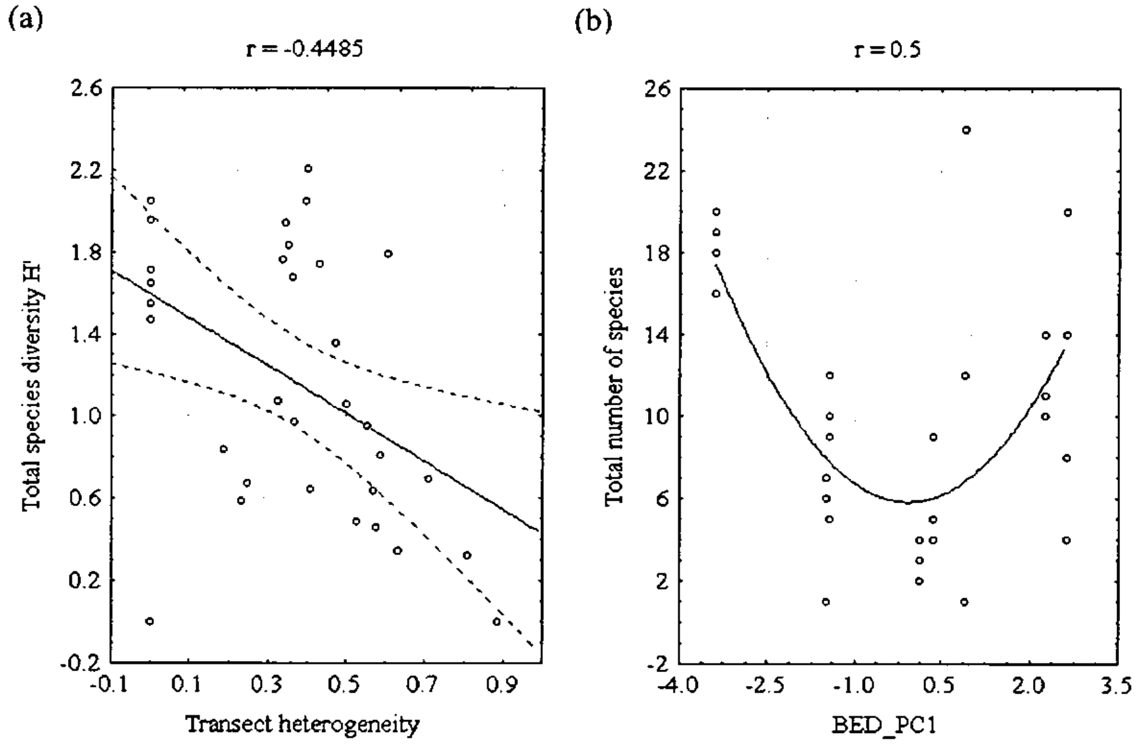


Figure 5.12 (a) Regression of total species diversity against increasing transect heterogeneity, with 95% confidence limits (b) 2nd-order polynomial regression equation of total species number against PC1 (representative of increasing seagrass habitat fragmentation).

It was hypothesised that the increase in habitat diversity would result in increased species diversity. For the measurements used, this would be shown as increases in diversity with increasing transect heterogeneity and fragmentation of the seagrass habitat. Results showed that total diversity had a negative relationship with transect heterogeneity (Figure 5.12a) and total species number had a weak negative association with increasing fragmentation. However, assessing the bivariate plots, it appeared that the relationship between total species number was better explained by a 2nd order polynomial equation (Figure 5.12b). One explanation for this is that, in more continuous and homogenous seagrass landscapes, there would be less edge effect (areas of enhanced species interactions; Saunders *et al.*, 1991; Fagan *et al.*, 1999), providing a more stable environment (less disturbance, physical and biological, predation) where more species can survive. Another explanation is that total species number reflects all the fish and decapods sampled, prey and predators alike, and, while smaller prey items (small prawns and shrimp) may find protection, so too might the predator species (larger wrasse and crabs) from their own predators. Bowden *et al.* (2001) proposed such predator-mediated coexistence as a possible reason for higher species numbers in large patches of seagrass. As the seagrass bed becomes more fragmented, species number declines, perhaps as the larger patches no longer afford protection to the higher-order predators. However, as the seagrass becomes more of a mosaic of habitats (seagrass, sand and macroalgae), with each habitat supporting certain species that are adapted to or 'prefer' that habitat, species number may increase. With increasing habitat diversity (and interspersion of habitats), species diversity increases (following predictions; Leopold, 1933). The various configurations of these mosaics may explain the greater variability in species number at this end of the scale (highly fragmented seagrass beds).

Both total diversity and total species number showed a positive relationship with depth. In fact, in all models of species number and densities, values were higher in deeper seagrass beds (Figure 5.11). This disagrees with the findings of Francour (1997) and Coles *et al.* (1993), but support the results of Bell *et al.* (1992) and Ruiz *et al.* (1993), who found an increase in large predatory fish with increasing depth. Bell *et al.* (1992) argued that, in shallower seagrass beds, not only is the vulnerability to avian predation greater, but that fewer species are able to tolerate larger fluctuations in temperature and oxygen. In Jersey, tidal ranges of up to 11m may exaggerate the fluctuations encountered in shallower beds, with the deeper seagrass offering a more stable environment, particularly during the day. Although salinity and temperature were measured at the time of sampling, and no significant patterns were found between sites, this snapshot may not reflect the recent history of salinity and temperature regimes, which may have influenced the fish and decapod densities at the time of sampling. Future studies could measure the variability range for these variables to take account of them in the models, they also need to take into account depth in the design stage and also assess patterns at different states of the tide.

In the model proposed by Salita (2000), as fragmentation increases, the number of small and cryptic fish species decreases and the number of larger benthic predators increases. Results of the present study showed that, while small juveniles of larger species (including, pollack, bib and black bream, three economically valuable species) decreased with fragmentation of the seagrass bed, the number of small permanent residents increased. There was also a 44% chance that the ranks of large permanent fish in each trawl matched that of the PC2 (increasing edge density and decreasing contagion). Survival of temporary juvenile fish may be improved in the contiguous seagrass landscapes, due to protection from predation, higher densities of smaller food items and greater environmental stability associated with larger 'core' areas (Salita, 2000; Bowden *et al.*, 2001; Hovel & Lipcius, 2001). It is also possible that juvenile fish may still show distributional patterns that are remnants of initial settlement. If so, present results conflict with studies suggesting that many small patches increase the probability of larvae or other immigrants encountering seagrass, increasing overall colonisation of the smaller patches compared to larger patches (Sogard, 1989; McNeill & Fairweather, 1993). Bowden *et al.* (2001), looking at the influence of seagrass patch size on the infauna, argued that the greater number of taxa found in larger patches may be due to greater immigration via dispersing larvae.

Temporary juveniles were also related positively with distance to the 10m isobath. One explanation for this could be that, further inshore, residual currents decrease in speed, facilitating settlement of juveniles. Interestingly, densities of black bream (*Spondyliosoma cantharus*) showed no relationship with fragmentation, but a strong significant association with canopy height during the day. Juveniles of this species are commonly associated with seagrass (Bauchot & Hureau, 1990; Costa *et al.*, 1994) and, similar to other fish inhabiting seagrass beds, appear to occupy the water column above the canopy at night (thus avoiding the trawl) and shelter in the seagrass bed during the day (Table 5.11 and see references in Bell & Pollard, 1989).

Greater edge density, and less continuous seagrass beds, may facilitate the foraging efficiency of larger permanent fish residents (Irlandi, 1994), but this group was also related positively to canopy height, perhaps indicating a trade off between the benefit of the canopy for their own protection and as a source of prey items, and the difficulties in moving and seeing prey within dense continuous seagrass (Holt *et al.*, 1983; Jordan, *et al.*, 1996). Trade off decisions are species and life-stage specific, and habitat patches can only be defined relative to a particular organism's perception and scaling of the environment. Therefore, just as in terrestrial systems, greater knowledge of the critical habitat characteristics of species is needed to make precise predictions as to what level of fragmentation results in a decrease of the viability of faunal populations in seagrass systems (Monkkonen & Reunarien, 1999).

One problem with assessing the effects of seagrass habitat configuration on ensemble variables is that a variety of responses would be expected depending on whether species have a fidelity to the core areas of the seagrass, the area of the patch edge or an alternative habitat (Bender *et al.*, 1998). The weak positive relationship between small permanent residents and seagrass fragmentation may be due to this group being dominated by two species of gobies, which were amongst the most dominant species (*Gobiusculus flavescens* and *Pomatoschistus minutus*). *Gobiusculus flavescens*, the two spot goby, is a water column species often associated with *Zostera* (Wheeler, 1969) and shows a positive relationship with estimated canopy height, but it is also found over bare sand (Chapter 3). *Pomatoschistus minutus* (sand goby) is a very abundant species on unvegetated sand but is uncommon in seagrass habitats (Chapter 3 Table 3.7). Sampling fragmented habitats would, therefore, result in greater overall total number of small permanent resident fish.

In terms of decapod crustaceans, previous studies have found that fragmented seagrass beds support more decapods than continuous (Eggleston *et al.*, 1998; Loneragan *et al.*, 1998; Hovel & Lipcius, 2001). However, in this study, decapod densities showed a weak inverse relation to PC2 (contagion and edge density) and were related positively to the epiphyte load, indicating that total decapod density is higher in more aggregated seagrass landscapes and at a higher seagrass plant complexity level. There are several possibilities why higher total decapod densities may be related to epiphytic load. Firstly, structurally complex epiphytes on the seagrass blades may increase the chances of larval settlement (Newell *et al.*, 1991). Smaller prey (grazing molluscs and amphipods) may also be more abundant where epiphytic load on the seagrass beds is high due to smaller perception windows (Milchakova, 2000). This may have a cascade effect, whereby, due to predation or food resources, smaller scale attributes affecting smaller sized organisms may indirectly affect the distributions of larger organisms and drive the higher level processes of population dynamics and community structure (Attrill *et al.*, 2000). Alternatively, epiphytic load may affect predation success indirectly, as it has been shown that the weight of the epiphytes can cause the blades of seagrass to bend which may create a better barrier to visual predation than if the leaves were erect (see Chapter 2).

One of the arguments for greater prawn and crab densities in fragmented seagrass beds is that predator efficiency is lower in fragmented seagrass beds. Hovel and Lipcius (2001) suggested that, although predators may not avoid patchy areas, foraging efficiency may be reduced since the search for appropriate feeding patches takes longer in fragmented seagrass. Conversely, others propose that patchiness facilitates foraging (Irlandi, 1994) and may lead to a higher proportion of active foraging species found on patchy beds. Salita *et al.* (2003) found that, in very fragmented seagrass habitats, there were high numbers of large benthic feeders (Salita *et al.*, 2003); in more continuous seagrass beds, these were replaced by high numbers of small, juvenile or cryptic species feeding on small epifauna or nekton, where protection from visual predators was afforded and the movements of larger species impeded (Salita *et al.*, 2003). Both explanations would support the results of the present study, which sampled across habitats, including unvegetated areas were the densities of some decapods may be reduced due to predation pressure.

There is also a need to reinforce the idea that fragmentation can have two elements: the disaggregation of seagrass patches into several small rather than a single large, or the reticulation of seagrass beds. Core area (the area of each patch deemed to be unaffected by the edges of the patch, where predation and foraging success and disturbance may be greater; Fagan *et al.*, 1999) decreases in both situations. It is suggested, that in landscapes where the seagrass forms separate patches on a matrix of unvegetated sand, a predator may move in-between patches of seagrass feeding at the edges. Holt *et al.* (1983) hypothesised that this type of heterogeneity was important for juvenile red drum. They found red drum to be more abundant in patchy areas than in homogenous stands of *Halodule wrightii* and suggested that this greater abundance be related to the juvenile fishes' requirements for open feeding areas adjacent to seagrass that provided nearby protection from larger predators. However, where seagrass is the matrix habitat with patch elements of bare sand, for larger predators, the seagrass and algae may act as barriers so that edge effects in the interior part of the seagrass landscape may be of a lower risk in terms of predation than outer edges or where edge density is low. In the present study, edge density has incorporated the fact that movement along suitable habitat patches is usually a function of the character of the intervening habitats. For these reasons, contrast weighted edge density was used which, in addition to standardising edge to a per unit area basis, reduces the length of each edge segment proportionate to a predetermined degree of contrast. Seagrass to unvegetated sand is assumed to have a greater contrast to that of seagrass to macro algal stands (Figure 5.4).

Seagrass beds are often quoted as offering good protection from predation (Orth *et al.*, 1984; Main, 1987; Rooker *et al.*, 1998a; Hindell *et al.*, 2000). Although many studies support this role, the level of protection available varies with the structure of the seagrass bed and is often limited to particular fish size classes (smaller species and juveniles) or cryptic species. There is often a balance between the benefits and costs of the structural complexity of seagrass habitats. Complexity benefits some smaller fish by providing refugia, yet is detrimental to visual predators by concealing their prey (Edgar & Shaw 1995a). Here, it was predicted that small [for example juvenile black bream (*Spondyliosoma cantharus*) and gobies such as *Gobiusculus flavescens*] and cryptic [for example pipefish (Sygnathidae) and fifteen-spined stickleback (*Spinachia spinachia*)] species of fish would increase, as the structural complexity of the seagrass plant stands increased (canopy height, homogeneity within the trawl swept area and epiphytic load). Results of the present study support this model, with total cryptic species increasing with canopy height, and densities of small permanent residents showing an inverse relationship with transect heterogeneity. *Gobiusculus flavescens* was associated positively with canopy height. It was also hypothesised that the abundance of large adult fish would decrease with increasing plant structure. Non-parametric multiple correlations (Gamma) supported this hypothesis, showing an increase in temporary mature fish densities (large adult fish which are not permanent residents of the seagrass bed, for example the benthic feeders such as rays, sole, mullet) with increased transect heterogeneity. However, this group also showed an increase with epiphytic load, which could not be explained, but may be due to a shared response to an unmeasured variable or a response to increased food items (for example epiphyte grazers).

5.5.2 Influence of habitat variables on night-time fauna

Diurnal patterns in seagrass mobile fauna are often distinctive (see Chapter 3 and Chapter 4 and references within). Borg *et al.* (1997) showed that, given the choice, juvenile cod preferred vegetated habitats of *Zostera marina*, the brown alga *Fucus vesiculosus* and algae of the genus *Cladophora* to bare sand. However, this preference was only apparent during the day. These authors proposed that the shelter provided by the macrophytes is not necessary at night. For those studies that have assessed diel variation in seagrass beds, similar strong patterns are evident (Robblee & Zieman 1984, Bauer 1985, Edgar & Shaw 1995a, Rountree & Able 1997, Mattila *et al.* 1999). In addition to diurnal movements to avoid predation, decapods are more active at night and some fish move to bare sand to feed (Summerson & Peterson, 1984; Jackson *et al.*, 2002). Day/night studies of seagrass versus bare sand and the influences of plant structure on fauna are common in the literature; however, few studies could be found that looked at the variation in influences of landscape patterns on fauna during the day and at night.

As expected, at night many of the patterns observed during the day broke down. This adds more value to the explanations given above relating to the use of the seagrass as a habitat for protection since this is likely to be a more important factor during the day, particularly for visual predators (Hindell *et al.*; 2000). At night, depth was a less important variable affecting the densities and number of species, perhaps as species move inshore where conditions are more favourable. The densities of large permanent residents showed an inverse relationship with depth. One explanation for this could be that these larger fish move into the shallow water to feed at night when the lower risk of avian predation may mean that they can exploit areas avoided during the day (Sogard *et al.*, 1987). However, some patterns were maintained. The density of cryptic species still showed an association with mean leaf height and it is proposed that as this group is adapted to living in the seagrass both in terms of morphological mimicry and their prey types, the species gains no advantage by moving into other areas at night. Other assemblage variables showed different relationships to the habitat and seagrass plant characteristics at night. Total density and diversity of species were related positively to distance to the 10 m isobath, perhaps as more species move inshore at night. Epiphytic load also appears as an important variable in a number of models. Chapter 3 and 4 illustrated that many decapod crustaceans become more active at night, and these are positively associated with epiphytic load for the reasons described earlier in this section.

5.5.3 Other influencing factors and study limitations

Despite the broad-scale heterogeneity in seagrass structure at both the plant and landscape scales (Figure 5.10), epibenthic fish and decapods showed a certain level of site integrity (see Figures 5.8 and 5.9). Variation in landscape configuration and seagrass plant characteristics may be one of several processes that determine the occurrence of a species at a site. Site differences may be due to the landscape-level factors measured and discussed above, but may also be due to recruitment from the plankton (Bell & Westoby, 1986; Bell *et al.*, 1988; controlled by water circulation processes, see Chapter 4) or proximity to influences, which were not measured in this study.

Many previous studies assessing the relationships between fauna and seagrass beds have been confounded by location (see Chapter 1 Section 1.6.1). Modelling has shown that much of the variation in abundance can be explained by two factors: variation in the currents delivering larvae and exposure of the site to wave action, which either kills larvae or re-transports them (Jenkins *et al.*, 1997a). The flow around Jersey appears essentially closed, and this aspect is thought to intensify the contrast of water properties across the frontal zones and have important implications for larval transport and retention (Pingree & Mardell, 1987). Although currents close to the shore are influenced by the shape of the coastline, with prominent headlands increasing the speed of tidal currents and causing gyres within adjoining bays (Barne *et al.,* 1995), on the whole, Jersey experiences relatively fast tidal currents. The present study attempted to incorporate current speed and hydrodynamics and potential larval supply by using the distance to the 10 m isobath as a surrogate. However, more hydrodynamic modelling is needed to understand larval transport close inshore around Jersey.

It is also unlikely that biologically-important (dependent) variables are determined by a strictly linear relationship. The ecological associations between habitat biological properties are generally more complex than can be described by simple linear models. Several studies have suggested that rates of predation do not decrease linearly with increasing seagrass structure (Nelson 1979; Gotceitas & Colgan, 1989). Many studies have identified a threshold both at the plant structure and landscape structure level (Figure 5.1). Such situations would mean that the linear models suggested here might not be appropriate to describe the relationship between abundance or diversity of fauna and the structure provided by the seagrass. In the present study, the R^2 values gave an approximation of the strength of any relationship and bivariate plots were observed and any non-linear relationships reported (Figure 5.12). The linear models observed may indicate that the range or detail of structures measured were not large enough to detect a threshold. Density of seagrass could not be measured during this study at a scale that would be applicable to the density of trawl samples, due to the subtidal nature of the seagrass beds and difficult diving conditions. However in Chapter 2 (Figure 2.10c), the majority of beds had shoot densities less than 550 shoots m^{-2}. Thresholds observed by other studies were in excess of 500 shoots m^{-2} (900 shoots.m^{-2} , Salita, 2000; 567 shoots.m^{-2} , Gotceitas & Colgan, 1989; 700 to 1000 shoots.m^{-2} , Gotceitas *et al.*, 1997).

5.5.4 Conclusions

Recent research and development plans for seagrass beds have requested landscape level approaches (Butler & Jernakoff, 1999) due to the management implications. For example, decisions over preservation are more likely to be a choice over different seagrass beds rather than parts of individual beds. In addition to offering a potentially important scale for establishing the influence of seagrass bed structure on megafauna, seagrass patch size, shape and leaf length are realistic scales for resource managers to monitor subtidal seagrass beds using the techniques described in Chapter 2. Understanding the influence of seagrass bed fragmentation or even cohesion on the distribution of fauna will inform decisions on management strategy and habitat restoration. If the organism-focused definition of a landscape is accepted, seagrass habitats would need to be managed across the full range of spatial scales.

6 Summary

6.1 Summary

Seagrass beds are thought to have a fundamental role in maintaining populations of commercially exploited fish and invertebrate species. They do this by providing one or more of the following: (1) a permanent habitat, allowing completion of the full life cycle, (2) a temporary nursery area for the successful development of the juvenile stages, (3) a feeding area for various life-history stages and (4) a refuge from predation. Unfortunately, these roles have been distilled from a disparate literature that is based upon different sampling methods, different seagrass species, different geographical locations, and different temporal and spatial scales. Little research establishing these roles has been conducted in Europe. Indeed, studies of this nature in British seagrass beds are totally lacking, even though their (presumed) importance is highlighted in British fisheries management and conservation strategies (e.g. UK Biodiversity Habitat Action Plans). Seagrass (of the genus *Zostera*) are included in some coastal Sites of Special Scientific Interest (SSSI), Ramsar sites (i.e. an area that has been designated a 'Wetland of International Importance' as defined by the 'Ramsar Convention' of 1971), Special Protected Areas (SPAs) under the EC Birds Directive, Marine Nature Reserves, Voluntary Marine Conservation Areas (VMCAs) and marine Special Areas of Conservation (SACs) (Holmes, 1983; Davison, 1997).

Despite such recognition, the distribution of seagrass around the British Isles has not been quantified rigorously at many locations. Chapter 1 highlighted that there are significant differences in the habitat roles of seagrass beds in relation to their morphology and location. Prior to the present study, the subtidal seagrass beds around Jersey were unmapped and knowledge of the associated fauna was limited to natural history observations made at the beginning of the 20th century (Sinel, 1906) and references of seagrass found in local fish species checklists (Le Sueur, 1967). It was, therefore, important (and the aim of Chapter 2) that the configuration and structure of the seagrass beds around Jersey (English Channel, 49°00N 02°00W) were comprehensively mapped prior to any assessment of the habitat value. The second aim of Chapter 2 was to assess the potential factors affecting the distribution and configuration of seagrass around Jersey, to identify both natural and anthropogenic effects, both now and in the future. In this study, analyses of aerial photography, diver surveys and an automated acoustic device (Biosonics DT4000) were brought together in a Geographical Information System to provide a multi-scale map of the subtidal *Zostera marina* around Jersey. The use of landscape metrics, widely employed in terrestrial ecology, enabled the configuration of the seagrass beds to be quantified and compared.

The findings of the mapping (Chapter 2) illustrated that the seagrass beds around Jersey differed in many of the attributes measured, both at a landscape level (for example, core area, edge density, patch size) and at the scale of the seagrass plant (for example, canopy height, density, epiphytic cover). These are all factors that have been shown previously to influence the distribution and composition of associated fauna. Difference in seagrass bed configuration and plant structure were related to relative exposure (REI), depth and characteristics of the sediment. For example, increased exposure was positively correlated with fragmentation of the seagrass beds (decrease in patch size and core area, and an increase in edge density). The seagrass was limited to the more sheltered north-eastern, eastern and southern coasts of Jersey and to a depth of 6m below chart datum.

Large tidal ranges found around Jersey result in the outer edges of some seagrass beds having up to 17m of water above them for periods of time. Such water depths limit the use of standard quantitative methods (throw traps and drop nets) for sampling the mobile macrofauna. More practical gear (such as trawls and beach seines), however, tend to be selective for/ against a particular faunal size class, habit or behaviour. No previous knowledge existed on the fauna inhabiting the subtidal seagrass beds around Jersey on which to base the choice of sampling method. Without employing a suite of sampling gears, inferences on the species inhabiting subtidal seagrass beds are limited to the selectivity of the gear used. The aim of Chapter 3 was, therefore, to trial different gears and sampling times to assess which methods gave the most comprehensive view of the species utiliing the seagrass beds, the results of which could be used as the basis for gear selection and to build a knowledge base of potential bias. Previous studies identified strong diel and tidal variability in the fauna inhabiting seagrass beds, therefore, the trial also made an assessment of optimum sampling time period. Five commonly used techniques (beam trawl, push net, beach seine, pots and diver survey) were compared in terms of species composition, species length-frequency distributions and operational efficiency (time cost). The different gears showed a high degree of species selectivity, with only 7% of species shared by all five methods. Beach seining and trawling sampled the greatest number of commercially exploited species (11 species) and trawling sampled the greatest total number of species (30 out of 43 in total). Based on these results, trawling and beach seining were selected to sample the optimum range of target species within the identified seagrass habitats. However, due to the depth limits of the beach seine, and the difficulty in accessing some of the seagrass beds from the shore, trawling was the main sampling method. Trawling showed positive size selectivity for small fish and decapod crustaceans, and under sampled larger more mobile species. Beach seining showed an opposite size bias and sampled species from the entire water column, which may have included species not strongly associated with the seagrass habitat. Both methods showed significant variability in fauna sampled at different times. For the trawling, significant differences in the density of fish and number of decapod species were observed for the two tidal states. Also, the number of exploited species caught was highest at night high tide. Diel differences in the fauna sampled were also strong, with some species only being sampled during either the day or night. Numbers of exploited species were highest at night, but overall species numbers were highest during the day. The decision was taken that sampling should be carried out both during the day and night, but because of the differences in depth of the various seagrass beds, sampling should be limited to one tidal state (low tide).

The variability in structure of seagrass beds, together with their role as nursery, foraging and protective habitats makes the inclusion of different levels of temporal and spatial scales important in seagrass studies. Chapters 4 and 5 examined the spatial and temporal utilisation of subtidal seagrass beds by fish, decapods and cephalopod molluscs in the coastal waters of Jersey. The seagrass beds studied supported a diverse large mobile fauna (46 species of fish, 40 species of decapod and 4 cephalopod mollusc species), including species exploited within the Normano-Breton Gulf (19, 6 and 3 species of fish, decapod and cephalopod respectively, with direct economic value).

To date, seagrass studies have identified that variability in species composition is linked to seagrass density, biomass and bed heterogeneity at a local scale, but at a larger scale hydrography becomes important, due to its influence on larval supply and habitat structuring. This disparity poses a problem for environmental managers when making decisions on the relative value of different seagrass beds. Should beds of a particular morphology or structure be made the priority for protection or are patterns of species occurrence largely due to the position of the bed (e.g. in relation to larval supply or spawning migration routes)? If this is the case, bed location may be a more important consideration than morphology. Current knowledge is derived largely from beds within estuaries or sheltered bays. However, Jersey possesses coastal seagrass beds and is surrounded by an intensified anticlockwise current, which further complicates the question of location for fisheries managers.

The aim of Chapter 4 was to examine whether local scale variability in large mobile fauna between beds was superseded by variability at a larger scale (the coastal location of the seagrass beds). Spatial scale was assessed using a three-factor nested ANOVA, with six random sites nested within geographic location (north east/ south of island), and sampled during the day and at night. Tests were run on individual species and on total fish, decapods and cephalopods, with the emphasis on exploited species. The temporal component of the study sampled three seagrass beds in the north-east of the island at three periods throughout the summer. Results from the temporal study aided the identification of permanent and temporary fish residents, utilising the seagrass bed as a nursery ground or temporary foraging area. Patterns in densities of these groups were analysed to see whether they varied with site and location and if patterns were consistent over time. Nine percent of the total numbers of fish were identified as juveniles, utilising the seagrass bed as a temporary nursery area (only specific size classes found). All of these temporary juveniles had economic value, for example, pollack (*Pollachius pollachius)* and black bream (*Spondyliosoma cantharus*). The largest proportion of total fish (74.7%) was small permanent residents in the seagrass bed (Gobidae and Gobiesocidae). Analysis of the small-scale temporal variability of fauna found that, due to the high numbers of temporary residents, there was a peak in both fish densities and species number, and densities of decapods, in July. Strong diel patterns further confirmed that significant day-night movements were occurring for certain species and that these patterns were repeated in time and space.

Gross measures of total abundance indicated that location of the site was not as important as the variability between individual sites. However, ANOVA on groups and individual species showed that patterns were not only site but species specific. For example, neither the economically important black bream (*Spondyliosoma cantharus*) nor the common prawn (*Palaemon serratus*) showed significant differences with location, although significant differences were observed between the northern sites (both species were numerically dominant in samples). In terms of assemblage composition, despite some degree of difference at the large location scale, there was a great deal of similarity in the assemblages of different seagrass beds. However, only five species of fish and six species of decapods were common to all sites. Similarities between sites are due to a few dominant common species, rather than subsets of the same fauna found in different degrees of relative abundance.

Results of Chapter 4 indicated that bed location was not as important as the variability between individual sites. The lack of a large-scale location effect may be explained by the fact that few of the species spawned offshore; the majority spawned within the seagrass beds as brooders or benthic spawners. It is suggested that only when seagrass beds are dominated by species that do not spawn locally, will patterns in seagrass fauna reflect larval supply. Overall, it would appear that post settlement/immigration processes such as predation, foraging success and emigration, supersede any larger-scale location effects (based on recruitment and immigration of fauna to the seagrass bed). These processes, and the resulting faunal composition, may be influenced by the structure and configuration of seagrass beds, which vary considerably around the coast of Jersey. Understanding the potential influence of seagrass bed structure on fauna not only identifies the most important habitats in terms of particular species, groups and overall biodiversity, but also enables predictions of the possible impacts on the fauna of different perturbation scenarios (for example fragmentation of the beds).

At the scale of individual seagrass beds, Chapter 5 aimed to assess whether the findings of models proposed by previous seagrass faunal studies applied to Jersey. The habitat characteristics of ten seagrass beds were examined as potential influences on fish and decapod assemblage composition. Faunal data was coupled with ecologically relevant seagrass habitat variables, from aerial photographic analysis (for example, seagrass core area, contiguity and other landscape metrics), digital echo-sounder data (for example, depth and canopy height) and diver surveys of the beds (for example, shoot density). The contributions of these variables as predictors of properties of the fish assemblages were evaluated using multiple linear regression models. Results indicated that shallow and deeper seagrass beds should be managed separately. Both species number and density increase of with increasing depth of the seagrass landscape, although at night, large mature fish may move into the shallower beds. Shallow-water beds are more prone to environmental fluctuations and, in some areas, activities on the lower shore (for example, boat launching, push netting and bait digging) may increase disturbance. Although these reasons were suggested to explain lower species diversity and 'habitat value' (for example, as a nursery for small juvenile species of fish), they also make them more vulnerable habitats in need of protection. Deeper seagrass beds appear more valuable as a habitat and are prone to different impacts (for example, anchor and mooring chain scarring or damage from the use of mobile gears).

6.2 Limitations and suggestions for further work

The sampling strategy used in the present study was designed to assess the relative spatial and temporal differences of seagrass beds in respect to fish, decapods and cephalopod molluscs. However, the review of the literature in Chapter 1 identified spatial and temporal patterns (see Figure 1.1 and 1.2 for summaries), which influence the fauna of seagrass at other study locations, but were not assessed during the present project (due to time constraints and difficult weather conditions). For example, in Chapter 4 temporal sampling was limited to a small time period, one summer's sampling. This limited time coverage may have important implications for the measurement of landscape variables. In some systems, patches of seagrass are temporally dynamic often showing cyclic variability in growth and extent (Chapter 1 Figure 1.2; see also Den Hartog, 1987; McNeill *et al.*, 1992; Worthington *et al.*, 1992; Glémarec *et al.*, 1996; Bell *et al.*, 1999) as are faunal distributions (Mattila, 1995), and temporal variation in the importance of seagrass beds may be stochastic. More long-term temporal studies of seagrass beds in this area are needed to confirm the patterns observed here and identify larger-scale temporal patterns and times when protection from disturbance for the seagrass beds is more important. This would allow for recruitment variability, migratory species and both the succession and die back of the seagrass habitats. Sampling in other seasons (Winter, Spring and Autumn) may distinguish other species, perhaps using the habitat as a winter refuge. It would also help to back up the conclusions reached regarding the temporal nature (in terms of habitat use) of the species observed in this study, and identify specific periods of immigration, emigration and ontogenetic shifts over the year. Temporal assessments would also help separate natural patterns from man-made perturbations and stochastic events such as disease and storms (but see Frost *et al.,* 1999). There are arguments as to the reliability of inferring the impacts of fragmentation from such studies without experimentally testing these predictions. Long-term monitoring should be set up to describe the seagrass beds in terms of their temporal variation configuration as well as smaller-scale changes in density and epiphyte index.

In terms of the different spatial scales known to influence seagrass fauna (Figure 1.1) Chapter 4 addressed shifts in the spatial variability of the seagrass large mobile fauna at the level of coastal location. Chapter 5 assessed bed morphology, location of the bed, site location in terms of other habitats, depth and some aspects of microhabitat structure. Further study, however, is required to test empirically some of the models proposed, possibly via manipulations of the seagrass beds or the use of ASU's. An examination of how microhabitat structure (Figure 1.1), bed morphology and landscape configuration effect smaller macrofaunal distributions (infauna and epifauna) in Jersey seagrass beds would be beneficial. Such studies would help in identifying any cascade effect, whereby, due to predation or food resources, smaller scale attributes affecting smaller sized organisms, may indirectly affect the distributions of larger organisms (Attrill *et al.*, 2000).

The assessment of habitat utilisation by fish was restricted towards the smaller (< 100 mm) and less mobile species (see Chapter 3 for more detail), and, therefore, may have underestimated the larger mobile predators. Similarly, the trawl will not have caught the smaller, newly-settled individuals, and the patterns reported are certainly influenced by substantial post-settlement patterns. Further study on the ichthyoplankton of the seagrass beds may answer questions about the influence of larval supply on species composition of the seagrass beds (see Tolan *et al.*, 1997; Jenkins *et al.*, 1998).

Another factor that needs to be considered is that the landscape mosaics looked at in this study do not exist in isolation. They have a structure that is determined at a broader scale (Kotliar & Wiens, 1990) and landscape boundaries are, to some extent, artificially imposed. Generally, landscapes occupy some spatial scale intermediate between an organism's normal home range and its regional distribution. One of the key principles of hierarchy theory and supply side ecology is that broader-scale process act to constrain or influence finer scale phenomena (Allen & Star, 1982). Ideally, landscape would be defined based upon each target species' short and long-range perceptual ability (Kolasa & Rollo, 1991), which are often not known. One suggestion is the calculation of habitat suitability index models for the species found (Kostecki, 1984).

6.3 Recommendations for management of Jersey seagrass beds

In Jersey, the management of seagrass landscapes has two main aims: conserving overall biodiversity and protecting habitats that serve a function for exploited species (for example, as a nursery or feeding ground)(States of Jersey Policy & Resources Committee, 2001). Juveniles of larger species (including pollack, bib and black bream) decreased in abundance with fragmentation of the seagrass, indicating that the nursery function may be lower in more fragmented beds. However, more fragmented beds may be important feeding grounds for larger fish of economic value (for example, wrasse, rays and even bass) particularly at night. Also, both the most fragmented seagrass beds (for example, La Coupe and Elizabeth Castle) and contiguous beds (for example, St Catherine and Les Elavees) support high species diversity (though assemblage composition differs). General advice to managers is, therefore to prevent fragmentation of the contiguous seagrass beds (or help to restore beds that have become fragmented via anthropogenic activities). Restoration of seagrass beds needs to be done with care, reflecting natural seagrass landscape configurations at each individual location (Bell *et al.*, 2001; Campbell, 2002). Monitoring at this level is perhaps the most cost effective (using remote sensing; aerial photography and the Biosonics equipment).

At the microhabitat level, factors such as canopy height and epiphytal load may affect the distributions of small and cryptic fish species and small decapod crustaceans, with knock on effects for higher trophic levels. Cryptic species may have a greater association with seagrass than other groups, which may associate with any structured habitat available (Heck *et al.*, 2003). For juvenile black bream (*Spondyliosoma cantharus*), a species of high economic value (States of Jersey Annual Fisheries Report, 2000), the seagrass beds are proposed as important nursery areas, relative to the canopy height (easily monitored using the Biosonics equipment, described in Chapter 2). Also, changes in epiphytic load and canopy height can be early indications of anthropogenic impacts on the seagrass beds, which may eventually result in larger scale habitat fragmentation (see discussion in Chapter 2). Therefore, some smaller-scale monitoring is also advisable.

The main factors impacting seagrass beds can be placed into three main categories; water clarity, water quality and physical damage. The potential impacts of these factors on the seagrass landscapes and consequently on the fauna (as suggested by the models in Chapter 5), their sources and possible mitigation, management and protection are outlined in Table 6.1.

In the 1930s an epidemic destroyed entire populations of *Zostera marina*. The 'wasting disease' as it has become known, resulted in diagnostic black lesions, which spread along the leaves in the space of a few weeks, making the brake off and eventually causing the death of the plant. After two or three weeks of constant defoliation the rhizomes of the plant become discoloured and perish (den Hartog, 1989). Effects on the structure of the habitat are likely to be seen as an initial reduction in canopy height, which models from Chapter 5 suggest may result in a decrease in fish diversity. Following the death of some plants small-scale fragmentation is likely, resulting in a decrease in the total number of species, fish density, decapod species number, decapod diversity and also a reduction in the number of juvenile fish. At some locations fragmentation may be exacerbated by currents preventing seagrass re-colonisation eventually increase in fragmentation either to a point where all the seagrass habitat is lost or where the landscape stabilises as a more heterogeneous mosaic of habitats. Initial decreases in total species number may then level off and start to increase (Figure 5.12) as increasing habitat diversity (and interspersion of habitats) results in increased species diversity, although results indicate that this may be due to an increase in small permanent fish as opposed to temporary juveniles (including exploited species, Table 5.11).

Early investigations lead to the conclusion that *Labyrinthula macrocystis*, an infectious slime mold protist, was the organism responsible (Young, 1943). However this theory lost credibility when *Labyrinthula* were found in large numbers on otherwise healthy plants (Rasmussen, 1977). Short *et al.* (1958) suggested that there were two forms, only one of which was pathogenic. Other theories on the cause of the disease included correlations with extremes of precipitation (Martin, 1954) and long term increases in water temperature (Rasmussen, 1977), both of which caused stress, which reduced the plants resistance to infection. There is evidence to suggest that unusually warm summers on the South West Coast of England during the 1980's may have stressed *Zostera marina* beds. A rise in temperature and decreased irradiance resulted in respiration outweighing photosynthesis and hence a reduction in the amount of available fixed carbon (Cleator, 1993). Other factors suggested to induce an epidemic include low irradiance (possibly due to increased turbidity), alterations in current flow and pollution (Short, et al., 1988; see Table 6.1 for potential sources in Jersey). Whilst a past epidemic cannot be regarded as a potential threat, recent discoveries of diseased plants have led scientists to believe that the wasting disease of the 1930's was not a unique event (Cleator, 1993b; Short, *et al.,* 1988). Although a natural event such as the wasting disease may be difficult to prevent with current knowledge, curtailing of stress factors such as pollution, may improve the *Zostera*'s survival ability in the event of another epidemic.

The most catastrophic losses of seagrass meadows since the 1930's wasting disease have been correlated with nutrient loading from coastal eutrophication (Burkholder, *et al.*, 1994). Some studies have shown that nutrient enrichment may increase production in *Zostera* (Tubbs & Tubbs, 1983; Zieman, 1975), however phytoplankton blooms and opportunistic algal growth (including epiphytes) may cause severe shading (Den Hartog, 1987). In addition a study carried out by Burkholder *et al.* (1994) indicated that water column nitrate enrichment could change internal nutrient balances and impair carbohydrate metabolism in *Zostera marina* visible as reduction in density, canopy height and possibly the impacts of *Sargassum* on *Zostera*, in terms of competition and degradation of the seagrass habitat are conflicting (see review in Davison, 1997) and the actual impacts on biodiversity and ecosystem function area largely unknown. With the occurrence of *Sargassum* around much of the coast of Jersey and its appearance in many of the seagrass landscapes (see Figure 5.4) study into the concerns would be valuable. Potential sources of nutrients in Jersey, which may cause enrichment, include run off from fertilised agricultural land and storm overflows from the sewage (under normal conditions the sewage receives full tertiary treatment and has since 1994). Continued monitoring of water quality by the States of Jersey Environmental Service Unit, is important in preventing serious water quality problems in Jersey.

Like many plants seagrasses are able to take up and concentrate heavy metals, organic compounds and substances such as Tributyltin (TBT), without any apparent adverse effects. In fact Francois *et al.* (1989) studied the decomposition of TBT in the tissue of seagrasses and found that the plants acted as detoxifiers, releasing monobutyltin in to the surrounding water. Chemical oceanographers are appreciating that seagrasses represent biotic heavy metal reservoirs (Mc Roy & Helfferich, 1980). However, unlike sediments, which are essentially heavy metal sinks, seagrass communities may remobilise and transport these elements to higher trophic levels.

Finally, the impacts can be of a more physical nature. Boat anchors, launching from the shore, propeller scarring, dredging and destructive fishing methods such as beam trawling, have all been shown to physically damage seagrass beds (De Jonge & De Jonge, 1992). *Zostera* roots are not very deep (20cm) and can be easily dislodged and removed. Seagrasses tend to grow in more sheltered parts of the island, for example St Catherine Bay (Chapter 2), which are equally as amenable to boat mooring and anchoring. Permanent boat moorings tend to have a localised impact (see Figure 2.11), with the anchor chain sweeping and scouring the immediate area of seagrass as the boat rotates with changes in the direction of currents and wind. Permanent moorings result in the fragmentation of the seagrass bed in a very different way to dragged anchors, mobile gear or dredging, creating small patches of bare sand in a matrix of seagrass, rather than un-vegetated channels dissecting seagrass beds into separate the different potential impacts on the fauna are discussed on page 213. There are methods employing sub-surface buoys that minimise the dragging of the anchor chain. It is suggested to managers that the use of such moorings is encouraged (for example through grants and subsidies) in at risk areas, such as St Catherine Bay, and also to try and ensure that any new moorings are located in unvegetated areas (aided by the maps produced in this study, Chapter 2). A general code of practice for all boat users should be provided to minimise damage to the seagrass beds.

Land claim (known as reclamation) and development are particularly important issues in Jersey due to its small size and dense population. Land is at a premium and infilling of intertidal zones as part of reclamation schemes are seen as a solution for development and to the problem of solid waste disposal. Land claim impacts the seagrass through direct loss of habitat and subsequent alterations of the dynamics of coastal processes. This may lead to fragmentation of the seagrass beds and the impacts on fauna described above. There is also a concern about the leaching of heavy metals from ash used as infill.

Many of these anthropogenic activities and also more natural occurrences such as severe storms can affect processes of sediment accretion and erosion and negatively influence water clarity (Table 6.1). This can affect the amount of light available for photosynthesis and so determines the depth to which the *Zostera* can grow. The models in Chapters 2 and 5 illustrated the importance of the depth in the value, with a common trend of increasing diversity with the depth of the seagrass beds. Loss of deeper beds may therefore have significant biodiversity implications and may impact larger fish, which come into the beds to feed at night (see Table 5.10). Both may affect the overall functioning of the ecosystem.

Table 6.2 and the issues discussed are just a guide, managers should be aware of cascade effects. For example, increased eutrophication has been shown to increase the growth of epiphytic algae on the seagrass (Den Hartog, 1987), which may create greater habitat complexity and result in an initial rise in species diversity. However, greater epiphytal loading also makes seagrass blades more prone to breakage during storms and can reduce canopy height directly. Epiphytic load may lower the amount of available PAR (Photosynthetically Active Radiation) for the seagrasses and hamper growth and ability to recolonise adjacent unvegetated patches. Loss of seagrass can also show a negative feedback. Sediments no longer stabilised by *Zostera* can result in increased turbidity, which can lead to further losses of seagrass, and the sediment characteristics may change making it unsuitable for recolonisation of the seagrass. It is suggested that the patches created by yachts in the sheltered St. Catherine Bay (Figure 2.11) would be more likely to recover through natural vegetative growth than the scars from dragged anchors in the seagrass in stringer current regimes for example in the Violet Channel, due to changes in the sediment.

for recolonisation of the seagrass. It is suggested that the patches created by yachts in the sheltered St. Catherine Bay (Figure 2.11) would be more likely to recover through natural vegetative growth than the scars from dragged anchors in the seagrass in stringer current regimes for example in the Violet Channel, due to changes in the sediment.

Table 6.1 Table illustrating the various factors impacting seagrass beds, their sources, influence on the fauna (based on models developed in Chapter 5) and threats to seagrass beds, and suggestions for management.

Factor	**Activity/source**	**Potential impacts on seagrass**	**Potential impact on fauna**	**Mediation/ Mitigation/ Management**
Water Clarity				
Turbidity	Natural: Storms, wind and wave action, run off from the land. Anthropogenic: Deposit extraction, dredging activities, and coastal development. Poor catchments management	• Increased stress increased susceptibility to wasting disease resulting in reduction in canopy height, fragmentation and even complete loss of habitat. • Restrict light levels and penetration of PAR (Photosynthetically active radiation), decrease in shoot density, increased canopy height • Reduce the depth limit of the seagrass beds, change in bed shape.	Models suggest that changes to the seagrass habitat described are likely to have the following impacts: Decrease in fish density and total number of species Decrease in the density of temporary juvenile fish (including many exploited species) Reduced depth limit may result in overall reduction in species number, diversity and density (fish and decapods) However, these changes may be confounded by the fact that increased turbidity may aid predator evasion, thus reducing the attraction of *Zostera* as a refuge (see page 22).	Limit anthropogenic activities, which may increase turbidity, to the winter when impact minimised. Consider the impact on the seagrass beds during Environmental Impact Assessments on a case-by-case basis. Monitor water quality and effectiveness of catchments management.
Water Quality				
Thermal changes	Natural/Anthropogenic: Climate change, severe winters and hot summers.	• Increased stress increased susceptibility to wasting disease resulting in reduction in canopy height, fragmentation and even complete loss of habitat.	Decrease in fish density and total number of species Decrease in the density of temporary juvenile fish (including many exploited species)	Follow Intergovernmental Panel on Climate Change (IPCC) advice on mitigation (Metz *et al.*, 2000).

Factor	**Activity/source**	**Potential impacts on seagrass**	**Potential impact on fauna**	**Mediation/ Mitigation/ Management**
Oil pollution	Oil spill from tanker Bilge from boats	• Oil on leaves may reduce PAR	Direct toxicity effect on the fauna	Jersey has a contingency plan important to reconsider the priority of areas containing seagrass within the contingency plan
Chemical Pollution	Point source discharges from industry. Leachates from coastal landfill sites. Fertiliser and herbicide run off from agricultural land Antifoul components (for example Tributyltin)	• *Zostera marina* accumulates heavy metals, TBT, other antifouling agents. • Growth inhibition and mortality. Visible as fragmentation and reduction in canopy height.	Accumulated chemical passed up the food chain. Habitat changes may lead to Decrease in fish density and total number of species Decrease in the density of temporary juvenile fish (including many exploited species)	Monitor water quality and effectiveness of catchments management.
Eutrophication	Sewage and agricultural runoff.	• Increased turbidity due to increased phytoplankton growth and subsequent impacts described above. • Increased nutrient inputs • Increased epiphytal load • Increased nitrate has also been linked to a deterioration of the meristem damage to plant, decreased density, • Promoted algal growth which may increase habitat heterogensity or compete for light resources, causing seagrass loss, fragmentation. • Low levels of nutrients may stimulate growth, increase canopy height, vegetative regrowth of unvegetated patches (decrease in fragmentation).	Increased epiphytic load may result in an increase in density of decapods, but a decrease in overall diversity. Increased habitat heterogeneity resulting from promoted algal growth may initially cause an increase in species diversity. Decrease in fragmentation may result in increased total species number.	Monitor water quality and effectiveness of catchments management.

Factor	**Activity/source**	**Potential impacts on seagrass**	**Potential impact on fauna**	**Mediation/ Mitigation/ Management**
Physical damage				
Direct: Removal, scouring, trampling. All resulting in direct damage to the seagrass canopy and rhizomes	Mobile gears, trampling by off-road vehicles, low water launching of pleasure craft, low water fishing, swimming, sailing. Boat anchoring, moorings. Land claim (known as reclamation) Direct habitat loss, smothering increased turbidity, changes in the hydrography erosions Jettites shading Channel dredging, coastal developments	• Seagrass roots are not very deep (20cm) can be easily dislodged • Rhizome damage may lead to fragmentation. • Reduction in canopy height	Decrease in fish density and total number of species Decrease in the density of temporary juvenile fish (including many exploited species)	These impacts identify considerable conflict between natural resources values and human values. Consideration of these issues within an Integrated Coastal Zone Management plan would be valuable. Encourage the use of mid water mooring buoys. Supply stakeholders with code of practice for protection of seagrass beds. Limit Already in place laws preventing the use of mobile gears within the bays and channels where seagrass occurs.
Indirect: Shading Any activity which effects the coastal processes of sedimentation and accretion	Introduction of non native species Sargassum Jetties/ structures which shade the seagrass. Seawalls Mariculture wracks	• Restrict light levels and penetration of PAR (Photosynthetically active radiation), decrease in shoot density, increased canopy height • Increase in habitat heterogeneity. • Increases in flow rate may facilitate fragmentation • Breakwater at St Catherine may actually have had a positive influence on the *Zostera* beds there by increasing shelter (lowering REI).	Shading may have similar impacts as turbidity. Though this may be offset by alternate structure as a refuge for fauna. Fragmentation may result in a Decrease in fish density and total number of species. Decrease in the density of temporary juvenile fish (including many exploited species)	Research into *Sargassum muticium* in Jersey to gauge actual impacts on the biodiversity and ecosystem function. Conservation of wildlife law includes provisions to prevent the spread of non-native marine species. Consider shading effects of new developments during Environmental Impact Assessments.

The season and frequency of activity is also important in determining the level of impact including turbidity less impact also whether populations are perennial or annual. Not all beds are impacted by the same activities. For example, shallow seagrass beds are more vulnerable to damage by launching boats on the shore and push netting by low water fishermen. However, anchoring and damage by mobile gear is more likely to impact deep-water beds.

Also, direct impacts on the fauna of the activities in Table 6.1 are not considered here. Although the seagrass plants themselves would seem to be resilient to pollution, not all the important constituents of the seagrass ecosystem are equally well protected (McRoy & Helfferich, 1977). When assessing the impacts of pollution on seagrass, the effects on associated flora and fauna are an important consideration, and therefore a baseline study of these would be useful taken into account in any EIA.

Zostera marina is undoubtedly very sensitive to anthropogenic influences, particularly in relation to eutrophication, pollution, turbidity, sedimentation and accretion. It is also apparent that *Zostera marina* has a poor ability to recover from such damage, being that it is long lived and has poor recruitment (from seeds). Recovery is most successful via vegetative growth. It is less likely that a population will recover in an area from seeding from another population. The species and habitat has, therefore, been classed as highly sensitive (Holt *et al.,* 1997) and Kinglisides (1995) proposes *Zostera marina* as a key species of Critical Ecological Capital (CEC), on the basis that it meets the criteria of *"providing an ecological basis for the existence and continuing functioning of a community...whose absence would cause the community to significantly alter, dysfunction or disappear"* (Masters & Gee, 1995). Due to the cost and limits to the success in restoration techniques *Zostera* also qualifies as CEC in terms of irreplacebility. In some areas seagrass transplantations for restoration purposes have been successful and guidance published (Campbell, 2002). However, restoration of seagrass beds needs to be done with care, reflecting natural seagrass landscape configurations at each individual location (Bell *et al.*, 2001). Landscape ecology studies such as the present one should be used as an aid for restoration efforts, most importantly in suggesting appropriate spatial configurations of restored seagrass to facilitate recruitment of fauna (Bell *et al.,* 1997).

Other methods of mitigation and protection include limiting physical disturbance to the winter when minimal impact can occur, monitoring of water quality and the designation of special areas of conservation (SAC) to protect seagrass areas from destructive fishing methods. The EC habitats directive (92/43/EEC) specifically mentions *Posidonia* seagrass protection could be achieved by referencing it individually (as proposed in the UK Habitat Action Plan for seagrass), its importance in comparison to *Posidonia* and at a local level must be more fully understood. However, *Zostera* beds are classed as priority habitats in UK Habitat Action Plans. Action plan objectives include maintaining the extent and distribution of seagrass beds in UK Waters, and to assess the feasibility of restoration of beds that have become damaged and degraded (UK Biodiversity Steering Group, 2000).

Due to its size and population pressures Jersey's marine environment is an area of intense activity where interactions between biological, physical, social and economic systems are constantly taking place. Current protection of seagrass beds in Jersey includes a ban on the use of mobile fishing gear within these shallow coastal zones. However, further legislation is needed to prevent boats from dragging their anchors whilst line fishing in the vicinity of a seagrass bed. Detailed monitoring of 'at risk' areas (for example, those seagrass beds in high exposure regimes and close to human activity such as at Elizabeth Castle) is needed to assess whether seagrass beds are receding and expanding. Aerial photographic-based maps provide a good inventory of the location and landscape configuration of the beds, and act as a baseline map for organising monitoring programs and for detecting large-scale changes in the seagrass distribution (for example Kendrick *et al.*, 1990). However, they can be costly and time consuming to carry out and analyse, and, for management purposes, earlier and smaller changes must be detected before they can escalate to a landscape disturbance response. It is suggested that permanent transects are set up and runs with the Biosonics DT4000^{TM} carried out regularly at set times of the year to monitor change more closely. It is also suggested that transects be positioned in the seagrass meadows in places that are representative of much larger areas of the meadow and in different directions across the meadow so that patterns can be detected from shallow to deeper water.,

Jersey is an island often noted for the fact that it nearly doubles in size on a low spring tided and much of the marine conservation around the coast of Jersey has concentrated in the past on the intertidal zone (Kindleysides, 1995). However, the subtidal area Jersey for which Jersey has conservation responsibility far out-weighs the area of land and intertidal. It is important that marine conservation does not stop at the low water mark (the upper limit of most of the *Zostera marina* beds). Out of sight, should not be out of mind. A strategy for the subtidal should be carried out, similar to the one produced by Kindleysides (1995) for the intertidal. There is a need to build awareness of the subtidal habitats, including the *Zostera* beds, in the general public and also focus education at particular groups (for example fishermen, anglers, yachtsmen) via the production of codes of practice.

In the year 2000 an area of 32.1 km^2 on the south east coast of Jersey was designated as Ramsar site, under the 'Ramsar Convention' (Convention on Wetlands of International Importance), in part due to the occurrence of the *Zostera* beds. One of the requirements under the Ramsar Convention is that governments all listed sites have a management plan in place and this is a key objective for the Environmental Service Unit (ESU) in future months. Since designation, the ESU have been developing a new digital map of the site to accurately describe the site's physical and ecological characteristics. The information from this present study should feed into this plan, which it is aimed will aid the process of coastal zone management within the Ramsar Site and form the basis of an Island-wide Integrated Coastal Zone Management Strategy to bring together stakeholders involved in the development, management, conservation and use of the coast (Environmental Service Unit, 2003). Such plans could ensure that the ecological requirements of *Zostera* are met and manage human activities currently taking place, to account for any anthropogenic threats that may affect the Jersey-wide *Zostera* resource. Table 6.1 considers some of the potential impacts of activities, developments and natural events, which may have detrimental impacts on the *Zostera* resource. This table used in conjunction with the multiple regression models developed in Chapter 5 (given in Appendix 1) may help managers assess risk during proposed developments or activities, to aid conservation of these important habitats.

7 References

7.1 References

Ackleson, S.G., Klemas, V., 1987. Remote sensing of submerged aquatic vegetation in lower Chesapeake Bay: A comparison of Landsat MSS to TM Imagery. *Remote Sensing of the Environment*, **22** (2), 235-248

Adams, S.M., 1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities: structural analysis. *Journal of Experimental Marine Biology and Ecology* **22**, 269-291.

Adams, S.M., 1976b. Feeding ecology of eelgrass fish communities. *Transactions of the American Fisheries Scociety* **105**, 514-519.

Allen, T.F.H., Starr, T.B., 1982. *Hierarchy: Perspectives for Ecological Complexity.* University of Chicago Press, Chicago. 310 pp.

Anderson, E.E., 1989. Economic benefits of habitat restoration: Seagrass and the Virginian Hard-Shell Blue Crab Fishery. North *American Journal of Fisheries Management* **9**, 140-149.

Ansari, Z.A., Rivonker, C.U., Ramani, P., Parulekar, A.H., 1991. Seagrass habitat complexity and macroinvertebrate abundance in Lakshadweep coral reef lagoons, Arabian Sea *Coral Reefs* **10**, 127-131.

Arkley, K., Jacklin, M.S., Boulter, M., Tower, J., 1996. The cuttlefish (*Sepia officianalis*) : A guide to its exploitation in UK waters. Sea-Fish Report No. SR467. Sea-Fish Industry Authority, Hull. 82 pp.

Arrivillaga, A., Baltz, D.M., 1999. Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. *Bulletin of Marine Science* **65**, 301-319.

Attrill, M.J., Strong, J.A., Rowden, A.A., 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* **23**, 114-121.

Bach, S.D., Thayer, G.W., La Croix, M.W., 1986. Export of detritus from eelgrass (*Zostera marina*) beds near Beaufort, north Carolina, USA. *Marine Ecology Progress Series* **28**, 265-278.

Baden, S.P., Pihl, L., 1984. Abundance, biomass and production of mobile epibenthic fauna in *Zostera marina* (L.) meadows, western Sweden. *Ophelia* **23**, 65-90.

Bajjouk, T., Guillamaumnt, B., Populus, J., 1996. The application of airborne imaging spectrometry system data to intertidal seaweed classification and mapping. *Hydrobiologia* **326**, 463-471.

Baltz, D.M., Rackocinski, C., Fleeger, J.W., 1993. Microhabitat use by marsh edge fishes in a Louisiana estuary. *Environmental Biology of Fishes* **36**, 109-126.

Barne, J.H., Robson, C.F., Kaznowska, S.S., Doody, J.P., Davidson, N.C. (eds.), 1995. *Coasts and seas of the United Kingdom. Region 5 north-east England: Berwick on Tweed to Filey Bay.* Joint Nature Conservation Committee, Peterborough.

Bauchot, M.L., Hureau, J.C., 1990. Sparidae. In: *Checklist of the fishes of the eastern tropical Atlantic* (eds Quéro, J.C., Hureau, J.C., Karrer, C., Post, A. and L. Saldanha). Paris, Unesco. 3 vol. pp. 790-812.

Bauer, R.T., 1985. Diel and seasonal variation in species composition and abundance of caridean shrimps (Crustacea, Decapoda) from seagrass meadows on the north coast of Puerto Rico. *Bulletin of Marine Science* **36**, 150-162.

Bax, N.J., 1998. The significance and prediction of predation in marine fisheries. *ICES Journal of Marine Science* **55**, 997-1030.

Belfield, P., 1999. *Belfield Tide Plotter 2000*, Version 3.1. Computer software program produced by the authors. Portions Crown Copyright.

Bell, J.D., Ferrell, D.J., McNeill, S.E., Worthington, D.G., 1992. Variation in assemblages of fish associated with deep and shallow margins of the seagrass *Posidonia australis. Marine Biology* **114**, 667-676.

Bell, J.D., Harmelin-Vivien, M.L., 1982. Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. I. Community structure. *Téthys* **10**, 337-347.

Bell, J.D., Pollard, D.A., 1989. Ecology of fish assemblages and fisheries associated with seagrasses. *Biology of seagrasses*, A.W.D. Larkum et al. (eds), Amsterdam: Elsevier Science, pp. 565-597.

Bell, J.D., Steffe, A.S., Westoby, M., 1988. Location of seagrass beds in estuaries: effects on associated fish and decapods. *Journal of Experimental Marine Biology and Ecology* **122**, 127-146.

Bell, J.D., Westoby, M., 1986a. Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. *Journal of Experimental Marine Biology and Ecology* **104**, 275-295.

Bell, J.D., Westoby, M., 1986b. Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. *Journal of Experimental Marine Biology and Ecology* **104**, 249-274.

Bell, J.D., Westoby, M., 1987. Effects of epiphytic alga on abundances of fish and decapods associated with the seagrass *Zostera capricorni. Australian Journal of Ecology* **12**, 330-337.

Bell, J.D., Westoby, M., Steffe, A.S., 1987. Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? *Journal of Experimental Marine Biology and Ecology* **111**, 133-144.

Bell, K.N.I., Cowley, P.D., Whitfield, A.K. 2001. Seasonality in frequency of marine access to an intermittently open estuary: implications for recruitment strategies. *Estuarine, Coastal and Shelf Science* **52**, 327-337.

Bell, S.S., Brooks, R.A., Robbins, B.D., Fonseca, M.S., Hall, M.O., 2001. Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation* **100**, 115-123.

Bell, S.S., Robbins, B.D., Jensen, S.L., 1999. Gap dynamics in a seagrass landscape. *Ecosystems* **2**, 493-504.

Bender, D.J., Contresas, T.A., Fahrig, L., 1998. Habitat loss and population decline: a meta analysis of the patch size effect. *Ecology* **79**, 517-533.

Biebl, R., McRoy, C.P., 1971. Plasmatic resistance and rate of respiration and photosynthesis of *Zostera marina* at different salinities and temperatures. *Marine Biology* **8**, 48-56.

Bierwith, P.N., 1993. Shallow seafloor reflectance and water depth derived by unmixing multispectral imagery. *Photogrammetric Engineering and Remote Sensing* **59**, 331-338.

Blaber, S.J.M., Blaber, T.G., 1980. Factors effecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology* **17**, 143-162.

Blaber, S.J.M., Brewer, D.T., Salini, J.P., Kerr, J.D., Conacher, C., 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, northern Australia. *Estuarine, Coastal and Shelf Science* **35**, 605-620.

Blanc, A., Daguzan, J., 1998. Artificial surfaces for cuttlefish eggs (*Sepia officianalis* L.) in Morbihan Bay, France. *Fisheries Research* **38**, 225-231.

Boesch, D.F., Turner, R.E., 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* **7**, 460-468.

Bone, Q., Marshall, N.B., Blaxter, J.H.S., 1996. Biology of Fishes. Second Edition. Chapman and Hall, London. 332 pp.

Borg, A., Pihl, L., Wennhage, H., 1997. Habitat choice by juvenile cod (*Gadus morhua* L.) on sandy soft bottoms with different vegetation types. *Hegoländer Meeresuntersuchungen* **51**, 197-212.

Bossy, S.F., 1998. Sea Fisheries Adviser, *personal communication*, 20th November.

Boström, C., Bonsdorff, E., 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the Baltic sea. *Journal of Sea Research* **37**, 153-166.

Bowden, D.A., Rowden, A.A., Attrill, M.J., 2001. Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. *Journal of Experimental Marine Biology and Ecology* **259**, 133–154.

Brook, I.M., 1977. Trophic relationships in a seagrass community (*Thallassia testudinum*), in Card Sound, Florida: fish diets in relation to macrobenthos and cryptic faunal abundance. *Transactions of the American Fisheries Society* **106**, 219-229.

Brothers, E.B., Thresher, R.E., 1985. Pelagic duration, disperal, and the distribution of Indo-Pacific coral-reef fishes. In *The Ecology of Coral Reefs,* Reaka, M.L., (ed). NOAA Symposium Series Undersea Research, Vol. 3. Maryland: National Oceanic & Atmospheric Administration. pp. 53–69.

Buckel, J.A., Stoner, A.W., 2000. Functional response and switching behaviour of young on the year piscivorous bluefish. *Journal of Experimental Marine Biology and Ecology* **245**, 25-41.

Burchmore, J.J., Pollard, D.A., Bell, J.D., 1984. Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* seagrass habitat in Port Hacking, New south Wales. *Aquatic Botany* **18**(1-2), 71-87.

Burkholder, J.M., Mason, M., Glasgow, H.B., 1992. Water column nitrate enrichment promotes decline of eelgrass *Zostera marina:* evidence from mesocosm experiments. Marine Ecology Progress Series **81**, 163-178.

Burrell, D. C., Schubel, J.R., 1977. Seagrass ecosystem oceanography. In C. P. McRoy & C. Helfferich, (eds) *Seagrass ecosystems: a scientific perspective.* Marcel Dekker, New York. pp 195–232.

Burrett, J.R., Chuter, D., 1991. Image correction of sidescan sonar data. *International Underwater Systems Design* **13**(5), 21- 24.

Burrough, P. A., 1986. Principles of Geographical Information Systems for Land Resources Assessment. Monographs on Soil and Resources Survey No. 12. Clarendon Press, Oxford.

Burrows, M.T., 1994. An optimal foraging and migration model for juvenile plaice. *Evolutionary Ecology* **8**, 125-149.

Butler, A., Jernakoff, P. (eds), 1999. *Seagrass in Australia: Strategic review and development of an R, D plan.* Collingwood, Australia: CSIRO Publishing.

Caddy, J.F., 1986. Modeling stock recruitment processes in Crustacea – some practical and theoretical perspectives. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 2330-2344.

Caloz, R., Collet, C., 1997. Geographic Information Systems (GIS) and remote sensing in Aquatic Botany: methodological aspects. *Aquatic Botany* **58**, 209-228.

Campbell, M.L., 2002. Getting the foundation right: A scientifically based management framework to aid in the planning and implementation of seagrass transplant efforts. *Bulletin of Marine Science,* **71**(3), 1405-1414.

Carr, M.H., 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* **75**, 1320-1333.

Carr, M.R., 1996. *PRIMER User Manual (Plymouth Routines in Multivariate Ecological Research).* Plymouth Marine Laboratory, Plymouth, 43 pp.

Carr, W.E.S., Adams, C.A., 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Transactions of the American Fisheries Society* **102,** 511-540.

CCL (Cockburn Cement Ltd), 2000. Seagrass Mapping: Owen Anchorage and Cockburn Sound 1999. Report to CCL prepared by NGIS, The University of WA, DA Lord and Associates, A Wyllie and Associates and Kevron Aerial Surveys. November 2000. Report No. 94/026/S3/2 (Cockburn Cement Ltd, Success, Western Australia), pp. 91.

Chauvaud, S., Bouchon, C., Maniere, R., 1998. Remote sensing techniques adapted to high resolution mapping of tropical coastal marine ecosystems (coral reefs, seagrass beds and mangrove). *International Journal of Remote Sensing* 19, 3625-3639.

Chauvaud, S., Bouchon, C., Maniere, R., 2001. Thematic mapping of tropical marine communities (coral reefs, seagrass beds and mangroves) using SPOT data in Guadeloupe Island. *Oceanologica Acta* 24, S3-S16.

Chessa, L.A., Scardi, M., Fresi, E., Saba, S., 1989. Consumers in *Posidonia oceanica* beds: 2. *Galathea squamifera* Leach (Decapoda Anomura). In: Boudouresque, C.F., Meinesz, A., Fresi, E., Gravez, V. (Eds.), *International Workshop on Posidonia Beds* 2. GIS Posidonie, Marseille, pp. 251–255.

Chuvieco, E., Congalton, R., 1988. Using cluster analysis to improve the selection of training statistics in classifying remotely sensed data. *Photogrammetric Engineering and Remote Sensing* **54**(9), 1275-1281.

Clancy, M., Cobb, J.S., 1997. Effect of wind and tidal advection on distribution patterns of rock crab *Cancer irroratus* megalopae in Block Island Sound, Rhode Island. *Marine Ecology Progress Series* **152**, 217–225.

Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology **18***, 117-143.

Clarke, K.R., Green, R.H., 1988. Statistical design and analysis of "biological effects" study. *Marine Ecology Progress Series **46***, 213-226.

Cleator, B., 1993. *The status of the genus Zostera in Scottish coastal waters*. Scottish Natural Heritage, Review No. 22, Edinburgh.

Cohen, D.M., T. Inada, T. Iwamoto and N. Scialabba, 1990. FAO species catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other Gadiform fishes known to date. FAO Fishery Synopsis (125, Vol. **10**):442 p.

Coles, R.G., Lee Long, W.J., Watson, R.A., Derbyshire, K.J., 1993. Distribution of seagrasses, and their fish and penaeid prawn communities, in Cairns Harbour, a tropical estuary, northern Queensland, Australia. *Australian Journal of Marine and Freshwater Research* **44**, 193-210.

Connolly, R., Jenkins, G., Loneragan, N., 1999. Seagrass dynamics and fisheries sustainability. In: *Seagrass in Australia: strategic review and development of an R, D plan.* Butler, A., Jernakoff, P.(eds), Collingwood, Australia: CSIRO Publishing, pp.25-64.

Connolly, R.M., 1994a. Removal of seagrass canopy: effects on small fish and their prey. *Journal of Experimental Marine Biology and Ecology* **184**, 99-110.

Connolly, R.M., 1994b. A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. *Australian Journal of Marine and Freshwater Research* **45**, 1033-1044.

Connolly, R.M., 1994c. The role of seagrass as preferred habitat for juvenile *Sillaginodes punctata* (Sillaginidae, Pisces): habitat selection or feeding. *Journal of Experimental Marine Biology and Ecology* **180**, 39-47.

Connolly, R.M., 1997. Differences in the composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. *Hydrobiologia* **346**, 137-148.

Cordrey, L. (ed.), 1997. *Action for Biodiversity in the south West: a Series of Habitat and Species Plans to Guide Delivery.* Royal Society for the Protection of Birds, Exeter.

Costa, M.J., Costa, J.L., Raposa de Almeida, P., Assis, C.A., 1994. Do eel grass beds and salt marsh borders act as preferential nurseries and spawning grounds for fish? An example of the Mira estuary in Portugal. *Ecological Engineering* **3**, 187-195.

Costanza, R., dArge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., vandenBelt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* **387**(6630), 253-260.

Costello, M.J., 1994. The BioMar (LIFE) project: developing a system for the collection, storage and dissemination of marine data for coastal management. In: *Classification of Benthic Marine Biotopes of the north-east Atlantic. Proceedings of a BioMar-LIFE Workshop*, Cambridge, 16-18 November 1994 (Hiscock, K., ed). Joint Nature Conservation Committee, Peterborough, pp.9-17.

Council of the European Community, 1992. *Habitats Directive*: *Conservation of natural habitats and of wild fauna and flora*. Council Directive 92/43/EEC.

Critchley, A.T., de Visscher, R.P.M., Nienhuis, P.H., 1990. Canopy Characteristics of the brown alga, *Sargassum muticum* in Lake Grevelingen, south-west Netherlands. *Hydrobiologia* **204/205**, 211-217.

Crutchley, S., 1997. *Designation of a Marine Protected Area in Jersey: Recommendations with special reference to Molluscs*. MSc Thesis, University College London. 83pp.

Culley, M., Farnham, W., Thorp, C., 1996. *An assessment of the Marine Communities present on the south Coast of Jersey from St Helier to La Rocque, July 1994*. The Marine Laboratory University of Portsmouth 49pp

Curran, P.J., 1985. *Principles of Remote Sensing*. Longman, London.

Dalla Via, J., Sturmbauer, C., Schönweger, G., Sötz,., Mathekowitsch, S., Stifter, M., Reiger, R., 1998. Light gradients and meadow structure in *Posidonia oceanica*: ecomorphological and functional correlates. *Mar. Ecol. Prog. Ser.*, 163: 267-278.

Dana, P.H., 2000. The Geographer's Craft Project, Department of Geography, University of Colorado. Boulder, United States. http://www.colorado.edu/geography/gcraft/notes/gps/gps_f.html . Last updated May 2000, Accessed by Author 8th October 2001.

Dauby, P., Khomsi, A., Bouquegneau, J., 1998. Trophic relationships within intertidal communities of the Brittany coasts: a stable carbon isotope analysis. *Journal of Coastal Research* **14**, 1202-1212.

Davison, D.M., 1997. The genus *Zostera* in the UK: A literature review identifying key conservation, management and monitoring requirements. Report to the Environment, Heritage Service, Department of the Environment (northern Ireland), Belfast.

De Jonge, V.N., De Jong, D.J., 1992. The role of light, tide and fisheries in the decline of *Zostera marina* L. in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* **20**, 161-176.

De Troch, M., Mees, J., Papadopoulos, I., Wkwabi, E.O., 1996. Fish communities in a tropical bay (Gazi Bay, Kenya): seagrass beds vs. unvegetated areas. *Netherlands Journal of Zoology* **46**, 236-252.

Den Hartog, C., 1970. *The seagrasses of the world*. Amsterdam: north Holland Publishing Company.

Den Hartog, C., 1971. The dynamic aspect in the ecology of sea-grass communities. *Thalassia jugoslavica* 7, 101–112.

Den Hartog, C., 1987. “Wasting disease” and other dynamic phenomena in *Zostera* beds. *Aquatic Botany* 27, 3-14.

Den Hartog, C., 1994. Suffocation of a littoral Zostera marina bed by Enteromorpha radiata. *Aquatic Botany* **47**, 21-28.

Dennison, W.C., Alberte, R.S., 1985. Role of daily light period in the depth distribution of *Zostera marina* (eelgrass). *Marine Ecology Progress Series* **25**, 51-61.

Diana, J.S., 1995. Foraging behaviour. In *Biology and ecology of fishes*, J.S. Diana (ed.), Carmel: Cooper Biological Science Press, pp.187-213.

Duarte, C.M., Sand-Jensen, Y K., 1990. Seagrass colonization: Patch formation and patch growth in *Cymodocea nodosa. Marine Ecology Progress Series* **65**, 193-200.

Duarte, C.M., 1991. Seagrass depth limits. *Aquatic Botany* **40**, 363-377.

Duarte, C.M., 1999. Seagrass ecology at the turn of the millenium: challenges for the new century. *Aquatic Botany*, 65: 7-20.

Duarte, C.M., Kalff, J., 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. *Limnol. Oceanogr.* 31, 1072-1080.

Eckman, J.E., 1987. The role of hydrodynamics in recruitment, growth and survival of *Argopecten irradians* (L.) and *Anomia simplex* (Dorbigny)within eelgrass meadows. *Journal of Experimental Marine Biology and Ecology* **106**, 165-191.

Eckman, J.E., Nowell, A.R.M., 1984. Boundary skin friction and sediment transport about an animal-tube mimic. *Sedimentology* **31**, 851-862.

Edgar, G.J., Shaw, C., 1995a. The production and trophic ecology of shallow-water fish assemblages in southern Australia. I. Species richness, size-structure and production of fishes in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* **194**, 53-81.

Edgar, G.J., Shaw, C., 1995b. The production and trophic ecology of shallow water fish assemblages in southern Australia. II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* **194**, 83-106.

Eggleston, D.B., Etherington, L.L., Ellis, W.E., 1998. Organism response to habitat patchiness: species and habitat dependent recruitment of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* **223**, 111-132.

Elliott, M., O'Reilly, M.G., Taylor, C.J.L., 1990. The Forth Estuary: A nursery and overwintering area for north Sea fishes. *Hydrobiologia* **195**, 89-103.

Emmerson, W.D., 1986. The Ecology of Palaemon pacificus (Simpson) associated with *Zostera capensis setchell. Transactions of the Royal Society of south Africa* **46**(1), 79-97.

English, S., Wilkinson, C., Baker, V., 1997. *Survey manual for tropical marine resources.* 2nd Edition. Australian Institute of Marine Science, Townsville, 368 pp.

Erdas Inc., 1991. Erdas Field Guide version 7.5. CST 1319. Produced at the Manchester Computing Centre in accordance with an agreement between the combined Higher education software Team (CHEST) and Erdas Inc. 2nd Edition. Chapter 6 Classification Pp 105 to 141

Fagan, W.F., Cantrell, R.S., Cosher, C., 1999. How habitat edges change species interactions. *American Naturalist* **153**, 165-182.

Farrell, T.M., Bracher, D., Roughgarden, J., 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnology and Oceanography* **36**, 279-288.

Fenton, G.E., Ritz, B.A., 1988. Changes in carbon and hydrogen stable isotope ratios of macroalgae and seagrass during decomposition. *Estuarine Coastal and Shelf Science* **26**, 429-436.

Ferguson R.L., Korfmacher, K., 1997. Remote sensing and GIS analysis of seagrass meadows in north Carolina, USA. *Aquatic Botany* **58**, 241-258

Ferrell, D.J., Bell, J.D., 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Marine Ecology Progress Series* **72**, 15-24.

Ferrell, D.J., McNeill, S.E., Worthington, D.J., Bell, J. D., 1993. Temporal and spatial Variation in the Abundance of Fish Associated with the Seagrass Posidonia australis in south-Eastern Australia. *Australian Journal of Marine and Freshwater Research* **44**, 881-899.

Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series 8*, 37-52.

Fonseca M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes near Beaufort, north Carolina, USA. *Marine Ecology Progress Series* 171, 109-121.

Fonseca M.S., Zieman, J.C., Thayer G.W., Fisher, J.S., 1983. The role of current velocity in structuring seagrass meadows. *Estuarine, Coastal and Shelf Science* **17**, 367-380.

Fonseca, M., Whitfield, P.E., Kelly, N.M., Bell, S.S., 2002. Modeling seagrass landscape pattern and associated ecological attributes. *Ecological Applications* **12**(1), 218-237.

Fonseca, M.S., Fisher, J.S., 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series* **29**, 15-22.

Fortes, M.D., 1991. Seagrass- Mangrove management – A key to marine coastal conservation in Asean region. *Marine Pollution Bulletin* **23**, 113-116.

Forward Jr., R.B., Frankel, D.A.Z., Rittschof, D., 1994. Moulting of megalopae from the blue crab *Callinectes sapidus*: effects of offshore and estuarine cues. *Marine Ecology Progress Series* **113**, 55-59.

Foster-Smith, R., Brown, C., Meadows, W.J., White, W., Limpenny, D.S., 2001. *Ensuring continuity in the development of broad-scale mapping methodology - direct comparison of RoxAnn and QTC-VIEW technologies*. CEFAS Lowestoft, Contract report AE0908, 113pp

Fourqurean, J. W., Willsie, A.W., Rose, C.D., Rutten, L.M., 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology* **138**, 341–354.

Francour, P., 1997. Fish assemblages of *Posidonia oceanica* beds at Port-Cros (France, NW Mediterranean): assessment of composition and long-term fluctuations by visual census. *P.S.Z.N.I. Marine Ecology* **18**, 157-173.

Francour, P., 1999. A critical review of adult and juvenile of adult and juvenile fish sampling techniques in *Posidonia oceanica* seagrass beds. *Naturalista Siciliana* **23**(Supplement), 33-57.

Francour, P., Liret, C., Harvey, E., 1999. Comparisons of fish abundance estimates made by remote underwater video and visual census. *Naturalista Siciliana* **23**(Supplement), 155-168.

Francois, R., Short, F.T., Weber, J.H., 1989. Accumulation and persistence of tributyltin in eelgrass (*Zostera marina*). *Environmental Science and Technology* **23**(2), 191-196.

Fraser, D.F., Gilliam, J.F., 1987. Feeding under predation hazard - response of the guppy and hart rivulus from sites with contrasting predation hazard. *Behavioural Ecology and Sociobiology* **21**, 203-209.

Froese, R., Pauly, D. (Editors), 2003. FishBase. World Wide Web electronic publication. www.fishbase.org, version 01 September 2003

Frost, M.T., Rowden, A.A., Attrill, M.J., 1999. Effect of habitat fragmentation on macroinvertebrate infaunal communities associated with the seagrass *Zostera marina* L. *Aquatic Conservation: Marine and Freshwater Ecosystems* **9**, 255-263.

Fry, B., 1981. Natural stable carbon isotope tag traces Texas shrimp migrations. *Fishery Bulletin* **79**, 337-345.

Gessner, F., 1971. Water permeability and photosynthesis in marine algae. *Botanica Marina* **14**(1), 29-31.

Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32**, 191-206.

Gibson, R.N., Pihl, L., Burrows, M.T., Modin, J., Wennhage, H., Nickell, L.A., 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series* **165**, 145-159.

Giesen, W.B.J.T., Van Katwijk, M.M., Den Hartog, C., 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquat. Bot.* 37, 71-85.

Gillanders, B.M., 1995. Feeding ecology of the temperate marine fish *Achoerodus viridis* (Labridae): size, seasonal and site specific differences. *Marine and Freshwater Research* **46**, 1009-1020.

Gilmore, R.G., 1990. Nekton: biomass and abundance. In: *Monographs on oceanographic methodology: seagrass research methods*. R.C. Phillips,, C.P. McRoy (eds), Paris:UNESCO.

Glémarec, M., Le Faou, Y., Cuq F., 1997. Long term changes of seagrass beds in the Glenan Archipelago (south Brittany). *Oceanologica Acta* **20**, 217-227.

Gore, R.H., Gallaher, E., Scotto, L.E., Wilson, K.A. 1981. Studies on decapod crustacea from the Indian River region of Florida. Community composition, structure, biomass, and species-aereal relationships of seagrass and drift algae-associated macrocrustaceans. *Estuarine Coastal and Shelf Sci*ence **12**, 485-508.

Gotceitas, V., Brown, J.A., 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*) - effects of predation risk. *Oecologia* **93**, 31-37.

Gotceitas, V., Colgan, P., 1989. Predator foraging success and habitat complexity – quantitative test of the threshold hypothesis. *Oecologia* **80**(2), 158-166.

Gotceitas, V., Fraser, S., Brown, J.A., 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**,1306-1319.

Gray, C.A., 1991a.Demographic patterns of the palaemonid prawn Macrobrachium intermedium in southeastern Australia: Spatial heterogeneity and the effects of species of seagrass. *Marine Ecology Progress Series* **75**(2-3), 239-249.

Gray, C.A., 1991b. Temporal variability in the demography of the palaemonid prawn *Macrobrachium intermedium* in two seagrasses. *Marine Ecology Progress Series* **75**(2-3), 227-237.

Gray, C.A., Bell, J.D., 1986. Consequences of two common techniques for sampling vagile macrofauna associated with the seagrass *Zostera capricorni*. *Marine Ecology Progress Series* **28**, 43-48.

Gray, C.A., Chick, R.C., McElligott, D.J., 1998. Diel changes in assemblages of fishes associated with shallow seagrass and bare sand. *Estuarine, Coastal and Shelf Science* **46**, 849-859.

Gray, C.A., McElligott, D.J., Chick, R.C., 1996. Intra- and inter- estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. *Marine and Freshwater Research* 47, 723-735.

Green, E.P., Mumby, P.J., Edwards, A.J., Clark, C.D., (Ed. A.J.Edwards), 2000. Remote sensing handbook for tropical coastal management. *Coastal Management Sourcebooks* 3, UNESCO, Paris. x + 316pp.

Green, E.P., Short, F.T., 2003. *World atlas of seagrasses.* UNEP, WCMC, London. 310pp.

Green, R.H., 1979. *Sampling Design and Statistical Methods for Environmental Biologists.* New York: John Wiley & Sons. 257 pp.

Greening, H.S., Livingston, R. J., 1982. Diel variation in the structure of seagrass-associated epibenthic macroinvertebrate communities. *Marine Ecology Progress Series* 7, 147-156.

Greenstreet, S.P.R., Tuck, I.D., Grewar, G.N., Armstrong, F., Reid, D.G., Wright, P.J., 1997. An assessment of the acoustic survey technique, RoxAnn, as a means of mapping seabed habitat. *ICES Journal of Marine Science*, 54, 939–959.

Grizzle, R.E., Short, F.T., Newell, C.R., Hoven, H., Kindblom, L., 1996. Hydrodynamically induced synchronous waving of seagrasses: 'monami' and its possible effects on larval mussel settlement. *Journal of Experimental Marine Biology and Ecology* **206**, 165-177.

Gubbay, S., 1993. *Management of Marine Protected Areas in the UK: Lessons from Statutory and Voluntary approaches.* Marine Conservation Society, Ross-on-Wye.

Guerao G, Ribera C., 2000. Population characteristics of the prawn *Palaemon serratus* (Decapoda, Palaemonidae) in a shallow Mediterranean Bay. *Crustaceana* **73**(4), 459-468.

Guidetti, P., 2000. Differences among fish assemblages with near shore *Posidonia oceanica* seagrass beds, rocky algal reefs and unvegetated sand habitats in the Adriatic Sea. *Estuarine Coastal and Shelf Science* **50**, 515-529.

Guidetti P., Bussotti S., 2000. Nearshore fish assemblages associated with shallow rocky habitats along the southern Croatian coast (eastern Adriatic sea). *Vie et Milieu-Life and Environment* **50**(3), 171-176.

Guillou, M., Michel, C., 1993. Reproduction and growth of *Sphaerechinus granularis* (Echinodermata: Echinoidea) in southern Brittany. *Journal of the Marine Biological Association of the United Kingdom* **73**, 179-192.

Gulland, J.A., 1980. Some problems of the management of shared stocks. FAO *Fisheries Technical Paper* **206,** 22 pp.

Gunton, A., 1997. Upper foreshore evolution and sea wall stability, Jersey, Channel Islands. *Journal of Coastal Research* **13**(3), 813-821.

Gustafson, E. J., 1998. Quantifying landscape spatial pattern: What is the state of the art. *Ecosystems,* 143-156.

Hale, J.A., Fraser, T.K., 2000. Image enhancements applied to scanned aerial photographs for benthic habitat mapping. *Proceedings of the Sixth International Conference on Remote Sensing for Marine and Coastal Environments*, Charleston, south Carolina (USA) 1-3 May 2000.

Halford, A.R., Thompson, A.A., 1994. Visual Census Surveys of Reef Fish. *Long term monitoring of the Great Barrier Reef, Standard Operational Procedure* No.3. Australian Institute of Marine Science.

Halliday, I.A., 1995. Influence of natural fluctuations in seagrass cover on commercial prawn nursery ground in a subtropical estuary. *Marine and Freshwater Research* **46,** 1121-1126.

Hamer, P.A., Jenkins, G.P., 1997. Larval supply and short-term recruitment of a temperate zone demersal fish, the King George whiting, *Sillaginodes punctata* Cuvier and Valenciennes, to an embayment in south-eastern Australia. *Journal of Experimental Marine Biology and Ecology* **208**(1-2), 197-214.

Hamilton L.J., Mulhearn P.J., Poeckert R., 1999. Comparison of RoxAnn and QTC-View acoustic bottom classification system performance for the Cairns area, Great Barrier Reef, Australia. *Continental Shelf Research*, 19(12): 1577-1597

Hanekom, N., Baird, D., 1984. Fish community structure in *Zostera* and non- *Zostera* regions of the Kromme estuary, St Francis Bay. South *African Journal of Zoology* **19,** 295-301.

Hannan, J.C., Williams, R.J., 1998. Recruitment of juvenile marine fishes to seagrass habitat in a temperate Australian Estuary. *Estuaries* **21**, 29-51.

Hare, J.A., Cowen, R.K., 1996. Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from south Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. *Limnology and Oceanography* **41**(6), 1264-1280.

Hart, D.D., Horwitz, R.J., 1991. Habitat diversity and the species–area relationship: alternative models and tests. In: *Habitat Structure: The Physical Arrangement of Objects in Space* (eds Bell, S.S., McCoy, E.D., Mushinsky, H.R.). Chapman, Hall, London. pp. 47–68.

Hartley, R., 1998. *Sed-Stat version 5.1.* University of Plymouth, Plymouth.

Hayward, P.J., Ryland, J.S., 1998. *Handbook of the marine fauna of north-West Europe.* Oxford University Press, Oxford.

Heck Jr, K.L., Able K.W., Roman, C.T., Fahay, M.P., 1995. Composition, abundance, biomass, and production of macrofauna in a New England esturay: Comparisons among eelgrass meadows and other nursery habitats. *Estuaries* **18**, 379-389.

Heck Jr, K.L., Hays, G., Orth, R. J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* **253**, 123–136.

Heck Jr, K.L., Thoman, T.A., 1981. Experiments on predator prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology.* **53** 125-134.

Heck Jr, K.L., Thoman, T.A., 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay *Estuaries* **7**, 70-92.

Heck Jr, K.L., Wilson, K.A., 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *Journal of Experimental Marine Biology and Ecology* **107**, 87-100.

Heck, Jr., K.L., Able, K.W., Fahay, M.P., Roman, C.T., 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows, species composition, seasonal abundance patterns and composition with unvegetated substrates. *Estuaries* **12**, 59-65.

Heck, Jr., K.L., Orth, R.J., 1980. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macro-invertebrate assemblages. In *Estuarine Perspectives,* V.S. Kennedy (ed.), New Yok: Academic Press, pp. 449-464.

Hempel, G., 1979. The egg stage. In: *The early life history of marine fish*, Parin,N.V. (ed.). University of Washington Press; Seattle. 83 pp.

Henderson, H.F., 1980. Some statistical considerations in relation to sampling populations of fishes. In: *Guidelines for sampling fish in inland waters*, Backiel, T & Welcomme, RL (eds). EIFAC Technical Papers no. 33, Rome. pp. 167-176.

Hettler, W.F., 1989. Nekton use of regularly-flooded saltmarsh cordgrass habitat in north Carolina, USA. *Marine Ecology Progress Series* **56**, 111-118.

Hily, C., Bouteille, M., 1999. Modifications of the specific diversity and feeding guilds in an intertidal sediment colonized by an eelgrass meadow (*Zostera marina*) (Brittany, France). *Comptes Rendus de L'Academie des Sciences Serie III – Sciences de la Vie-Life Sciences* **322** (12), 1121-1131.

Hindell, J.S., Jenkins, G.P., Keough, M.J., 2000. Variability in abundance of fishes associated with seagrass habitats in relation to diets of predatory fishes. *Marine Biology* **136**, 725-737.

Holmes, N.T.H., 1983. *The distribution of Zostera and Ruppia in the Fleet.* Nature Conservancy Council CSD Report, No. 500 (Contractor: Alconbury Environmental Consultants)

Holt, S.A., Kitting, C.L., Arnold, C.R., 1983. The distribution of young red drums among different seagrass meadows. *Transactions of the American Fisheries Society* **112**, 267-271.

Holt, T.J., Hartnoll, R.G., Hawkins, S.J., 1997. *Sensitivity and vulnerability to man-induced change of selected communities: intertidal brown algal shrubs, Zostera beds and Sabellaria spinulosa reefs.* Research Report No. 234. English Nature, Peterborough.

Hootsman, M.J.M., Vermaat, J.E., Van Virssen, W., 1987. Seed bank development, germination and early survival of two seagrass species from the Netherlands, *Zostera marina* and *Zostera noltii*. *Aquatic Botany* **28**, 275-285.

Hovel, K.A., Lipcius, R.N., 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control Blue crab survival. *Ecology*, **82**(7), 1814-1829.

Huh, S.H., 1984. Seasonal variations in populations of small fishes concentrated in shoalgrass and turtlegrass meadows. *The Journal of the Oceanological Society of Korea* **19**, 44-55.

Hundley, A., 1994. Report on the use of an acoustic method for mapping seagrass density and location. *Offshore Scientific Services*, Report No. 940401, New south Wales, Australia.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54,** 187–211.

Irlandi, E.A., 1994. Large-scale and small-scale effects of habitat structure on rates of predation – How percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* **98**(2), 176-183.

Irlandi, E.A., 1996. The effects of seagrass patch size and energy regime on growth of a suspension feeding bivalve. *Journal of Marine Research* **54**, 161-185.

Irlandi, E.A., Ambrose Jr,W.G., Orlando, B.A., 1995. Landscape ecology and the marine environment how spatial configuration of seagrass habitat influences growth and survival of the Bay Scallop. *Oikos* **72**, 307-313.

Irlandi, E.A., Peterson, C.H., 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. *Oecologia* **87**, 307-318.

Irving, R., Mackenzie, G., Reid, T., 1998. *Coral Cay Conservation Sub Aqua Club, Isles of Scilly 1997 Expedition Report.* Unpublished report, Coral Cay Conservation Ltd, London

Jackson, E.L., Rowden, A. A., Attrill, M. J., Bossy, S. F. and Jones, M. B. (2002). Comparison of fish and mobile macroinvertebrates associated with seagrass and adjacent sand at St. Catherine Bay Jersey (English Channel): Emphasis on commercial species. *Bulletin of Marine Science* **71**(3), 1333-1341.

Jackson, E.L., Rowden, A.A., Attrill, M. J., Bossy, S. F. and Jones, M. B. (2001). The importance of seagrass as a habitat for fishery species. *Oceanography and Marine Biology: An Annual Review* **39**, 269-303.

Jackson, J.R., Noble, R.L., 1995. Selectivity of sampling methods for juvenile Largemouth Bass in assessments of recruitment processes. North *American Journal of Fisheries Management* **15**, 408-418.

Jacobs, R.P., 1980. Effects of the Amoco Cadiz oil spill on the seagrass community at Roscoff, with special reference to the benthic infauna. *Marine Ecology Progress Series* **2**, 207-212.

Jacobs, R.P.W.M., 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. *Aquatic Botany* 7, 151-172.

Jaeger, J.A.G., 2000. Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landscape Ecology* **15**, 115-130.

Janssen, L.L.F., van der Wel, F.J, 1994. Accuracy assessment of satellite derived land cover data: a review. *Photogrammetric Engineering and Remote Sensing*, **60**: 419-426.

Jansson, B.O., Aneer, G., Nellbring, S., 1985. Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as estimated by SCUBA census. *Marine Ecology Progress Series* **23**, 31-43.

Jenkins, G.P., Black, K.P., Keough, M.J., 1999. The role of passive transport and the influence of vertical migration on the pre-settlement distribution of a temperate, demersal fish: numerical model predictions compared with field sampling. *Marine Ecology Progress Series* 184, 259-271.

Jenkins, G.P., Black, K.P., 1994. Temporal variability in settlement of a coastal fish (*Sillaginoides punctata*) determined by low-frequency hydodynamics, *Limnology and Oceanography* **39**(7), 1744-1754.

Jenkins, G.P., Black, K.P., Wheatley, M.J., Hatton, D.N., 1997a. Temporal and spatial variability in recruitment of a temperate, seagrass associated fish is largely determined by physical processes in the pre- and post-settlement phases. *Marine Ecology Progress Series* **148**, 23-35.

Jenkins, G.P., Keough, M.J., Hamer, P.A., 1998. The contributions of habitat structure and larval supply to broad-scale recruitment variability in a temperate zone, seagrass-associated fish. *Journal of Experimental Marine Biology and Ecology* **226**, 259-278.

Jenkins, G.P., May, H.M.A., Wheatley, M.J., Holloway, M.G., 1997b. Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip and Corner Inlet, Victoria, Australia, with emphasis on commercial species. *Estuarine, Coastal and Shelf Science* **44**, 569-588.

Jenkins, G.P., Shaw, M., Stewart, B.D., 1993. Spatial variation in food limited growth of juvenile Greenback flounder, *Rhombosolea tapirina*: evidence from otolith daily increments and otolith scaling. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2558-2567.

Jenkins, G.P., Sutherland, C.R., 1997. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: Colonisation and turn-over rates of fishes associated with artificial macrophyte beds of varying physical structure. *Journal of Experimental Marine Biology and Ecology* **218**, 103-125.

Johnson, L.B., Cage, S.H., 1997. Landscape approaches to the analysis of aquatic ecosystems. *Freshwater Biology* **37**, 113-132.

Jones, G.P., 1991. Post-recruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In *The ecology of fishes on coral reefs*. P.F. Sale, (ed.), San Diego: Academic Press, pp.294-328

Jordan, F., Bartolini, M., Nelson, C., Patterson, P., Soulen, H.L., 1996. Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **208**, 45-56.

Joyeux, J. C., 1999. The abundance of fish larvae in estuaries: within- tide variability at inlet and immigration. *Estuaries* **22**, 889-904.

Kaiser, M.J., Rogers, S.I., McCandless, D.T., 1994. Improving quantitative surveys of epibenthic communities using a modified 2m beam trawl. *Marine Ecology Progress Series* **106**, 131-138.

Karnofsky, E.B., Atema, J., Elgin, R.H., 1989. Field observations of social behaviour, shelter use and foraging in the lobster, *Hommarus americanus*. *Biological Bulletin* **176**, 239-246.

Keddy, P.A., 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. *Aquatic Botany* **14**, 41-58.

Kelly, M. G., 1980. Remote sensing of seagrass beds. In: *Handbook of Seagrass Biology: An Ecosystem Perspective*, Phillips, R.C. & C.P. McRoy (eds.), Garland STMP Press, New York, pp. 69-85.

Kendrick G.A., Eckersley, J., Walker, D.I., 1999. Landscape-scale changes in seagrass distribution over time: a case study from Success Bank, Western Australia. *Aquatic Botany* **65**(1-4), 293-309.

Kendrick, G.A., Hegge, B.J., Wyllie, A., Davidson, A., Lord, D.A., 2000. Changes in seagrass cover on Success and Parmelia Banks, Western Australia between 1965 and 1995. *Estuarine Coastal and Shelf Science* **50**, 341-353.

Kendrick, G.A., Huisman, J.M., Walker, D.I., 1990. Benthic macroalgae of Shark Bay, Western Australia. *Botanica Marina* **33**(1), 47-54.

Kentula, M.E., McIntire, C.D., 1986. The autecology and production dynamics of eelgrass (*Zostera marina* L) in Netarts Bay, Oregon. *Estuaries* 9, 188-199.

Kenworthy, W.J., Zieman J.C. Thayer, G.W., 1982. Evidence for the influence of seagrass on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, north Carolina (USA). *Oecologia* 54, 152-158.

Kenyon, R.A., Loneragan, N.R., Hughes, J., Staples, D.J., 1997. Habitat preference of juvenile tiger prawns *Penaeus esculentus* and *P. semisulcatus* in the western Gulf of Carpentaria, Australia. *Estuarine Coastal and Shelf Science* **45**, 393-403.

Kikuchi, T., 1974. Japanese contributions on consumer ecology in eelgrass (*Zostera marina*) beds, with special reference to trophic relationships and resources in inshore fisheries. *Aquaculture* **4**, 145-160.

Kikuchi, T., Pérès, J.M., 1977. Consumer ecology of seagrass beds. In: *Seagrass Ecosystems; A Scientific Perspective*. McRoy, C. P. & Helfferich, C. (eds). Marcel Dekker, New York.147-193.

Kindleysides, D., 1995. Conserving the intertidal Biodiversity of Jersey: a Strategy. Master of Science Thesis, Univeristy College London, UK.

Kirkman, H., Kuo, J., 1990. Pattern and process in southern Western Australian seagrasses. *Aquatic Botany* 37(4), 367-382.

Kirkman, H., 1990. Seagrass distribution and mapping. In *Seagrass Research Methods. Monographs on oceanographic methodology 9*. Phillips, R.C., McRoy, C.P. (eds). UNESCO, Paris.

Kirkman, H., 1996. Baseline and Monitoring Methods for Seagrass Meadows. *Journal of Experimental Management* 47, 191-201.

Kirkman, H., Kirkman, J.A., 2000. The management of seagrasses in south- east Asia and Australia. *Biologia Marina Mediterranea* 7(2): 305-319.

Kjelson, M.A., Colby, D.R., 1977. The evaluation and use of gear efficiencies in the estimation of estuarine fish abundance, p416-424. *In* M. Wiley (ed.), *Estuarine Processes*, Vol. **2**. Academic Press, New York.

Kjelson, M.A., Johnson, G.N., 1978. Catch efficiencies of a 6.1-meter otter trawl for estuarine fish populations. *Transactions of the American Fisheries Society* **107**, 246-254.

Klumpp, D.W., Howard, R.K., Pollard, D.A., 1989. Trophodynamics and nutritional ecology of seagrass communities. *Biology of Seagrasses*, A.W.D. Larkum et al. (eds), Amsterdam: Elsevier Science, pp. 394-437.

Klumpp, D.W., Nichols, P.D., 1983. Studies of food-chains in seagrass communities. 4. Nutrition of the southern sea garfish *Hyporhampus melanochir*: gut passage rate and daily consumption of two food types and assimilation of seagrass components. *Marine Ecology Progress Series* **12**, 207-216.

Kolasa, J., Rollo, D.C., 1991. Heterogeneity of heterogeneity: a glossary. In: *Ecological heterogeneity*, J. Kolasa & S.T.A. Pickett, eds. Springer-Verlag, New York. pp 1-23.

Kostecki, P.T., 1984. Habitat suitability index models: spotted seatrout. *US Fisheries and Wildlife Service*. FWS/OBS-82/10.75. 22 pp.

Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos* **59**, 253-260.

Kuipers, B.R., Maccurrin, B., Miller, J.M., Van de Veer, H.W., Witte, J.I.J., 1992. Small trawls in juvenile flatfish research: their development and efficiency. *Netherlands Journal of Sea Research* **29**(1-3), 109-117.

Kulczycki, G.R., Virnstein, R.W., Nelson, W.,G., 1981. The relationship between fish abundance and algal biomass in a seagrass-drift algae community. *Estuarine, Coastal and Shelf Science* **12**, 341-347.

Laffaille, P., Brosse, S., Feunteun E., Baisez, A., Lefeuvre, J.C., 1998. Role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel Bay. *Hydrobiologia* **374**, 121-133.

Langton, R.W., Steneck, R.S., Gotceitas, V., Juanes, F., Lawton, P., 1996. The interface between fisheries research and habitat management. *Journal of Fisheries Management* **16**, 1-7.

Larkum, A.W.D., McComb, A.J., Shepherd, S.A. (eds) 1989. *Seagrass biology: an Australian perspective*, Amsterdam: Elsevier.

Lathrop, R.G., Styles, R.M., Seitzinger, S.P., Bognar, J.A., 2001. Use of GIS Mapping and Modelling Approaches to examine the spatial distribution of seagrasses in Barnegat Bay, New Jersey. *Estuaries* 24(6a), 904-916.

Le Sueur, R.F., 1967. *The marine fishes of Jersey*. Sociète Jersiaise, Jersey. 33 pp.

Leadbitter, D., Leelong W., Dalmazzo, P., 1999. Seagrasses and their management- implications for research. In: *Seagrass in Australia: Strategic review and developemnet of an R, D Plan*. Butler, A. and Jernakoff, P. (eds). CSIRO, Collingwood. 140-171.

Ledoyer, M., 1969. Ecologie de la faune vagile des biotopes méditerranéens accessibles en scaphandre autonome. *Tethys* **1**, 291-308.

Lee Long, W.J., McKenzie, L.J., Roelofs, A.J., Makey, L.J., Coles, R.G., Roder, CA., 1998. Baseline Survey of Hinchinbrook Region Seagrasses - October (Spring) 1996. *Research Publication* No. **51**, Great Barrier Reef Marine Park Authority, Townsville.

Lehmann, A., Jacquet J.M., Lachavanne, JB., 1997. A GIS approach of aquatic plant spatial heterogeneity in relation to sediment and depth gradients, Lake Geneva, Switzerland. *Aquatic Botany* 58, 347-361.

Lehmann, A., Lachavanne, J.B., 1997. Geographic Information Systems and remote sensing in Aquatic Botany. *Aquatic Botany* 58, 195-207.

Leopold, A., 1933. Game Management. Charles Scribners, New York.

Levin, P., Petrik, R., Malone, J., 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia* **112**, 55-63.

Lewis, F.G., Stoner, A.W., 1983. Distribution of macrofauna within seagrass beds – An explanation for patterns of abundance. *Bulletin of Marine Science* **33**(2), 296-304.

Lewis, F.G., 1984. Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. *Marine Ecology Progress Series*, **19**(1-2), 101-113.

Lewis, G.F., Stoner, A.W., 1981. An examination of methods for sampling macrobenthos in seagrass meadows. *Bulletin of Marine Science* **31**, 116-124.

Li, H., Reynolds, J.F., 1995. On definition and quantification of heterogeneity. *Oikos* **73**, 280-284.

Lillesand, T.M., Kiefer, R.W., 2000. *Remote sensing and image interpretation.* 4th Edition. John Wiley, Sons, Chichester.

Lillycrop, W.J., Estep, L.L., 1995. Generational advancements in coastal surveying, mapping. *Sea Technology* 36(6): 10-16.

Lipcius, R.N., Eggleston, D.B., Miller, D.L., Luhrs, T.C., 1998. The habitat-survival for Caribbean spiny lobster: an inverted size effect and non-linearity in mixed algal and seagrass habitats. *Marine and Freshwater Research* **49**, 807-816.

Livingston, J. R., 1984. The relationship of physical factors and biological response in coastal seagrass meadows. *Estuaries* **7**, 377-390.

Loneragan, N.R., Bunn, S.E., Kellaway, D.M., 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. *Marine Biology* **130**, 289-300.

Lonergan, N. R., Kenyon, R. A., Staples, D.J., Poiner, I. R., Conacher, C. A., 1998. The influence of seagrass type on the distribution and abundance of post-larval and juvenile tiger prawns (*Penaeus esculentus* and *Penaeus semisulcatus*) in the western Gulf of Carpentaria, Australia. *Journal of Experimental Marine Biology and Ecology* **228**, 175-195.

Longhurst, A., 1999. Does the benthic paradox tell us something about surplus production models? *Fisheries Research* **41**, 111-117.

Lubbers, L., Boynton, W.R., Kemp, W.M., 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. *Marine Ecology Progress Series* **65**, 1-14.

Maceina, M.J., Shireman, J.V., Langeland, K.A., Canfield, D.E., 1984. Prediction of submersed plant biomass by use of a recording fathometer. *Journal of Aquatic Plant Management* **22**, 35-38.

Maceina, M.J., Shireman, J.V., Langland, K.A., Canfield, D.E., 1984. Prediction of submerged plant biomass by use of recording fathometer. *Journal of Aquatic Plant Management* **22**, 35-38.

Main, K.L., 1987. Predator avoidance in seagrass meadows: prey behaviour, microhabitat selection, and cryptic coloration. *Ecology* **68**, 170-180.

Mann, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic Coast of Canada. I: Zonation and biomass of seaweeds. *Marine Biology*, **12**(1), 1-10.

Manzanera, M., Romero, J., 2000. Multifractal structure in *Posidonia oceanica* meadows. *Biologia Marina Mediterranea* 7(2), 389-392.

Martin, A. C., 1954. A clue to the eelgrass mystery. *Transactions of the 19th north American Wildlife Conference Washington, D. C.*, pp. 441-449.

Martin, F.D., Cooper, M., 1981. A comparison of fish faunas found in pure stands of two tropical Atlantic seagrasses, *Thalassia testudinum* and *Syringodium filiforme*. North*east Gulf Science* **5**, 31-37.

Mason D.M., Brandt S.B., 1999. Space, time, and scale: new perspectives in fish ecology and management. *Canadian Journal of Fisheries and Aquatic Science* **56** (supplement1), 1-3.

Mattila, J., Chaplin, G., Eilers, M.R., Heck, K.L., O'Neal, J.P., Valentine, J.F., 1999. Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). *Journal of Sea Research* **41**, 321-332.

McConnaughey, T., McRoy, C. P., 1979. ^{13}C Label identifies eelgrass (*Zostera marina*) carbon in an Alaskan estuarine food web. *Marine Biology* **53**, 263-269.

McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: www.umass.edu/landeco/research/fragstats/fragstats.html

McGarigal, K., Marks, B.J. , 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351, USDA Forest Service, Pacific northwest Research Station, Portland, Oregon.

McNeill, S.E., Bell, J.D., 1992 Comparison of beam trawls for sampling macrofauna of *Posidonia* seagrass. *Estuaries* **15**(3), 360-367.

McNeill, S.E., Fairweather, P.G., 1993. Single large or several small marine reserves? An experimental approach with seagrass fauna. *Journal of Biogeography* **20**, 429-440.

McNeill, S.E., Worthington, D.G., Ferrell, D.J., Bell, J.D., 1992. Consistently outstanding recruitment of five species of fish to a seagrass bed in Botany Bay, NSW. *Australian Journal of Ecology* **17**, 359-365.

McRea, J.E., Greene, G., O'Connell, M., Wakefield, W.W., 1999. Mapping marine habitats with high resolution sidescan sonar. *Oceanologia Acta* 22, 679-686.

McRoy, C. P., Helfferich, C. (eds) 1977. *Seagrass Ecosystems; a scientific perspective.* New York: Marcel Dekker.

McRoy, C.P. (ed.) 1973. *Seagrass ecosystems: recommendations for research programs. Proceedings of the International Seagrass Workshop.* Leiden, The Netherlands, 22 to 26 October 1973, Leiden: National Science Foundation.

Meng, L., Powell, C.J., 1999. Linking juvenile fish and their habitats: an example from Narragansett Bay, Rhode Island. *Estuaries* **22**, 905-916.

Micheli, F., Peterson, C.H., 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology* **13**(4), 896-881.

Middleton, M.J., Bell, J.D., Burchmore, J.J., Pollard, D.A. Pease, B.C., 1984. Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New south Wales. *Aquatic Botany* **18**, 89-109.

Milchakova, N.A., 2000. The dynamics of the encrusting layer on *Zostera marina* L. leaves in Sevastopol Bay. *Biologia Marina Mediterranea*, **7**(2), 255-264.

Millar, R.B., 1992. Estimating the size-selectivity of fishing gear by conditioning against total catch. *Journal of the American Statistical Association*, **87**(420), 962-968.

Miller, R.E., Campbell, D.W., Lunsford, P.J., 1980. Comparison of sampling devices for the juvenile blue crab, *Callinectes sapidus*. *Fisheries Bulletin, U.S.* **78**, 196-198.

Miner, S.P., 1993. Application of acoustic hydrosurvey technology to the mapping of eelgrass (*Zostera marina*) distribution in Humboldt Bay, California. In: *Proceedings, 6th Symposium on Coastal and Ocean Management*, New Orleans, LA, July 19-23.

Misund, O.A., Luyeye, N., Coetzee, J., Boyer, D., 1999. Trawl sampling of small pelagic fish off Angola: effects of towing speed, tow duration, and time of day. *ICES Journal of Marine Science* **56**, 275-283.

Monkkonen, M., Reunarien, P., 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* **84**(2), 302-305.

Moore, K. A., Wilcox, D. J., Orth, R. J., 2000. Analysis of the abundance of submersed aquatic vegetation communities in the Chesapeake Bay. *Estuaries* 23, 115-127.

Mumby, P.J., Green, E.P., 2000. Mapping coral reefs and macroalgae. In: Remote sensing handbook for tropical coastal management. *Coastal Management Sourcebooks* 3, UNESCO, Paris. x + 316pp.

Mumby, P.J., Green, E.P., Edwards, A.J., Clark, C.D., 1997. Measurement of Seagrass standing crop using satellite and digital airborne remote sensing. *Marine Ecology Progress Series* **159**, 51-60.

Mumby, P.J., Green, E.P., Edwards, A.J., Clark, C.D., 2000. Cost-effectiveness of remote sensing for costal management. In Green, E.P., Mumby, P.J., Edwards, A.J., Clark, C.D. (Ed. Edwards, A.J.) *Remote Sensing Handbook for Tropical Coastal Management, Costal Management Sourcebooks* 3, UNESCO Publishing, France. p271-291.

Munro, C., Nunny, R., 1998. Isles of Scilly Subtidal Habitat and Biotope Mapping Survey. *English Nature Research Report* No.276. English Nature, Peterborough.

Muus, B.J., Nielsen, J.G., 1999. *Seafish*. Blackwell Science, Oxford (UK). 340 pp.

Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., van't Hof, T., den Hartog, C., 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine Coastal and Shelf Science* **51**(1), 31-44.

Nelson, T. A., 1997. Interannual variance in a subtidal eelgrass community. *Aquatic Botany* **56**, 245-252.

Nelson, W.G., 1979. An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. *Journal of Experimental Marine Biology and Ecology* **39**, 231-264.

Nelson, W.G., Bonsdorff, E., 1990. Fish predation and habitat complexity: are complexity thresholds for real? *Journal of Experimental Marine Biology and Ecology* **141**, 183-194.

Newell, C.R., Hidu, H., McAlice, B.J., Podniesinski, G., Short, F., Kindblom, L., 1991. Recruitment and commercial seed procurement of the blue mussel *Mytilus edulis* in Maine. *Journal of the World Aquacultural Society* **22**, 134-152.

Nixon, S.W., Oviatt, C.A., 1973. Ecology of a New England salt marsh. *Ecological Monographs* **43**, 363-498.

Norris, J.G., Wyllie-Echevverria S., Mumford T., Bailey A., Turner, T., 1997. Estimating Basal Area coverage of subtidal seagrass beds using underwater videography. *Aquatic Botany* **58**, 269-287.

Nouvel H., Holthuis L.B., 1957. Les Processidae (Crustacea Decapoda Natantia) des eaux européennes. *Zoologische Verhandelingen Leiden* **32**, 1-81.

Novak, R., 1984. A Study in Ultra-Ecology: Microorganisms on the Seagrass *Posidonia oceanica* (L.) Delile. *Marine Ecology 5(2), 143-190.*

O'Brien, C.J.1994. Ontogenetic changes in the diet of juvenile brown tiger prawns, *Penaeus esculentus*. *Marine Ecology Progress Series* **112**, 195-200.

Olney, J.E., Boehlert, G.W., 1988. Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay. *Marine Ecological Progress Series* **45**, 33-43.

Orbi, A., Salomon, J.C., 1988. Tidal dynamics in the vicinity of the Channel Islands. *Oceanologica Acta* **11**(1), 55-64.

Orth, R. J., 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: *Plant-Animal Interactions in the Marine Benthos* (eds John, D.M. Hawkins, S.J. and J. H. Price). Systematics Ass. Spec. Vol. No. **46**. Clarendon Press, Oxford, pp. 147-164.

Orth, R., 1976. The demise and recovery of eelgrass, *Zostera marina*, in Chesapeake Bay, Virginia. *Aquatic Botany* **2**, 141-159.

Orth, R.J., 2000. Protection and restoration of seagrasses: addressing global concerns from a local perspective in Chesapeake Bay, USA. *Biologia Marina Mediterranea* **7**(2), 401-404.

Orth, R.J., Heck, K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. *Estuaries* **7**, 339-350.

Orth, R.J., Moore, K.A., 1983. Submersed vascular plants: techniques for analyzing their distribution and abundance. *Marine Technological Society Journal* **17**, 38-52.

Orth, R.J., van Montfrans, J., 1982. Predator- prey interactions in a *Zostera marina* ecosystem in the lower Chesapeake Bay, Virginia. In: *Interactions of resident consumers in a temperate estuarine seagrass community: Vaucluse shores, Virginia USA*. R.J. Orth, J. van Montfrans (eds), Virginia: VIMS-SRAMSOE **267**, 81-94.

Orth, R.J., van Montfrans, J., 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs. *Callinectes sapidus*.I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Marine Ecological Progress Series* **41**, 283-294.

Paiva, P.C., 2001. Spatial and temporal variation of a nearshore benthic community in southern Brazil: Implications for the design of monitoring programs. *Estuarine Coastal and Shelf Science* **52**(4), 423-433.

Pallot, A., 2002. Meteorological Department, Jersey Airport, *personal communication*, 25th May.

Pardieck, R.A., Orth, R.J., Diaz, R.J., Lipcius, R.N., 1999. Ontogenetic changes in habitat use by postlarvae and young juveniles of the blue crab. *Marine Ecology Progress Series* **186**, 227-238.

Parsley, M.J., Palmer, D.E., Burkhardt, R.W., 1989. Variation in capture efficiency of a beach seine for small fishes. North *American Journal of Fisheries Management* **9**, 239-244.

Pasqualini, V., Clabaut, P., Pergent, G., Benyoussef, L., Pergent-Martini, C., 2000. Contribution of side scan sonar to the management of Mediterranean littoral ecosystems. *International Journal of Remote Sensing* **21**, 367-378.

Pasqualini, V., Pergent-Martini, C., Clabaut, P., Marteel, H., Pergent, G., 2001. Integration of aerial remote sensing, photogrammetry, and GIS technologies in seagrass mapping. *Photogrammetric Engineering and Remote Sensing* **67**, 99-105.

Pasqualini, V., Pergent-Martini, C., Clabaut, P., Pergent, G., 1998. Mapping of *Posidonia oceanica* using Aerial Photographs and Side Scan Sonar: Application off the Island of Corsica (France). *Estuarine, Coastal and Shelf Science* **47**, 359-367.

Patton, D.R. 1975. A diversity index for quantifying habitat edge. *Wildlife Society Bulletin* **3**, 171-173.

Paulij, W.P., Herman, P.M.J., Roozen, M.E.F., Denuce, J.M., 1991. The influence of photoperiodicity on hatching of *Sepia officianalis*. *Journal of the Marine Biological Association of the United Kingdom* **71**(3), 665-678.

Pawson, M., 1995. Biogeographical identification of English Channel fish and shellfish stocks. MAFF, Fisheries Laboratory, Lowestoft, Fisheries Research Technical Report no. 99, 72 pp.

Perkins-Visser, E., Wolcott, T.G., Wolcott, D.L., 1996. Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Experimental Marine Biology and Ecology* **198**, 155-173.

Petersen, C.G.J., Boysen-Jensen 1911. Valuation of the sea I. Animal life of the sea bottom, its food and quantity. *Report of the Danish Biological Station* **20**, 1-81.

Petrik, R., Levin, P.S., 2000. Estimating relative abundance of seagrass fishes: a quantitative comparison of three methods. *Environmental Biology of Fishes* **58**, 461-466.

Phillips, R.C., 1969. Temperate grass flats. In: *Coastal ecological systems of the United States*, **2**, Odum, H. T., Copeland, B. J. & McMahan, E. A. (eds). Report of the Federal Water pollution Cont. Admin, 737-773.

Phillips, R.C., McRoy, C.P. (eds) 1980. *Handbook of seagrass biology: an ecosystem perspective*. New York: Garland STPM.

Phillips, R.C., McRoy, C.P. (eds) 1990. *Monographs on oceanographic methodology: Seagrass research methods*, Paris: UNESCO.

Phillips, R.C., Meñez, E.G., 1988. *Seagrasses*. Smithsonian Contributions to Marine Sciences, 34. Washington D.C: Smithsonian Institution Press.

Pierce, C.L., Rasmussen, J.B., Leggett, W.C., 1990. Sampling littoral fish with a seine: Corrections for variable capture efficiency. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1004-1010.

Pihl, L., 1986. Exposure, vegetation and sediment as primary factors for mobile faunal community structure and production in shallow marine soft bottom areas. *Netherlands Journal of Sea Research* **20**, 75-83.

Pihl Baden, S., Pihl, L., 1984. Abundance, biomass and production of mobile epibenthic fauna in *Zostera marina* (L.) meadows, western Sweden. *Ophelia* **23**. 65-90.

Pihl, L., Rosenberg, R., 1982. Production, abundance and biomass of mobile epibenthic marine fauna in shallow waters, Western Sweden. *Journal of Experimental Marine Biology and Ecology* **57**(2-3), 273-301.

Pile, A.J., Lipcius, R.N., Van Montfrans, J., Orth, R. J., 1996. Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecological Monographs* **66**, 277-300.

Pingree, R.D., Forster, G.R., Morrison,G.K., 1974. Turbulent convergent tidal fronts. *Journal of the Marine Biological Association of the United Kingdom* **54**, 469-479.

Pingree, R.D., Maddock, L., 1979. The tidal physics of headland flows and offshore tidal bank formation, *Marine Geology*, **32**, 269-289.

Pingree, R.D., Mardell, G.T., 1987. Tidal flows around the Channel Islands, *Journal of the Marine Biological Association of the United Kingdom*, **67**, 691-707.

Pingree, R.D., Mardell, G.T., Maddock, L., 1985. Tidal mixing in the Channel Isles Region derived from the results of Remote Sensing and measurements at sea. *Estuarine, Coastal and Shelf Science* **20**(1), 1-18.

Pohle, D.G., Bricelj, V.M., Garcia- Esquivel, Z., 1991. The eelgrass canopy: an above-bottom refuge from benthic predators for juvenile bay scallops *Argopecten irradians. Marine Ecology Progress Series* **74**, 47-59.

Pollard, D.A., 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. *Aquatic Botany* **18**, 3-42.

Poumian-Tapia, M., Ibarra-Obando, S.E., 1999. Demography and biomass of the seagrass *Zostera marina* in a Mexican coastal lagoon. *Estuaries* **22**(4), 837-847.

Primavera, J.H., 1997. Fish predation on mangrove-associated penaeids - The role of structures and substrate. *Journal of Experimental Marine Biology and Ecology* **215** (2), 205-216.

Quéro, J-C, Vayne, J-J. (eds), 1998. *Les fruits de la mer et plantes marines des pêches françaises*. Delacaux et Niestlé, Paris. 256 pp.

Quéro, J-C. (ed), 1997. *Les poissons de mer des pêches françaises*. Delacaux et Niestlé, Paris. 304 pp.

Raposa, K.B., Oviatt, C. A., 2000. The influence of contiguous shoreline type, distance from shore, and vegetation biomass on nekton community structure in eelgrass beds. *Estuaries* **23**, 46-55.

Rasmussen, E., 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In *Seagrass ecosystems; a scientific perspective*. C.P. McRoy,, C. Helfferich (eds). New York: Marcel Dekker, pp. 1-52.

Reiger, H.A., Robson, D.S., 1966. Selectivity of gill nets, especially to lake whitefish. *Journal of the Fisheries Research Board of Canada* **23**, 423-454.

Remillard, M.M.,Welch, RA., 1992. GIS Technologies for Aquatic Macrophyte studies: 1. Database development and changes in the Aquatic Environment. *Landscape Ecology* 7(3), 151-162.

Reusch, T.B.H., 1998. Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. *Marine Ecology Progress Series* **167**, 149-153.

Riley, J. D. (1971). The Riley Push Net. In: *Methods for the Study of Marine Benthos*, Holme, N. A. and McIntyre, A. D. (eds). Blackwell Scientific publications, Oxford (IBP Handbook, No. 16). 286-290.

Robbins B.D., Bell, S.S., 2000. Dynamics of a subtidal seagrass landscape: Seasonal and annual change in relation to water depth. *Ecology* **81**, 1193-1205.

Robbins, B.D., Bell, S.S., 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trends in Evolution and Ecology* **9**, 301-304.

Robblee, M.B., Zieman, J.C., 1984. Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bulletin of Marine Science* **34**, 335-345.

Robertson, A.I., Dixon, P., Daniel, P.A., 1988. Zooplankton dynamics in mangrove and other nearshore habitats in tropical Australia. *Marine Ecology Progress Series* **43**, 139-150.

Robinson, C.L.K., Levings, C.D., 1995. An overview of habitat classification systems, ecological models, and geographic information systems applied to shallow foreshore marine habitats. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* **2322**, 65 pp.

Rogers, S.I., Rijnsdorp, A.D., Damm, U., Vanhee, W., 1998. Demersal fish populations in the coastal waters of the UK and continental NW Europe from beam trawl survey data collected from 1990 to 1995. *Journal of Sea Research* **39**(1-20), 79-102.

Ronnback, P., 1999. The ecological basis for economic value of seafood production supported by mangrove ecosystems. *Ecological Economics* **29**, 235-252.

Rooker, J.R., Dennis G.D., 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science* **49**, 684-698

Rooker, J.R., Holt, G.J., Holt, S.A., 1998a. Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: is early life survival enhanced by seagrass meadows? *Marine Biology* **131**, 145-151.

Rooker, J.R., Holt, S.A., Holt, G.J., Fuiman, L.A., 1999. Spatial and temporal variability in growth, mortality, and recruitment potential of post settlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. *Fishery Bulletin* **97**, 581-590.

Rooker, J.R., Holt, S.A., Soto, M.A., Holt, G.J., 1998b. Post settlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries* **21**, 318-327.

Roper, A., 1999. Jersey fisherman, *pers. comm.*, 5th August.

Rosenberg, A., Bigford, T.E., Leathery, S., Hill, R.L.., Bickers, K., 2000. Ecosystem approaches to fishery management through essential fish habitat. *Bulletin of Marine Science* **66**(3), 535-542.

Rountree, R.A., Able, K.W., 1997. Nocturnal fish use of New Jersey marsh creek and adjacent bay shoal habitats. *Estuarine, Coastal and Shelf Science* **44**, 703-711.

Rozas, L.P., Minello, T.J., 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries* **20**, 199-213.

Rozas, L.P., Minello, T.J., 1998. Nekton use of saltmarsh, seagrass, and nonvegetated habitats in a south Texas (USA) Estuary. *Bulletin of Marine Science* **63**, 481-501.

Rozas, L.P., Odum, W.E., 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia* **77**, 101-106.

Ruiz, G.M., Hines, A.H., Posey, M.H., 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Marine Ecology Progress Series* **99**, 1-16.

Ryer, C.H., van Montfrans, J., Orth, R.J., 1990. Utilization of seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. II. Spatial and temporal patterns of moulting. *Bulletin of Marine Science* **46**, 95-104.

Sabol, B., McCarthy, E., Rocha, K., 1997. Hydroacoustic basis for detection and characterization of eelgrass (*Zostera marina*). In: Proceedings, *4th Conference on Remote Sensing for Marine and Coastal Environments*, Orlando, Florida, 17-19 March.

Sabol, B.M., Burczinski, J., 1998. Digital echo sounder system for characterizing vegetation in shallow-water environments. *Proceedings of the Fourth European Conference on Underwater Acoustics*. Alippi, A and Cannelli, GB. (eds), Rome, Italy.

Sabol, B.M., Melton, R.E., 1995. *Development of an automated system for detection and mapping of submersed aquatic vegetation with hydro acoustic and global positioning system technologies, Report 1 - The Submersed Aquatic Vegetation Early Warning System (SAVEWS) - System Description and User's Guide* (Version 1.0). Joint agency Guntersville Project Aquatic Plant Management. 37 pp.

Sabol, B.M., Shafer, D.J., Melton, E., 1996. Mapping seagrasses for dredging operations. Environmental Effects of Dredging, D-96-1.

Sale, P.F., Douglas, W.A., Doherty, P.J., 1984. Choice microhabitats by coral-reef fishes at settlement. *Coral Reefs* **3**, 91-99.

Salita, J.T., 2000. The influence of spatial arrangement of seagrasses on fish abundance in Bolinao, northern Philippines. *ZMT Bremen Contribution 10*. Zentrum für Marine Tropenökologie (ZMT), Bremen, pp 85.

Salita, J.T., 2003. Field evidence on the influence of seagrass landscape on fish abundance in Bolinao, northern Philippines. *Marine Ecology Progress Series* **247**, 183-195.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **51**,18-32.

Savino, J. F., Stein, R. A., 1982. Predator-prey interactions between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* **111**, 255-256.

Schmidt, T.W., 1989. Food habits, length-weight relationship and condition factor of young great Barracuda, *Syphraena barracuda* (Walbaum), from Florida Bay, Everglades National Park, Florida. *Bulletin of Marine Science* **44**, 163-170.

Scott, J.K., 1981. The seagrass fish fauna of Geographe Bay, Western Australia. *Journal of the Royal Society of Western Australia* **63**, 97-102.

Sea-fish Industry Authority 1996. Trap fishing for cuttlefish. *Sea-fish Industry Authority, Hull.* Video, 24 minute run time.

Sebens, K.P., 1991. Habitat structure and community dynamics in marine benthic systems. In *Habitat structure*, S.S. Bell (ed), Chapman & Hall, London. pp. 211-234.

Sedberry, G.R., Carter, J., 1993. The fish community of a shallow tropical lagoon in Belize, Central America. *Estuaries* **16**, 198-215.

Shabmann, L.A., Capps Jr, O., 1985. Benefit of taxation for environmental improvement: a case example from Virginia's soft crab fishery. *Land Economics* **61**, 398-418.

Shanks, A.L., Wright, W.G., 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. *Journal of Experimental Marine Biology and Ecology* **114**(1), 1-13.

Shaw, M., Jenkins, G. P., 1992. Spatial variation in feeding, prey distribution and food limitation of juvenile flounder *Rhombosolea tapirina* Gunther. *Journal of Experimental Marine Biology and Ecology* **165**, 1-21.

Sheridan, P., 1997. Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, U.S.A. *Estuarine Coastal and Shelf Science* **44**, 455-469.

Short, F.T., Ibelings, B.W., den Hartog, C., 1988. Comparison of a current eelgrass disease to the wasting disease in the 1930s. *Aquatic Botany* **30**, 295-304.

Short, F.T., Wyllie-Echeverria, S., 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* **23**(1): 17-27.

Siljeström, P., Moreno, A., Rey, J., Carbó, R., 2001. Potential of hydro-acoustic measurements in the cartography of *Cymodocea nodosa* meadows. *Proceedings of the 36th European Marine Biology Symposium: A Marine Science odyssey into the 21st Century*, Maó, 17 to 22 September 2001. Abstract only.

Simenstad C.A, Cordell, J.R., 2000. Ecological assessment criteria for restoring anadromous salmonid habitat in Pacific northwest estuaries. *Ecological Engineering*, **15**(3-4), 283-302.

Sinel, J.,1906. *An outline of the natural history of our shores*. Swan Sonnenschein & Co., London. pp.347.

Smaldon G., Holthuis L.B., Fransen C.H.J.M., 1993. *British coastal shrimps and prawns*. Linnean Society Synopsis British Fauna (n.s.) **15**(i-vii) (Second Edition). Academic Press, London, + 1-142.

Snedecor, G.W., Cochran, W.G., 1980. *Statistical methods*. Iowa State University Press, Ames. 507 pp.

Sogard, S. M., 1989. Colonisation of artificial seagrass by fishes and decapod crustaceans: importance of proximity to natural eelgrass. *Journal of Experimental Marine Biology and Ecology* **133**, 15-37.

Sogard, S.M., Able, K.W., 1991. A comparison of eelgrass, sea lettuce, macroalgae and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine, Coastal and Shelf Science* **33**, 501-519.

Sogard, S.M., Olla, B.L., 1993. The influence of predator presence on utilization of artificial seagrass habitats by juvenile walleye pollock, *Theragra chalcogramma*. *Environmental Biology of Fishes* **37**, 57-65.

Sogard, S.M., Powell, G.V.N., Holmquist, J.G., 1987. Epibenthic fish communities on Florida Bay Banks: Relationships with physical parameters and seagrass cover. *Marine Ecology Progress Series* **40**, 25-39.

Sogard, S.M., Powell, G.V.N., Holmquist, J.G., 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. *Bulletin of Marine Science* **44**(1), 179-199.

Sogard, S.M., Powell, G.V.N., Holmquist, J.G., 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. *Bulletin of Marine Science* **44**, 179-199.

Sotheran, I.S., Foster Smith, R.L., Davies, J., 1997. Mapping of Marine Benthic Habitats Using Image Processing Techniques within a Raster Based Geographic Information System. *Estuarine, Coastal and Shelf Science* **44**, 25-31.

Spitzer, P.M., Mattila, J., Heck Jr, K.L., 2000. The effects of vegetation density on the relative growth rates of juvenile pinfish, *Lagodon rhomboides* (Linneaus), in Big Lagoon, Florida. *Journal of Experimental Marine Biology and Ecology* **244**, 67-86.

Spyker, K.A., van den Berghe, E., 1995. Diurnal Abundance Patterns of Mediterranean Fishes Assessed on Fixed transects by Scuba divers. *Transactions of the American Fisheries Society* **124**, 216-224.

States of Jersey Department of Agriculture and Fisheries, 2000. *Fisheries section annual report 1999*. States of Jersey Department of Agriculture and Fisheries, Trinity, Jersey. 18 pp.

States of Jersey Department of Agriculture and Fisheries, 2001. *Fisheries section annual report 2000*. States of Jersey Department of Agriculture and Fisheries, Trinity, Jersey. 18 pp.

States of Jersey Policy and Resources Committee, 2001. Jersey into the Millenium: A sustainable future. States of Jersey Government Report, St. Helier, Jersey, 122 pp.

StatSoft Inc., 1998. *STATISTICA for Windows [Computer program manual]*. Tulsa, Oklahoma: StatSoft, Inc., 2300 East 14th Street, Tulsa, OK 74104, phone: (918) 749-1119, fax: (918) 749-2217, email: info@statsoft.com, WEB: http://www.statsoft.com

StatSoft, Inc., 2003. *Electronic Statistics Textbook*. Tulsa, Oklahoma: StatSoft. WEB: http://www.statsoft.com/textbook/stathome.html.

Stoner, A.W., 1980. The role of seagrass biomass in the organisation of benthic macrofaunal assemblages. *Bulletin of Marine Science* **30**, 537-551.

Stoner, A.W., 1983. Distribution of fishes in seagrass meadows: role of macrophyte biomass and species composition. *Fisheries Bulletin, U.S.* **81**, 837-846.

Stoner, A.W., 1991. Diel variation in the catch of fishes and peneid shrimps in a tropical estuary. *Estuarine Coastal and Shelf Science* **33**, 57-69.

Stoner, A.W., Lewis, F.G., 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical seagrass meadows. *Journal of Experimental Marine Biology and Ecology* **94**, 19-40.

Støttrup, J.G., Nielsen, J.R., Krog, C., Rasmussen, K., 1994. Results on the extensive production of north Sea cod, *Gadus morhua* L., and their growth and distribution subsequent to the release in the Limfjord, Denmark. *Aquaculture and Fisheries Management* **25** (Supplement 1), 143-159.

Strauss, R.E., 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* **108**, 344-352.

Summerson, H.C., Peterson, C.H., 1984. Role of predation in organising benthic communities of a temperate zone seagrass bed. *Marine Ecology Progress Series* **15**, 63-77.

Syvret, A., 1998, Société Jersiaise, Marine Biologist. *Pers. comm.*, 20th November.

Szedlmayer, S.T., Able, K.W., 1996. Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey Estuary. *Estuaries* **19**, 697-709.

Tanaka, S., Sugimura, T., 2001. A new frontier of remote sensing from IKONOS images. *International Journal of Remote Sensing* **22**(1), 1-5.

Thayer, G.W., Adams, S.M., LaCroix, M. W., 1975. Structural and functional aspects of a recently established *Zostera marina* community. *Estuarine Research* **1**, 518-540.

Thayer, G.W., Chester, A.J., 1989. Distribution and abundance of fishes among basin and channel habitats in Florida bay. *Bulletin of Marine Science* **44**, 200-219.

Thomas, G.L., Thiesfield, S.L., Bonar, S.A., Crittenden, R.N., Pauley, G.B., 1990. Estimation of submergent plant biovolume using acousitc range information. *Canadian Journal of Fisheries and Aquatic Science* **47**, 805-812.

Thomas, J.L., Zimmerman, R.J., Minello, T.J., 1990b. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texan Bays. *Bulletin of Marine Science* **46**, 115-125.

Thresher, R. E., Gunn, J. S., 1986. Comparative analysis of visual census techniques for highly mobile, reef associated piscivores (Carangidae). *Environmental Biology of Fishes* **17**(2), 93-116.

Thresher, R.E., Nichols, P.D., Gunn, J.S., Bruce, B.D., Furlani, D.M., 1992. Seagrass detritus as the basis of a coastal planktonic food chain. *Limnology and Oceanography* **37**, 1754-1758.

Tolan, J.M., Holt, S.A., Onuf, C.P., 1997. Distribution and community structure of ichthyoplankton in Laguna Madre seagrass meadows: potential impact of seagrass species change. *Estuaries* **20**, 450-464.

Townsend, E.C., Fonseca, M.S., 1998. Bioturbation as a potential mechanism influencing spatial heterogeneity of north Carolina seagrass beds. *Marine Ecology Progress Series* **169**, 123-132.

Tubbs, C. R., Tubbs, J.M., 1983. The distribution of *Zostera* and its exploitation by wildfowl in the Solent, southern England. Aquatic Botany **15**, 223-239

Tupper, M., Boutilier, R.G., 1995. Effects of habitat on settlement, growth and postsettlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1834-1841.

Tupper, M., Hunte, W., 1994. Recruitment dynamics of coral-reef fishes in Barbados. *Marine Ecology Progress Series* **108**, 225-235.

Turk, S.M., 1986. The three species of eelgrass (*Zostera*) on the Cornish coast. *Cornish Studies* **14**, 15-21

Turner, M. G., Gardner, T.H. (eds). 1991. *Quantitative methods in landscape ecology.* Springer-Verlag, New York.

Turner, M. G., Gardner, T.H. (eds)., 1991. Quantitative methods in landscape ecology. Springer-Verlag, New York.

Turner, S.J., Hewitt, J.E., Wilkinson, M.R., Morrisey, D.J., Thrush, S.F., Cummings, V.J., Funnell, G., 1999. Seagrass patches and landscapes: the influence of wind wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries* **22**, 1016-1032.

UK Biodiversity Steering Group, 1995. Biodiversity: The UK Steering Group Report, Volume II: Action Plans. HMSO, London

Underwood A.J., 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Annual Review of Oceanography and Marine Biology* **19**, 513-605.

Underwood, A.J., 1992. Competition and marine plant-animal interactions. In: *Plant-Animal Interactions in the Marine Benthos,* D. John, S. J. Hawkins and J. Price (eds). Systematics Association Special Volume No. 46, Clarendon Press, Oxford. pp 443-475.

Underwood, A.J., 1997. *Experiments in Ecology. Their logical design and interpretation using analysis of variance.* Cambridge University Press, Cambridge. 504 pp.

Underwood, A.J., Chapman, M.G., 1997. Subtidal assemblages on rocky reefs at a cliff-face sewage outfall (north Head, Sydney, Australia): What happened when the outfall was turned off? *Marine Pollution Bulletin* **33**(7-12), 293-302.

Valle, C.F., O'Brien, J.W., Wiese, K.B., 1999. Differential habitat use by California halibut, *Paralichthys californicus*, barred sand bass, *Paralabrax nebulifer,* and other juvenile fishes in the Alamitos Bay, California. *Fishery Bulletin* **97**, 646-660.

Vance, D.J., Staples, D.J., Kerr, J.D., 1985. Factors affecting year-to-year variation in the catch of banana prawns (*Penaeus merguiensis*) in the Gulf of Carpentaria, Australia. *Journal of Conservation, Central Institute of Economic Management* **42**(1), 83-97.

Walker, D.I., 1988. Methods for monitoring seagrass habitat. *VIMS Working Paper* **18**. Melbourne, Australia.

Walker, D.I., Lukatelich, R.J., Bastyan, G., McComb, A.J., 1989. Effect of boat moorings on seagrass beds near Perth, Western-Australia. *Aquatic Botany* **36**(1), 69-77.

Warburton, K., 1989. Catchability variation in short beam trawl hauls. *Fisheries Research* **7**, 55-63.

Wassenberg, J.J. Blaber, S.J.M., Burridge, C.Y., Brewer, D.T., Salini, J.P., Gribble, N., 1997. The effectiveness of fish and shrimp trawls for sampling fish communities in tropical Australia. *Fisheries Research* **30**, 241-251.

Wathne, F.W., 1977. Performance of trawls used in resource assessment. *Marine Fisheries Review* **39**(6), 16-23.

Webb, D.G., 1991. Effect of predation be juvenile pacific salmon on marine harpacticoid copepods. I. Comparisons of patterns of copepod mortality with patterns of salmon consumption. *Marine Ecology Progress Series* **72**, 25-36.

Webster, P.J., Rowden, A.A., Attrill, M.J., 1998. Effect of shoot density on the infaunal macro-invertebrate community within a *Zostera marina* seagrass bed. *Estuarine, Coastal and Shelf Science* **47**(3), 351-357.

Weinstein, W.P., Brook, H. A., 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. *Marine Ecology Progress Series* **12**, 15-27.

Weinstein, W.P., Heck, K.L., Jr., 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure and community ecology. *Marine Biology*, **50**(2), 97-107.

Werner, E.E., Hall, D.J., 1988. Ontogenetic habitat shifts in bluegill: the foraging rate predation risk trade off. *Ecology* **69**, 1352-1366.

Wheeler, A., 1969. *The Fishes of the British Isles and north-West Europe*. Michigan State University Press, East Lansing. 613 pp.

Wheeler, A., 1980. Fish-algal relations in temperate waters. In *The shore environment: ecosystems 2*, J.H. Price et al. (eds), London; Academic Press, pp. 677-698.

Wheeler, A., 2001. Formerly of British Museum of Natural History, London. Pers.comm, 15th March.

Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E., 1986. *Fishes of the north-eastern Atlantic and the Mediterranean*. Vol. II. UNESCO 517-1007.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**, 385-397

Wilson, D.P., 1949. The decline of *Zostera marina* L. at Salcombe and its effects on the shore. *Journal of the Marine Biological Association* **28**(2), 395-413

Wilson, K.A., Heck, K.L., Able, K.W., 1987. Juvenile blue crab, *Callinectes sapidus*, survival - an evaluation of eelgrass, *Zostera marina*, as refuge. *Fishery Bulletin* **85**, 53-58.

Winer, B.J. 1971. *Statistical Principles in Experimental Design, Second Edition*. McGraw-Hill, Inc., New York. 907 pp.

With, K.A., Crist, T.O., 1995. Critical thresholds to landscape structure. *Ecology* **76**(8), 2446-2459.

Wood, E.J.F., Odum, W.E., Zieman, J.C. (1969). Influence of seagrass on the productivity of coastal lagoons. In *Memoirs Symposium International Costeras* (UNAM-UNESCO), November 28-30, pp. 495-502.

Worthington, D. G. Ferrell, D. J., McNeill, S. E., Bell, J. D., 1992b. Effects of the shoot density of seagrass on fish and decapods: are correlations evident over large spatial scales? *Marine Biology* **112**, 139-146.

Worthington, D.G. Ferrell, D.J., McNeill, S.E., Bell, J.D., 1992a. Growth of four species of juvenile fish associated with the seagrass *Zostera capricorni* in Botany Bay, New south Wales. *Australian Journal of Marine and Freshwater Research* **43**, 1189-1198.

Worthington, D.G., Fowler, A.J., Doherty, P.J., 1995. Determining the most efficient method of age determination for estimating the age structure of a fish population. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2320-2326.

Worthington, D.G., Westoby, M., Bell, J.D., 1991. Fish larvae settling in seagrass: effects of leaf density and an epiphtic alga. *Australian Journal of Ecology* **16**, 289-293.

Young, P.C., 1981. Temporal changes in vagile epibenthic fauna of two seagrass meadows (*Zostera capricorni* and *Posidonia australis*). *Marine Ecology Progress Series* **5**, 91-102.

Young, P.C., Carpenter, S.M., 1977. Recruitment of postlarval Penaeid prawns to nursery areas in Moreton Bay, Queensland. *Australian Journal of Marine and Freshwater Research* **28**, 745-773.

Zimmerman, R.J., Minello, T.J., 1984. Densities of *Penaeus aztecus*, *Penaeus setiferus* and other macrofauna in a Texas saltmarsh. *Estuaries* **7**, 421-433.

Zupo, V., Nelson, W.G., 1999. Factors influencing the association patterns of *Hippolyte zostericola* and *Palaemonetes intermidius* (Decapoda: Natantia) with seagrasses of the Indian River Lagoon, Florida. *Marine Biology* **134**, 181-190.

Appendix 1

Appendix 1: Multiple linear regression equations for predicting potential affect of changes in seagrass structure on faunal ensemble variables.

Where:
't' is transect heterogeneity,
'e' is epiphytal load index,
'd' is depth in metres,
'c' is estimated canopy height,
'a' is percentage of algae (based on trawl swept area),
'$PC1$' is the first Principle Component representative of fragmentation
'$PC2$' is the second Principle Component representative of habitat heterogeneity
'$PC3$' is the third Principle Component representative of distance to 10m isobath.

Day

Dependent variables (y)	**=**	$\alpha + \beta(t) + \beta(e) + \beta(d) + \beta(c) + \beta(PC1) + \beta(PC2) + \beta(PC3)$
Total species number	=	$-1.39 + [0.91(d)] + [-0.4(PC1)] + [0.58(PC3)]$
Total density	=	$0.14 + [0.91(e)] + [0.48(d)] + [0.49(c)] + [-0.45(PC1)] + [-0.49(PC2)]$
Total diversity	=	$0.97 + [-0.47(t)] + [0.51(d)]$
Fish species number	=	$-0.48 + [0.9(d)] + [-0.32(PC1)] + [0.75(PC3)]$
Fish density	=	$0.08 + [-0.4(t)] + [0.57(d)] + [0.23(a)] + [0.29(PC3)]$
Fish diversity	=	$-0.46 + [0.79(d)] + [0.32(c)] + [0.8(PC3)]$
Decapod species number	=	$4.03 + [-0.27(t)] + [0.76(d)] + [-0.34(c)] + [-0.41(PC1)] + [0.28(PC3)]$
Decapod density	=	$1.72 + [0.64(e)] + [-0.25(c)] + [-0.44(PC2)]$
Decapod diversity	=	$0.26 + [-0.4(t)] + [0.6(d)]$
Fish Groups		
Temporary juveniles	=	$-0.01 + [0.87(d)] + [-0.36(PC1)] + [0.54(PC3)]$
Permanent juveniles		No multiple linear regression model. See table 5.10
Small permanents	=	$0.002 + [-0.57(t)] + [0.5(PC1)]$
Cryptic permanents	=	$-0.13 + [0.34(d)] + [0.46(c)]$
Large permanents		No multiple linear regression model. See table 5.10
Temporary mature		No multiple linear regression model. See table 5.10

Night

Dependent variables (y)	**$= \alpha + \beta(t) + \beta(e) + \beta(d) + \beta(c) + \beta(PC1) + \beta(PC2) + \beta(PC3)$**
Total species number	$= 11.79 + [-0.32(t)] + [0.39(PC3)]$
Total density	$= 0.62 + [0.73(e)] + [0.31(PC3)]$
Total diversity	$= 1.66 + [-0.45(e)]$
Fish species number	$= 3.22 + [0.64(PC3)]$
Fish density	No multiple linear regression model. See table 5.10
Fish diversity	$= 4.34 + [0.35(e)] + [0.20(a)] + [0.38(PC1)] + [0.72(PC3)]$
Decapod species number	$= 4.03 + [-0.27(t)] + [0.76(d)] + [-0.34(c)] + [-0.41(PC1)] + [0.28(PC3)]$
Decapod density	= No multiple linear regression model. See table 5.10
Decapod diversity	$= -0.8 + [0.64(e)]$
Fish Groups	
Temporary juveniles	No multiple linear regression model. See table 5.10
Permanent juveniles	No multiple linear regression model. See table 5.10
Small permanents	$= 0.04 + [0.38(PC1)] + [-0.29(PC2)]$
Cryptic permanents	$= -0.04 + [0.48(d)] + [0.67(c)] + [-0.28(PC1)] + [0.32(PC3)]$
Large permanents	$= 0.05 + [-0.46(d)] + [0.4(c)]$
Temporary mature	No multiple linear regression model. See table 5.10