2007

APPLICATION OF SURFACE-OCEAN REMOTE-SENSING TO THE CHARACTERISATION OF BIOGEOGRAPHIC PATTERNS OF BENTHIC FAUNA IN A TEMPERATE SHELF SEA

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http://hdl.handle.net/10026.1/2507

http://dx.doi.org/10.24382/1530

University of Plymouth

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APPLICATION OF SURFACE-OCEAN REMOTE-SENSING TO THE
CHARACTERISATION OF BIOGEOGRAPHIC PATTERNS OF BENTHIC
FAUNA IN A TEMPERATE SHELF SEA

KIRSTEN ALEXANDRA RICHARDSON, M.Sc., B.Sc. (Hons.)

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

DOCTOR OF PHILOSOPHY

School of Biological Sciences
Marine Ecology Research Centre

In collaboration with
Plymouth Marine Laboratory

May 2007
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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 without prior agreement of the Graduate Committee. This study was financed with the aid of a studentship from the Natural Environment Research Council and carried out in collaboration with Plymouth Marine Laboratory. The work described in this thesis was conducted by the author, under the supervision of Dr. N.J. Hardman-Mountford, M. Kendall and Prof. J.I. Spicer.

This research has used data sets not collected by the candidate (remotely-sensed data, MRCS model data and bed-stress data from Pingree and Maddock’s 1977 model of tidal residuals). Consequently, this data has previously been used in publications and theses. The epibenthic survey data was collected by the author and has not yet been published. The processing, application and interpretation of the data within this thesis is completely the work of the author and is to the best of the author’s knowledge, completely original.

Throughout the thesis all sources of information have been specifically acknowledged by means of reference.

Presentation and Conferences Attended:


Poster presentation

Oral Presentation

Contributing Author:


Word count of main body of thesis: 49,262

Signed: ........................................

Date: 10th September 2007
ABSTRACT

APPLICATION OF SURFACE-OCEAN REMOTE-SENSING TO THE CHARACTERISATION OF BIOGEOGRAPHIC PATTERNS OF BENTHIC FAUNA IN A TEMPERATE SHELF SEA

KIRSTEN ALEXANDRA RICHARDSON, M.SC., B.SC. (HONS.)

Ecosystem scale, adaptive management of the marine environment, emphasised by the Convention on Biological Diversity, requires a clear understanding of the spatial and temporal dynamics of the system in question. Classical species-based biogeography alone is not sufficient to describe those dynamics at the appropriate scale for whole ecosystem management. A novel, multidisciplinary, complex systems approach has been developed for characterising the biogeographic distribution of benthic fauna in a temperate shelf sea system through application of remote sensing to the principles of benthic-pelagic coupling.

A six year time series of satellite remote sensing data (AVHRR SST and SeaWiFS Chl-a, L\textsubscript{wN}(555, 670)) was analysed using multivariate statistical techniques to identify the emergent patterns (temporal and spatial) of water column physical structure and associated patterns of productivity in North-West European Shelf waters. Three persistent biogeographic regions were identified from horizontal patterns in sea surface properties. Comparison with the results of an epibenthic field survey, have shown gradients of epibenthic megafaunal distribution to correspond closely to the biogeographic regions identified by remote sensing. The application of this technique to marine monitoring programmes and ecosystem management is discussed.
“Ocean, n. A body of water occupying about two-thirds of a world made for man – who has no gills.”

*Ambrose Bierce (1842 – 1914?)*

ACKNOWLEDGEMENTS

I am profoundly grateful to my supervisors, Mike Kendall, Nick Hardman-Mountford and John Spicer, for their unwavering support and patience. They have provided both academic guidance and friendship, which I very much appreciate. I would also like to thank Tony Hawkins for his encouragement during the initial stages of this project.

From PML, I would like to thank the Remote Sensing Group (RSDAS), who explained the intricacies of remote-sensing to me and provided me with the AVHRR and SeaWiFS images of the English Channel, Jerry Blackford, who taught me to programme in FORTRAN and Francis Gilbert and Katy Lewis who provided me with data from the Medium Resolution Continental Shelf (MRCS) model. I am grateful to Dave Robins for his support, guidance, and friendship.

I could not have completed this thesis without the help of the crew of the “Plymouth Quest”. Their knowledge of the western English Channel and the operation of benthic sampling gear was an invaluable resource, as was their knowledge of the best “fish and chips” shop in Newlyn. Amanda Beesley’s assistance in counting and identifying a vast number of animals was also much appreciated.

I am indebted to my friends for their encouragement and support through what has been a difficult few years: Olivia and Ricardo (and Javi), Hazel and Mike, Nova, Gareth and Bec and James.

Finally I would like to thank my parents, without whose love and support I could not have completed this journey.
## CONTENTS

<table>
<thead>
<tr>
<th>Contents</th>
<th>i</th>
</tr>
</thead>
<tbody>
<tr>
<td>List of figures</td>
<td>vii</td>
</tr>
<tr>
<td>List of tables</td>
<td>xvi</td>
</tr>
<tr>
<td>List of Acronyms</td>
<td>xvii</td>
</tr>
</tbody>
</table>

### Chapter 1

**Introduction, research aims and general background**

1. **Introduction and rationale**
   1.1 Application of the "Ecosystem Approach" in Regional Seas  
   1.2 Biogeographic distribution patterns of epibenthic fauna in UK Regional Seas.  
   1.3 Linking environmental conditions to the distribution of epibenthic fauna  
   1.4 Water column structure and satellite remote-sensing  
   1.5 Ecological pattern as an emergent property of a complex adaptive system

2. **Research aims and thesis outline**
   2.1 Research aims  
   2.2 Thesis outline

3. **The study area**

4. **Remotely-sensed data**
   4.1 A brief history  
   4.2 Remotely-sensed oceanographic data  
   4.3 Variables used in this study
### 1.5  
**Tidal currents: linking the sea-surface and the seabed**

1.5.1  
Tidal currents  

1.5.2  
Tidal velocity  

1.5.3  
Vertical structure of tidal currents within the water column  

1.5.4  
Bed-stress  

1.5.5  
Dissipation of tidal energy  

1.5.6  
Stratified or well-mixed water column?  

1.5.7  
Summary  

### Chapter 2

An Investigation of the suitability of remotely-sensed surface-ocean data as a means of describing the spatial and temporal heterogeneity of water column physical structure and patterns of productivity in the English Channel.

#### 2.1  
**Introduction**  

#### 2.2  
**Methods**  

2.2.1  
Data acquisition and pre-processing  

2.2.2  
Converting digital numbers to real world values  

2.2.3  
Selection of a map projection  

2.2.4  
Detection of cloud contamination  

2.2.5  
Spatial variability statistics  

2.2.6  
Temporal variability statistics  

#### 2.3  
**Results**  

2.3.1  
Cloud contamination  

2.3.2  
Spatial variability: time-series mean and standard deviation for each remotely-sensed variable  

2.3.3  
Intra-annual variability  

2.3.4  
Inter-annual variability and time series analysis  

#### 2.4  
**Discussion**  

2.4.1  
Cloud cover  

2.4.2  
Intra-annual variability  

2.4.3  
Inter-annual variability  

2.4.4  
Significance of observations  

#### 2.5  
**Conclusions**
Chapter 3

The Application of remote-sensing to the identification of persistent ecological provinces in the English Channel

3.1 Introduction

3.2 Principal Components Analysis (PCA)

3.3 Methods

3.3.1 Data preparation
3.3.2 T-mode Principal Components Analysis
3.3.3 Interpretation of PC/eigenvector modes
3.3.4 Initial selection of PC/eigenvector modes
3.3.5 Identification of ecological sub-provinces from selected PC/eigenvector modes
3.3.6 Testing the sub-province structure

3.4 T-Mode PCA of the remotely-sensed data: Results and interpretation

3.4.1 SST: Results
3.4.2 SST: Interpretation
3.4.3 log(Chl-a): Results
3.4.4 log(Chl-a): Interpretation
3.4.5 L_11,.,.,(555): Results
3.4.6 L_11,.,.,(555): Interpretation

3.5 Identification and validation of sub-provinces: Results

3.5.1 Identification of sub-provinces
3.5.2 Testing of sub-provinces

3.6 Identification and validation of sub-provinces: Discussion

3.7 Overall Conclusions
Chapter 4

The relationship between the English Channel remotely-sensed sub-provinces and the spatial heterogeneity of seabed environmental variables.

4.1 Introduction

4.1.1 Linking water column structure and seabed environmental variables

4.1.2 Selection of seabed data

4.2 Methods

4.3 Results

4.3.1 Variation in water depth (m) (MRCS bathymetry data) in the English Channel

4.3.2 Mean depth (m) (MRCS bathymetry data) of each sub-province

4.3.3 Variation in bed-stress estimates (dynes cm⁻²) in the English Channel (Pingree and Maddock's 1977 model of tidal residuals)

4.3.4 Mean bed-stress (dynes cm⁻²) in each sub-province (Pingree and Maddock's 1977 model of tidal residuals)

4.3.5 Comparison of sub-sample water depth (m) (MRCS bathymetry data) and SST, log(Chl-a) and L₅₅₅ values.

4.3.6 Comparison of sub-sample bed-stress estimates (dynes cm⁻²) (Pingree and Maddock's 1977 model of tidal residuals) and SST, log(Chl-a) and L₅₅₅ values.

4.3.7 Relationship between water depth (m) and bed-stress (dynes cm⁻²)

4.4 Discussion

4.5 Overall Discussion and Conclusions

Chapter 5

Remotely-sensed sub-province structure related to the biogeographic distribution of epibenthic megafauna in the English Channel

5.1 Introduction
5.2  *Validity of the sub-province structure at a reduced spatial scale* 133

5.2.1  Methods 133

5.2.2  Results 136

5.2.3  Discussion on the validity of sub-province structure at reduced spatial scale 144

5.3  *Predicting the biogeographic distribution of epibenthic fauna from the remotely-sensed sub-province structure.* 148

5.3.1  Methods 148

5.3.2  Results 157

5.3.3  Discussion on the biogeographic distribution of epibenthic fauna 177

5.4  *Conclusions* 180

Chapter 6

*Overall discussion and conclusions* 181

6.1  *Introduction* 181

6.2  *An investigation of the suitability of remotely-sensed surface-ocean data as a means of describing the spatial and temporal heterogeneity of water column physical structure and associated patterns of primary productivity in the English Channel.* 181

6.3  *Application of remote-sensing to the identification of persistent spatial structure (sub-provinces) within the spatial and temporal heterogeneity of physical water column structure and associated patterns of productivity in the English Channel.* 184

6.4  *The relationship between the sub-province structure detected from remotely-sensed data and the spatial variation in seabed physical variables used to describe the distribution of benthic fauna in existing studies.* 186
6.5 Predicting the biogeographic distribution of epibenthic megafauna in the English Channel from the structure of the remotely-sensed sub-provinces.

6.6 Additional factors influencing the spatial distribution of epibenthic fauna in the English Channel.

6.7 Implications and final conclusions

6.8 Suggestions for further work

References

Appendices

A3.1 Selection PC/eigenvector modes \( \log(\text{Chl}-a) \)

A3.2 Selection PC/eigenvector modes \( L_w(555) \)

A5.1 Location of sample stations (latitude and longitude) in the Lands End – Portland test area

A5.2 "Plymouth Quest"

A5.3 Full list of species found in each sub-province

A5.4 Regression analysis plots for the relationship between sample stations in terms of similarity of remotely-sensed variables vs. similarity of epibenthic fauna (untransformed data for all epibenthic species and \( \sqrt{n} \)-transformed data for each separate phyla).

A5.5 Distribution of echinoderm species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages

A5.6 Distribution of crustacean species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages

A5.7 Distribution of mollusc species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages
LIST OF FIGURES

1.1 Map of the English Channel: the area in which this study is focused. 15

1.2 Summary of the link between water column structure in shelf seas and seabed environmental conditions. 27

2.1 Schematic of spatial variability statistics 34

2.2 Schematic of temporal variability statistics 35

2.3 Comparison of the mean monthly percentages of cloud cover for AVHRR and SeaWiFS data between January 1998 and December 2003. 37

2.4.a Temporal mean SST (°C) for the English Channel. 39

2.4.b SST (°C) temporal standard deviation for the English Channel. 39

2.5.a Temporal mean log(Chl-a) (mg m⁻³) for the English Channel. 41

2.5.b Temporal standard deviation log(Chl-a) (mg m⁻³) for the English Channel. 41

2.6.a Temporal mean $L_{\lambda_\lambda}(555)$ (mW cm⁻² µm⁻¹ sr⁻¹) for the English Channel. 43

2.6.b Temporal standard deviation $L_{\lambda_\lambda}(555)$ (mW cm⁻² µm⁻¹ sr⁻¹) for the English Channel. 43

2.7.a Temporal mean $L_{\lambda_\lambda}(670)$ (mW cm⁻² µm⁻¹ sr⁻¹) for the English Channel. 44

2.7.b Temporal standard deviation $L_{\lambda_\lambda}(670)$ (mW cm⁻² µm⁻¹ sr⁻¹) for the English Channel. 44

2.8 12 month spatial mean time-series for SST (°C) (whole English Channel area) for time period January 1998 to December 2003. 46

2.9 Temporal monthly mean SST (°C) for the English Channel. 47

2.10 12 month spatial mean time-series for log(Chl-a) (mg m⁻³) (whole English Channel area) for the time period January 1998 to December 2003. 48
2.11 Temporal monthly mean log(Chl-α) (mg m⁻³) for the English Channel.

2.12 12 month spatial mean time-series for $L_{\mu W}(555)$ (mW cm⁻² μm⁻¹ sr⁻¹) (whole English Channel area) for the time period January 1998 to December 2003.

2.13 12 month spatial mean time-series for $L_{\mu W}(670)$ (mW cm⁻² μm⁻¹ sr⁻¹) (whole English Channel area) for the time period January 1998 to December 2003.

2.14 Temporal monthly mean $L_{\mu W}(555)$ (mW cm⁻² μm⁻¹ sr⁻¹) for the English Channel.

2.15 Temporal monthly mean $L_{\mu W}(670)$ (mW cm⁻² μm⁻¹ sr⁻¹) for the English Channel.

2.16 72 month spatial mean time-series for SST (°C).

2.17 72 month spatial mean time-series for log(Chl-α) (mg m⁻³).

2.18 72 month spatial mean time-series for $L_{\mu W}(555)$ (mW cm⁻² μm⁻¹ sr⁻¹).

2.19 72 month spatial mean time-series for $L_{\mu W}(670)$ (mW cm⁻² μm⁻¹ sr⁻¹).

2.20 Annual net heating cycle at the sea surface. Adapted from Pingree (1980).

3.1 Schematic of the mathematical break-down of T-mode Principle Components Analysis (PCA) as applied to remotely-sensed data.

3.2 Schematic of the unsupervised classification process.

3.3 The grid used to spatially re-sample the remotely-sensed data in order to test the spatial structure of the proposed sub-provinces.

3.4.a SST. The Guttman Criterion.

3.4.b SST. Logarithmic Eigenvalue Curve (LEV).
3.4.c SST. North et al. (1982) Rule of thumb for testing uniqueness of PC/eigenvector modes. 85

3.5 SST eigenvector loadings (temporal aspect of the PC/eigenvector mode). Each eigenvector relates to a corresponding PC image. 87

3.6 SST PC Images. 88

3.7 Log(Chl-a) eigenvector loadings (temporal aspect of the PC/eigenvector mode). Each eigenvector relates to a corresponding PC image. 90

3.8 Log(Chl-a) PC Images. 91

3.9 $L_{W555}$ eigenvector loadings (temporal aspect of the PC/eigenvector mode). Each eigenvector relates to a corresponding PC image. 94

3.10 $L_{W555}$ PC Images. 94

3.11 English Channel Sub-Provinces identified from steady state spatial patterns in the mean 12 month image time-series of remotely-sensed SST, log(Chl-a) and $L_{W555}$. 97

3.12 The grid used to spatially re-sample the remotely-sensed data overlaid on the sub-province image so that the location of each grid square in terms of the three sub-provinces can be observed. 97

3.13 NMDS ordination of the relationship between sub-samples in terms of 3 x 12 month time-series (SST, log(Chl-a) and $L_{W555}$) data extracted for each sub-sample location as part of the spatial re-sampling process. 100

3.14 SST. Mean 12 month time-series for each sub-province calculated from the sub-samples within that sub-province. 95% confidence limits are indicated for each month. 101

3.15 log(Chl-a). Mean 12-month time-series for each sub-province calculated from the sub-samples within that sub-province. 95% confidence limits are indicated for each month. 102
3.16 $L_{wn}(555)$. Mean 12 month time-series for each sub-province calculated from the sub-samples within that sub-province. 95% confidence limits are indicated for each month.

3.17 Summary of the gradients in water column stability, SST, $L_{wn}(555)$ and $\log$(Chl-a) values that characterise the sub-province structure.

4.1 Pingree and Maddock's contour map of bed-stress (dynes cm$^{-2}$) variation in the English Channel region.

4.2 MRCS bathymetry data for the English Channel region. Coloured according to 10m depth intervals (0m $>$ 120m). Resolution is approximately 7.4 km$^2$.

4.3 Frequency distribution of bathymetry values (20 m intervals) sub-sampled from MRCS model bathymetry data (7.4 km$^2$ grid resolution).

4.4 Mean water depth (m) (MRCS bathymetry data) of sub-samples in each of the three sub-provinces. 95% confidence intervals are indicated.

4.5 Frequency distribution of bed-stress estimates (5 dynes cm$^{-2}$ intervals) from Pingree and Maddock's (1977) model of tidal residuals within the English Channel sub-samples.

4.6 Mean bed-stress (dynes cm$^{-2}$) value of sub-samples in each of the three sub-provinces. 95% confidence intervals are indicated.

4.7.a Water depth (m) (MRCS bathymetry data) sub-sample values plotted against mean annual sub-sample values for SST ($^\circ$C) ($r = 0.65 (p < 0.01)$).

4.7.b Water depth (m) (MRCS bathymetry data) sub-sample values plotted against mean annual sub-sample values for $\log$(Chl-a) (mg m$^{-3}$) ($r = -0.715 (p < 0.01)$).

4.7.c Water depth (m) (MRCS bathymetry data) sub-sample values plotted against mean annual sub-sample values for $L_{wn}(555)$ (mW cm$^{-2}$ $\mu$m$^{-1}$ sr$^{-1}$) ($r = -0.436 (p < 0.05)$).
4.8 NMDS ordination comparing the relationship between the 12 month mean time-series of the remotely-sensed variables (SST, log(Chl-a), L{\text{\textsc{M}}}(555)) in the English Channel. Water depth (m) overlaid.

4.9.a Bed-stress (dynes cm\(^{-2}\)) (Pingree and Maddock's 1977 model) sub-sample values plotted against mean annual sub-sample values for SST (°C) \((r = -0.336 \ (p < 0.10))\).

4.9.b Bed-stress (dynes cm\(^{-2}\)) (Pingree and Maddock's 1977 model) sub-sample values plotted against mean annual sub-sample values for log(Chl-a) (mg m\(^{-3}\)) \((r = 0.464 \ (p < 0.01))\).

4.9.c Bed-stress (dynes cm\(^{-2}\)) (Pingree and Maddock's 1977 model) sub-sample values plotted against mean annual sub-sample values for \(L_{\text{\textsc{M}}}(555)\) (mW cm\(^{-2}\) \(\mu m^{-1}\ sr^{-1}\)) \((r = 0.531 \ (p < 0.01))\).

4.10 NMDS ordination comparing the relationship between the 12 month mean time-series of the remotely-sensed variables (SST, log(Chl-a), \(L_{\text{\textsc{M}}}(555)\)) in the English Channel. Bed-stress estimates (dynes cm\(^{-2}\)) are overlaid.

4.11 Water depth (m) (MRCS bathymetry data) sub-sample values plotted against bed-stress (dynes cm\(^{-2}\)) sub-sample estimates from Pingree and Maddock's (1977) model of tidal residuals in the English Channel.

5.1 Map of the Lands End – Portland area of the English Channel displaying the location of the three sub-provinces.

5.2 Location of the 31 x 1 km\(^2\) sample stations in the Lands End – Portland test area.

5.3 NMDS ordination of the relationship between the remotely-sensed properties of the 31 x 1 km\(^2\) sample stations in the Lands End – Portland test area of the English Channel.
5.4 SST (°C) monthly means with 95% confidence intervals of each sub-province, calculated from the SST mean monthly values of each of the sample stations contained within that sub-province: a) original allocation of sample stations to sub-provinces and b) allocation of sample stations to sub-provinces as indicated by the clusters identified in the NMDS ordination in figure 5.3.

5.5 log(Chl-a) (mg m⁻³) monthly means with 95% confidence intervals of each sub-province, calculated from the log(Chl-a) mean monthly values of each of the sample stations contained within that sub-province: a) original allocation of sample stations to sub-provinces and b) allocation of sample stations to sub-provinces as indicated by the clusters identified in the NMDS ordination in figure 5.3.

5.6 Lₜₜ(555) (mW cm⁻² μm⁻¹ sr⁻¹) monthly means with 95% confidence intervals of each sub-province, calculated from the Lₜₜ(555) mean monthly values of each of the sample stations contained within that sub-province: a) original allocation of sample stations to sub-provinces and b) allocation of sample stations to sub-provinces as indicated by the clusters identified in the NMDS ordination in figure 5.3.

5.7.a SST (°C). Annual mean values plotted against annual range values of the remotely-sensed variables at each of the 31 x 1 km² sample stations in the Lands End – Portland test area.

5.7.b log(Chl-a) (mg m⁻³). Annual mean values plotted against annual range values of the remotely-sensed variables at each of the 31 x 1 km² sample stations in the Lands End – Portland test area.

5.7.c Lₜₜ(555) (mW cm⁻² μm⁻¹ sr⁻¹). Annual mean values plotted against annual range values of the remotely-sensed variables at each of the 31 x 1 km² sample stations in the Lands End – Portland test area.

5.8 Geographic translation of the revised allocation of the 31 x 1 km² sample stations to sub-provinces (SP').

5.9 The mini-Agassiz trawl used in the macro-scale survey of mega epibenthic fauna in the Lands End – Portland test site.

5.10 Schematic of the division of each 1 km² sample station into quadrants for replicate sample collection.
5.11 Sample stations in the Lands End – Portland test area where it was possible to collect four replicate benthic trawls. The stations where it was not possible to obtain samples are indicated by white markers.

5.12 Schematic of the comparison between the two similarity matrices (non-parametric Regression Analysis and Coefficient of Determination) detailing the relationship between the sample stations in the Lands End – Portland test area in terms of a) epibenthic faunal assemblage and b) remotely-sensed variables.

5.13 Percentage contribution of each phyla (echinoderms, crustaceans and molluscs) to the total number of species recorded in the bio-geographical survey.

5.14 Mean number of individuals \(N\) recorded at each sample station (calculated from the four replicate trawls). The mean numbers of echinoderms, crustaceans and molluscs are shown as a percentage of the total \(N\).

5.15 Comparison of the NMDS ordinations of the relationship between the Lands End – Portland test area sampling stations in terms of a) epibenthic faunal assemblage (Bray-Curtis similarity) – Station mean abundances, b) epibenthic faunal assemblage (Bray-Curtis similarity) - All replicate samples and c) remotely-sensed variables (Euclidean distance).

5.16 Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and \(\sqrt{\text{V}}\)-transformed epibenthic assemblages (Bray-Curtis similarities).

5.17 Substrata type (Folk Classification 1954) for each sample station overlaid on the NMDS ordination of the relationship between sample stations in terms of epibenthic assemblage.

5.18 Depth class (10 m intervals) recorded from the MRCS model bathymetry data (≈ 7.4 km x 7.4 km grid) for each sample station overlaid on the NMDS ordination of the relationship between sample stations in terms of epibenthic assemblage.
5.19 Comparison of the mean number of individuals (N) of epibenthic fauna found in each sub-province for: a) the full compliment of species identified in the 2004 survey, b) echinoderm species, c) crustacean species and d) mollusc species.

5.20 Comparison of the mean number of species (S) of epibenthic fauna found in each sub-province for: a) the full compliment of species identified in the 2004 survey, b) echinoderm species, c) crustacean species and d) Mollusc species.

5.21 Comparison of the mean value of Simpson’s Index (1 - λ) for the epibenthic fauna found in each sub-province for: a) the full compliment of species identified in the 2004 survey, b) echinoderm species, c) crustacean species and d) mollusc species.

5.22 Comparison of the mean Taxonomic Distinctness (Δ*) of epibenthic fauna found in each sub-province for: a) the full compliment of species identified in the 2004 survey, b) echinoderm species, c) crustacean species and d) mollusc species.

5.23 The two gradients of epibenthic species distribution observed in the Lands End – Portland test area: a) The Lyme Bay gradient covering SP1’ and SP2’ and b) the Western gradient covering SP2’ and SP3’.

A3.1.a log(Chl-a). The Guttman Criterion.

A3.1.b log(Chl-a). Logarithmic Eigenvalue Curve (LEV).


A3.2.a Lwa(555). The Guttman Criterion.

A3.2.b Lwa(555). Logarithmic Eigenvalue Curve (LEV).


A5.2 “The Plymouth Quest” berthed at Sutton Harbour Marina in Plymouth’s Barbican area. “Quest” is a 21.5 m L.O.A. wet fish stern trawler.
A5.4.a Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and untransformed epibenthic assemblages (Bray-Curtis similarities).

A5.4.b Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and $\sqrt{N}$-transformed echinoderm assemblages (Bray-Curtis similarities).

A5.4.c Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and $\sqrt{N}$-transformed crustacean assemblages (Bray-Curtis similarities).

A5.4.d Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and $\sqrt{N}$-transformed mollusc assemblages (Bray-Curtis similarities).

A5.5 Distribution of echinoderm species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages.

A5.6 Distribution of crustacean species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages.

A5.7 Distribution of mollusc species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages.
## LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Equations necessary to convert 8bit image DNs to real world physical values for each water column variable. Supplied by NERC Remote Sensing Data Analysis Service (RSDAS), Plymouth Marine Laboratory.</td>
</tr>
<tr>
<td>3.1</td>
<td>Allocation of sub-samples to sub-provinces.</td>
</tr>
<tr>
<td>3.2</td>
<td>Pairwise comparisons (ANOSIM) to test for statistical differences between the three sub-provinces, based on the remotely-sensed properties of the sub-samples.</td>
</tr>
<tr>
<td>5.1</td>
<td>Allocation of sample stations to sub-provinces in the Lands End – Portland test area.</td>
</tr>
<tr>
<td>5.2</td>
<td>Pairwise comparisons (ANOSIM) to test for statistical differences between the three sub-provinces, based on the remotely-sensed properties of the sample stations in the Lands End – Portland area.</td>
</tr>
<tr>
<td>5.3</td>
<td>Revised allocation of sample stations to sub-provinces (cluster arrangement) in the Lands End – Portland test area.</td>
</tr>
<tr>
<td>5.4</td>
<td>Sample stations (revised sub-province allocation) in the Lands End – Portland test area where it was possible to obtain four replicates trawls of epibenthic fauna.</td>
</tr>
<tr>
<td>5.5</td>
<td>List of species found to occur in only one of the three sub-provinces.</td>
</tr>
<tr>
<td>5.6</td>
<td>List of species found to occur in all three sub-provinces.</td>
</tr>
<tr>
<td>5.7</td>
<td>Pairwise comparisons between sub-provinces in a one-way ANOSIM to test for statistical difference between the epibenthic faunal assemblages of those sub-provinces.</td>
</tr>
<tr>
<td>5.8</td>
<td>( R^2 ) values for the distribution of each epibenthic phyla and the variation in remotely-sensed properties at the 20 sample stations in the Lands End – Portland test area.</td>
</tr>
<tr>
<td>5.9</td>
<td>Average Bray-Curtis dissimilarity, combined species richness and number of species in common (expressed as percentage in parenthesis) for each pair of sub-provinces.</td>
</tr>
<tr>
<td>5.10</td>
<td>The sub-set of 30 species identified in the SIMPER analysis of the three sub-provinces</td>
</tr>
<tr>
<td>A5.1</td>
<td>Location of sample stations (latitude and longitude) in the Lands End – Portland test area.</td>
</tr>
<tr>
<td>A5.3</td>
<td>Full list of species found in each sub-province.</td>
</tr>
</tbody>
</table>
LIST OF ACRONYMS

ANOSIM – Analysis of Similarities
ATSR – Along Track Scanning Radiometer
AVHRR – Advanced Very High Resolution Radiometer
BGS – British Geological Survey
BML – Bottom mixed Layer
CAS – Complex Adaptive Systems
CBD – Convention on Biological Diversity
CDOM – Coloured, Dissolved Organic Matter
Chl-a – Chlorophyll-a (mg m⁻³)
CZCS – Coastal Zone Colour Scanner
DEFRA – Department of the Environment, Farming and Rural Affairs
DN – Digital Number
DSRS – Dundee Satellite Receiving Station
EM – Electromagnetic
ERS-1 RA – Earth Resources Satellite -1 Radar Altimeter
ERS-1 SAR – Earth Resources Satellite -1 Synthetic Aperture Radar
ERS-1 SCATT – Earth Resources Satellite -1 Scatterometer
ERS-2 SAR – Earth Resources Satellite -2 Synthetic Aperture Radar
ERS-2 SCATT – Earth Resources Satellite -2 Scatterometer
ERSEM – European Regional Seas Ecosystem Model
ERTS – Earth Resource Technology Satellites
ESSA – Environmental Science Services Administration
GAC – Global Area Coverage
HDF – Hierarchical Data Format
HRPT – High-Resolution Picture Transmission
IOCCG – International Ocean-Colour Coordinating Group
LAC – Local Area Coverage
LEV graph – log(eigenvalues) graph
LME – Large Marine Ecosystems
\( L_{\text{W}}(555) \) – Water Leaving Radiance at 555nm (mW cm⁻² μm⁻¹ sr⁻¹)
$W_{\lambda}(670)$ - Water Leaving Radiance at 670nm ($\text{mW cm}^{-2} \mu\text{m}^{-1} \text{sr}^{-1}$)

MANOVA - Multivariate Analysis of Variance

MCS - Marine Conservation Society

MRCS - Medium Resolution Continental Shelf Model

NAO - North Atlantic Oscillation

NASA - National Aeronautics and Space Administration

NEODC - NERC Earth Observation Data Centre

NERC - Natural Environment Research Council

NMDS - Non-metric Multi-Dimensional Scaling

NOAA - National Oceanic and Atmospheric Administration

NSCATT - NASA’s Scatterometer

PC - Principle Component

PCA - Principal Components Analysis

PML - Plymouth Marine Laboratory

POL - Proudman Oceanographic Laboratory

POLCOMS - Proudman Oceanographic Laboratory Coastal Ocean Modelling System

RCEP - Royal Commission on Environmental Pollution

RSDAS - NERC Remote Sensing Data Analysis Service

SAR - Synthetic Aperture Radar

SeaWiFS - Sea viewing Wide Field-of-view Sensor

SIMPER - Similarity Percentages

SIMPROF - Similarity Profiling

SML - Surface Mixed Layer

SMMR - Scanning Multi-channel Microwave Radiometer

SP - Sub-Province

SPM - Suspended Particulate Matter

SSM/I - Special Sensor Microwave Imager

SST - Sea Surface Temperature ($^\circ\text{C}$)

TIROS-1 - Television and Infrared Observation Satellite 1

TOPEX/Poseidon - NASA’s ocean Topography Experiment

UN - United Nations

UNEP - United Nations Environment Programme

WWF - World Wildlife Fund

xviii
CHAPTER 1

INTRODUCTION, RESEARCH AIMS AND GENERAL BACKGROUND

1.1 Introduction and rationale

1.1.1 Application of the “Ecosystem Approach” in Regional Seas

Continental shelf-seas cover only a very small percentage of the Earth’s surface (≈ 6%) yet they are hugely important both ecologically and economically (e.g. Constanza et al. 1997). Shelf-seas draw down and store 20 - 50% of the carbon dioxide that is collectively stored by the global oceans (Thomas et al. 2004) and shelf-sea zooplankton communities provide the basis for more than 95% of the world’s estimated fisheries yield (Walsh 1988). The demands of the expanding human population are impacting shelf-seas both directly (e.g. the unsustainable exploitation of fish stocks) and indirectly (e.g. climate change) (RCEP 2004; Sabine et al. 2004; WWF 2006).

The recognition that small-scale\(^1\), single species approaches to conservation and environmental management are inadequate to address the impact of humans on the environment (Franklin 1993; Gaston and Blackburn 1999; Lawton 1999; Wieters 2001) has lead to the initiation of a holistic “ecosystem approach” (UN 1992; UNEP 1995).

Ecosystems are defined in Article II of the Convention on Biological Diversity (CBD) as:

"Dynamic complexes of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit."

\(^1\) In this thesis the terms “small-scale” and “fine-scale” are used to imply limited size or scope and the terms “large-scale”, “broad-scale” and “macro-scale” are used to indicate that a study or approach is wide-ranging or expansive.
Ecosystems are complex and dynamic: they vary in space, time and over a range of scales (Levin 1992). A method of management that encompasses this variability is essential to the delivery of an ecosystem approach. The process of “adaptive management” recognises the complex nature of ecosystems and is based on the development of management practices that are structured to allow modification in response to feedback from ecological monitoring (Yoccoz et al. 2001; Mee 2004). Therefore adaptive management has been identified as a key mechanism in the ecosystem approach (Laffoley et al. 2004; UNEP 2004).

The UK government is committed to encouraging the application of an ecosystem approach to the marine environment by 2010, in order to secure the targets of halting the decline of biodiversity and achieving sustainable development in the marine environment (CBD 2000; DEFRA 2004). The UK’s jurisdictional waters have been subdivided into Regional Seas: medium-scale marine ecosystems that reflect the ecology, distribution of natural resources and socio-economic uses of the area concerned (DEFRA 2004; Turnbull 2004; DEFRA 2005). Examples of UK Regional Seas include the Irish Sea, the western English Channel and Western Approaches and the southern North Sea. The ecosystem approach is to be applied at the Regional Seas level. Therefore an understanding of the physical and biological patterns of variability, at the same broad-scale at which the environment is being managed, is essential for the process of adaptive management. The effects of environmental conditions or other organisms on a particular species, in a specific place, can be determined from small-scale investigations. However, without corresponding broad-scale investigations, it is impossible to determine if results simply reflect the eccentricities of individual species and specific sites, or if they are revealing the operation of a more universal process (Brown and Maurer 1989; Brown 1995).
1.1.2 Biogeographic distribution patterns of epibenthic fauna in UK Regional Seas.

Epibenthic fauna are the animals that live at the sediment-water interface of the benthic environment. Epibenthic communities are important to shelf-sea ecosystems in terms of the bioturbation of surface sediments, nutrient cycling and detrital decomposition (Pearson 2001; Rosenberg 2001). The epibenthos are also a critical food source for higher trophic levels and are a valuable resource for fisheries (Petersen 1918; Caddy 1989; Collie et al. 1997; Pauly et al. 2002). Additionally, epibenthic species are relatively sessile and long lived, making them sensitive indicators of change in the marine environment (Blacker 1957; Reiss and Kroncke 2005).

There is a strong history of benthic sampling in the shelf-seas that surround the UK, dating back to the classical works of Petersen (1913; 1918) and Thorson (1957). Following Petersen’s studies, biogeographic investigations of the patterns of distribution of benthic fauna tended to focus on infaunal rather than epifaunal benthic species sampling: an inequality that has been attributed to the difficulties involved in quantitatively sampling the epibenthos (Rees et al. 1999; Reiss and Kroncke 2004).

The biogeographic distribution of epibenthic fauna in UK Regional Seas has been linked to a multitude of environmental factors. Substratum type has traditionally been regarded as the fundamental factor in determining the distribution and abundance of benthic fauna (e.g. Petersen 1913; Jones 1950; Thorson 1957) although several more recent studies have had difficulty in linking substratum type to epibenthic faunal distributions (Basford et al. 1990; Duineveld and van Noort 1990; Duineveld et al. 1991; Reiss and Kroncke 2004).

Descriptions of the biogeographic distribution of epibenthic species' in UK Regional Seas are most abundant for the North Sea. Dyer et al. (1982; 1983), Frauenheim et al. (1989), Duineveld and van Noort (1990), Jennings et al. (1999), Zuhlke et al. (2001), Callaway et al. (2002) and Reiss and Kroncke (2004) all reported differences between the northern and southern sections of the North Sea in terms of epibenthic community structure. Frauenheim et al. (1989) linked the observed differences in
distribution to the influence of different water masses while Duinevald and van Noort (1990), Jennings et al. (1999) and Callaway et al. (2002) found temperature to be the main factor influencing the spatial variation in epibenthic communities. Dyer et al. (1983) and Zuhlke et al. (2001) reported that the north-south differences in the community structure of epibenthic fauna occurred along the northern edge of Dogger Bank; the location of the 50 m depth contour. Duinevald and van Noort (1990), Zuhlke et al. (2001), Calloway et al. (2002) and Reiss and Kroncke (2004) also describe a distinction between coastal and offshore epibenthic faunal communities in the southern region of the North Sea.

The epibenthos of the Irish Sea and Celtic Sea are not as well sampled at those of the North Sea. Rees and Walker (1991) and Hensley (1996) reported on epibenthic biodiversity in the north of the Irish Sea, while Hartley (1979) and Mackie et al. (1995) have described patterns of distribution in the southern Irish Sea and Celtic Sea. Mackie et al. (1995) described species rich assemblages in offshore areas of gravel and offshore areas of medium sand with distinctive *Venus verrocosa* communities interspersed among areas of hard ground.

In the English Channel, Holme's (1961; 1966) surveys are the only studies that have sampled epibenthic fauna across the entire region. As with the studies conducted in the North Sea (e.g. Jennings et al. 1999), Holme (1961; 1966) found that the biogeographical differences between the epibenthic communities of the English Channel could be related to temperature variation. Holme (1961; 1966) additionally reported an east-west faunal boundary in the central region of the English Channel. Cabioch's (1961; 1968) detailed surveys of the French side of the English Channel highlighted the influence of tidal current velocity (e.g. bed-stress) on the distribution of the epibenthos. Bed-stress, defined in terms of the tidal velocity at 1 m above the seabed, has also been indicated in several smaller-scale studies (e.g. Warwick and Uncles 1980) as being an influential factor in determining the distribution of benthic fauna. Ellis and Rogers (2000) focused on the distribution of echinoderm species. They identified an east-west faunal boundary and a north-south faunal boundary in the English Channel with the east-west faunal boundary being consist with that described by Holme (1961; 1966). Freeman and Rogers (2003) also reported on epibenthic species distributions in the eastern basin of the English Channel. They highlighted substratum type, sea-surface temperature (SST), depth and tidal current velocity related measures (e.g. bed-stress) as being key to the distribution of
epibenthic fauna. However, Freeman and Rogers (2003) also stated that no single environmental factor could adequately describe epibenthic distribution patterns.

Rees et al. (1999) have conducted the most extensive survey to date, in terms of area covered: they collected samples in the coastal regions of England and Wales and also in the North Sea. Rees et al. (1999) concluded that substratum type was the main physical structuring force behind the biogeographic distribution of epibenthic fauna in their survey. However, they also specified that correlations between epibenthic distribution patterns and patterns of variability in coastal influences (e.g. proximity to estuaries), depth, tidal current velocity and SST could be detected.

Additionally, primary productivity and chlorophyll-a (Chl-a) concentrations in sediment are thought to influence epibenthic communities (Creutzberg 1985; Basford et al. 1989; Hamerlynck and Mees 1991).

1.1.3 Linking environmental conditions to the distribution of epibenthic fauna

Macro-scale heterogeneity in biogeographic species distributions may be influenced by heterogeneity in environmental conditions. The distinctive pattern of abundance and distribution displayed by a particular species is a reflection of that species' requirements for environmental conditions (Hutchinson 1957; Brown 1995; Levin 1999). Patterns observed in the heterogeneity of environmental conditions could potentially facilitate an understanding of biogeographic patterns of epibenthic species' distributions. However, this depends on the strength of the association between species and environment. Patterns observed in the distribution of epibenthic mega-fauna will also undoubtedly be influenced by factors other than variation in environmental conditions e.g. population dynamics (Gaston and Blackburn 2000). Moreover, the existence of species-based macro-ecological pattern in the marine environment has been successfully demonstrated by Foggo et al. (2003) in their work on British estuarine macro-invertebrates.

Considering the pressing need to adaptively manage (develop management practices that respond to advances in ecological monitoring) the UK marine ecosystem for a whole ecosystem perspective, current knowledge regarding the distribution of
epibenthic species at a Regional Seas scale is woefully inadequate. Macro-scale studies of epibenthic species distributions are patchily distributed both temporally (throughout the last 50 years) and spatially (in terms of study locations around the British Isles). The variety of types of sampling method used and the time scale over which the epibenthic surveys of the UK shelf-seas have been conducted (almost 50 years from Holme’s surveys of the English Channel to the most recent studies of that region) constrains any kind of synthesis of the collected data (Rees 1996; Rees et al. 1999). Even less is known about how the distributions of epibenthic species vary in time. Long-term studies (e.g. Clarke and Frid 2001) are more prevalent than investigations into intra-annual variation (e.g. Reiss and Kroncke 2004) and although long-term studies are important from a monitoring perspective, information regarding intra-annual variation is also essential for establishing natural levels of variability within and between ecosystems (Hardman-Mountford et al. 2005). Macro-scale spatial studies of epibenthic species distributions that also incorporate temporal variation are logistically almost impossible.

The subtidal environment can not be easily accessed by humans: we require specialist equipment in order to collect benthic samples and these samples essentially amount to a collection of brief snapshots of ecological structure (Solan et al. 2003). Any perception of structure or pattern in the distribution of the epibenthos is thus totally dependent on the sampling method used. This limitation was elegantly described by Petersen (1913):

“A dredging ship may be compared with an air-ship towing a dredge over Copenhagen, catching a policeman in one street and a perambulator in another; and from these it draws conclusions as to the whole population of the town.”

The disparate nature of existing information on the biogeographic distribution of epibenthic fauna in UK regional shelf seas and the logistical constraints of conducting a systematic sampling programme at the regional seas scale limits investigation of species-based macro-ecological pattern. However, a good understanding of spatial and temporal variation in the environmental conditions that influence epibenthic species distributions could potentially act as a surrogate.
Exactly which environmental conditions influence the distribution of epibenthic species in UK shelf-seas is not entirely clear. The approaches adopted in existing studies (e.g. Rees et al. 1999), to relate biogeographic patterns of epibenthic species distributions to environmental conditions, have been developed from traditional small-scale studies where the focus is single point data (Hare 1996; Raffaelli et al. 2003). Single point data, when used to examine environmental variability over large spatial scales, may be misleading and analyses that explicitly identify the larger scale patterns of variability are essential. None of the existing studies of epibenthic fauna adequately address patterns of spatial and temporal heterogeneity in environmental conditions at the scale at which the study was conducted i.e. the Regional Seas scale.

### 1.1.4 Water column structure and satellite remote-sensing

All of the environmental factors that have been identified by existing studies as influencing the biogeographic distribution of epibenthic fauna in UK shelf-seas (SST, bed-stress, tidal velocity, substratum type, depth and primary productivity), are linked to the dynamics of water column structure. Shelf-sea water column structure at the scale of UK Regional Seas is determined by the balance between surface-heat flux and wind and tide induced mixing (Simpson and Hunter 1974; Pingree et al. 1975a; Simpson et al. 1977; Pingree and Griffiths 1978; Pingree 1980; Rippeth et al. 2005). Variations within this balance result in most UK shelf-seas either remaining well-mixed throughout the year, or undergoing seasonal stratification (Pingree and Griffiths 1978). Seasonally stratified regions endure a much smaller annual range in SST than well-mixed regions. Water depth is also an important factor in the water column structure model (Simpson and Hunter 1974) as is tidal velocity, which is directly related to tidal mixing. Moreover, tidal velocity is proportional to bed-stress (Pingree and Maddock 1977; Pingree 1980; Pingree et al. 1984) and bed-stress is crucial to the distribution of seabed sediments, hence affecting patterns of substratum type (Stride 1963; 1965; 1973; Pingree and Maddock 1977; Hamilton 1979). Bed-stress also has implications in terms of food availability for benthic organisms (Wildish 1977). Additionally, the physical variation in water column structure affects primary productivity. Seasonally stratified regions are characterized by peaks in productivity with the spring and autumn bloom events, whereas productivity in well-mixed regions tends to remain at a higher level
throughout the year (Pingree *et al.* 1975b; Pingree *et al.* 1976; Holligan and Harbour 1977; Pingree 1978; Holligan 1981; Spooner 2001). A detailed review of this relationship between the environmental factors associated with the biogeographic distribution of epibenthic fauna and the established model of water column structure in shelf-seas can be found in section 1.5 of this chapter.

Pattern in the vertical structure of the water column can be detected from horizontal patterns at the sea-surface (Platt and Sathyendranath 1999). Satellite remote-sensing of surface-ocean properties has been frequently and successfully used to detect patterns of spatial and temporal heterogeneity in water column structure and associated patterns of productivity (e.g. Paden *et al.* 1991; Fang and Hsieh 1993; Hernandez-Guerra and Nykjaer 1997; Longhurst 1998; Tseng *et al.* 2000; Yoder *et al.* 2002). Remote-sensing data have the potential to provide extensive spatial and temporal coverage of sea-surface properties and is easily and freely available (Kerr and Ostrovsky 2003; Turner *et al.* 2003).

The boundaries between regions with different water column structures are often subtle gradients that vary in space and time. The spatial and temporal resolution and cohesion of remotely-sensed data (e.g. uninterrupted coverage of a whole regional sea area (1000's of km$^2$) at a spatial resolution of 1 km$^2$ and with a temporal resolution of one week) enables the detection of subtle gradients in the spatial and temporal heterogeneity of physical and biological sea-surface properties. Multivariate variance partitioning methods, such as Principal Components Analysis (PCA), have been widely applied to remotely-sensed data in order to detect these spatial and temporal gradients (Fang and Hsieh 1993; Gallaudet and Simpson 1994; Hare 1996; Otero and Siegel 2004; Palacios 2004). Variance partitioning methods have also recently been implemented as a means of identifying and classifying ecological regions or provinces in the oceans from remotely-sensed data. Hardman-Mountford (2000) and Hardman-Mountford and McGlade (2002) identified persistent co-varying ecological regions in the Gulf of Guinea Large Marine Ecosystem (LME) using remotely-sensed SST data. Additionally, Hardman-Mountford *et al.* (In Press) used remotely-sensed measurements of chlorophyll-$a$ (Chl-$a$) to address the validity of identifying ecological provinces in the global ocean. This method of ecological sub-province identification successfully incorporates macro-scale spatial and temporal heterogeneity of environmental conditions.
1.1.5 Ecological pattern as an emergent property of a complex adaptive system

Ecological pattern was defined by Hutchinson (1953) as:

"The structure which results from the distributions of organisms in, or from their interactions with their environment".

Hutchinson (1953) also stated that the concept of ecological pattern is essentially a steady state, rather than an equilibrium phenomenon. The definition of a "steady state" is borrowed from Physics and refers to the condition of a system when some or all of the quantities describing it are independent of time but not necessarily in thermodynamic or chemical equilibrium.

Hutchinson's notion of ecological pattern as a steady state phenomenon is fundamental to an understanding of ecosystems as Complex Adaptive Systems (CAS). CAS are characterised by large numbers of diverse components. These components interact with each other in a non-linear manner (frequently involving response delays and feedback loops) and become hierarchically organized into arrangements which are determined and reinforced by flows and interactions amongst the components (Simon 1962; Levin 1992; Holland 1995; Levin 1999; Levin 2002; Wu and Marceau 2002). Hence CAS are thermodynamically open and exchange mass and or energy with their environment.

Structure, pattern and function are emergent properties of the interactions between the many diverse components of a CAS (Dooley 1997). Therefore, ecological pattern is an emergent property of an ecosystem (Levin 1999; Levin 2002). The definition of ecological pattern as a steady state phenomenon implies that the variables that specify the relationship between the components of the pattern are not fixed, but that the integrity of the pattern endures. Platt and Sathyendranath (1999) liken the concept of ecological pattern as a steady state phenomenon to the seasonal manifestations of a river:

"... a river is the same river, even though its manifestation during spring floods is so different from that at the end of the summer drought ..."

Any description of pattern must also be at a scale that will determine the appropriate level of simplification and aggregation for the specified problem or phenomenon of interest (Levin 1992; Goldenfeld and Kadanoff 1999). If a scale of description is too large for the system
concerned then critical internal heterogeneity may be averaged out. A scale of description that is
too small may over complicate any identification of pattern by including small-scale
idiosyncratic variability that is a product of processes acting at different spatial scales (Brown
1995). In order to understand human behaviour, we would not build a model describing what
every single cell in the body is doing. The same is true for an ecosystem: we do not expect to
understand ecosystem dynamics by accounting for the interactions of every single species
(Levin 1992). The incorporation of too many processes and parameters may also obscure the
desired qualitative understanding (Goldenfeld and Kadanoff 1999): patterns that emerge from
complex systems do not always require complex explanations (Levin 1999).

A complex adaptive systems approach that incorporates Hutchinson’s (1953) definition of
pattern as a steady state phenomenon was used by Hardman-Mountford (2000), Hardman-
Mountford and McGlade (2002) in their delineation of ecological provinces in the Gulf of
Guinea LME and by Hardman-Mountford et al. (In Press) in their description of ecological
provinces in the global ocean. The studies listed above employed remotely-sensed surface-
ocean data in their investigation and demarcation of steady-state pattern in surface-ocean
properties. The work of Hardman-Mountford and colleagues (2000; 2002; In Press) is only one
step towards a top-down approach to describing the hierarchical structure of marine ecosystems
that is necessary for a holistic systems-based understanding of these ecosystems (Gaston and
Blackburn 1999). However, the usefulness of this type of approach has been demonstrated in
terrestrial systems by Wu and David (2002) in their hierarchical decomposition of the urban
landscape of Phoenix, Arizona.
1.2 Research aims and thesis outline

1.2.1 Research aims

There are two primary aims to this thesis. The first is to investigate the potential application of remotely-sensed surface-ocean data to the characterization of ecological provinces (defined as persistent, spatially co-varying regions) based on the patterns of spatial and temporal heterogeneity of shelf-sea water column structure and associated patterns of productivity. The second aim is to investigate the possibility of relating the water column ecological provinces to biogeographic distribution patterns of epibenthic fauna in a UK Regional Sea.

The English Channel was selected as the focus of the study as this region has been the subject of extensive oceanographic study for over 100 years (Southward et al. 2005).

In order to accomplish the aims of this thesis the following steps were undertaken:

i. Investigate the suitability of remotely-sensed surface-ocean data as a means of describing the spatial and temporal heterogeneity of water column physical structure and associated patterns of productivity in the English Channel.

ii. Investigate the application of remote-sensing data, via a holistic, systems type approach, to the identification of persistent ecological regions (steady state patterns) within the spatial and temporal heterogeneity of physical water column structure and associated patterns of productivity of the English Channel.

iii. Investigate the relationship between the remotely-sensed ecological regions detected from the remote-sensing data and the seabed environmental variables that have been linked to the biogeographic distribution of epibenthic fauna in existing studies.

iv. Compare the biogeographic patterns of distribution of epibenthic megafauna with the structure of the remotely-sensed ecological regions.
1.2.2 Thesis outline

As now should be evident, Chapter 1 of this thesis outlines the rationale and the aims of the study and gives a brief description of the study area. The section on Remotely-Sensed Data describes the basic principles of remote-sensing and details the remotely-sensed variables that were used in this study. The following section, Tidal Currents: Linking the Sea-Surface and the Seabed, explains the physics of the link between the remotely-sensed sea-surface variables and the environmental variables that have been identified as influencing the macro-scale distribution of epibenthic fauna in UK Regional Seas.

In Chapter 2, the patterns of spatial and temporal variability in physical water column structure and associated patterns of productivity that could be detected from the selected remotely-sensed variables were compared with documented patterns of water column variability in the study region. Although water column structure in the English Channel has been well described, it had not been determined solely from remotely-sensed data prior to this study. Before any form of variance partitioning method could be applied to the remote-sensing data it was necessary to determine if the data included the appropriate level of spatial and temporal variability to describe the phenomena of interest.

Chapter 3 describes the application of variance partitioning methods, coupled with a complex systems type approach, to the identification of persistent ecological regions in the English Channel. This study represents the first attempt to apply this method to a shelf-sea region.

In Chapter 4 the structure of the ecological regions, identified in the previous chapter, were related to the environmental variables that have been indicated in the literature as influencing the biogeographic distribution patterns of epibenthic fauna in UK shelf-seas.

Chapter 5 tests the validity of the ecological province structure at a reduced spatial scale and compares that structure with the distribution of epibenthic megafauna observed in a survey of the western English Channel during 2004.

Chapter 6 reviews the conclusions made in each chapter and relates them to the primary aims of the study. Potential applications of the thesis are discussed as are possible areas for future work.
1.3 The study area

The English Channel covers an area of approximately 75,000 km$^2$ and is a typically funnel shaped tidal shelf-sea (Reynaud et al. 2003) (figure 1.1) and is situated close to the margins of the north-west European Continental Shelf. The distance, due south-west, from Lands End to the shelf-break is approximately half the distance from the Western Approaches to the Dover Straits (Pingree 1980; Larsonneur et al. 1982). Water depth decreases from 200 m at the shelf-break to $\approx 110$ m in the Western Approaches and once within the confines of the English Channel, decreases in a west to east direction to the Dover Straits ($< 40$ m) and towards both the English and French coasts. The shallow eastern basin of English Channel is geologically young compared to the markedly deeper western sector (Larsonneur et al. 1982; Waller and Long 2003).

The English Channel has been the subject of extensive oceanographic study for over 100 years (Southward 1995; Southward et al. 2005), partly due to the situation of the UK's oldest marine laboratory, the Marine Biological Association, in Plymouth. Of particular note is the prolific work of Pingree and co-workers (Pingree et al. 1975a; Pingree and Maddock 1977; Pingree and Griffiths 1978; Pingree and Maddock 1978; Pingree 1980; Pingree et al. 1984) and influential papers by Maddock and Swann (1977), Southward and Butler (1972). These are complemented by recent work by Spooner (2001). The net surface heat flux (Pingree 1980; Spooner 2001) and tidal mixing (principally the $M_2$ semi-diurnal lunar tide) (Pingree and Maddock 1977; 1978; Pingree 1980; Pingree et al. 1984) are identified as the key mechanisms responsible for the physical structure of the water column of the English Channel.

Patterns of productivity in the English Channel have also received considerable attention (Pingree et al. 1975b; Pingree et al. 1976; Holligan and Harbour 1977; Holligan 1981). The seasonal patterns of phytoplankton distribution have been identified in relation to the physical structure of the water column, with particular reference to water column stability (Holligan and Harbour 1977). Therefore both the physical oceanographic dynamics and patterns of primary productivity of the English Channel are relatively well documented and understood.

Studies of the distribution and diversity of benthic fauna in the English Channel also have a long history: from the work of Allen (1899) and Ford (1923) in early part of the 20th century, to Holme (1953; 1961; 1966; 1983; 1984; 1985) and Cabioch (1961; 1968) and more recent
studies such as Sanvincente-Anorve et al (1996), Vallet and Dauvin (1998), Rees et al (1999), Ellis and Rogers (2000), Newell et al (2001) and Freeman and Rogers (2003). Most of these studies are limited to particular areas of the English Channel, for example Plymouth (e.g. Ford 1923), Roscoff (e.g. Cabioch 1961) or the eastern basin (e.g. Ellis and Rogers 2000). Holme's surveys of the 1960's (1961; 1966) are the only studies to sample benthic fauna across the entire English Channel.
Figure 1.1: Map of the English Channel: the area in which this study is focused.
1.4 Remotely-sensed data

1.4.1 A brief history

Remote sensing can be defined as the collection and interpretation of information about a distant target with which the sensor has no contact (Turner et al. 2003). This description encompasses a wide range of data types, including variations in acoustic wave distributions, electromagnetic energy distributions or force distributions. For the purpose of this study "remote sensing" will refer to the detection of electromagnetic (EM) energy by sensors mounted on satellites.

The concept of observing earth from space received its first impetus as early as 1890 when Ludwig Rahrmann used a rocket propelled camera system to obtain a birds eye photographic view of the Earth (American Society of Photogrammetry, 1983). Advances in earth observation over the last century have been by-products of the development of meteorological satellites, such as the US National Aeronautics and Space Administration’s (NASA) Television and Infrared Observation Satellite (TIROS-1), the use of which proved that the Earth’s weather systems could be observed from space (Lillesand and Kiefer 1987). In 1966 the US Environmental Science Services Administration (ESSA) and NASA began work on an experimental system designed to test the feasibility of collecting remotely-sensed data from unmanned satellites. The first of these Earth Resources Technology Satellites (ERTS), later renamed LANDSAT, was launched in 1972 (Lillesand and Kiefer 1987). The range of sensors and satellites employed in collecting and recording remotely-sensed data has increased significantly from the time when the first of the LANDSAT satellites was launched, more than 30 years ago. The high spatial and temporal resolution provided by remotely-sensed data makes those data applicable to a whole range of disciplines from meteorology and geology (NOAA 1985), to defence (Brandli 1978) and conservation (Kerr and Ostrovsky 2003; Turner et al. 2003). Lillesand and Kiefer (1987) provide a detailed review of the history of remote-sensing.

There are two primary types of sensor employed in remote-sensing: passive sensors and active sensors. Passive sensors record a radiation signal emitted directly from the earth. Active sensors send a pulse of radiation to the earth, which is then altered and returned or bounced back to the sensor. Both passive and active sensors record the intensity of a signal in a “band”
or “channel” (a wavelength interval of specified width within the EM spectrum) (Turner et al. 2003). Remotely-sensed data are usually arranged in a matrix of pixels, the size of which is determined by the spatial resolution of the sensor. The spatial resolution is the area of the Earth’s surface that is represented by each pixel; the finer the resolution, the smaller the area. Therefore, remotely-sensed data with a spatial resolution of 4km, would refer to data in a matrix of 4km x 4km pixels. Temporal resolution (also known as “revisit time”) indicates the time period between which the satellite makes repeat passes over the object or area that is being sensed. Greater temporal resolution is usually achieved at the sacrifice of spatial resolution (Turner et al. 2003). In order for a satellite to pass over the same place at an increased frequency, it must have an increased field of view and thus loses some of its ability to detect objects at a finer scale. Optical sensors that record information in the visible and infrared range of the EM spectrum are cloud limited. Temporal resolution becomes important when attempting to obtain clear information from areas that are repeatedly veiled by cloud or other atmospheric phenomena (Turner et al. 2003). The specific wavelength intervals of the electromagnetic spectrum that a sensor can detect are known as its spectral resolution. The way in which different objects reflect and emit electromagnetic radiation is termed their spectral signature. The greater the number of spectral bands present in the spectral signature of an object, the more unique features of the object that can be identified.

1.4.2 Remotely-sensed oceanographic data

Remotely-sensed oceanographic data have been available since the mid 1960s (Sherman 1985) and include data recorded by both passive and active sensors. Primary examples of parameters measured by passive sensors are sea-surface temperature (SST) from infrared radiometry (Advanced Very High Resolution Radiometer (AVHRR), Along Track Scanning Radiometer (ATSR)), ocean colour and sea ice from visible radiometry (Coastal Zone Colour Scanner (CZCS), Sea viewing Wide Field-of-view Sensor (SeaWiFS)) and brightness emissivity derived sea ice and global SST from passive microwave sensors (Scanning Multichannel Microwave Radiometer (SMMR), Special Sensor Microwave Imager (SSM/I)). Parameters measured by active sensors include: sea surface height or topography from radar altimeter (GEOSAT, Earth Resources Satellite-1 Radar Altimeter (ERS-1 RA), NASA’s ocean Topography Experiment (TOPEX/Poseidon)), sea surface roughness and winds from synthetic aperture radar (Earth Resources Satellite-1 Synthentic Aperture Radar (ERS-1 SAR), Earth Resources Satellite-2 Synthentic Aperture Radar (ERS-2 SAR)) and sea state
from scatterometers (Earth Resources Satellite-1 Scatterometer (ERS-1 SCATT), Earth Resources Satellite-2 Scatterometer (ERS-2 SCATT), NASA’s Scatterometer (NSCAT)).

1.4.3 Variables used in this study

1.4.3.i Sea surface temperature (SST)

The physical properties of sea water relevant to fluid dynamics are functions of pressure, temperature and salinity (Pond and Pickard 1983). The most important feature in dynamical oceanography is the quantitative manner in which sea water density varies with changes in temperature, salinity and pressure (Pond and Pickard 1983). Density increases as temperature decreases and as pressure and salinity increase. Temperature in the form of sea surface temperature (SST) is the only one of these variables directly available as remotely-sensed data and has been successfully used as a means of identifying spatial variability in water masses in several studies (Paden et al. 1991; Fang and Hsieh 1993; Gallaudet and Simpson 1994; Hare 1996; Hernandez-Guerra and Nykjaer 1997; Hardman-Mountford and McGlade 2002). Distinctive fluctuations in external physical forcing mechanisms, such as solar irradiation, air-sea heat flux and wind and tidal mixing act with the basic principles of fluid dynamics to produce variation in shelf sea SST (Spooner 2001).

SST data from AVHRR sensors were used for this study. The AVHRR sensors are situated on the NOAA polar orbiting satellites and have a five channel scanning radiometer with a spatial resolution of 1.1 km (known as local area coverage (LAC)). Global area coverage (GAC), a lower resolution product (4 km) is created by on-board averaging of data (DSRS). The sensors are receptive in the visible, near-infrared and infrared ‘window’ regions of the EM spectrum, are accurate to within ± 0.6°C (Keogh et al. 1999), orbit the earth every 102 minutes and have a swath width in excess of 2600 km (Rao et al. 1990).

1.4.3.ii Ocean colour

The same suite of external forcing mechanisms that influence temperature distribution, also affects the spatial and temporal distribution of dissolved and suspended matter in mid-latitude shelf seas. Remote-sensing of suspended matter involves analysis of the variation in magnitude and spectral quality of the water leaving radiation (IOCCG 2000). A combination of this analysis and a sound understanding of the optical properties of the medium, allow quantitative information on the type of substances present in the water and their
concentrations to be extracted (IOCCG 2000). Four main components of sea water are recognised from a practical, optical perspective: pure water, phytoplankton, inorganic suspended particulate matter (SPM) and "yellow substances" or coloured, dissolved organic matter (CDOM) (Hooker et al. 1992). The components listed above are measured by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) sensor. SeaWiFS is part of NASA's "Mission to Planet Earth" and is located aboard the OrbView-2 satellite, which was launched by the Orbital Sciences Corporation in 1997 (Lavender and Groom 1999). NASA have financed the development and acquired the rights to use SeaWiFS data for academic research (Lavender and Groom 1999) and as such, all investigators wishing to use SeaWiFS imagery must register with NASA. SeaWiFS has a near-polar sun-synchronous (maintains a constant angle with respect to the sun) orbit and is able to tilt to avoid sunglint on the sea (NEODC). Full spatial resolution (1 km) local area coverage (LAC) is transmitted continuously and can be acquired by any licensed receiving station around the world. Data at lower spatial resolution (4 km) global area coverage (GAC) are also transmitted. SeaWiFS receives information from eight, 20 nm wide, spectral bands: six of these are in the visible range of the EM spectrum and two are in the near-infrared range.

The physical structure of water masses has been shown to be reflected in biological pattern: extent and development of the thermocline, areas of mixing and frontal systems all have important consequences for the temporal and spatial distribution of phytoplankton (Pingree et al. 1975b; Pingree et al. 1976; Rippeth 2005; Rippeth et al. 2005). Phytoplankton are pervasive in the euphotic zone of temperate shelf-seas and form the base of the aquatic food-web. Concentration of Chlorophyll-a (Chl-a), the main phytoplankton photosynthetic pigment, is often utilised as a proxy for phytoplankton biomass (IOCCG 2000). Increases in biomass are due to gross primary productivity and losses of biomass are primarily the product of respiration, mortality and zooplankton grazing. Gross primary productivity can be described as the total quantity of carbon or energy fixed during photosynthesis. Photosynthesis also requires the presence of inorganic nutrients, many of which are available as aqueous compounds in sea water. Community structure of the phytoplankton and the physiological state of the cells (e.g. nutrient status and photoadaptation) can greatly affect the pigment composition of a water sample (IOCCG 2000).

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2 Sunglint: The portion of shortwave radiation illuminating a water surface that is reflected back to space. This reflection appears in visible imagery as a bright area on an otherwise dark water area when winds are light and the water surface is smooth. The rougher the water, the more diffuse the glint pattern.
Measurements of Chl-\(a\) concentration from ocean colour sensors have been used in order to determine patterns of spatial and temporal heterogeneity in the oceans, both in conjunction with SST data (Baldacci et al. 2001; Yoder et al. 2002; Palacios 2004) and with other ocean colour products (Otero and Siegel 2004). The majority of ocean colour research has been focused in oceanic Case I (IOCCG 2000) waters where the optical properties are dominated by phytoplankton pigments (Morel and Prieur 1977) and comparatively little work has been carried out in Case II waters, where CDOM and SPM play a significant role in the optical properties (Lavender and Groom 1999; IOCCG 2000; Binding et al. 2003). Case I waters (typically the open ocean) exhibit strong absorption by algal pigments in the blue/green range of the EM spectrum (maximum absorption at \(\lambda = 445\) nm) and weak absorption in the green/yellow range (\(\lambda = 550-580\) nm) (IOCCG 1998). Changes in the ratio of reflectance of blue/green light are interpreted as changes in Chl-\(a\) concentration (IOCCG 2000). The SeaWiFS algorithm for the retrieval of Chl-\(a\) concentration uses ratios of reflectance from the blue/green and green/yellow wavelengths (O'Reilly et al. 1998), as spectral ratios are less likely to be affected by error than absolute values (IOCCG 1998). However, wavelengths that are used as signal carriers for a given variable (e.g. Chl-\(a\)) can become contaminated by the signal of another variable (e.g. SPM or CDOM). This is the situation in Case II waters (typically coastal and shelf seas), which contain large quantities of yellow substances and SPM. Yellow substances have a significant influence on the reflectance ratio of blue/green light, making it very difficult to distinguish them from phytoplankton pigments (IOCCG 1998; 2000). Inorganic nutrient (primarily nitrogen, phosphate and silicate) and light availability are the most significant limiting factors to primary production in shelf seas (Sverdrup 1953; Raymont 1963; Pingree et al. 1977; Walsh 1988). Terrestrial run-off is an important source of nutrients, freshwater and sediment for coastal oceans (Otero and Siegel 2004), but high levels of SPM in shelf seas may also limit productivity owing to a reduction in photic depth (Binding et al. 2003). Case II waters can be interpreted by the SeaWiFS two-wavelength, Chla-\(a\) retrieval algorithm, as Case I waters with high Chl-\(a\) concentrations (IOCCG 1998). Therefore great care must be taken in interpreting Chl-\(a\) ocean colour images from shelf sea waters.

For the reasons mentioned above, measures of reflectance by suspended sediments have been used in conjunction with ocean colour Chl-\(a\) data (Yoder et al. 2002; Otero and Siegel 2004) or incorporated in region-specific algorithms (Baldacci et al. 2001; Binding et al. 2003). Comparison of the remote sensing reflectance (sr\(^{-1}\)) at different wavelengths shows a distinct peak at approximately 555 nm and a lesser peak at approximately 670 nm, for Case II waters (IOCCG 2000). Otero and Siegel's (2004) study of the Santa Barbara Channel, US, found that
Water leaving radiance at 555 nm ($L_{W\lambda}(555)$) from the SeaWiFS sensor was a good proxy for suspended sediments, whilst Binding et al. (2003) found using water–leaving radiance at 665 nm ($L_{W\lambda}(665)$) to be most effective in an algorithm for retrieval of estimates of SPM concentration, from the Irish Sea.

SeaWiFS ocean colour data on Chl-\textit{a} concentration and water-leaving radiance at 555 nm ($L_{W\lambda}(555)$) and 670 nm ($L_{W\lambda}(670)$) were used in conjunction with AVHRR SST data, for the purpose of this study. The SST, Chl-\textit{a}, $L_{W\lambda}(555)$ and $L_{W\lambda}(670)$ data will be collectively referred to as the "remotely-sensed variables". Data were available from both SeaWiFS ocean colour products and AVHRR SST covering the time period from 1997 to 2003. A temporal dimension is essential for assessing the dynamic structure of water masses as many key processes have strong intra-annual (seasonal) (Pingree 1980) and inter-annual variability (Southward et al. 1975). Longer phase patterns such as the North Atlantic Oscillation (NAO) (Garcia-Soto et al. 2002) and sun-spot cycles (Southward et al. 1975) can also affect water mass structure but act outside of the time frame of this study.

1.5 Tidal currents: linking the sea-surface and the seabed

Water column structure in shelf seas is determined by the balance between surface heat flux and tidal-mixing (Simpson and Hunter 1974; Pingree and Maddock 1977; Pingree and Griffiths 1978; Pingree 1980; Simpson et al. 1996; Rippeth et al. 2005). The surface-ocean dynamics that are a result of these physical factors can be observed from remotely-sensed images of the sea-surface. The physical principles of the link between water column structure, bathymetry, bed-stress and seabed sediment distribution, in the context of the English Channel, are described below.

1.5.1 Tidal currents

Tidal currents are the oscillating horizontal movement of sea water associated with the vertical rise and fall of the tide. They are caused predominantly by astronomical forces: the simultaneous action of the gravitational forces of the Earth, Sun and
Moon and the revolution about one another of the Earth and Moon and the Earth and Sun. The Earth/Moon pair exert the greatest effect on the tides as the shorter distance from the Moon to Earth outweighs the greater mass of the Sun (Pond and Pickard 1983). The principle lunar semi-diurnal tidal constituent \( (M_2) \), first described for the English Channel by Doodson and Corkan (1932), is a product of the gravitational forces and rotation of the Earth/Moon pair. The \( M_2 \) tide is the most important tidal constituent in the English Channel (Pingree and Maddock 1977; Pingree and Griffiths 1978; Pingree 1980; Sinha and Pingree 1997): it has an amplitude that is approximately three times that of the principal solar semi-diurnal tidal constituent \( (S_2) \) (Pingree 1980). Furthermore, approximately 90% of the kinetic energy of tidal currents in the Celtic Sea and western English Channel is contained in the semi-diurnal frequencies and 75% of this total is the result of the \( M_2 \) tidal component (Pingree 1980).

### 1.5.2 Tidal velocity

When investigating the effect of tidal mixing on hydrographic properties, it is the magnitude of the horizontal oscillatory movement, the tidal velocity, which is important. Tidal velocity can be described by \( u \) and \( v \) components which correspond to the velocity of the tidal current in east/west and north/south directions respectively. The total horizontal tidal velocity \( (\text{cm s}^{-1}) \) is equal to the magnitude of the vector \( U \) which can be calculated using equation 1.1:

\[
\text{Equation 1.1: } |U| = \sqrt{u^2 + v^2}
\]

Where \( u \) = velocity of the tidal current in east/west direction and \( v \) = velocity of the tidal current in north/south directions respectively. The magnitude of horizontal tidal velocity can vary considerably over hundreds, or even tens, of metres (Pond and Pickard 1983). Tidal velocity in the English Channel and Celtic Sea ranges from weak \( (0.3 \text{ ms}^{-1}) \) in open water (e.g. Nymphe Bank in the Celtic Sea) to very strong \( (4.6 \text{ ms}^{-1}) \) in the central English Channel (e.g. the “Narrows” between the Isle of Wight and Cherbourg). As water depth decreases from the shelf edge to the coast, the amplitude and velocity of the tidal wave progressively increases (Mann and Lazier 1996). Tidal velocity also increases as the width
between coastal boundaries decreases: a mechanism that conserves the volume of water transported per second through any given section of a channel (Pingree and Maddock 1977).

1.5.3 *Vertical structure of tidal currents within the water column*

Variation in the velocity of tidal currents with depth is also essential in the investigation of hydrographic properties. The movement of tidal currents across the seabed produces a frictional bed-stress, which decreases the velocity of the tidal current. In well-mixed water at depths of about 100 m, the magnitude of the tidal velocity one metre above the seabed is approximately half that of the sea-surface and on average, the tidal velocity at the sea-surface is 1.15 times greater than the mean value for the water column (Cartwright 1961).

The decreased tidal velocity at the sea bed, owing to the frictional effect of bed-stress, results in tidal currents at the sea bed reaching their maximum velocity in the tidal cycle prior to sea-surface tidal currents (Proudman 1953). The time difference between reaching maximum tidal velocity at the sea bed and at the sea-surface can be as much as 20 min (Pingree and Griffith 1974). However, the tidal velocity has been shown to increase logarithmically with height above the sea bed (Charnock 1959; Dyer 1971), so sea-surface tidal velocity can be used to give an indication of seabed tidal velocity and also bed-stress with the use of an appropriate drag coefficient (Pingree and Maddock 1977).

Turbulent eddies formed by tidal current shear in the surface layer also transmit motion from the surface to deeper water. The magnitude of eddy viscosity (parcels of water are exchanged, rather than molecules, between parts of a moving fluid, which causes much greater internal friction) and the extent to which the turbulence in the surface layer is vertically diffused are dependent on the gradient of seawater density in relation to depth (Simpson *et al.* 1996).

1.5.4 *Bed-stress*

Bed-stress ($T_B$ (dynes cm$^{-2}$)) is the mean change in momentum of the tidal current at the seabed, during a tidal cycle. The seabed provides a frictional resistive force to the flow of the tidal current: tidal velocity is reduced and momentum is transferred. Bed-stress is defined in terms of the tidal velocity at one metre above the seabed (Pingree 1980) as follows:
Equation 1.2: $T_B = \rho C_D |U|^2$

where $\rho$ is the density of sea water, $C_D$ is the drag coefficient and $|U|$ is the magnitude of tidal velocity. The drag coefficient is the squared ratio of frictional velocity to tidal velocity. Pingree (1980) lists approximate mean values for $\rho (\approx 1.0365 \text{ g cm}^{-3})$ and $C_D (\approx 0.0025)$ for the Celtic Sea and the English Channel. The similarity between the spatial distribution of bed-stress and sea-surface tidal velocity in the English Channel (both estimated from a numerical model), has been examined by Pingree and Maddock (1977) and Pingree (1980). The relationship between bed-stress distributions and the erosion and deposition of seabed sediment in the English Channel, has also been observed by Pingree and Maddock (1977).

High values of bed-stress result in the erosion of sediments, therefore bedrock is associated with high bed stress values and sediments of fine granulometry (i.e. mud or sand) are linked to low bed stress values. A strong level of comparability is also evident between Hamilton’s (1979) map of sand transport paths (see also Stride 1973) over the seabed of the English Channel and Celtic Sea and Pingree and Maddock’s (1977) predicted spatial distribution of bed-stress. The regions of the English Channel that are indicated as “sand in transit over basal conglomerate” (Hamilton 1979) are those that experience the greatest values of bed-stress. The more stable areas of the English Channel bed-load (e.g. sediment not in transit) are those with low values of bed-stress.

1.5.5 Dissipation of tidal energy

Work (joules) is done against bed-stress as the tidal currents oscillate and a proportion of the total energy of tidal currents is dissipated. The total energy input from astronomical forces to global tidal energy is estimated at $5 \times 10^{12}$ Watts: between 44% and 56% of this energy is dissipated (mostly in shallow seas) by frictional stresses, i.e. bed-stress (Pond and Pickard 1983). Approximately 10% of the global dissipation of the $M_2$ tide occurs on the north-west European continental shelf (Pingree 1980) and approximately 1.2% of the total global input to tidal energy is dissipated within the English Channel (calculated from estimates of energy input by Pond and Pickard (1983) and dissipation by Pingree (1980)).
The scalar product of bed-stress and tidal velocity can be used as a measure of the rate of dissipation of tidal energy per square centimetre. Bed-stress is proportional to the square of the tidal velocity, therefore, the distribution of energy dissipation will be proportional to the tidal velocity cubed (Pingree 1980) (equation 1.3):

\[ E = U \cdot T_B = \rho \cdot C_D \cdot |U|^3 \]

where \( D \) refers to the rate of energy dissipation in ergs s\(^{-1}\), \( T_B \) is bed-stress, \( \rho \) is the density of sea water, \( C_D \) is the drag coefficient and \( |U| \) is the magnitude of tidal velocity.

The spatial distribution of \( D \) (mean value for the water column) also strongly resembles the spatial distribution of sea-surface tidal velocity (Pingree 1980). The majority of tidal energy in the English Channel is dissipated in the "Narrows" between the Isle of Wight and the Cherbourg Peninsula, where high values of sea-surface tidal velocity are also recorded (Pingree 1980).

1.5.6 Stratified or well-mixed water column?

The propensity of the water column to stabilise and stratify under the influence of the net surface heat flux can be measured by the ratio of production of potential energy required to maintain vertically well-mixed conditions to the rate of tidal energy dissipation (Pingree and Griffiths 1978). This ratio is proportional to the mass of the water column \( (\rho h) \) divided by the mean tidal energy dissipation rate (equation 1.3).

Simpson and Hunter (1974) have argued that the change from well-mixed to stratified conditions occurs at critical values of this parameter (equation 1.4):

\[ S = \log_{10} \left[ \frac{h}{C_D \cdot |U|^3} \right] \]

where \( S \) is the stratification parameter and \( h \) is the depth of the water column. The critical value at which the water column undergoes the transition from well-mixed to stratified conditions is \( S = 1.5 \) (cgs units). Simpson and Hunter's (1974) analysis of the stratification parameter in the Irish Sea has been extended to the Celtic Sea, English Channel and North Sea by Fearnhead (1975), Hughes (1976), Simpson (1976), Simpson et al. (1977) and Pingree and Griffiths (1978). The variables
necessary to calculate the stratification parameter can be easily obtained from hydrographic data or from numerical models (Pingree 1980) making it a convenient method for assessing the stratification potential of shelf seas. Pingree and Griffiths (1978) compared the predicted position of fronts (stratification parameter calculated from a numerical model of the $M_2$ tide) to the observed position of fronts (determined from infrared satellite images and field measurements of SST) on the north-west European continental shelf. Despite the simplifying assumptions of their numerical model (e.g. tidal velocity was assumed to be constant with depth), the predicted and observed position of fronts were in “remarkable agreement” (Pingree and Griffiths 1978).

The distribution of the stratification parameter in the English Channel also reflects the spatial variation of sea-surface tidal velocity (Pingree 1980). The structure of the water column affects the vertical diffusion of motion from turbulent surface eddies. In well-mixed conditions density varies little with depth: the water column is easily overturned by turbulent mixing and the motion of turbulent eddies at the sea-surface is readily transferred to water close to the seabed. Density increases sharply with depth in stratified conditions, which serves to dampen and suppress the transfer of turbulent motion from the sea-surface to the seabed.

1.5.7 Summary

The link between the vertical structure of the water column and distribution of seabed sediment is summarized in figure 1.2. Variation in water column structure and associated patterns of productivity, between well-mixed and stratified regions, has been detected using surface-ocean remotely-sensed SST and Chl-a data (Bisagni et al. 2001; Yoder et al. 2002). Simpson and Hunter’s (1974) Stratification Parameter ($S$), the ratio of water mass (product of depth and density) to energy dissipation, is a proven indicator of water column structure. Tidal energy is dissipated as tidal currents work against bed-stress. The rate of energy dissipation is proportional to bed-stress, which is also proportional to tidal velocity and bed-stress has been shown to have a direct effect on the distribution of seabed sediment. Therefore, the patterns of spatial variability in bed stress, water depth and substratum type in the English Channel should, in theory, relate to water column structure.
Water column structure in shelf seas is determined by the balance between surface heat flux and tidal mixing and can be observed from surface-ocean remotely-sensed properties.

Gravitational and rotational forces of sun, moon and earth create tidal currents.

Velocity \((U)\) of tidal currents in the horizontal plane has east/west \((u)\) and north/south \((v)\) components and can exhibit spatial variation on a scale of tens of metres.

\[ |U| = \sqrt{u^2 + v^2} \]

Tidal velocity also varies with depth \((h)\).

Tidal velocity close to the sea-bed is less than at the sea-surface owing to loss of momentum caused by bed-stress \((T_B)\). The relationship between \(h\) and \(U\) is generally logarithmic so \(U\) at the seabed can be predicted from surface values of \(U\).

Clear agreement between predicted \((S)\) and observed \((\text{infrared images of the surface-ocean})\) areas of well-mixed and stratified water.

Simpson and Hunter's Stratification Parameter \((S)\) uses a critical value \((S = 1.5)\) of the ratio of water mass to rate of tidal energy dissipation to determine where change from stratified to well-mixed conditions will occur.

\[ S = \log h / C_B |U|^3 \]

Work (joules) is done against bed-stress \((T_B)\) as the tidal currents flow over the sea-bed and a proportion of tidal energy is dissipated. Rate of dissipation of tidal energy \((D)\) is product of \(T_B\) and \(U\):

\[ D = U \cdot T_B = \rho C_B |U|^3 \]

Bed-stress \((T_B)\) is directly linked to the distribution of seabed sediments.

Bed-stress is the change in momentum of the tidal current at the seabed caused by friction.

\[ T_B = \rho C_B |U|^3 \]

Figure 1.2: Summary of the link between water column structure in shelf seas (which can be identified from remotely-sensed surface-ocean properties) and the seabed environmental conditions that have been linked to the biogeographic distribution of epibenthic fauna in existing studies of the English Channel.
CHAPTER 2

AN INVESTIGATION OF THE SUITABILITY OF REMOTELY-SENSED SURFACE-OCEAN DATA AS A MEANS OF DESCRIBING THE SPATIAL AND TEMPORAL HETEROGENEITY OF WATER COLUMN PHYSICAL STRUCTURE AND PATTERNS OF PRODUCTIVITY IN THE ENGLISH CHANNEL.

2.1 Introduction

The concept of finding an appropriate scale at which to investigate the emergent structure of complex systems has undergone considerable discussion in the ecological literature (e.g. Levin 1992). A similar problem has been addressed by Gallaudet and Simpson (1994) in the oceanographic literature: they defined two particular types of essential dimensionality in oceanographic data: “geometric dimensionality” which refers to the temporal and spatial scale of the data and “geophysical dimensionality” which refers to the number of significant physical processes or dynamics represented within the data.

Prior to any attempts to identify ecological provinces in the English Channel from surface-ocean remotely-sensed variables, it was necessary to assess whether the available remotely-sensed data provided a suitable level of description (geometric dimensionality) to capture the phenomenon of interest (geometric dimensionality) (Goldenfeld and Kadanoff 1999). In this study, the phenomena of interest are emergent broad-scale patterns in the spatial and temporal heterogeneity of water column physical structure and phytoplankton biomass, linked to primary production.

The water column structure and associated patterns of phytoplankton biomass/productivity in the English Channel have been well documented (e.g. Holligan and Harbour 1977; Pingree 1980; Southward et al. 2005). Although remote-sensing data has previously been used in conjunction with oceanographic and biological models in
the English Channel (Pingree and Griffiths 1978; Pingree 1980; Spooner 2001), this thesis represents the first attempt to infer the spatial and temporal heterogeneity of water column structure and productivity using only remotely-sensed data.

The aim of this chapter is, therefore, to investigate whether the available remotely-sensed data (AVHRR SST and SeaWiFS Chl-α, \(L_{\text{W}}(555)\) and \(L_{\text{W}}(670)\)) has sufficient geometric and geophysical dimensionality to describe the documented spatial and temporal variability of physical water column structure and associated patterns of productivity. If the remotely-sensed data has sufficient geometric and geophysical dimensionality then it should be possible to identify a greater annual range of SST (°C) in the shallow coastal regions than in the western basin of the English Channel (Pingree 1980). The greater thermal stability of the western English Channel is a product of tidal seasonal stratification and the annual net heating cycle at the sea surface (Pingree 1980; Spooner 2001; Rippeth et al. 2005). The influence of the annual net heating cycle should also be identifiable in the annual SST range recorded i.e. the highest SST should occur in September at the end of the annual net heating phase and the lowest SST should occur in March at the end of the annual net cooling phase. Phytoplankton blooms (Spring and Autumn) in the western English Channel (Pingree et al. 1976; Holligan and Harbour 1977) should be identifiable from the Chl-α data set as should the seasonal, tidal front, also located in the western English Channel (Pingree and Griffiths 1978; Longhurst 1998b). A distinction between the Case II eastern basin of the English Channel and the oceanic/Case I influenced western approaches should be identifiable from the water leaving radiance data (\(L_{\text{W}}(555)\) and \(L_{\text{W}}(670)\)) (IOCCG 2000).
2.2 Methods

2.2.1 Data acquisition and pre-processing

Data from both the AVHRR and the SeaWiFS sensors are transmitted to the Dundee Satellite Receiving Station (DSRS) at the University of Dundee which records and archives data for the European shelf-seas, north-east Atlantic Ocean and Mediterranean Sea. Raw data are then distributed, via the internet, to NASA and to Plymouth Marine Laboratory (PML).

The NERC Remote Sensing Data Analysis Service (RSDAS) at PML pre-processes both the AVHRR and the SeaWiFS data from level 0 (raw High-Resolution Picture Transmission (HRPT) format) and level 1 (raw Hierarchical Data Format (HDF)) respectively, to level 3 data (weekly composite images used in this study) (Lavender and Groom 1999). The data pre-processing for both AVHRR and SeaWiFS data involves calibration, atmospheric and radiometric correction, cloud clearing (pixels obscured by cloud are recoded with a value of zero), inference of geophysical properties and processing of daily images into weekly composite images. The time series of data used for this study runs from the beginning of January 1998 to the end of December 2003, giving a total of 310 weekly composite images. This six year time period was the duration for which SeaWiFS ocean colour products are currently readily available. The spatial resolution of the data was 1 km\(^2\) for SeaWiFS products and 4 km\(^2\) for AVHRR SST data. Each 4km\(^2\) pixel of the AVHRR SST data was divided into 4 x 1 km pixels so that it could be compared with the SeaWiFS data.
2.2.2 Converting digital numbers to real world values

For both the AVHRR and SeaWiFS products, each pixel in the weekly composite 8bit images had a digital number value (DN) which required conversion to a physical value. Satellite sensors measure the radiation from each pixel, recording it as a DN from 0 to 255: each DN is given a greyscale value, with 0 relating to black and 255 relating to white. Table 2.1 contains the equations required to convert DNs for each water column variable to physical values.

Table 2.1. Equations necessary to convert 8bit image DNs to real world physical values for each water column variable. Supplied by NERC Remote Sensing Data Analysis Service (RSDAS), Plymouth Marine Laboratory.

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<thead>
<tr>
<th>Water Column Variable</th>
<th>Conversion Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>SST</td>
<td>$SST = (0.1DN) + 5$</td>
</tr>
<tr>
<td>Chl-a</td>
<td>$Chl-a = 10^{0.015DN - 2}$</td>
</tr>
<tr>
<td></td>
<td>$\log(Chl-a) = 0.015DN - 2$</td>
</tr>
<tr>
<td>$L_{WN}(555)$</td>
<td>$L_{WN}(555) = 0.02DN$</td>
</tr>
<tr>
<td>$L_{WN}(670)$</td>
<td>$L_{WN}(670) = 0.01DN$</td>
</tr>
</tbody>
</table>

The conversion from DNs to physical values for SST and the water-leaving radiance variables is a linear function. However, the conversion for DNs to Chl-a concentration is an exponential function. A logarithmic transformation of the Chl-a values (see table 2.1), which exhibit a linear relationship with the DNs, was used in order to maintain assumptions of normality for further parametric statistical analysis. As the primary concern of this study is spatial and temporal variability, $\log(Chl-a)$ values are as appropriate as direct Chl-a concentrations.

All land pixels were re-coded with a value of zero and were masked out to prevent any distortion of the analysis of the sea-surface data.
2.2.3 Selection of a map projection

A spherical Earth is assumed for all the remotely-sensed input images. Therefore, a Mercator projection is used. The Mercator projection (devised by Gerardus Mercator in 1569) has straight meridians and parallels that intersect at right angles. The Mercator projection is a conformal map and as such, preserves angles: any straight line is a line of constant bearing, otherwise known as a loxodrome or rhumb line. Size and distance are exaggerated in northern latitudes but shape is maintained reasonably well. In north-west European seas, coastline structure is preserved effectively by the Mercator projection.

2.2.4 Detection of Cloud Contamination

Both the AVHRR and the SeaWiFS sensors are optical sensors; their ability to record information is limited by the presence of cloud or other atmospheric phenomena. Precipitation over the Celtic Sea and the English Channel is largely oceanic in origin, with greater rainfall in the winter months than in the summer months (Pingree 1980; Perry and Hollis 2005). In order for precipitation to occur cloud must be present. This would suggest that contamination is most likely to be greater during the winter months than during the summer. Cloud contamination refers to the “non-land” pixels that were recoded with a value of zero, during the cloud removal procedures of data pre-processing. Pixels that are cloud-contaminated are effectively missing data points in the matrix of pixels that make up each image. The degree of cloud contamination in the remotely-sensed data set was assessed, to ensure that errors in the process of analysis and interpretation of results did not occur as a direct result of this phenomenon.

Each weekly composite image for each of the water column variables was reclassified to a binary image: cloud pixels retained their value of zero and non-cloud pixels were recoded to have a value of one. The percentage of cloud-contaminated pixels in each weekly composite layer was determined from counts of pixels present with a value of zero, exclusive of land areas. In order to detect any seasonal patterns of cloud contamination that may have influenced patterns in the remotely-sensed data, monthly mean percentages (12 values averaged over the whole remotely-sensed time-series) of cloud-contaminated pixels for each sensor (AVHRR and SeaWiFS) were calculated. Corresponding standard deviation values were also calculated.
2.2.5. Spatial variability statistics

The temporal mean and standard deviation for the whole time-series and the temporal mean for each month were calculated for each of the remotely-sensed variables (figure 2.1 and equation 2.1).

\[
\overline{X} = \frac{\sum_{t=1}^{t=n} (\chi_{it})}{n}
\]

In equation 2.1, \( \overline{X} \) is the temporal mean pixel value, \( t = 1, 2, 3 \ldots n \) is the time-step and \( i \) and \( j \) are the pixel dimensions of the image. The resulting descriptive statistical images showed the mean spatial pattern for the whole time-series, and also any seasonal and spatial variability that may be present.

The temporal mean and standard deviation images were all coloured using a Histogram Equalisation Model (Gonzalez and Wintz 1977) rather than according to value. The Histogram Equalisation Model is a non-linear stretch that redistributes pixel values so that there are approximately the same number of pixels with each value within a given range: the result approximates a flat histogram. The model does not alter pixel value, however, it does significantly increase the colour contrast within an image, which greatly facilitates the visualisation and identification of pattern.

Figure 2.1: Schematic of spatial variability statistics: calculating the temporal mean image, where \( \overline{X} \) is the temporal mean pixel value, \( t = 1, 2, 3 \ldots n \) are the time steps or input layers and \( i \times j \) are the pixel dimensions of the image.
2.2.6. Temporal variability statistics

Each weekly composite image, for each remotely-sensed variable, was averaged spatially (whole English Channel) to create a time-series of data (figure 2.2 and equation 2.2).

\[
\bar{\chi} = \frac{\sum (\chi_{ij})}{m}
\]

In equation 2.2, \(\bar{\chi}\) is the spatial mean value for the image, \(i\) and \(j\) are the pixel dimensions of the image (where \(i = 1, 2, 3, \ldots I\) and \(j = 1, 2, 3, \ldots J\)) and \(m\) is the total number of pixels in the image. The monthly mean values, for each successive month of the time-series (72 months for each variable), were then calculated from the weekly spatial mean time-series.

![Figure 2.2: Schematic of temporal variability statistics: calculating the spatial mean time-series, where \(\chi\) is the spatial mean value for the image, \(t = 1, 2, 3, \ldots, n\) are the time steps or input layers and \(i \times j\) are the pixel dimensions of the image.](image)

Intra-annual variability in the data was investigated by calculating an overall monthly mean time-series (12 months) from the 72 month spatial mean time-series. Inter-annual variation in the 72 month spatial mean time-series was examined using a standard time-
series decomposition (Chatfield 1984; Bowerman and O'Connell 1993). A 12-point centred moving average (which deseasonalised the data) was applied to the 72 successive monthly mean values and this was plotted with the mean value for the whole time-series, the full 72 month spatial mean time-series and 12 month spatial mean time-series for each remotely-sensed variable.

The 12 month spatial mean time-series for LWN(555) and LWN(670) were statistically compared via calculation of a Spearman Rank correlation coefficient ($r$) to determine if it was necessary to use both measures of water leaving radiance. A strong correlation between the two variables would suggest a repetition of information. The pixel values of the temporal mean and temporal standard deviation images for $L_{WN}(555)$ and $L_{WN}(670)$ were also compared and signal to noise ratios calculated in order to determine which variable produced a better optical signal for the English Channel region.
2.3 Results

2.3.1 Cloud contamination

The comparison of the monthly mean percentages of cloud-contaminated pixels for each sensor (AVHRR and SeaWiFS) showed that the SeaWiFS data suffered from cloud contamination more than the AVHRR data (figure 2.3). The SeaWiFS mean value of cloud contamination for the whole remotely-sensed time-series of images was 23.4%. This value was 2.7 times greater than the whole time-series mean value of cloud contamination for the AVHRR sensor (8.7%). Clear differences in cloud-cover between the winter months (October to March) and the summer months (April to September) also existed. The mean percentage of cloud contamination in the AVHRR images for the winter months was 15.96%, which decreased to a mean value of 4.9% during the summer months. The difference between winter and summer mean cloud-contamination values for the SeaWiFS data was even more pronounced than the AVHRR values: 30.81% in winter, decreasing to a value of 12.4% for summer.

Figure 2.3: Comparison of the mean monthly percentages of cloud cover for AVHRR and SeaWiFS data between January 1998 and December 2003 (standard deviations indicated).
Cloud-contamination percentages were also calculated for the temporal mean monthly images for each remotely-sensed variable. No cloud contamination was found in these images. The temporal averaging process had the effect of interpolating pixel values through time to create a complete pixel matrix with no missing values.

2.3.2 **Spatial variability: time-series mean and standard deviation for each remotely-sensed variable**

2.3.2.1 **SST**

The temporal mean SST image (figure 2.4.a) for the whole time series exhibits a slightly colder average SST value (12.6°C) for the immediate coastal regions and eastern English Channel, than the average SST value for the western and mid region of the English Channel (13.6°C). The temporal standard deviation image (figure 2.4.b) of the whole SST time series clearly shows that the eastern English Channel is also the area of highest variance. The area of high variability extends from the Straits of Dover, west along the Channel to Portland on the English coast and St. Malo on the French coast. The western English Channel exhibits less variance in SST, particularly in the western mouth of the channel between Lands End and Brittany. A distinct SST gradient exists in the mid-western English Channel (Start Point to Guernsey area) which may be indicative of the western English Channel front (Pingree and Griffiths 1978).

The temporal mean and temporal standard deviation images are calculated from the whole image time-series (310 weekly composite images covering the period from January 1998 to December 2003). Any cloud contamination present in the images (pixels re-coded with a value of zero) will be included in the calculations. The standard deviation values detailed in figure 2.4.b (12.6 - 3.3°C) are an artefact of cloud contamination. The monthly temporal averaging process had the effect of interpolating pixel values through time to completely remove any cloud contamination (see section 2.3.1 on cloud contamination). Therefore, the variance structure of the whole-time series can be verified by comparison with the variance structure observed in the examination of the 12 month temporal mean time-series images. The cloud contamination artefact will also apply to the whole time-series temporal standard deviation images produced from the SeaWiFS data (log(Chl-a), $L_{w}(555)$ and $L_{w}(670)$).
Figure 2.4.a: Temporal mean SST (°C) for the English Channel derived from AVHRR weekly composite images for the period January 1998 to December 2003.

Figure 2.4.b: SST (°C) temporal standard deviation for the English Channel derived from AVHRR weekly composite images for the period January 1998 to December 2003.
2.3.2.ii Log(Chl-a)

The temporal mean log(Chl-a) image (whole time series) (figure 2.5.a) strongly resembled the temporal standard deviation image for the whole time series of SST (figure 2.4.b), i.e. the highest mean log(Chl-a) values were associated with the greatest variations in temperature. The only notable difference between the two images was that the mean log(Chl-a) values were high around the coast of Cornwall and Brittany, despite these western English Channel areas experiencing a lesser degree of variation in temperature. The mean log(Chl-a) values found in the Dover Straits, the Bay of Seine and around the Isle of Wight appeared to be at least three times greater than those found in the western English Channel between the Lizard and Brittany. Figure 2.5.b, the log(Chl-a) temporal standard deviation image for the whole time series, showed the greatest variation in log(Chl-a) values to occur in shallow waters on both the French and English sides of the Channel, in the Straits of Dover and in the Bristol Channel. The main body of water in the central and western channel exhibits considerably less variation in log(Chl-a) values. However, the English Channel consists mostly of Case II waters and the log(Chl-a) signal was likely to be contaminated by CDOM and SPM concentrations. The effect of the CDOM and SPM concentrations is potentially less in the western English Channel owing to the oceanic influence of the Atlantic (Case I waters).
Figure 2.5.a: Temporal mean $\log(\text{Chl-a})$ (mg m$^{-3}$) for the English Channel derived from SeaWiFS weekly composite images for the period January 1998 to December 2003.

Figure 2.5.b: Temporal standard deviation $\log(\text{Chl-a})$ (mg m$^{-3}$) for the English Channel derived from SeaWiFS weekly composite images for the period January 1998 to December 2003.
2.3.2.iii $L_{W(555)}$ and $L_{W(670)}$

High mean values of $L_{W(555)}$ were displayed along both the French and English coasts (figure 2.6.a) compared to the mean values displayed in the western English Channel. These high values were probably representative of high concentrations of suspended matter present in the water column. The English coast between Dungeness and Brighton and around the Isle of Wight exhibited slightly larger areas of high $L_{W(555)}$ values than the French coast. River outlets on the French coast, for example the Seine (Avoine 1987), were particularly evident as sources of suspended matter. An area in the central English Channel region, extending from the Isle of Wight and Southampton area to Cherbourg, Cap de la Hague and round to the Channel Islands and St Malo, also showed high values of $L_{W(555)}$. The western English Channel region had the lowest values and exhibited the least variance (figure 2.6.b). As with both $log(Chl-a)$ values and SST, the greatest amount of variance in $L_{W(555)}$ mean values was found in the coastal regions, particularly in the vicinity of the Isle of Wight, the Straits of Dover and the Channel Islands. A clear distinction in values of $L_{W(555)}$ to the east and west of a line between Portland and Cap de la Hague was apparent in the temporal standard deviation image (figure 2.6.b), which could be interpreted as a divide between Case I (in the west) and Case II waters (in the east). These observations also held true for the temporal mean (figure 2.7.a) and standard deviation images (figure 2.7.b) (whole time series) for $L_{W(670)}$. However the $L_{W(670)}$ data showed markedly less overall variability than the data recorded at $L_{W(555)}$. 


Figure 2.6.a: Temporal mean $L_{\text{WN}}(555)$ (mW cm$^{-2}$ $\mu$m$^{-1}$ sr$^{-1}$) for the English Channel derived from SeaWiFS weekly composite images for the period January 1998 to December 2003.

Figure 2.6.b: Temporal standard deviation $L_{\text{WN}}(555)$ (mW cm$^{-2}$ $\mu$m$^{-1}$ sr$^{-1}$) for the English Channel derived from SeaWiFS weekly composite images for the period January 1998 to December 2003.
Figure 2.7.a: Temporal mean $L_{WM}(670)$ (mW cm$^{-2}$ μm$^{-1}$ sr$^{-1}$) for the English Channel derived from SeaWiFS weekly composite images for the time period January 1998 to December 2003.

Figure 2.7.b: Temporal standard deviation $L_{WM}(670)$ (mW cm$^{-2}$ μm$^{-1}$ sr$^{-1}$) for the English Channel derived from SeaWiFS weekly composite images for the period January 1998 to December 2003.
2.3.3 Intra-annual variability

2.3.3.i SST

The 12 month spatial mean time-series values (figure 2.8) showed March to be the coldest month and August to be the warmest month. The temporal mean monthly images (figure 2.9) showed the coldest areas of the English Channel to be located around the coastal regions of the eastern English Channel during the first quarter of the year. This cold region extended from Portland to the Straits of Dover on the English coast and as far west as St Malo on the French coast, with an average SST of 6.5°C for the quarter. The coastal region to the west of the English Channel (Portland to Lands End and the coast of Brittany) was considerably warmer on average during January, February and March (mean SST of approximately 10°C) than the eastern coastal regions. The warmest SST in the English Channel during the first quarter of the year were found in the deeper water between Lands End and Ushant at the western mouth of the English Channel (mean SST of 11°C). This body of warm water extended westwards out into the Celtic Sea towards the shelf break and eastwards as far as Portland (mean SST of 9.8°C) in the deeper water of the mid English Channel.

The English Channel warmed quickly through April, May and June (second quarter) and reached SSTs of between 10.9°C and 15.3°C by June. The coastal waters of the eastern English Channel warmed first of all; the French coast prior to the English coast. By June both coasts were warmer, by a mean value of 4.4°C, than the deeper water in the mid region of the eastern English Channel. The warmer coastal regions had a western limit of the Isle of Wight on the English side of the English Channel but extended all the way around the Breton coast on the French side. An initial observation of the western English Channel area during the second quarter of the year gave the impression that the warmer water was retreating from this area. However, this was not the case: the main water body in the western English Channel was, like the rest of the channel, increasing in temperature, but at a slower rate than the eastern coastal waters.
The water body to the west of Start Point had a mean SST of approximately 15°C by June, with the exception of the cooler patches (mean SST of approximately 11°C) that persisted around Start Point, the Lizard, Lands End and the western tip of Brittany. This structure was maintained into the third quarter of the year, through July and August, with coastal areas of the eastern English Channel reaching a maximum of 18.8°C by August. The main body of water in the western English Channel achieved a mean of approximately 17.5°C, with the cooler patches in the eastern mid English Channel and around Lands End, the Lizard and the coast of Brittany reaching a mean temperature of 14.2°C. During June, July and August a steep temperature gradient is evident in the western English Channel highlighting the western English Channel front (Pingree and Griffiths 1978). This observation concurred with the gradient observed in the temporal mean SST image for the whole time series (figure 2.4.a).

In September the whole of the eastern English Channel was within the mean SST range of 16.9 – 17.9°C. By October the coastal waters were beginning to lose heat (16.3°C). However, the deeper water in the eastern and mid-English Channel was still comparatively warm (17.8°C). The suggested frontal system in the western English Channel retreated and broke down during October and November. In the final quarter of
the year (October, November and December) a return to the SST structure observed in
the first quarter images could be seen. The coastal waters lost heat quickly attaining a
mean SST value of 6.7°C by December, the mid-English Channel also cooled and the
western main water body was again the warmest area of the English Channel with a
mean SST value of 12.2°C.

SST (°C) range for each month.

<table>
<thead>
<tr>
<th></th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
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<tr>
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<td>17.9</td>
<td>16</td>
<td>13.7</td>
<td>12.2</td>
</tr>
</tbody>
</table>

Figure 2.9: Temporal monthly mean SST (°C) for the English Channel derived from AVHRR weekly composite images for the period January 1998 to December 2003.
The fluctuations in SST that were observed in the 12 temporal monthly mean images corresponded with the structure observed in temporal standard deviation image for the whole time series (figure 2.4.b). The areas of the English Channel that displayed greatest variance in SST were the eastern coastal regions which had a mean SST fluctuation of approximately 12.6°C. The mid-English Channel region (deeper water east of Portland and Cap de la Hague) had a mean annual SST fluctuation of approximately 8.8°C and the more stable western English Channel encountered an annual SST fluctuation of approximately 7.1°C.

2.3.3.ii Log(Chl-a)

The 12 month spatial mean time-series values for log(Chl-a) (figure 2.10) in the English Channel showed an increase of more than 500% from January to May. The mean value then fell slightly in June before increasing again during July and August, when the maximum mean monthly value for the English Channel was reached. September through to December saw an almost linear decrease in log(Chl-a) values until the lowest mean monthly value was seen in December.

![Figure 2.10: 12 month spatial mean time-series for log(Chl-a) (mg m⁻³) (whole English Channel area) for the time period January 1998 to December 2003.](image-url)
Figure 2.11: Temporal monthly mean log(chlorophyll-a) (mg m\(^{-3}\)) for the English Channel derived from SeaWiFS weekly composite images for the period January 1998 to December 2003.

The temporal mean monthly images (figure 2.11) showed the eastern English Channel to be consistent in its pattern of log(Chl-a) values, throughout the year. Comparatively high values of log(Chl-a) compared with the rest of the English Channel area were found on the coasts, from the Straits of Dover as far west as Portland on the English coast and from Dover to St. Malo on the French coast.
The influence of CDOM and SPM on the reflectance ratios of the SeaWiFS Case I Chl-a algorithm must be taken into consideration. The coastal areas of the English Channel are subject to terrestrial run-off and are likely to contain high CDOM and SPM loads.

During the second quarter of the year (April, May and June) the areas of high log(Chl-a) in the coastal regions of the eastern English Channel were observed to extend towards the mid eastern English Channel region. Throughout this quarter, the greatest log(Chl-a) values were found along the French coast, particularly in regions where there was river discharge, for example, around the mouth of the Seine. The third quarter of the year (July, August and September) saw the high values of the eastern English Channel retreat again towards coastal regions and by the final quarter of the year, the pattern of log(Chl-a) distribution in the eastern English Channel had returned to that which was observed in the course of the first quarter.

The western English Channel area (west of Portland and Cap de la Hague) appeared to behave rather differently in terms of horizontal log(Chl-a) distribution. In the autumn and winter months an area of relatively high log(Chl-a) values could be found between Portland and Start Point on the English Coast. This area appeared to retreat back to the boundary of the eastern English Channel (Portland) during the second quarter of the year. The main body of water in the western English Channel showed a large area of comparatively low log(Chl-a) values which reached into the Channel from the Celtic sea and extended as far east as Start Point and the coast of Brittany. This area of comparatively low log(Chl-a) values were constant throughout the first quarter of the year, but began to exhibit an increase in the second quarter (April, May and June). By July an area of high log(Chl-a) values, was apparent in the mid Channel between Start Point and the Lizard and the Breton coast. A steep gradient between high and low productivity was also evident running across a line between the Lizard and the Breton coast. During August the log(Chl-a) values decreased slightly only to peak again in September. The area of autumnal increase in log(Chl-a) values was situated further west towards the entrance to the Celtic Sea and a productivity gradient symptomatic of a front could be observed between Start Point and Ushant. The final quarter of the year saw a return to the distribution patterns observed during the first quarter.
2.3.3.iii $L_{WN}(555)$ and $L_{WN}(670)$

The 12 month spatial mean time-series values for $L_{WN}(555)$ (figure 2.12) and $L_{WN}(670)$ (figure 2.13) followed an almost identical pattern. However, the observed values of $L_{WN}(555)$ were approximately five times greater than those of $L_{WN}(670)$. Both water-leaving radiance variables exhibited their highest mean annual values in January and February (0.31 mW cm$^{-2}$ µm$^{-1}$ sr$^{-1}$ and 1.5 mW cm$^{-2}$ µm$^{-1}$ sr$^{-1}$ for $L_{WN}(670)$ and $L_{WN}(555)$ respectively). A rapid decrease was observed between February and June, where the lowest mean annual values were reached for both variables (0.095 mW cm$^{-2}$ µm$^{-1}$ sr$^{-1}$ and 0.57 mW cm$^{-2}$ µm$^{-1}$ sr$^{-1}$ for $L_{WN}(670)$ and $L_{WN}(555)$ respectively). Levels of water-leaving radiance increased steadily from July until October at an approximate rate of 0.03 mW cm$^{-2}$ µm$^{-1}$ sr$^{-1}$ per month for $L_{WN}(670)$ and 0.09 mW cm$^{-2}$ µm$^{-1}$ sr$^{-1}$ per month for $L_{WN}(555)$. Both variables exhibited a decrease of around 25% in water-leaving radiance values between October and December. Statistical comparison of the 12 month spatial mean time-series for $L_{WN}(555)$ and $L_{WN}(670)$ revealed a Correlation Coefficient ($r$) value of 0.974 ($p < 0.01$), implying a very strong correlation between the patterns of intra-annual variability of the two variables. A strong degree of similarity between the two variables could also be observed from the temporal mean seasonal cycle images (figure 2.14 and 2.15).

![Graph showing the 12 month spatial mean time-series for $L_{WN}(555)$](image)

**Figure 2.12:** 12 month spatial mean time-series for $L_{WN}(555)$ (mW cm$^{-2}$ µm$^{-1}$ sr$^{-1}$) (whole English Channel area) for the time period January 1998 to December 2003.
High values of $L_{WN}(555)$ and $L_{WN}(670)$ were present around all coasts, especially on the English coast from the Straits of Dover to the Isle of Wight, on the French coast at areas of river discharge and around the Channel Islands. The mid-region of the eastern English Channel exhibited low values of both variables as did the western English Channel (west of Start Point and Cap de la Hague).

During March and April the area of high $L_{WN}(555)$ and $L_{WN}(670)$ values around the Isle of Wight extended across the English Channel, in a wide band, to Cherbourg and Cap de la Hague. Values in the western English Channel also began to increase around the Breton coast and extended to half way across the western mouth of the English Channel. In May and June, the band of high values between the Isle of Wight and Cherbourg retreated, with lower values observed in the deeper water of the mid-English Channel. $L_{WN}(555)$ and $L_{WN}(670)$ values on the French coast at the eastern end of the English Channel also decreased and an area of high values appeared in the western mouth of the English Channel.
Figure 2.14: Temporal monthly mean $L_{FR}(555)$ (mW cm$^{-2}$ um$^{-1}$ sr$^{-1}$) for the English Channel derived from SeaWiFS weekly composite images for the period January 1998 to December 2003.

By July, $L_{FR}(555)$ and $L_{FR}(670)$ values along the French coast were much reduced from the values displayed during the winter months. The high values that appeared to be moving in from the Celtic Sea, were visible around the southern coast of Devon and Cornwall.
These high values also extended across the English Channel to just north of the Breton coast, where a sharp decline in water-leaving radiance values could then be observed. An area of comparatively low \( L_{\text{WN}}(555) \) and \( L_{\text{WN}}(670) \) values reached north and east, skirting the Channel Islands and into the mid English Channel waters between Portland and Cherbourg.

![Map of the English Channel with LWN values](image)

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<th>Mar</th>
<th>Apr</th>
<th>May</th>
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</table>

**Figure 2.15:** Temporal monthly mean \( L_{\text{WN}}(670) \) (mW cm\(^{-2}\) \(\mu m\)^{-1} sr\(^{-1}\)) for the English Channel derived from SeaWiFS weekly composite images for the period January 1998 to December 2003.
During August and September, $L_{wN}(555)$ and $L_{wN}(670)$ values in the western English Channel decreased and a band of high values between the Isle of Wight and Cherbourg again developed, as was noted during March. Water-leaving radiance values along the French coastal regions of the eastern English Channel also increased. By October the pattern of both $L_{wN}(555)$ and $L_{wN}(670)$ values had returned to that detected for the winter months.

The temporal standard deviation images for $L_{wN}(555)$ (figure 2.6.b) and $L_{wN}(670)$ (figure 2.7.b) indicated that the areas of highest variation were the coastal regions, especially in the vicinity of the Isle of Wight and the Channel Islands. The temporal mean monthly images showed these areas to have consistently high levels of suspended matter relative to the western English Channel. Analysis of the range of maximum values, observed over the 12 month period, showed that the variation experienced in the coastal regions of the eastern and central English Channel is greater than that experienced in the western English Channel: by a factor of 4.8 for values of $L_{wN}(555)$ and a factor of 10.6 for values of $L_{wN}(670)$.

### 2.3.4 Inter-annual variability and time series analysis

#### 2.3.4.i SST

The centred moving average for the 72 month spatial mean time-series (figure 2.16) fluctuated around the overall mean value for the time series (12.06°C), with the fluctuations appearing to correspond to the annual range of maximum and minimum SST. Fluctuations that were marginally above the time series mean were exhibited during 1999, 2001 and 2003: these years showed maximum annual SST range (between 9.42°C and 9.66°C). The intervening years, 1998, 2000 and 2002 displayed a lesser degree of annual SST range (between 7.06°C and 7.58°C). The alternating pattern in scope of annual range from 1998 to 2003 suggested a two yearly cycle in the data. The final year of the time series (2003) was a notably warm year (Luterbacher et al. 2004) with the annual maximum SST reaching approximately 1°C higher than any other year in the time series (and 1.2°C higher than the mean seasonal maximum for this time-series). Overall, the 72 month spatial mean time-series varied only slightly from the 12 month spatial mean time-series indicating that the dominant mode of variability in this data set was intra-annual.
Figure 2.16: 72 month spatial mean time-series for SST (°C) for the period January 1998 – December 2003, compared to the same data with a smoothing function (12 point centred moving average) applied, the 12 month spatial mean time-series and the spatial mean for the whole time series.

2.3.4.ii Log(Ch-a)

The 72 month spatial mean time-series for log(Chl-a) was displayed in figure 2.17. Values of the centred moving average were predominantly below the time-series mean of -0.275 mg m⁻³ with the exception of values for 2001 and 2003, which were mostly greater than the time-series mean. The maximum monthly mean values for 2001 and 2003 are also notably higher than the maximum values of the 12 month spatial mean time-series. The minimum values for the first half of the time-series (1998 – 2000) are considerably lower (an average of 29%) than the minimum values of the 12 month time-series mean. The log(Chl-a) 72 month spatial mean time-series also mapped closely to the 12 month spatial mean time-series, although the signal was not as clear as in the SST 72 month time-series.
2.3.4.iii \( L_{WN}(555) \) and \( L_{WN}(670) \)

Observations of inter-annual temporal variability for both \( L_{WN}(555) \) and \( L_{WN}(670) \) were similar (figures 2.18 and 2.19 respectively). The centred moving average for both variables fluctuated closely around the 72 month time-series mean (0.927 and 0.184 mW cm\(^{-2}\) \( \mu \)m\(^{-1}\) sr\(^{-1}\) for \( L_{WN}(555) \) and \( L_{WN}(670) \) respectively), with the exception of 1998 and 2003. In 1998 particularly high values of suspended matter concentrations could be observed for the month of January; 42% higher than those observed for the 12 month spatial mean time-series maximum for \( L_{WN}(555) \) and 55% greater for \( L_{WN}(670) \). During the latter part of 2002 and into 2003 the centred moving average for both suspended matter variables dropped more noticeably below the time series mean. The annual range of values for \( L_{WN}(555) \), for 2003, was 24.5% less than the annual mean range and 11% less for \( L_{WN}(670) \). For both \( L_{WN}(555) \) and \( L_{WN}(670) \), the 72 month spatial mean time-series closely tracked the 12 month spatial mean time-series, once again indicating that intra-annual variation was the dominant mode of variability in this data set.
Figure 2.18: 72 month spatial mean time-series for $L_{\text{WN}}(555)$ (mW cm$^{-2}$ $\mu$m$^{-1}$ sr$^{-1}$) for the period January 1998 – December 2003, compared to the same data with a smoothing function (12 point centred moving average) applied, the 12 month spatial mean time-series and the spatial mean for the whole time series.

Figure 2.19: 72 month spatial mean time-series for $L_{\text{WN}}(670)$ (mW cm$^{-2}$ $\mu$m$^{-1}$ sr$^{-1}$) for the period January 1998 – December 2003, compared to the same data with a smoothing function (12 point centred moving average) applied, the 12 month spatial mean time-series and the spatial mean for the whole time series.
2.4 Discussion

The aim of this chapter was to assess the suitability of remotely-sensed data (SST, log(Chl-a) and water-leaving radiance at 555 nm and 670 nm: six year time-series from 1998 to 2003) as a means of describing the spatial and temporal heterogeneity of water column physical structure and associated patterns of productivity in the English Channel. The spatial and temporal analysis that was conducted in this chapter is discussed in terms of intra-annual and inter-annual for each remotely-sensed variable.

2.4.1 Cloud cover

Data from the SeaWiFS sensor (log(Chl-a), $L_{wm}(555)$ and $L_{wm}(670)$) contained more cloud-contamination that the AVHRR SST data. A distinct increase in the percentage of cloud-contamination during the winter months (October to March) compared to during the summer (April to September) was also detected. However, when the 12 month temporal mean image time-series was calculated, for each of the remotely-sensed variables, no cloud-contamination was detected. The temporal averaging process interpolated pixel values through time to create a complete pixel matrix with no missing values. The limitations of this process of temporal interpolation was that pixel values in the 12 month temporal mean image time-series, for some areas of the English Channel, may be the result of data from just one year of the full time-series (1998 – 2003), rather than a true mean value. The chance of data anomalies influencing the observed spatial variability in the 12 month temporal mean time-series was, therefore, increased.

2.4.2 Intra-annual variability

2.4.2.1 SST

The 12 month spatial mean time-series for SST (figure 2.8) was extremely similar to the annual net heating flux (figure 2.20) for temperate shelf seas (Pingree 1980). The negative phase of the annual net heating flux cycle runs from late October to March annually, and the net heating stage of the cycle occurs between April and September. Changes in the annual net heating flux are affected by a range of meteorological
variables: down-welling irradiance at the sea surface and the air/sea temperature difference exert the greatest influence. At the scale of the whole English Channel (= 75,000 km²), meteorological fields are thought to be primarily responsible for the mean seasonal pattern of sea surface temperature (Edinger et al. 1968; Pingree 1980; Spooner 2001).

Figure 2.20: Annual net heating cycle at the sea surface, Q(H), in cal cm⁻² month⁻¹, where Q is the heat flux downwards and H is the water depth. Adapted from Pingree (1980).

SST within the English Channel region did not have a uniform spatial distribution. Therefore, atmospheric forcing was not the only physical mechanism influencing variance in SST distribution. Tidal currents and water depth vary over smaller scales than meteorological fields and have a significant effect on the hydrography of shelf-seas (Pingree and Maddock 1977; 1978; Pingree 1980; Pingree et al. 1984). Pingree (1980) states that the distribution of hydrographic properties in the English Channel may only be fully understood by paying attention to the important role of tides in mixing properties, both vertically and horizontally. The effects of net surface heating are redistributed vertically by wind and tidal mixing. Stabilisation of the water column (stratification) occurs when surface heating produces more buoyancy than can be mixed.
away by the production of mechanical energy due to wind mixing from the surface and tidal mixing from below.

During the winter months, low irradiance and air temperature result in a negative heat flux into the water column producing convective overturn, which in addition to seasonally increased, wind induced mixing, maintains a well mixed water column. The spatial distribution of SST observed in the first quarter of the year (12 temporal monthly mean images – figure 2.9) is most likely to be a function of water depth. The shallowest region of the English Channel in the east exhibits the coldest annual mean temperatures, whilst the deeper water at the western mouth of the English Channel is, on average, some 4.5°C warmer.

In March the heat flux becomes positive and the water column has the potential to become stratified by way of the mean buoyancy flux due to heating exceeding the mean mixing energies due to wind and tide (Pingree and Pennycuick 1975; Spooner 2001). The eastern end of the English Channel (from the Dover Straits to Portland and Cherbourg), the Golfe de St Malo, the Channel Islands and the Breton coast are all subject to a greater tidal velocity than the rest of the western English Channel (Pingree, 1980). Pingree and Griffith’s (1978) predicted positions of Simpson and Hunter’s (1974) stratification parameter (S) suggest that this greater tidal amplitude exceeds a certain threshold, causing sufficient mixing to prevent stratification (S<1). The only exception to this relationship is a strip across the English Channel from Newhaven to Dieppe which experiences tidal amplitudes equivalent to the main western English Channel, and is identified as transitional water by Pingree and Griffiths (1978). The weaker tidal amplitudes of the western English Channel allow seasonal stratification to develop. The transitional waters of the western English Channel extend out to the shelf break beyond Ushant and intrude upon the predominantly stratified waters of the Celtic Sea (Longhurst 1998b).

The second and third quarters (April to September) of the 12 month temporal mean image time-series clearly reflected the patterns of tidal amplitude and stratification potential described above. In the eastern English Channel and Golfe de St Malo, the shallow coastal waters warmed quickly with the advent of the positive heat flux. These were the areas of the English Channel that exhibited the greatest variation in annual temperature range.
The onset of stratification in the western English Channel was evident from May and the eastward advance of a tidal front (running from Start Point and looping around the cost of Brittany to Ushant) was clear between May and August. Maddock and Swan (1977) identified a rapid increase in surface mixed layer temperatures at the onset of stratification at E1. Stratification was determined to reach its maximum in August, after which it began to recede owing to a decrease in solar heating and an increase in wind induced mixing. During September and October, the front observed in the western English Channel retreated back towards the western mouth of the channel. This observation concurred with the western English Channel front described by Pingree and Griffiths (1978) and Longhurst (1998a). The areas of cooler water noted in the Narrows (between the Isle of Wight and the Cherbourg Peninsula), around Lands End, the Lizard and the Breton coast during July, August and September were due to the particularly high tidal amplitudes that occur at these points: a common anomaly around headlands (Pingree 1980). Tidal mixing distributes the positive surface heat flux energy vertically. Therefore, these areas stood out in sharp contrast to the warm surface mixed layer of the adjacent stratified region.

The well-mixed eastern English Channel continued to warm in accordance with the net positive heat flux, until the final quarter of the seasonal cycle where the shallow coastal waters responded rapidly to the negative heat flux. Heat loss to the atmosphere is slower in the deeper mid-regions of the eastern English Channel (Pingree 1980). Disintegration of the frontal system in the western English Channel was also evident during this final quarter of the seasonal cycle.

2.4.2.ii Log(Chl-a)

The 12 month spatial mean time-series for log(Chl-a) follows the same seasonal pattern observed by Holligan and Harbour (1977) at E1. Low light levels during the winter months result in low productivity and hence low Chl-a values. As seasonal stratification commences in the spring, with the advent of the positive phase of the annual net heat flux, productivity increases massively and spring blooms occur. In the summer months, Chl-a values in the surface mixed layer (SML) decrease as available nutrients become depleted. The thermocline acts as a barrier to vertical mixing, reducing the vertical flux of nutrients from the nutrient replete bottom mixed layer (BML) (Spooner 2001). Sporadic mixing events in the autumn, followed by temporary re-stratification, restock the available nutrient supply in the SML resulting in an autumn bloom. Rippeth (2005)
and Rippeth et al. (2005) have also shown that mixing at the thermocline, in summer stratified shelf-seas, is largely responsible for sub-surface Chl-a maxima that can be detected in the summer months, between the spring and autumn bloom events. Similarity between the 12 month spatial mean time-series of log(Chl-a) values and SST was observed. Both phytoplankton productivity and sea surface heat flux are directly linked to levels of irradiance. Therefore, it is hardly surprising that they exhibit similar seasonal patterns.

The 12 temporal mean log(Chl-a) images exhibited a marked contrast between the east and west English Channel. The eastern English Channel displayed consistently high levels of log(Chl-a), particularly the coastal regions. The corresponding temporal monthly mean SST images confirmed that this area was well mixed throughout the year and as such had the potential to provide a good supply of inorganic nutrients to phytoplankton communities. However, the continued re-suspension of inorganic and organic material in the water column by mixing processes has the potential to limit light availability and thus limit productivity. The very clear distinction between the east and west of the English Channel that is evident in the whole time series temporal standard deviation image for $L_{wv}(555)$, must be considered in the interpretation of intra-annual spatial patterns of log(Chl-a) distribution. The east of the Channel (east of Portland and Cherbourg) experiences high variability of water leaving radiance at 555nm (shown to be a good estimate of SPM (IOCCG 1998; 2000; Otero and Siege 2004)), has high tidal velocity and is no deeper than 60m. The combination of these factors leads to the very strong probability that the eastern English Channel is a Case II area of water. Therefore, measures of log(Chl-a) must be interpreted with care, as the high quantities of CDOM and SPM will affect the reflectance ratios used in the Chl-a retrieval algorithm. The apparent high values of log(Chl-a) will consist of a combination of SPM, CDOM and chlorophyll-a values.

Light and inorganic nutrient supply (especially nitrate, phosphate and silicate) are the most significant limiting factors to phytoplankton productivity in temperate shelf seas. Both of these factors are controlled by the same physical forcing mechanisms that are responsible for the SST variability described in this thesis. In seasonally stratified waters, such as those found in the western English Channel, timing of the spring bloom is typically controlled by the onset of stratification. Seasonal changes in the spatial distribution of log(Chl-a) in the western English Channel were evident from May in the temporal monthly mean images. The autumn phytoplankton bloom (September) was
most clearly evident. The September bloom also strongly resembles the spatial pattern of the western English Channel tidal front as it retreats westwards. $\log(\text{Chl-}a)$ values for the last quarter of the year then decreased, corresponding to the break down in stratification and declining solar irradiance levels. Observations of the development of the spring bloom in the western English Channel made by Pingree et al. (1976) agreed with the patterns retrieved from the SeaWiFS data.

2.4.2.iii $L_{\text{WN}}(555)$ and $L_{\text{WN}}(670)$

Examination of the temporal monthly mean images for $L_{\text{WN}}(555)$ and $L_{\text{WN}}(670)$ emphasised the high degree of similarity between the two variables. The similarity in spatial variation was also apparent when comparing the whole time-series temporal standard deviation images for both variables. Both measurements of water-leaving radiance showed the greatest levels of intra-annual variation to be around the French and English coasts. Areas of riverine input (e.g. the Baie du Seine) exhibited decidedly high values. Terrestrial run-off and sediment output from estuaries are most likely to be responsible for this phenomenon (Otero and Siegel 2004).

The difference between well mixed and seasonally stratified regions of the English Channel was also evident from the temporal monthly mean images: the western English Channel exhibited consistently lower values of the water-leaving radiance variables than the well mixed eastern region of the English Channel. The spatial variation in tidal velocity (Pingree, 1980), which is in primarily responsible for the division of stratified and well mixed water in the Channel, is also clearly reflected in the temporal monthly mean images for $L_{\text{WN}}(555)$ and $L_{\text{WN}}(670)$. Additionally, the area of extreme tidal velocity in the Narrows displayed high values of both variables, throughout the year. The major intra-annual variation in the values of $L_{\text{WN}}(555)$ and $L_{\text{WN}}(670)$ for the western English Channel, mirrored the advance of the seasonal tidal front and the phytoplankton bloom episodes. Phytoplankton bloom conditions result in increased quantities of dissolved organic matter (CDOM) in the water column (Barnes and Hughes 1988), which will increase reflectance in the green/yellow range of the electromagnetic spectrum.
2.4.3 Inter-annual variability

The investigation of inter-annual variation primarily emphasised the strength of the seasonal signal. A potential biannual cycle was observed in the SST 12-point centred moving average which may be a result of climatic forcing by the North Atlantic Oscillation (NAO). The NAO is the primary large-scale mode of natural climatic variability in the study region (Osborn 2004); it affects the winter climate of Europe by altering the winter storm track across the Atlantic but it is a 'noisy' phenomenon with no clear long-term trend (the best predictions to date have not been able to capture more than 10% of its year-to-year variance) (Osborn 2004). The six year time-series (January 1998 – December 2003) of available remotely-sensed data was not extensive enough to detect inter-annual trends in the physical forcing mechanisms that affect water column structure in the English Channel.

2.4.4 Significance of observations

The fundamental forcing mechanisms of spatial and temporal heterogeneity in physical structure and primary productivity of the water column, have been documented in the extensive history of oceanographic research that has been conducted in the English Channel (e.g. Holligan and Harbour 1977; Pingree 1980). The analysis of the remotely-sensed data conducted in this chapter, clearly show spatially and temporally cohesive patterns in the selected water column variables (SST, log(Chl-a) and water-leaving radiance at 555 nm and 670 nm) that correspond with those key forcing mechanisms.

Concerns regarding the effectiveness of the Chl-a retrieval algorithm in Case II waters may be addressed by using the corresponding spatial and temporal patterns, determined from the water-leaving radiance variables, as a mask. Case II waters with high SPM and CDOM loads have been shown to produce peaks of reflectance at 555 nm and 670 nm (IOCCG 2000). Measurements of water-leaving radiance at 555 nm and 670 nm can be employed to determine where contamination of the chlorophyll-a signal in the green/yellow wavelengths, by SPM and CDOM, is likely to occur.

There was a substantial degree of similarity in the spatial and temporal variability observed in $L_{WN}(555)$ and $L_{WN}(670)$. The spatial mean seasonal cycles of $L_{WN}(670)$ and
were also highly correlated ($r = 0.97$, $p < 0.01$). The spatial variability observed in the whole time series temporal means of the two water-leaving radiance variables were virtually identical to each other, except that the mean values of $L_{WN}(555)$ are five times as great as those recorded for $L_{WN}(670)$. However, the time series standard deviations for both variables were of the same order of magnitude, which suggested that the $L_{WN}(555)$ data had a greater signal-to-noise ratio than $L_{WN}(670)$ (IOCCG 1998). This observation was corroborated by the clarity of the spatial pattern of variation in the time series standard deviation image for $L_{WN}(555)$ compared to that of $L_{WN}(670)$. The distinct divide between high variability of $L_{WN}(555)$, east of Portland on the English coast and Cherbourg on the French coast, and low variability to the west (not apparent in the $L_{WN}(670)$ standard deviation image), showed a potential division of the English Channel into turbid coastal Case II waters to the east and more oceanic type Case I waters in the west.

The temporal resolution of the data (six years) was not sufficient to identify long term cycles such as those observed by Maddock and Swan (1977) at E1. However, in temperate shelf-sea regions such as the English Channel, the most significant temporal mode of variability is intra-annual (Pingree 1980). The examination of inter-annual variability in the 72 month spatial mean time-series data for each of the remotely-sensed variables, showed no convincing evidence of inter-annual trends, but did emphasise the seasonal signal. The purpose of the time-series analysis was to resolve the temporal aspect of the geometric dimensionality of water column physical structure and associated patterns of productivity in the English Channel. The observations of intra-annual variability in the remotely-sensed data were consistent with all the major documented geophysical properties of the English Channel system (geophysical dimensionality). Intra-annual variation was considered to be the dominant type of temporal variability and it was concluded that the time-series of remotely-sensed data used in this study was sufficient to describe that variability. Therefore the SST, Chl-$a$ and $L_{WN}(555)$ data sets meet the specifications of geometric and geophysical dimensionality.

Additionally, the concerns regarding the removal of cloud-contamination from the remotely-sensed images using temporal interpolation appeared to be unfounded. The 12 temporal monthly mean images were effective in reproducing the essential spatial and temporal heterogeneity of water column physical structure and associated patterns of productivity.
2.5 Conclusions

The results of this descriptive study suggest that remotely-sensed data are a suitable means of describing the spatial and temporal heterogeneity of water column physical structure and associated patterns of productivity in the English Channel. The patterns observed in the spatial and temporal seasonal analysis of the AVHRR SST data were consistent with documented patterns in the key physical forcing mechanisms (surface heat flux and tidal mixing), that affect the stability of the water column (e.g. Pingree 1980; Rippeth et al. 2005). The SST 12 month spatial mean time-series also displayed consistency with the effects of the net surface heat flux and associated meteorological variables (air/sea temperature difference and solar irradiance (Spooner 2001)) at the scale of the whole English Channel. Whereas the temporal mean monthly images of SST displayed spatial patterns in accordance with the theory that tidal mixing is the primary physical forcing mechanism within the English Channel region (Simpson et al. 1977; Pingree and Griffiths 1978; Pingree 1980; Rippeth et al. 2005).

Intra-annual variability of log(Chl-a) ocean colour data, from the SeaWiFS sensor, convincingly echoed the confirmed seasonal variation in physical structure of the English Channel. The 12 month spatial mean time-series for log(Chl-a) followed the seasonal pattern of Chl-a concentrations recorded by Holligan and Harbour (1977) at E1 and the pattern of development of the seasonal phytoplankton bloom in the western English Channel is consistent with Pingree et al (1976) and with observations of the tidal front in that region (Pingree and Griffiths 1978; Longhurst 1998a). Concerns regarding the accuracy of the Chl-a signal in Case II waters were addressed via an informal comparison of the log(Chl-a) and water-leaving radiance data.

The observations of water-leaving radiance at 555 nm and 670 nm ($L_{WN}(555)$ and $L_{WN}(670)$), were extremely similar both temporally and spatially. However, $L_{WN}(555)$ demonstrated a greater signal-to-noise ratio, which was particularly evident in the distinctions between Case I and Case II waters that can be made from the $L_{WN}(555)$ data. Owing to the degree of similarity between the two water-column variables, it was considered necessary to use only $L_{WN}(555)$ in further stages of analysis.

The available remotely-sensed data (AVHRR SST and SeaWiFS Chl-a, $L_{WN}(555)$ and $L_{WN}(670)$) were found to have sufficient geometric and geophysical dimensionality to
describe the documented patterns of spatial and temporal variability in physical water column structure and associated patterns of productivity. Therefore, the data set could be confidently subjected to variance partitioning methods, such as principle component analysis, in order to identify ecological provinces based on these physical processes.
CHAPTER 3

THE APPLICATION OF REMOTE-SENSING TO THE IDENTIFICATION OF PERSISTENT ECOLOGICAL PROVINCES IN THE ENGLISH CHANNEL

3.1 Introduction

Hardman-Mountford (2000), Hardman-Mountford and McGlade (2002) and Hardman-Mountford et al. (2006) have developed a complex systems approach to defining ecological provinces in the ocean. The approach applies variance partitioning methods to remotely-sensed surface-ocean data in order to detect persistent spatial pattern in the temporal and spatial variability of a system. Pattern, according to Hutchinson's (1953) steady state definition, is an emergent property of a complex system (Levin 1999; Wu and David 2002). Variance partitioning methods are a means of detecting pattern.

The variance partitioning method used by Hardman-Mountford (2000), Hardman-Mountford and McGlade (2002) and Hardman-Mountford et al. (2006) was Principle Components Analysis (PCA). PCA has been widely applied to remotely-sensed oceanographic data as a means of determining modes of spatio-temporal co-variability (e.g. Paden et al. 1991; Fang and Hsieh 1993; Yoder et al. 2002). However, prior to the work of Hardman-Mountford (2000), Hardman-Mountford and McGlade (2002) and Hardman-Mountford et al. (2006), PCA had not been utilized for the identification of ecological provinces from remotely-sensed data.

Before PCA can be applied to such a data set, it is essential to establish whether that data set meets the specified geometric and geophysical dimensionality of the system that is being examined (Gallaudet and Simpson 1994). In the preceding chapter (Chapter 2), it was determined that the documented intra-annual variability of water column structure and associated patterns of productivity in the English Channel (e.g. Pingree 1980) could be identified using monthly mean images (January – December) of remotely-sensed SST, $\log(\text{Chl-a})$ and $L_W(555)$ data. Therefore, the mean monthly images provided the necessary
geometric dimensionality to describe the geophysical dimensionality of water column dynamics in the English Channel.

The aim of this chapter was to investigate the application of remotely-sensed data, via a complex systems approach, to the identification of persistent ecological regions within the English Channel. This study was the first attempt to apply the method developed by Hardman-Mountford (2000), Hardman-Mountford and McGlade (2002) and Hardman-Mountford et al. (2006) to a shelf-sea region. It was also the first attempt to combine remotely-sensed SST, \( \log(\text{Chl-a}) \) and \( L_{\text{wN}}(555) \) data to identify ecological provinces: Hardman-Mountford (2000) and Hardman-Mountford and McGlade (2002) used SST data and Hardman-Mountford et al. (2006) used Chl-a data.

The method of identification of ecological provinces using PCA of remotely-sensed images is in its infancy. Hardman-Mountford (2000) and Hardman-Mountford and McGlade (2002), who pioneered the method, employed a combination of time-series analysis, linear regression and the calculation of power spectra to quantitatively assess the relationship between co-varying regions that were identified directly from PCA. Hardman-Mountford et al. (2006) further developed the method by investigating the application of objective multivariate statistical methods to the identification of provinces. The method used in this thesis was developed in parallel to the method used by Hardman-Mountford et al. (2006). Therefore, no direct reference to existing methodologies can be made. The methods section of this chapter (section 3.3) also outlines the rationale behind the development process.
3.2 Principal Components Analysis (PCA)

Principal Components Analysis (PCA), also referred to as Empirical Orthogonal Function Analysis (EOF Analysis) is an objective multivariate statistical technique (Emery and Thomson 2001). Analysis of large scale, multi-dimensional data sets, where many of the dimensions are highly correlated, requires specialist statistical tools. PCA is exploratory and as such does not conform to the controlled and replicated situations that are required for confirmatory statistical techniques (e.g. analysis of variance) (Hare 1996). PCA essentially seeks to extract dominant underlying gradients of variation that account for the major patterns across all of the original variables. The input data set is decomposed into uncorrelated linear combinations of the variables, variance is preserved and mean square approximate errors are minimized (Fung and LeDrew 1987; Gallaudet and Simpson 1994; Emery and Thomson 2001). The aim is that a few major gradients will explain much of the variability in the total data set and that any noise in the data will be separated from those major gradients.

The value of PCA as a tool for isolating sources of data variability in oceanographic and meteorological investigations has been recognised for over 50 years (Preisendorfer 1988). Fukuoka (1951) was the first to apply PCA to a meteorological question, although it was not widely adopted as a technique until the work of Lorenz (1956) and Kutzbach (1967). PCA was introduced to the oceanographic community by Davis (1976) and has since become a routinely used technique in physical oceanography and meteorology.

When PCA is applied to remote-sensing, the output is a series of ranked Principal Component (PC) images with associated eigenvectors. The eigenvectors can be interpreted as a weighting, or loading, through time for each PC image. The PC images are the spatial output from the analysis and are calculated as the sum of each of the samples (pixels) through time, weighted by the eigenvector. Each PC image with its associated eigenvector is termed a "mode". The eigenvalues (or ranking) provide a measure of the total fraction of the variance that is explained by each PC/eigenvector mode (Otero and Siegel 2004).

Ordinarily, most of the variance is explained by the first few PC/eigenvector modes whose pattern can be interpreted in terms of physically meaningful processes. A direct physical or mathematical relationship between PC/Eigenvector modes and any related physical processes does not necessarily exist: empirical models do not inevitably tally with the true modes of
physical behaviour (Emery and Thomson 2001). More than one physical mechanism may contribute to the variance found in a single PC/eigenvector mode, or a single mechanism may be spread across several PC/eigenvector modes. Usually, in data sets that contain one or more strong signals, most of the fundamental variability is encapsulated in the first few PC/eigenvector modes (Hare 1996).

It is very important to use an appropriate level of description (geometric dimensionality) to capture the phenomenon of interest (geophysical dimensionality). If the geometric dimensionality of the input data is not sufficient to encompass the geophysical dimensionality of the system being investigated, then the PCA is unlikely to yield robust results. The results of PCA are highly dependent upon the input data: a characteristic that is clearly illustrated by Gallaudet and Simpson's (1994) discussion of studies using PCA in the Santa Barbara Channel. It is essential that interpretation is based in a detailed knowledge of the system under investigation (Hardman-Mountford 2000): a point that is demonstrated by Eastman and Fulk's (1993) discovery that an artefact in their data, due to sensor drift, could be identified in one of their resulting PC/eigenvector modes.

The two most commonly used forms of PCA for dealing with spatio-temporal data are known as T-mode (spatial) PCA and S-mode (temporal) PCA (Preisendorfer 1988). T-mode PCA describes how spatial modes vary in time, whereas S-mode PCA describes how temporal modes vary in space (Hare 1996). S-mode PCA is the more widely used method (e.g. Hare 1996; Ryan et al. 1999; Baldacci et al. 2001; Yoder et al. 2002; Ho et al. 2004; Otero and Siegel 2004; Palacios 2004). However, it has been suggested in a number of studies that T-mode PCA is a more effective method for determining persistent patterns of spatial variance (Paden et al. 1991; Fang and Hsieh 1993). S-mode and T-mode PCA have been compared and have been shown to produce similar results. However, T-mode PCA tended to represent dominant spatial patterns more clearly (Hernandez-Guerra and Nykjaer 1997; Tseng et al. 2000; Bisagni et al. 2001). The process of computing S-mode PCA involves the removal of the temporal mean. Therefore, the dominant spatial structure. T-mode PCA was the method applied to the detection of ecological provinces by Hardman-Mountford (2000), Hardman-Mountford and McGlade (2002) and Hardman-Mountford et al. (2006) and is the method used in this study.
3.3 Methods

3.3.1 Data preparation

Mean images for each month of the year (January – December) were calculated from a six year time-series (1998 – 2003) of AVHRR SST and SeaWiFS log(Chl-a) and LwN(555) data (see Chapter 2). The 12 mean monthly images for each of the remotely-sensed variables were used as input data for the T-mode PCA. The PCA was conducted separately for each remotely-sensed variable, so for example, the SST input data consisted of 12 images or variables with each image representing a time-step. The images were made up of pixels and each pixel represented a spatial sample. For the English Channel data, image dimensions in terms of pixels, were 588 x 354. Therefore, each of the 12 SST variables was effectively a data matrix with 208,152 data points.

Each input variable (image) was spatially normalised to have a mean of zero and unit standard deviation. Spatial normalisation was achieved using the following equation:

\[ x'_{ij} = \frac{(x_{ij} - \bar{Y})}{\sigma} \]

where \( x_{ij} \) is the pixel value at pixel location \( ij \), \( \bar{Y} \) is the mean value of all pixels in the layer and \( \sigma \) is the standard deviation of all pixels in the layer. Spatial normalisation prior to PCA assists interpretation of the output PC images, by presenting them as positive and negative deviations from the image mean.
3.3.2 T-mode Principle Components Analysis

T-mode PCA, which describes how spatial modes vary in time, was employed for the purposes of this study. In T-mode PCA, the pixel locations represent the samples (rows) and the time steps represent the variables (columns) of the input matrix. The T-mode PCA was performed using a modified version of the PCA routine in the ERDAS Imagine® Spatial Modeller software package. The modification involved replacing the calculation of a covariance matrix with the calculation of a correlation matrix. The correlation matrix normalises the input variables. Although the data had already been spatially normalised, the correlation matrix additionally temporally normalises the input variables, so that each input variable (time step) has an equal contribution to the total temporal variance. Non-normalised PCA allows input variables with greater levels of variance to contribute more to the total temporal variance than those with lower levels of variance. Fung and LeDrew (1987) and Eastman and Fulk (1993) concluded that normalised PCA was more effective than non-normalised PCA at detecting change in earth observation time-series data sets, as it prevented dominant features from masking more subtle changes in the data.

The output from the PCA is comprised of the PC/eigenvector modes and the eigenvalues (figure 3.1). The first PC/eigenvector mode accounts for the variance indicated by the largest eigenvalue and so on for each consecutive PC/eigenvector mode. There are as many PCs, eigenvectors and eigenvalues as there are input variables (time steps). In this study 12 input variables were used for each of remotely-sensed variable.
Figure 3.1: Schematic of the mathematical break-down of T-mode Principle Components Analysis (PCA) as applied to remotely-sensed data.
3.3.3 Interpretation of PC/eigenvector modes

An understanding of how the PC/eigenvector data were presented is necessary in order to relate the patterns observed in the PC images and corresponding eigenvector loadings, to the spatial and temporal heterogeneity present in the system. It was possible to determine regions of pixels that co-varied in time from the spatial variability described by the PC images. The PC image was calculated as the sum of each of the pixels (samples) through time, weighted by the eigenvector loading. The value for each time step of the eigenvector loading described how the spatial variability displayed in the PC image correlated to the observed variability at that particular time step. A strong positive eigenvector loading indicated that the spatial variability displayed by the PC image was present, an eigenvector loading of zero implied that there was no correlation and a strong negative eigenvector loading indicated that spatial variability, opposite to that which is displayed in the PC image, was present.

Spatial variability displayed in the PC images was denoted by spatially normalised units: the sign (positive or negative value) of these units indicated the comparative relationship of the pixels in the image. Pixels with a positive value (coloured red) showed where co-varying regions of pixels occurred and pixels with a negative value (coloured blue) showed areas of pixels that were uncorrelated. The pixel colouration was a gradient: strong positive correlation (red), to a weak correlation (white), to a strong negative correlation (blue). The areas of black pixels denoted the pivot point or zero line between the positive and negative correlation gradient. It was relative spatial gradients that were most important for the interpretation of pattern from the underlying data set, rather than absolute values. Therefore, legend values were not added to the PC images.
3.3.4 Initial selection of PC/eigenvector modes

To facilitate the interpretation of PC/eigenvector modes in terms of meaningful physical pattern, it is essential to keep only modes that represent more than sampling error or environmental noise (Hare 1996). If too few modes are retained then “under-factoring” or loss of signal may occur and if too many are kept then “under-filtering” will result from the retention of noise (Hare 1996). Statistical methods to determine how many PC/eigenvector modes represent signal are numerous and in some cases rather subjective. These include various selection rules such as Cattell’s “Scree Test” (1966), the “LEV Graph” (Craddock and Flood 1969; Farmer 1971) and the “Guttman Criterion” (Guttman 1954); also comparisons with randomly generated products, such as “Rule N” which is based in Monte-Carlo procedures (Preisendorfer 1988). Permutation methods for correlation coefficients (Potter et al. 2001) may also be used as may North et al.’s (1982) uniqueness test for establishing the uniqueness of PC/eigenvector modes. A useful method for deciding how many PC/eigenvector modes to retain is to utilise a number of the tests that have been mentioned above and compare the results (Hare, 1996). For the purpose of this study the Guttman Criterion, the LEV graph and the North et al.’s (1982) uniqueness test were used.

3.3.4.i The Guttman Criterion

The Guttman criterion (Guttman 1954) may be used when the input data set has been normalised or a correlation matrix is used, as was the case in this study. According to the Guttman Criterion, only PC/eigenvector modes with a value greater than or equal to one are deemed to be significant. In a typical normalised data set, each variable has unit standard deviation: any individual PC/eigenvector mode should account for the variance of at least a single variable if it is to be retained for interpretation (Hare, 1996). PC/eigenvector modes that have an eigenvalue of less than one are dismissed as noise.

3.3.4.ii LEV Graph

The log(eigenvalues) (LEV) are plotted against their root (PC/eigenvector mode number) and a straight line is drawn through the higher number roots (Craddock and Flood 1969). Farmer (1971) demonstrated that a PCA of random data produces a straight line LEV graph. Therefore, PC/eigenvector modes that lie above the line were retained, as these were considered to be non-random.
3.3.4.iii North et al.'s (1982) uniqueness test for PC/eigenvector modes

It is possible for consecutive PC/eigenvector modes with eigenvalues of similar magnitude to become mixed, forming "degenerate multiplets". The uniqueness of PC/eigenvector modes is established by the separation of their particular eigenvalues. North et al.'s (1982) uniqueness test states that an eigenvalue ($\lambda_a$) must be separated from a neighbouring eigenvalue ($\lambda_b$) as follows (equation 3.2);

$$\Delta_{ab} = \lambda_a - \lambda_b$$

by more than its sampling error, calculated as follows (equation 3.3);

$$\sigma_{\lambda_a} = \lambda_a (2 / n)^{1/2}$$

(where $\sigma_{\lambda_a}$ is the standard error of the eigenvalue and $n$ is the degrees of freedom) or they are judged to form part of a degenerate multiplet and their PC/eigenvectors are a random mixture of the true PC/eigenvector mode (Hare 1996). The cut off point for using a subset of PC/eigenvector modes to efficiently represent a large data set should not fall in the middle of a degenerate multiplet, as there is no justification for keeping part of the multiplet and abandoning the rest (North et al. 1982).

A combination of the Guttman Criterion, the LEV graph and North et al's (1982) uniqueness test was used to establish which of the PC/eigenvector modes accounted for at least one variable, were unique and contained non-random processes. These selected PC/eigenvector modes were discussed in terms of the emergent patterns of water column structure and associated patterns of productivity that could be identified.
3.3.5 Identification of ecological sub-provinces from selected PC/eigenvector modes

The use of the term “province” stems from Longhurst’s work on the global oceans (Longhurst 1998). The scale at which this study is focused is within the scale of Longhurst’s provinces. Therefore, the ecological provinces identified in this study were termed “sub-provinces”. Having established that the PC/eigenvector modes, for each remotely-sensed variable, described identifiable, real features of the system being studied, a further level of selection was applied to the modes. Only PC/eigenvector modes that described persistent, spatially co-varying regions were retained. If a strong, persistent spatial structure exists in a region, it will often be identified in the first or second PC/eigenvector mode. The eigenvector loadings will display a temporal signal that is either always positive or always negative, thereby indicating that the spatial structure of the PC image is always present. Eigenvector loadings that have reduced or near constant temporal variability are generally associated with PC images that resemble the temporal mean image for the time-series that is being investigated (Hernandez-Guerra and Nykjaer 1997). While these PC/eigenvector modes may resemble the temporal mean image, they are statistically different. The steady state patterns that they detect are a real part of the variance structure of the region being studied hence their value for sub-province identification.

The PC image components of the PC/eigenvector modes that displayed persistent, spatial structure were subjected to an unsupervised classification routine. Essentially unsupervised classification is a multivariate clustering routine. The selected PC images were the variables used and the pixel locations were the samples. Euclidean distance was employed as the distance metric between samples and K-mean clustering was used to group the samples (K-mean clustering algorithm ERDAS Imagine ®). Each group of samples equated to a sub-province. The output from the classification was an image where each pixel was assigned a value according to its group thereby producing a geographical translation of the sub-province structure. This process is summarised in figure 3.2.
Figure 3.2: Schematic of the unsupervised classification process. PC images displaying persistent spatial gradients were selected and used as the input variables used. The pixel locations were the samples. Euclidean distance was employed as the distance metric and K-mean clustering was used to group the samples. The output image is a geographical translation of the clustering.

It is important to remember that the sub-province structure was defined from persistent, spatial gradients. These spatial gradients were steady state patterns (i.e. independent of time but thermodynamically open). Therefore, sub-province boundaries were points of maximum gradient rather than absolute boundaries.

Although unsupervised classification is generally considered to be an objective approach (Sabins 1987), there is still a strong element of subjectivity attached. The clustering algorithm used required the user to specify the number of clusters into which the data should be
separated. Hence the unsupervised classification process is an iterative one. The number of clusters is specified based on the user’s knowledge of the area that is being imaged, the classification is computed and the results are determined satisfactory if the classification can be interpreted in terms of known patterns and features of the area (Short 2005). The persistent spatial structures identified in the PC images and their interpretation in terms of water column structure, were used as a guide for the number of clusters selected.

3.2.6 Testing the sub-province structure

Spatial analysis re-sampling methods advocated by Fortin (1999) and Anselin (1992) were used in conjunction with objective multivariate statistical techniques to test the sub-province structure identified in the unsupervised classification. The data used for the sub-province validation were the original image time-series (12 monthly mean images) of the three remotely-sensed variables that were used as the input data for the T-mode PCA. The data were spatially re-sampled by extracting a series of sub-samples from each image time-series using a sampling grid of 0.25°N by 0.25°W squares. The grid squares were separated by a distance of 0.5°N and 0.5°W (figure 3.3). The spatial mean of the pixels enclosed in each grid square was calculated for each time step in the time-series. Therefore, each sub-sample consisted of a 12 month time-series. A total of 32 sub-samples were extracted. Each sub-sample was then classified as belonging to one of the three sub-provinces according to its geographical location.
Figure 3.3: The grid used to spatially re-sample the remotely-sensed data in order to test the spatial structure of the proposed sub-provinces. Each grid square was 0.25°N by 0.25°W and was separated from any other grid square by a distance of 0.5°N and 0.5°W.

The extracted data were normalised to allow for comparison between the three remotely-sensed variables and similarity between the sub-samples was quantified using Euclidean distance. One-way Analysis of Similarities (ANOSIM routine in PRIMER V.6 (Clarke and Green 1988)) was used to determine if there was a statistically significant difference between the remotely-sensed properties of the sub-samples in different sub-provinces. A global test (among all three sub-provinces) and pairwise comparisons between each sub-province were carried out.

Although the normalized remotely-sensed data satisfies the multivariate normality assumptions, the non-parametric ANOSIM procedure was selected in preference to the parametric Multivariate Analysis of Variance (MANOVA). By selecting the sub-samples independently from the sub-province structure, it was not possible to ensure that sample sizes for each sub-province were equal. Therefore, the small and unequal sample size considerably increased the risk of occurrence of Type I errors when calculating the MANOVA test-statistic (e.g. Wilks'λ; (Zar 1999)). The non-parametric permutation procedure combined with a
Monte Carlo test approach to generation of significance levels (Hope 1968), utilised in the ANOSIM procedure, circumvents the problems of unequal group sample sizes.

Non-metric Multi-Dimensional Scaling (NMDS) and Hierarchical Cluster Analysis (Group Average Method with Similarity Profiling (SIMPROF – PRIMER V.6) at $p < 0.01$) (see Clarke and Warwick 2001 for all) were also applied to the sub-sample similarity matrix. These techniques allow a more detailed examination of the relationship between the sub-samples. The clusters resulting from the Hierarchical Cluster Analysis were overlaid on the NMDS ordination to verify the mutual consistency of the two representations. The sub-province to which each sub-sample was allocated was also displayed on the ordination plot. Agreement between the patterns detected in the multivariate analysis of the objectively re-sampled data and the structure of the sub-provinces was interpreted as validation of the sub-province structure.

Finally, the mean 12 month time-series and 95% confidence limits were calculated for each remotely-sensed variable in each of the sub-provinces. These mean time-series and 95% confidence limits allowed a basic assessment of intra-annual variability in sub-province structure in terms of each of the remotely-sensed variables. The sub-provinces are defined as thermodynamically open regions. Therefore, the variables describing the structure of those regions and the relationship between regions are not fixed values.
3.3 T-Mode PCA of the remotely-sensed data: Results and interpretation

3.3.1 SST: Results

According to the various selection criteria applied to the eigenvalues, between three (Guttman criteria and North et al.'s (1982) uniqueness test) and six (LEV graph) of the twelve PC/eigenvector modes produced by the T-mode PCA of the SST data should be retained (figures 3.4.a to c). The first three PC/eigenvector modes accounted for 94% of the variance. The remaining PC/eigenvector modes were discarded, as individually they explained very little of the total variance (6%) and their interpretation, in terms of known water-column features, was ambiguous.

Figure 3.4.a: SST. The Guttman Criterion: The SST data is normalised therefore each variable has unit standard deviation. Any individual PC/eigenvector mode should account for the variance of at least a single variable if it is to be retained for interpretation. Only PC/eigenvector modes with an eigenvalue ≥ 1 are retained.
Figure 3.4.b: SST. Logarithmic Eigenvalue Curve (LEV): PC/eigenvector modes that lie above the straight line drawn through the higher number roots are retained. Farmer (1971) demonstrated that a PCA of random data produces a straight line LEV graph. Therefore, PC/eigenvector modes that lie above the line were retained, as these were considered to be non-random.

Figure 3.4.c: SST. North et al. (1982) Rule of thumb for testing uniqueness of PC/eigenvector modes. Adjacent PC/eigenvector modes with eigenvalues of similar magnitude can become mixed, forming “degenerate multiplets”. An eigenvalue must be separated from its adjacent eigenvalue by more than its sampling error (error bars displayed above) in order for it to be considered separate and not part of a degenerate multiplet. The cut off point for retaining PC/eigenvector modes should not fall in the middle of a multiplet.
3.3.1.i SST PC/eigenvector modes 1 and 2

The uniqueness test (North et al. 1982) indicates that PC/eigenvector modes one and two are a degenerate multiplet (figure 3.4.c). Degenerate multiplets are formed when adjacent PC/eigenvector modes with eigenvalues of similar magnitude become mixed. However, PC/eigenvector modes 1 and 2 are interpretable in terms of known physical oceanographic features and they jointly explain 81.77% of the variance in seasonal SST. The eigenvector loading for the SST PC1 image (figure 3.5) remained positive throughout the 12 monthly time steps, implying that the gradient observed in the SST PC1 image is persistent throughout the year. Although the eigenvector loading was consistently positive, it was weaker between April and November, than between December and March and the lowest eigenvector loading occurred in September. This variation in the eigenvector loading indicated that the gradient of spatial variation shown in the SST PC1 image was stronger during the winter months than in the summer. The SST PC1 image (figure 3.6.a) displayed a clear gradient from the persistent spatial structure of the western English Channel to areas of high variability in the eastern coastal areas.

The second PC/eigenvector mode was responsible for 34.82% of the total variance. The eigenvector loading for the SST PC2 image followed a comparable seasonal pattern to that of the eigenvector loading for SST PC1 (figure 3.5): strong positive loading between December and March, decreasing to a minimum in September, except the eigenvector loading for PC2 became negative between May and November. The SST PC2 image (figure 3.6.b) showed a similar spatial gradient of increasing variability in an eastwards direction, to that observed in the SST PC1 image. However, between May and October this gradient was reversed (negative eigenvector loading).
Figure 3.5: SST eigenvector loadings (temporal aspect of the PC/eigenvector mode). Each eigenvector relates to a corresponding PC image (indicated in the legend).

3.3.1.ii SST PC/eigenvector mode 3

The third PC/eigenvector mode explained 12.23% of the total variance and was considered to be independent of the first two PC/eigenvector modes (figure 3.6.c). The eigenvector loading for the SST PC3 image was positive between February and August (maximum positive loading occurred in May) and negative between September and January (maximum negative loadings occurred in October and November). The spatial gradient displayed in the SST PC3 image indicated a sharp difference in SST from the central English Channel region (east of Start Point and excluding coastal regions) to the area to the west of Start Point and the coastal regions of the eastern English Channel during May and October/November.
Figure 3.6: SST PC Images. The percentage of variance in the SST temporal mean seasonal cycle explained by each PC/eigenvector mode is displayed at the bottom of each image, as is the colour scale. Blue represents a strong negative correlation between pixels, red represents a strong positive correlation, white represents a weak correlation and black represents the boundaries between areas of positive and negative correlation (i.e. zero correlation).

3.3.2 SST: Interpretation

Although the strength of the SST PC1 eigenvector loading varied during the 12 month time-series, overall it remained consistently positive, indicating that the spatial gradients displayed in the SST PC1 image were persistent throughout the year. Therefore, the SST PC1 image spatial gradient fulfils Hutchinson’s (1953) definition of pattern as a steady state: independent of time but not necessarily in thermodynamic of chemical equilibrium. The spatial gradient that is evident in the SST PC1 image relates to the greater thermal stability of the seasonally stratified western English Channel compared to the high annual variability in SST experienced by the shallow, well-mixed coastal regions of the eastern English Channel. The SST PC1 eigenvector loading weakened between April and September reflecting the phase of rapid increase in SST under the net heating phase of the annual net heating cycle. The western
English Channel has higher SST values during the winter months than the shallow coastal regions. However, the eastern coastal regions show a greater rate of increase in SST during the net heating cycle than the western Channel region and by September, the eastern English Channel is on average 3 – 4 °C warmer than the western English Channel.

The east/west divide in the English Channel was also clearly visible in the SST PC2 image. The negative eigenvector loading between April and November also relates to the net heating phase of the annual net heating cycle. The eastern coastal regions rapidly warm by around 10°C during this time. The period between April and November, in the western English Channel, is that between the onset and breakdown of summer stratification (Pingree and Griffiths 1978; Pingree 1980). As the net cooling phase of the annual net heating cycle begins (October), SST decreases and the mean buoyancy flux, due to heating, no longer exceeds the mean mixing energies due to wind and tides and the water column undergoes a transition from stratified to mixed.

Both the first and second SST PC/eigenvector modes essentially describe the same gradient: the change from the seasonally stratified, low SST variability region in the western English Channel to the well mixed, high SST variability eastern coastal regions.

The third PC/eigenvector mode (figure 3.6.c) highlights the main body of water in the eastern basin of the English Channel. The sharp gradient between the coasts and the deeper water of the central English Channel, visible in the SST PC3 image, emphasised the depth related differences between these two areas where the water column structure is dominated by tidal mixing. The rate of heat loss to and gain from the atmosphere is slower in the deeper regions of the mid-eastern English Channel than in the shallow coastal waters (Pingree 1980).
3.3.3 log(Chl-a): Results

Only the first two PC/eigenvector modes from the log(Chl-a) T-mode PCA were retained: they jointly explain 88.61% of the total variance. The first two PC/eigenvector modes were considered to be independent from each another and from the other PC/eigenvectors under North et al. s (1982) test for uniqueness. These two modes were also identified by the Guttman Criterion. The PC/eigenvector selection tests for the PCA of the log(Chl-a) data are included in Appendix A3.1.

3.3.3.1 log(Chl-a) PC/eigenvector mode 1

The first log(Chl-a) PC/eigenvector mode explained 81.08% of the total variance in log(Chl-a). A clear east/west divide could be seen in the English Channel, similar to that displayed in SST PC/eigenvector modes 1 and 2. The eigenvector loading remained almost constant throughout the 12 month time-series, indicating that the spatial gradients displayed by the log(Chl-a) PC1 image are a persistent feature of the English Channel system (figure 3.7). The log(Chl-a) PC1 image (figure 3.8.a) displayed a gradient from the high variability but low log(Chl-a) values of the western English Channel to the low variability but high log(Chl-a) values of the eastern coastal regions.

![Figure 3.7: Log(Chl-a) eigenvector loadings (temporal aspect of the PC/eigenvector mode). Each eigenvector relates to a corresponding PC image (indicated in the legend).](image-url)
3.3.3 ii log(Chl-a) PC/eigenvector mode 2

The second log(chl-a) PC/eigenvector mode determined 7.53% of the total spatial and temporal variance in log(Chl-a) values and was not as immediately decipherable as the first log(Chl-a) PC/eigenvector mode. The eigenvector loadings were negative between October and April but were strongly positive between May and September, reaching a peak in July (figure 3.7). The log(Chl-a) PC2 image (figure 3.8.b) showed a steep meridional gradient (north/south) in log(Chl-a) values in the eastern English Channel (east of Start Point and Cherbourg). The log(Chl-a) PC2 image also detected an area of spatially co-varying log(Chl-a) values (May to September) in the central western English Channel.

![Log(Chl-a) PC Images](image)

Figure 3.8: Log(Chl-a) PC Images. The percentage of variance in the SST temporal mean seasonal cycle explained by each PC/eigenvector mode is displayed at the bottom of each image, as is the colour scale. Blue represents a strong negative correlation between pixels, red represents a strong positive correlation, white represents a weak correlation and black represents the boundaries between areas of positive and negative correlation (i.e. zero correlation).

3.3.4 log(Chl-a): Interpretation

The same physical mechanisms that shape the spatial and temporal variation of SST in the English Channel also affect the spatial and temporal variation in log(Chl-a) values. Clear gradients existed between the shallow eastern coastal regions, the deeper waters of eastern basin and the western English Channel: the same persistent pattern of spatial variation that predominates in the SST data.
The greater tidal velocity and the shallower water of the eastern English Channel result in the water column maintaining a well mixed state throughout the year (Pingree 1980). The mixing process ensures a supply of inorganic nutrients to the water column, which along with light, are the most significant limiting factors to primary production in temperate shelf seas. A continuous supply of nutrients and higher levels of solar irradiation afforded by shallow coastal waters should provide ideal conditions for primary production and hence high levels of log(Chl-a). However, the analysis of water leaving radiance at 555 nm ($L_{W555}$) conducted in Chapter 2, suggested that the east of the English Channel could be classified as optically complex CASE II waters. CASE II waters contain high levels of suspended particulate matter (SPM) and coloured dissolved organic matter (CDOM) which can affect the reflectance ratios in the algorithms used to retrieve chlorophyll-a concentrations (IOC 2000). In CASE II waters, what appear to be measures of high chlorophyll-a concentration may in fact be a combination of chlorophyll-a, SPM and CDOM.

The high variability of log(Chl-a) values exhibited by the western English Channel reflected the annual cycle of primary productivity in seasonally stratified temperate shelf seas (Holligan and Harbour 1977). Low productivity winter months are followed by a spring bloom, sub-surface chlorophyll-a maxima during the summer months and an autumn bloom as stratification begins to break down (Rippeth 2005; Rippeth et al. 2005).

The key feature of the second PC/eigenvector mode was the meridional gradient in the eastern English Channel (figure 3.8.b). The eastern English Channel remains well mixed throughout the year ensuring a continued supply of inorganic nutrients to the water column. However, the waters around the French coast (Dover Straits to Cherbourg) are shallower than those on the English coast (Dover to Start Point) and are also more transparent owing to a weaker tidal velocity and thus less suspended sediment (Pingree 1980). The result is a greater availability of solar irradiation which causes the French coastal regions to reach a state of net primary production before the English Coastal regions.
3.3.5 \( L_{WN}(555) \): Results

Only the first two PC/eigenvector modes of the \( L_{WN}(555) \) PCA were retained as they were considered to be independent from the other PC/eigenvector modes and from each other. These two PC/eigenvector modes were also identified by the Guttman Criterion. The two PC/eigenvector modes jointly explain 91.13% of the total variance. North et al.'s (1982) test for uniqueness and the Guttman Criterion have proved to be the more suitable tests for PC/eigenvector selection for this study. The LEV graph tended to overfactor considerably, by identifying PC/eigenvector modes that explained a very small percentage of the overall variance and that could not be interpreted in terms of meaningful water column structure. The PC/eigenvector selection tests for the PCA of the \( L_{WN}(555) \) data are included in Appendix A3.2.

3.3.5.i \( L_{WN}(555) \) PC/eigenvector mode 1

The first \( L_{WN}(555) \) PC/eigenvector mode explained 82.2% of the total spatial and temporal variance. The eigenvector loadings were consistently strong and positive throughout the annual cycle (figure 3.9) indicating that the spatial gradient observed in the \( L_{WN}(555) \) PC1 image was a persistent structure. The PC1 image (figure 3.10.a) displayed a sharp gradient from the areas of high \( L_{WN}(555) \) values (around the Isle of Wight and the Kent and Sussex coast, the Channel Islands and river mouths e.g. the Seine and the Somme) to the comparatively low \( L_{WN}(555) \) values of the western English Channel.

3.3.5.ii \( L_{WN}(555) \) PC/eigenvector mode 2

The second PC/eigenvector mode is responsible for 8.93% of the total variance. The eigenvector loadings for the \( L_{WN}(555) \) PC2 image were similar to the eigenvector loadings for the \( \log(\text{Chl}-a) \) PC2 image. The eigenvector loadings were positive between May and September and negative from October to April (figure 3.9). The \( L_{WN}(555) \) PC2 image (figure 3.10.b) reflects the seasonal variation in \( L_{WN}(555) \). The eastern coastal regions exhibit their lowest \( L_{WN}(555) \) values during the early summer and this is also the time period when the greatest \( L_{WN}(555) \) values occur in the western English Channel.
Figure 3.9: $L_W(555)$ eigenvector loadings (temporal aspect of the PC/eigenvector mode). Each eigenvector relates to a corresponding PC image (indicated in the legend).

Figure 3.10: $L_W(555)$ PC Images. The percentage of variance in the SST temporal mean seasonal cycle explained by each PC/eigenvector mode is displayed at the bottom of each image, as is the colour scale. Blue represents a strong negative correlation between pixels, red represents a strong positive correlation, white represents a weak correlation and black represents the boundaries between areas of positive and negative correlation (i.e. zero correlation).
3.3.6 $L_{WN}(555)$: Interpretation

As with the first PC/eigenvector modes for both SST and $\log$(Chl-$a$), the spatial variation displayed by the first $L_{WN}(555)$ PC/Eigenvector mode represented a steady state pattern. The areas of particularly high tidal velocity around Portland Bill, Cap del la Hague and the Channel Islands (Pingree and Maddock 1977; 1978; Pingree 1980) produce consistently high values of $L_{WN}(555)$, which are reflected in the $L_{WN}(555)$ PC1 image. Areas of riverine input could also be easily identified e.g. the mouth of the Seine. $L_{WN}(555)$ values in coastal regions are highest during the winter months due to increased riverine input (increased precipitation results in more terrestrial run-off (Binding et al. 2003)) and increased mixing due to the effect of wind at the sea-surface. The western English Channel experiences generally lower values and less variability of $L_{WN}(555)$ than the coastal regions. The distinction between the optical quality of the water column on the French and English coasts of the eastern basin of the English Channel was clearly evident.

3.4 Identification and testing of sub-provinces: Results

3.4.1 Identification of sub-provinces

Persistent spatial gradients that could be explained in terms of meaningful features of water column structure and primary productivity were identified in the first PC/eigenvector mode for each remotely-sensed variable (SST, $\log$(Chl-$a$) and $L_{WN}(555)$). The first two SST PC/eigenvector modes were considered to be part of a degenerate multiplet. However, both modes essentially depicted the same pattern: the difference between the thermally stable, seasonally stratified regions and the well-mixed regions with high annual variability in SST. Therefore, the part of the variance structure that was a persistent feature i.e. that which was displayed in the first PC/eigenvector mode, was retained. Three PC images (SST PC1, $\log$(Chl-$a$) PC1 and $L_{WN}(555)$ PC1) were selected as the input images for the unsupervised classification.
The process of unsupervised classification is an iterative procedure and relies upon the user's knowledge of the features identified in the area that is being studied. Two distinct gradients in spatio-temporal co-variability were identified in all three of the PC images that were selected for use as input images in the unsupervised classification. The first was the gradient from immediate coastal areas to the eastern basin of the English Channel. The second was the gradient from the eastern basin of the English Channel to the western basin. As discussed in the sections on interpretation of PC/eigenvector modes, these gradients are consistent with known features of thermal stability and tidal mixing within the English Channel. Therefore, the a priori selection of clusters to be identified in the unsupervised classification routine was set at three to reflect the three areas separated by the gradients detailed above.

The results of the unsupervised classification routine clearly highlighted the three areas (sub-provinces) identified in the PC images (figure 3.11). Sub-province 1 (SP1) encompassed the coastal regions of the English Channel and was most prevalent in the Dover Straits, around the Channel Islands and along the English Coast from Lyme Bay to Eastbourne. Sub-province 2 (SP2) dominated the eastern basin of the English Channel and extended around the English and French coasts of the western English Channel and sub-province 3 (SP3) dominated the main water body of the western English Channel.

3.4.2 Testing of sub-provinces

A total of 32 sub-samples were extracted from the 12 month image time-series for each remotely-sensed variable using the spatial re-sampling grid (figure 3.12). Each sub-sample was allocated to one of the three sub-provinces based on its location (table 3.1 and figure 3.12).
Figure 3.11: English Channel Sub-Provinces identified from steady state spatial patterns in the mean 12 month image time-series of remotely-sensed SST, log(Chl-a) and LWN(555). The mean 12 month image time-series for each variable were calculated from a time-series of weekly composite images that covered the period from the start of January 1998 to the end of December 2003. Sub-provinces were identified using an un-supervised classification routine.

Figure 3.12: The grid used to spatially re-sample the remotely-sensed data overlaid on the sub-province image so that the location of each grid square in terms of the three sub-provinces can be observed. Each grid square was 0.25°N by 0.25°W and is separated from any other grid square by a distance of 0.5°N and 0.5°W.
The use of an objective spatial re-sampling method, such as the grid employed in this study, meant that it was not possible to ensure that equal numbers of sub-samples were extracted from each sub-province.

Table 3.1: Allocation of sub-samples to sub-provinces.

<table>
<thead>
<tr>
<th>Sub-Province (SP)</th>
<th>Sub-Samples Allocated to Sub-Province</th>
<th>Total Number of Sample Stations per Sub-Province</th>
</tr>
</thead>
<tbody>
<tr>
<td>SP1</td>
<td>13, 16, 20, 22, 23, 25, 32</td>
<td>7</td>
</tr>
<tr>
<td>SP2</td>
<td>1, 8, 18, 19, 21, 24, 26, 27, 28, 29, 30, 31</td>
<td>12</td>
</tr>
<tr>
<td>SP3</td>
<td>2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 14, 15, 17</td>
<td>13</td>
</tr>
</tbody>
</table>

The global test of the one-way ANOSIM \( R = 0.57, p < 0.001 \) indicated that a statistically significant difference existed between the three sub-provinces in terms of the remotely-sensed properties of the sub-samples within those sub-provinces. The \( R \)-value of 0.57 suggested that sub-provinces were overlapping but definitely distinct from one another.

In the pairwise comparisons (table 3.2) the SP1 and SP3 sub-samples displayed the greatest level of distinction. The SP1 and SP2 sub-samples were overlapping but undoubtedly different and the SP2 and SP3 sub-samples showed a moderate degree of difference.

Table 3.2: Pairwise comparisons (ANOSIM) to test for statistical differences between the three sub-provinces, based on the remotely-sensed properties of the sub-samples.

<table>
<thead>
<tr>
<th>ANOSIM Pairwise Comparisons</th>
<th>R value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SP1 vs SP2</td>
<td>( R = 0.55 )</td>
<td>( p &lt; 0.002 )</td>
</tr>
<tr>
<td>SP1 vs SP3</td>
<td>( R = 0.93 )</td>
<td>( p &lt; 0.001 )</td>
</tr>
<tr>
<td>SP2 vs SP3</td>
<td>( R = 0.36 )</td>
<td>( p &lt; 0.001 )</td>
</tr>
</tbody>
</table>
The same similarity matrix that was used as the basis for the one-way ANOSIM test was also used to produce an NMDS ordination (figure 3.13). The Kruskall stress value (Kruskal 1964; Kruskal and Wish 1978) of the 2D ordination equalled 0.1, indicating that it was a good representation of the relationship between the sub-samples. The relationship displayed in figure 3.13 strongly reflected the relationships between the sub-samples of each sub-province that were identified in the ANOSIM pairwise comparisons. The SP3 sub-samples were all clustered to the left-hand side of the ordination and the SP1 sub-samples were located to the right. The SP2 sub-samples were located centrally and were mostly closer to the SP3 sub-samples than to the SP1 sub-samples. However, the sub-samples were not clearly delineated into three groups that were representative of the three sub-provinces. Instead the sub-samples displayed a gradient from the SP3 sub-samples located in the Western Approaches, through the SP2 sub-samples in the mid Channel, to the English side of the eastern basin and the Dover Straits (SP1 sub-samples). The clusters \(p < 0.01\) (Hierarchical Cluster Analysis and SIMPROF) overlaid on figure 3.13 emphasised the south-west Channel to north-east Channel gradient.

The clusters also highlighted two additional aspects of the relationship between the sub-samples:

- The affinity between the sub-samples located at the eastern side of SP3 (e.g. 14 and 17) and the SP2 sub-samples that cover the area around the Cherbourg Peninsula and the French side of the eastern basin.

- The marked difference between the sub-samples located on the French (e.g. 26, 28 and 30) and English sides of the eastern basin (e.g. 23, 25 and 27).

The monthly mean SST values for each sub-province calculated from the sub-samples located within that sub-province are displayed in figure 3.14. SP3 displayed a notably smaller annual range of SST than either SP1 or SP2. SP1 experienced the greatest annual range of SST of the three sub-provinces. The three sub-provinces were distinct from one another in terms of SST from December to April; the mean SST value for each sub-province during this time period is outside of the 95% confidence intervals of the other two sub-provinces. The monthly mean SST values for all three sub-provinces increased sharply between May and August and during this period none of the sub-provinces could be considered independent from one another.
A greater level of distinction between the three sub-provinces was noted in the log(Chl-a) monthly mean sub-province values (figure 3.15). SP1 exhibited the highest log(Chl-a) values, closely followed by SP2. SP3 displayed considerably lower values than either of the other two sub-provinces. However, peaks in log(Chl-a) values were detected for SP3 during May, July and September. SP3 was distinct from both SP1 and SP2 throughout the mean 12 month period. SP2 and SP1 were also distinct from one another for the majority of the seasonal cycle, apart from during May (a log(Chl-a) peak was detected for SP2 in May), June and July where the 95% confidence intervals for the SST mean values overlap.
The distinction between sub-provinces was also weakest from May to July for the $L_{WN}(555)$ monthly mean values (figure 3.16). SP3 and SP2 were not distinct from one another during this period and SP1 was not distinct from SP2 or SP3 in July. However, between August and April, the three sub-provinces were clearly different from one another. SP1 displayed the highest and also the greatest range in $L_{WN}(555)$ monthly mean values, with the highest values occurring during the winter months. The SP3 monthly mean LWN(555) values were the lowest and also had the lowest annual range.
Figure 3.15: $\log(\text{Chl-a})$. Mean 12 month time-series for each sub-province calculated from the sub-samples within that sub-province. 95% confidence limits are indicated for each month.

Figure 3.16: $L_{\text{uw}}(555)$. Mean 12 month time-series for each sub-province calculated from the sub-samples within that sub-province. 95% confidence limits are indicated for each month.
3.5 Identification and validation of sub-provinces: Discussion

Three sub-provinces (SP1, SP2 and SP3) were identified within the English Channel region from persistent spatial gradients detected in remotely-sensed SST, \( \log(\text{Chl-a}) \) and \( L_{\text{w}(555)} \) data. The clear structure detected in multivariate analysis of the spatially re-sampled, remotely-sensed variables (12 month time-series) was in agreement with the hypothesised sub-province structure. A global ANOSIM test of the re-sampled data confirmed that three overlapping but definitely different structures could be identified from the English Channel surface-ocean remotely-sensed data. The corresponding pairwise comparisons (all significant at the 1% level) emphasised a gradient from the SP1 sub-samples to those of SP3 via the SP2 sub-samples. The SP2 sub-samples were considered to be more similar to the SP3 sub-samples than to the SP1 sub-samples.

Further examination (NMDS ordination – figure 3.13) showed the gradient between the sub-provinces to have a strong west to east 'direction': from the Ushant area of the Western Approaches to the Kent and Sussex coast and the Dover Straits. The clear difference between the English and French sides of the eastern basin was also incorporated in this gradient. Aspects of the steady state gradients that were identified in the first PC/eigenvector modes for each of the remotely-sensed variables, could also be detected in the gradient between sub-provinces. Gradients of increasing annual range in SST, increasing annual range and mean values of \( L_{\text{w}(555)} \), and decreasing annual range but increasing mean values of \( \log(\text{Chl-a}) \) corresponded to the west to east gradient. These gradients are summarised in figure 3.17.

A key transitional period in terms of intra-annual variation in physical water column structure and primary productivity in the English Channel appeared to be in the rapid heating phase of the annual net heating cycle (April to July). During this period the coastal waters of the English Channel become warmer than the main western Channel water mass, which stratifies. Peaks in phytoplankton biomass and hence primary productivity occur in the western English Channel which also have the effect of increasing levels of CDOM in the water column (Pingree et al. 1976). The increased phytoplankton population depletes inorganic nutrients from the water column and in coastal regions, the levels of SPM and CDOM from riverine input and terrestrial run-off are reduced owing to reduced precipitation during the summer months (Binding et al. 2003; Perry and Hollis 2005). A comparison of mean intra-annual variability in SST, \( \log(\text{Chl-a}) \) and \( L_{\text{w}(555)} \) values, for each sub-province, revealed that the
period of rapid annual net heating is also the period when the three sub-provinces are least
distinct from one another and the gradient that defines their structure is at its weakest.

Figure 3.17: Summary of the gradients in water column stability, SST, $L_{\text{air}}(555)$ and $\log(\text{Chl-a})$ values that
classify the sub-province structure.
3.6 Overall Conclusions

The method of sub-province identification from remotely-sensed data that was in part developed via this thesis, has been shown to be a valid means of detecting and defining steady state patterns in the spatial and temporal heterogeneity of shelf sea water column physical structure and primary productivity. T-mode PCA successfully highlighted persistent spatial gradients in the remotely-sensed SST, log(Chl-a) and $L_{w555}$ data that could be interpreted in terms of meaningful biophysical water column dynamics. Moreover, the unsupervised classification routine combined with spatial re-sampling and multivariate statistical analysis proved to be an efficient means of identifying sub-province structure.

The structure of the three English Channel sub-provinces (SP1, SP2 and SP3) was clearly related to the established model of shelf sea water column structure: the balance between annual net heating at the sea-surface and mixing due to wind and tides. The sub-provinces incorporate a west to east spatial gradient of decreasing physical water column stability and intra-annual variability in primary productivity, into a simple spatial framework. This type of simple framework, that includes the essential emergent patterns of spatial and temporal heterogeneity of a system, has the potential to provide a useful environmental baseline for ecosystem scale adaptive management of regional shelf seas (Hardman-Mountford et al. 2005). The possible application of the sub-province identification method to the wider UK continental shelf seas should be further investigated.
CHAPTER 4

THE RELATIONSHIP BETWEEN THE ENGLISH CHANNEL REMOTELY-SENSED SUB-PROVINCES AND THE SPATIAL HETEROGENEITY OF SEABED ENVIRONMENTAL VARIABLES.

4.1 Introduction

4.1.1 Linking water column structure and seabed environmental variables

Recent studies by Rees et al. (1999) and Freeman and Rogers (2003) have linked the biogeographic distribution of epibenthic fauna in the English Channel to heterogeneity in substratum type, depth, tidal current velocity, bed-stress and SST. The physical/environmental factors listed above are all related to water column structure. Bed-stress is measured in terms of the tidal velocity at 1 m above the seabed and has been shown to play an important role in the distribution of seabed sediments (Stride 1963; 1965; 1973; Hamilton 1979). Water column structure in shelf seas is dominated by the balance between surface heating and tidal mixing. A measure of the tendency of the water column to stratify under the influence of the net surface heat flux (Simpson and Hunter's (1974) stratification parameter \( S \)) can be calculated from the ratio of water mass (density multiplied by depth) and mean tidal energy dissipation.

The methods used to relate species distributions to environmental conditions in existing studies tend to focus on environmental data from point locations. Patterns in the spatial and temporal heterogeneity of environmental conditions, at the scale at which the study is being conducted, are rarely addressed (Hare 1996; Raffaelli et al. 2003). In the preceding chapter, three sub-provinces were identified within the English Channel region. Spatially and temporally cohesive surface-ocean remote-sensing data were employed to detect the sub-provinces and their structure was found to closely correspond to the established model of variation in water column structure (Simpson and Hunter 1974; Pingree and Griffiths 1978; Pingree 1980; Rippeth et al. 2005). Therefore, the sub-provinces
reflect vertical, as well as horizontal variability and as such could relate to spatial heterogeneity in the seabed environmental factors that are linked to water column processes e.g. bed-stress. The aim of this chapter was to investigate the relationship between the remotely-sensed sub-provinces and the seabed environmental factors that have been linked to the distribution of epibenthic fauna in the English Channel.

4.1.2 Selection of seabed data

It was determined that spatially cohesive seabed data would be the most appropriate form of data to compare to the remotely-sensed variables, as both seabed and sea-surface data could then be compared using the same analytical methods. A variety of spatially cohesive data relating to seabed environmental factors exist for the English Channel. Possible sources of seabed data were therefore reviewed and numerous limitations to use were encountered. An example is the British Geological Survey (BGS) digital seabed sediment data. The BGS data were deemed to be inappropriate for use in this study owing to their limited coverage of the English Channel and also due to the caveat attached to the data, by BGS (BGS 2003; Smith 2003), regarding its accuracy.

Tidal velocity data from the Medium Resolution Continental Shelf (MRCS) model were also considered for use in this study. The MRCS model functions over a much larger spatial area than that which was required for this study. The model covers the north-west European continental shelf region (12 °W to 13 °E and 48 °N to 62 °N) and operates on an approximately 7.4 km x 7.4 km resolution grid. This causes problems when a subset of the overall model data is extracted i.e. for the English Channel region. The rules that govern distribution or spatial interaction in the model variables may extend beyond the boundaries of the area that is taken as a subset. This is referred to as an “edge effect” (Vidal Rodeiro and Lawson 2005) and can result in the propagation of errors within the subset of model data. The process of calibrating the model data for the English Channel region was beyond the scope of this thesis, hence, the MRCS tidal velocity data were also judged unsuitable for use in the seabed/remotely-sensed sub-province relationship.
Finding spatially cohesive data relating to seabed environmental/physical factors that could also be legitimately compared to the surface-ocean remotely sensed data proved to be extremely difficult. Two sources of seabed environmental data were selected for comparison with the remotely-sensed sub-provinces: Bathymetry data from the MRCS model and estimates of bed-stress (dynes cm$^{-2}$) from Pingree and Maddock's (1977) 2-D model of tidal residuals in the English Channel.

4.1.2.1 Medium Resolution Continental Shelf (MRCS) Model Bathymetry Data
The MRCS model is a coupled hydrodynamic-ecosystem model that has been developed by PML, Proudman Oceanographic Laboratory (POL) and the UK Metrological Office. POL provides the hydrodynamic component from the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS) (Holt and James 2001; Holt et al. 2004) and PML supplies the ecosystem component from the European Regional Seas Ecosystem Model (ERSEM) (Baretta et al. 1995; Blackford et al. 2004). The model covers the north-west European continental shelf region (12 °W to 13 °E and 48 °N to 62 °N) and operates on an approximately 7.4 km x 7.4 km resolution grid.

Temporal variation in bathymetry on the scale of the whole English Channel occurs over geological time scales and is caused by events such as tectonic subsidence or post-glacial sea-level rises, for example the rapid sea-level rise in the early Holocene that flooded the Straits of Dover (Larsonneur et al. 1982; Waller and Long 2003). Temporal variation in oceanographic properties such as SST and tidal velocity at the equivalent scale (whole English Channel) occur within much shorter temporal dimensions, e.g. seasonal or inter-annual variation. The movement of bed-load sediments, which lie over bed-rock on the sea-floor, is directly affected by tidal velocity. The morphology of the bed-rock, sources of sediment supply and tidal velocity all combine to form sediment patches, ripples and waves. These variations in sediment topography are transient and are frequently destroyed or modified by storms and then restructured by tidal flow (Hamilton 1979). Therefore, small scale variations in bathymetry do occur on a time scale that equates to that of the variation in shelf-sea water column structure.
However, this variation is only really relevant at the scale of a few km$^2$. The detail of sediment topographical features is lost when bathymetric values are averaged over larger areas such as the ≈7 km$^2$ grid of the MRCS model. On the scale of the whole English Channel and at a resolution such as the one employed by the MRCS model, bathymetric variation is exclusively spatial. For this reason, subsets of the MRCS bathymetry data were not subject to the same potential problems of edge effects as the tidal velocity data: there are no complex temporal processes acting beyond the boundaries of the subset of bathymetry data that may influence the values of the data within the subset.

4.1.2.ii Pingree and Maddock’s (1977) model of tidal residuals

Pingree and Maddock’s (1977) 2-D hydrodynamic numerical model of the principal semi-lunar tide (M$_2$) in the English Channel operates on a 5 nautical mile grid system (≈ 9.3 km$^2$). The x-axis points along the main axis of the English Channel in a 075°N direction: the horizontal velocity component, $u$, acts in the same direction as the x-axis and the second horizontal velocity component, $v$, is transverse to $u$. The equations of motion used in the development of the model were integrated vertically, from sea-surface to seabed to reduce the number of spatial parameters from three $(x, y, z)$ to two $(x, y)$. The model effectively reproduces the key tidal residuals in the M$_2$ tide and its associated harmonics (M$_4$ and M$_6$) e.g. the clockwise eddy in Lyme Bay and the double low tides at Portland. Pingree and Maddock calculated the average velocity of $U$ over one complete tidal cycle (≈ 12.4 hrs at a one-minute time-step) of the M$_2$ tide. The value of $U$ used in the calculation of bed-stress (dynes cm$^{-2}$) (see section 1.5.4 of this thesis) was the mean tidal velocity for the whole water column (surface to seabed) averaged over one tidal cycle of the M$_2$ tide. The density of seawater ($\rho$) and the drag coefficient ($C_D$) were considered as constants.
4.2 Methods

Estimates of bed-stress (dynes cm\(^{-2}\)) were extracted from Pingree and Maddock’s (1977) contour map of variations in bed-stress in the English Channel (figure 4.1). Hence, the values of bed-stress used in this analysis are only an estimate: they were not calculated directly from the tidal velocity model data. The contour map was digitised and geo-referenced using ArcGIS and then imported to ERDAS Imagine® for sub-sampling.

Bathymetry data (mean value for each MRCS grid square) covering the English Channel region were extracted from the MRCS model and the resulting matrix was converted to a raster image, subset to the same coordinates as the remotely-sensed data and coloured according to 10 m depth intervals using ERDAS Imagine® (Figure 4.2).

Figure 4.1: Pingree and Maddock’s contour map of bed-stress (dynes cm\(^{-2}\)) variation in the English Channel region. The bed-stress values are calculated from Pingree and Maddock’s model of tidal residuals (Pingree and Maddock 1977). This map was adapted from Pingree’s summary of the oceanography of the English Channel and Celtic Sea (1980).
The spatial re-sampling grid (32 x 0.25 °W x 0.25 °N grid squares each separated by a distance of 0.5 °W and 0.5 °N) used in Chapter 3 of this thesis (figure 3.3) was also used to objectively sample the MRCS bathymetry data and to extract bed-stress estimates from Pingree and Maddock’s (1977) model. Spatial mean bathymetry values (m) and bed-stress values (dynes cm$^2$) were calculated for each grid square (AOI procedures). Each grid square was categorised, depending upon its location within the English Channel, as belonging to one of the three oceanographic sub-provinces defined in Chapter 3 (see table 3.1). The mean and 95% confidence intervals of the bed-stress and bathymetry sub-samples, for each sub-province, were calculated and frequency distributions were plotted to gauge the range and distribution of both bed-stress and bathymetry within the English Channel.

The 12 month temporal mean times-series images for SST, log(Chl-a) and $L_{WN}(555)$, calculated in Chapter 2 of this thesis and used as the basis for the T-mode PCA in Chapter 3, were sub-sampled using the spatial re-sampling grid as part of the sub-province validation process in Chapter 3.
The 12 month spatial mean time-series values that were extracted for each grid square and for each of the remotely-sensed variables in Chapter 3 of this thesis, were also used in this Chapter to compare the patterns of spatial and temporal heterogeneity observed in the remote-sensing data with patterns observed in the bed-stress and bathymetry data. Mean annual values for each grid sub-sample were calculated for each remotely-sensed variable from the extracted 12 month spatial mean time-series data.

The relationship between the mean bed-stress estimates and the annual mean values of each of the surface-ocean variables (SST, log(Chl-a) and $L_w N(555)$ sub-samples) was plotted and Product Moment Correlation Coefficients ($r$) were calculated. This procedure was repeated for the bathymetry sub-samples.

An NMDS ordination of the relationship between the grid sub-samples, based on the mean 12 month time-series for each of the three remotely-sensed variables, was calculated in Chapter 3 (figure 3.13). The sub-province in which each sub-sample was located was indicated on the ordination. This NMDS ordination clearly exhibited the gradients in SST, log(Chl-a) and $L_w N(555)$ that were observed in the T-mode PCA analysis (also Chapter 3) and formed the basis of the remotely-sensed sub-province classification. Therefore, the ordination was an ideal base on which to overlay values via a "bubble" plot, of the estimated bed-stress and MRCS bathymetry values for each sub-sample. The addition of the bed-stress and bathymetry values (depth (m)) gave an indication of whether the spatial variation of these seabed environmental variables in the English Channel, corresponds to the gradients observed in the surface-ocean remotely-sensed variables.

Finally, the MRCS bathymetry sub-sample values and the bed-stress estimates were plotted against one another and a Product Moment Correlation Coefficient ($r$) was calculated in order to assess the relationship between the two seabed variables.
4.3 Results

4.3.1 Variation in water depth (m) (MRCS bathymetry data) in the English Channel

The water depth values of the sub-samples ranged from 5.81 m on the coast near Dieppe (sub-sample 30) to 122.05 m in the Western Approaches, south-west of Ushant (sub-sample 4). The majority of the sub-samples (62.5%) had bathymetry values between 40 m and 100 m, 12.5% had values of greater than 100 m and 25% had values less than 40 m (figure 4.3).

![Figure 4.3](image.png)

*Figure 4.3:* Frequency distribution of bathymetry values (20 m intervals) sub-sampled from MRCS model bathymetry data (7.4 km² grid resolution)
4.3.2 Mean depth (m) (MRCS bathymetry data) of each sub-province

The SP3 sub-samples ranged between depths of 122.05 m in the Western Approaches (sub-sample 4) and 69.72 m at the eastern boundary of the sub-province (sub-sample 17) and had a mean value of 91.63 m (figure 4.4). The water depth of SP2 sub-samples ranged between 64.09 m (sub-sample 8) at Ushant and 15.87 m (sub-sample 19) in the Baie du Saint-Brieuc. The mean water depth value for the SP2 sub-samples was 48.96 m. The SP1 sub-samples had a mean water depth of 39.74 m. However, there was a marked difference between the depth of the SP1 sub-samples from the English coastal region (13, 16, 20, 23 and 25) and those from the Channel Islands (22) and the Dover Straits (32). The mean water depth of the SP1 English coast sub-samples was 61.07 m compared to a mean bathymetry value of only 11.3 m for the Channel Islands and Dover Straits sub-samples.

![Figure 4.4: Mean water depth (m) (MRCS bathymetry data) of sub-samples in each of the three sub-provinces. 95% confidence intervals are indicated.](image)

The 95% confidence intervals for the mean water depth (m) values for sub-provinces 1 and 2 are overlapping, whereas the 95% confidence intervals for the mean depth value for SP3 were outside of the confidence interval range of the mean values of both SP1 and SP2.
4.3.3 Variation in bed-stress estimates (dynes cm\(^{-2}\)) in the English Channel
(Pingree and Maddock’s 1977 model of tidal residuals)

The bed-stress sub-samples (mean value for one tidal cycle) for the English Channel region, extracted from Pingree and Maddock’s contour map, ranged from 1.5 dynes cm\(^{-2}\) (sub-sample 9 – St. Austell Bay) to 35 dynes cm\(^{-2}\) (sub-sample 21 – Cap de la Hague). However, 75% of the sub-samples had bed-stress values of less than or equal to 10 dynes cm\(^{-2}\) (figure 4.5). The sub-samples with bed-stress values greater than 10 dynes cm\(^{-2}\) were located in the Golfe de St Malo (sub-samples 19 and 22), in the Narrows between the Cherbourg Peninsula and the Isle of Wight (sub-samples 20, 21, 23, 24 and 25) and in the Dover Straits (sub-sample 32). Sub-samples 21 (Cap de la Hague) and 24 (Cherbourg) have exceptionally high values of bed-stress (35 and 30 dynes cm\(^{-2}\) respectively) for the English Channel Region.

Figure 4.5: Frequency distribution of bed-stress estimates (5 dynes cm\(^{-2}\) intervals) from Pingree and Maddock’s (1977) model of tidal residuals within the English Channel sub-samples.
4.3.4 Mean bed-stress (dynes cm\(^2\)) in each sub-province (Pingree and Maddock’s 1977 model of tidal residuals)

The SP3 sub-samples had the lowest mean value of bed-stress at 3.79 dynes cm\(^2\) (figure 4.6), with the lowest SP3 bed-stress value occurring in St Austell Bay (sub-sample 9) and the greatest SP3 bed-stress value occurring at the eastern boundary of SP3 (sub-sample 17). SP2 encompassed a wide range of bed-stress values: from 3 dynes cm\(^2\) south-west of Eastbourne (sub-sample 29) to the extreme values of sub-samples 21 and 24 (Cherbourg Peninsula). The mean bed-stress value for the SP2 sub-samples is 10.19 dynes cm\(^2\). With the exception of sub-samples 21 and 24, the values of the SP2 bed-stress sub-samples ranged between 3 dynes cm\(^2\) and 11.67 dynes cm\(^2\) (mean value of 6.13 dynes cm\(^2\)). It was clear that the very high bed-stress values that occurred around the Cherbourg Peninsula considerably skewed the mean bed-stress value for the SP2 sub-samples. The SP1 sub-samples had the highest mean bed-stress value (13.31 dynes cm\(^2\)) of the three English Channel sub-provinces and, like the SP2 bed-stress sub-samples encompassed a wide range of values. The greatest SP1 bed-stress value occurred at sub-sample 23 (\(T_b = 20\) dynes cm\(^2\)), which is located in the Narrows to the south of the Isle of Wight. The Narrows region in the centre of the English Channel appeared to experience greater tidal velocity and bed-stress than the Dover Straits.

![Figure 4.6: Mean bed-stress (dynes cm\(^2\)) value of sub-samples in each of the three sub-provinces. 95% confidence intervals are indicated.](image)

As with the sub-province mean water depth values, the 95% confidence intervals for the mean bed-stress values for SP1 and SP2 are not distinct from one another. The confidence intervals around the SP3 mean bed-stress value separate it from SP1 but not from SP2.
4.3.5 Comparison of sub-sample water depth (m) (MRCS bathymetry data) and SST, log(Chl-a) and $L_{WN}(555)$ values.

The water depth sub-samples are positively correlated ($r = 0.65$, $p < 0.01$) with the annual mean SST sub-samples (figure 4.7.a) and negatively correlated with both the annual mean log(Chl-a) ($r = -0.715$, $p < 0.01$) and $L_{WN}(555)$ ($r = -0.436$, $p < 0.05$) sub-samples (figure 4.7.b and c respectively).

Figure 4.7.a: Water depth (m) (MRCS bathymetry data) sub-sample values plotted against mean annual sub-sample values for SST (°C) ($r = 0.65$ ($p < 0.01$)).

The difference in water depth between the French and English coasts was clearly displayed in figures 4.7.a – c: the comparison between the bathymetry sub-sample values and the annual mean sub-sample values of each of the remotely-sensed variables. The French and English coast SP1 sub-samples had similar annual values of SST (averages of 12.52 °C and 12.51 °C respectively) and log(Chl-a) (0.432 mg m$^{-3}$ and 0.461 mg m$^{-3}$ respectively). The exception was sub-sample 22 (Jersey), which has the lowest annual mean SST value (12.02 °C) of all the English Channel sub-samples and the lowest SP1 annual mean log(Chl-a) value (0.073 mg m$^{-3}$). In addition to being considerably deeper than the French coast SP1 sub-samples, the English coast SP1 sub-samples also had a greater annual mean $L_{WN}(555)$ value: 2.33 compared to 1.55 mW cm$^{-2}$ μm$^{-1}$ sr$^{-1}$ for the French coast.
These correlations between water depth and the remotely-sensed variables were less evident when the water depth sub-sample values were overlaid on the NMDS ordination of the 12 month mean times series values of SST, log(Chl-a) and $L_{W(555)}$ (figure 4.8).

Figure 4.7.b: Water depth (m) (MRCS bathymetry data) sub-sample values plotted against mean annual sub-sample values for log(Chl-a) (mg m$^{-3}$) ($r = -0.715$ ($p < 0.01$)).

Figure 4.7.c: Water depth (m) (MRCS bathymetry data) sub-sample values plotted against mean annual sub-sample values for $L_{W(555)}$ (mW cm$^{-2}$ μm$^{-1}$ sr$^{-1}$) ($r = -0.436$ ($p < 0.05$)).
Figure 4.8: NMDS ordination (Euclidean distance is used as the distance measure) comparing the relationship between the 12 month mean time-series of the remotely-sensed variables (SST, log(Chl-a), $L_{W(555)}$) in the English Channel. The ordination is based on sub-samples of the data (32 x 0.25 °W x 0.25 °N grid squares each separated by a distance of 0.5 °W and 0.5 °N). The water depth (m) value for each sub-sample, extracted from the MRCS model bathymetry data, is listed next to each sub-sample and indicated by the “bubble” scale.

The deepest sub-samples displayed the highest annual mean SST and lowest annual mean log(Chl-a) and $L_{W(555)}$ values. However, sub-samples 19, 8 and 22 (Baie de Saint-Brieuc, Ushant and Jersey) and 13, 16, 20, 23 and 25 (English coast from Lyme Bay to Bognor Regis) are conspicuous in that they do not match this general trend. The position of sub-samples 19, 8 and 22, relative to the other sub-samples, was most strongly influenced by their annual mean SST values. Sub-sample 19 has the highest annual mean SST value in SP2 and sub-samples 8 and 22 have the coldest annual mean SST values from all of the English Channel sub-samples. The stretch of English coast from Lyme Bay to Bognor Regis (sub-samples 13, 16, 20, 23 and 25) has the highest annual mean levels of $L_{W(555)}$ and log(Chl-a) of all of the English Channel sub-samples, despite being distinctly deeper than the other coastal sub-samples. A west to east gradient in terms of sub-sample geographical location in the English Channel exists in the NMDS ordination in figure 4.8. The gradient of decreasing water depth displayed by the overlaid depth values corresponded to the west to east gradient.
4.3.6 Comparison of sub-sample bed-stress estimates (dynes cm\(^{-2}\)) (Pingree and Maddock's 1977 model of tidal residuals) and SST, log(Chl-a) and \(L_{wn}(555)\) values.

Both the log(Chl-a) and \(L_{wn}(555)\) sub-sample values exhibited positive correlations with the bed-stress sub-sample values \((r = 0.46, p < 0.01\) and \(r = 0.53, p < 0.01\) respectively) (figure 4.5.b and c). No positive correlation existed between the SST sub-sample annual mean values and the bed-stress sub-samples \((r = -0.336, p < 0.1)\) (figure 4.5.a).

The positive correlation between the bed-stress sub-samples and the log(Chl-a) and \(L_{wn}(555)\) sub-samples was reflected in figure 4.10: the NMDS ordination of the 12 month mean times series values of SST, log(Chl-a) and \(L_{wn}(555)\) with bed-stress estimates overlaid. The general gradient observed in figure 4.10 suggested that low values of bed-stress were associated with low values of log(Chl-a) and \(L_{wn}(555)\) and with low annual variability in SST and vice versa. However, whilst the majority of the sub-samples with bed-stress values greater than 10 dynes cm\(^{-2}\) (SP1 sub-samples 20, 22, 23, 25 and 32) were located to the right of the NMDS plot, in agreement with the suggested gradient, sub-samples 19, 21 and 24 (all belonging to SP2) were located centrally.
These three sub-samples had higher annual mean SST values and lower annual mean Chl-a and $L_{WN}(555)$ values than the other sub-samples with bed-stress values greater than 10 dynes cm$^{-2}$.

Figure 4.9.b: Bed-stress (dynes cm$^{-2}$) (Pingree and Maddock's 1977 model) sub-sample values plotted against mean annual sub-sample values for $\log$(Chl-a) (mg m$^{-3}$) ($r = 0.464$ ($p < 0.01$)).

Figure 4.9.c: Bed-stress (dynes cm$^{-2}$) (Pingree and Maddock's 1977 model) sub-sample values plotted against mean annual sub-sample values for $L_{WN}(555)$ (mW cm$^{-2}$ μm$^{-1}$ sr$^{-1}$) ($r = 0.531$ ($p < 0.01$)).
Figure 4.10: NMDS ordination (Euclidean distance is used as the distance measure) comparing the relationship between the 12 month mean time-series of the remotely-sensed variables (SST, log(Chl-a), Lw;v (555)) in the English Channel. The ordination is based on sub-samples of the data (32 x 0.25 °W x 0.25 °N grid squares each separated by a distance of 0.5 °W and 0.5 °N). The bed-stress estimate (dynes cm$^{-2}$) for each sub-sample, extracted from Pingree and Maddock's 1977 model of tidal residuals in the English Channel, is listed next to each sub-sample and indicated by the "bubble" scale.
4.3.7 Relationship between water depth (m) and bed-stress (dynes cm$^{-2}$)

The bathymetry sub-samples exhibited a negative correlation ($r = -0.5, p < 0.01$) with the bed-stress estimates extracted from Pingree and Maddock's (1977) model. The extreme bed-stress values of sub-samples 21 and 24 stood out in scatter plot of the two variables (figure 4.11), as did the difference in bathymetry values between the French (22 and 32) and English coast (13, 16, 20, 23 and 25) SP1 sub-samples. A definite divide between SP1 sub-samples was also evident in terms of bed-stress: sub-samples 30 and 16 had bed-stress values of 4.5 and 7.5 dynes cm$^{-2}$ respectively compared to the rest of the SP1 sub-samples, which had a mean bed-stress value of 16.25 dynes cm$^{-2}$.

![Figure 4.11: Water depth (m) (MRCS bathymetry data) sub-sample values plotted against bed-stress (dynes cm$^{-2}$) sub-sample estimates from Pingree and Maddock's (1977) model of tidal residuals in the English Channel. Sub-sample data points are coloured according to the sub-province (proposed in Chapter 3) in which the sub-sample is located and sub-sample number is indicated. Correlation coefficient: $r = -0.5$ ($p < 0.01$).](image)
4.4 Discussion

A clear agreement existed between gradients of bed-stress and water depth in the English Channel and the structure of the remotely-sensed sub-provinces. A gradient of increasing water depth was detected from SP3 (western basin of the English Channel) to SP1 (eastern coastal regions); this gradient reflects the morphology of the English Channel (Reynaud et al. 2003).

The bed-stress estimates also exhibited a general gradient between the sub-provinces, with SP3 displaying lower mean bed-stress values than SP2 and SP1. Most of the bed-stress sub-samples had values of less than 10 dynes cm$^2$. The sub-samples with bed-stress values greater than 10 dynes cm$^2$ were all located in close proximity to features of the French and English coast that are known to cause tidal current shear and the formation of turbulent eddies. Sub-samples 20, 23 and 25 (SP1), located on the British coast between Swanage and Bognor Regis in the Narrows, experience a high degree of turbulent tidal motion from current shear around the Isle of Wight (Grijalva 1962; Hyacinthe and Kravtchenko 1970; Pingree and Maddock 1977).

Extreme values of bed-stress were recorded for sub-samples 21 and 24 located at Cherbourg and Cap de la Hague. The prominent nature of the Cherbourg Peninsula also creates two turbulent eddies (Grijalva 1962; Pingree and Maddock 1977; Pingree et al. 1984; Sinha and Pingree 1997). An anti-clockwise eddy from Cap de la Hague (sub-sample 21) south-west into the Golfe de St Malo (sub-sample 22) and a clockwise eddy from Cherbourg (sub-sample 24) south-east into the Bay of Seinne. Sub-sample 22 is additionally affected by tidal current shear around the Channel Islands (Pingree and Maddock 1977; Pingree et al. 1984). The extreme bed-stress values estimated for sub-samples 21 and 24 are a product of the increased tidal velocity through the Narrows and the morphology of the Cherbourg Peninsula. The French coast is shallower than the English coast (Pingree 1980) and the well-mixed condition of the water column (a consequence of the low bathymetry values and the high tidal velocity) enables vertical diffusion of the surface turbulence.
The bed-stress value estimated for sub-sample 32 (16.25 dynes cm\(^{-2}\)) is not as great as the values estimated in the Narrows region of the English Channel. Although the tidal velocity and therefore bed-stress, in the Dover Straits, is considerably increased by the close proximity of the French and English Coasts, it is not amplified by tidal current shear from prominent features of coastal morphology to the same degree as the body of water in the Narrows.

A positive correlation between SST and bathymetry was detected. Annual SST range in deeper, more stable (seasonally stratified) regions is considerably less than in shallow well-mixed coastal regions where the effects of the net surface heat flux is more pronounced. In each correlation between bathymetry and the remotely-sensed variables, the SP2 sub-samples 1 and 5 (Lands End and the Lizard respectively) stand out. This is primarily due to their depth; between 10 and 30 m deeper than the other SP2 sub-samples. Sub-samples 1 and 5 display a similar mean annual temperature to the other SP2 sub-samples, but have lower annual mean \(\log(Chl-a)\) and \(L_{WN}(555)\) values. Although coastally located, they are also located in the western mouth of the English Channel and in areas where the gradient between the three sub-provinces is very steep. The remaining SP2 sub-samples are all located in the central and eastern regions of the Channel. The low annual mean \(\log(Chl-a)\) and \(L_{WN}(555)\) values recorded at sub-samples 1 and 5 are consistent with those recorded for the SP3 sub-samples. The deeper more thermally stable water results in less turbulent motion from tidal mixing and seasonal stratification. Therefore, the volumes of SPM and CDOM present in the water column (\(L_{WN}(555)\)) are likely to be lower. The SP3 sub-samples undergo peaks in \(\log(Chl-a)\) concentration that are consistent with the phytoplankton blooms that have been observed in the western English Channel (e.g. Holligan and Harbour 1977).

The bathymetry sub-samples displayed a strong negative correlation with the annual mean values for the \(\log(Chl-a)\) sub-samples. Annual mean \(\log(Chl-a)\) values were also shown to be positively correlated with bed-stress, although the correlation was weaker. Phytoplankton productivity in temperate shelf-seas is limited by light and inorganic nutrient supply. Light availability increases in shallow water and nutrients are more readily available in areas where sediment is periodically re-suspended through the action of bed-stress. The quantity of SPM and CDOM in the water column (indicated by \(L_{WN}(555)\) values) is also tied to the relationship between water column stability and light and nutrient availability. The Dover Straits are a good example of this relationship: productive, shallow, well-mixed water with a good nutrient supply. However, the greatest annual mean sub-sample values of \(\log(Chl-a)\) and \(L_{WN}(555)\) were found to occur in the deeper water of the English coast around the Isle of Wight (sub-samples 23, 23 and 25 and to a lesser extent sub-samples 13 and 16). Simpson and Hunter's
(1974) stratification parameter (S) is key to understanding these apparent anomalies between water depth and productivity in the coastal regions of the English Channel. The bed-stress values for the area around the Isle of Wight were some of the highest estimated from Pingree and Maddock's (1977) model. Bed-stress is directly proportional to tidal energy dissipation and the ratio of water mass (the product of density and depth) to energy dissipation forms the basis of Simpson and Hunter's parameter. Although the water depth around the Isle of Wight is significantly deeper than on the French coast, the high level of energy dissipation in the Narrows (the majority of tidal energy dissipation in the English Channel occurs here (Pingree 1980)) sufficient to maintain a well-mixed water column. Distributions of phytoplankton in the English Channel have been considered in terms of S; where water depth is scaled by the extinction coefficient (the rate of attenuation of sunlight in the water column with depth) (Pingree 1978; 1980).

The SP2 sub-samples, 19, 21, 22 and 24 were also an exception to the pattern of high log(Chl-a) and $L_{WN}(555)$ values linked with shallow, well-mixed water. Sub-samples 21 and 24 (Cherbourg Peninsula) had bed-stress values 10 dyne cm$^{-2}$ greater than the sub-samples on the English side of the Narrows and were approximately 30 m shallower. However, the mean annual log(Chl-a) values for the Cherbourg Peninsula sub-samples (21 and 24) were relatively low compared to the other sub-samples that were located in well-mixed coastal waters. The clockwise (Cherbourg) and anticlockwise (Cap de la Hague) eddies that are a product of the increased tidal velocity in the Narrows and the morphology of the Cherbourg Peninsula transport nutrients and sediment towards the French coast on either side of the Peninsula (Kenyon and Stride 1970; Pingree et al. 1984). The added tidal current shear caused by the Channel Islands resulted in the high annual mean $L_{WN}(555)$ values and low annual mean log(Chl-a) values observed at sub-sample 22. High levels of turbulent motion and SPM limit light availability and hence limit primary productivity. The turbulent motion documented in the region of the Channel Islands also enhances the process of rapid heat loss and gain, hence the low annual mean SST value for sub-sample 22. Sediment and nutrients transported by the Cherbourg eddy into the more stable Bay of Seinne, coupled with the riverine input from the Seinne itself and the Somme, help to maintain the high levels of primary productivity observed along the eastern section of the French coast (e.g. sub-sample 30). The effects of the Cherbourg Peninsula and Channel Island turbulence did not appear to reach as far as sub-sample 19 (SP2), which was located in shallow coastal water the Golfe de St Malo and had a relatively high bed-stress value (11.67 dyne cm$^{-2}$) and moderate log(Chl-a) and $L_{WN}(555)$ values.
4.5 Overall Discussion and Conclusions

The inaccessible nature of the seabed and the fact that it is not a static environment combine to make the collection and collation of spatially and temporally cohesive seabed physical data extremely difficult.

The comparison of bed-stress estimates from Pingree and Maddock's (1977) model, with the MRCS bathymetry data and sub-samples of the surface-ocean variables, revealed relationships between the surface and sea-bed physical variables that have the potential to corroborate the definition of the three biophysical oceanographic sub-provinces. Owing to the coarse estimates of bed-stress extracted from Pingree and Maddock's contour map, the correlations and patterns discussed cannot be considered as a robust test of the relationship between the sea-surface and the seabed.

However, the comparisons between the surface and seabed variables highlighted two important points:

First, the interplay between water depth and tidal velocity is critical to understanding physical processes on the scale of the English Channel. Simpson and Hunter's (1974) stratification parameter \( S \) incorporates both depth and tidal velocity. The established paradigm of water column mixing and vertical structure in shelf seas on which the parameter it is based, still remain central to the understanding of shelf sea processes (Rippeth 2005; Rippeth et al. 2005). A comparison between \( S \), calculated from a 2-D model of tidal dynamics in the English Channel (i.e. Pingree and Maddock, 1977), and the persistent spatial patterns identified in the surface-ocean variables (from PCA in Chapter 3) would be a better approach to testing the link between physical variables at the sea-surface and the seabed.

Second, whilst the basic spatial and temporal patterns of water column can be elucidated from SST data, the \( \log(\text{Chl-a}) \) and \( L_wN(555) \) data are invaluable in terms of refining those basic patterns. For example, the distinction between productive well mixed areas and those, like sub-sample 22 in the Channel Islands region, where the effects of high tidal velocity and current shear are amplified by shallow water resulting in limited phytoplankton production.
The problems encountered in finding suitable, spatially cohesive data, relating to physical conditions on the seabed of the English Channel, emphasises the need for alternative methods of characterising the bio-geographic distribution of benthic fauna. The link between surface-ocean properties and seabed physical conditions needs to be tested more conclusively. However, the basic patterns and correlations between the two sets of variables that are discussed in this chapter point to a positive outcome.
CHAPTER 5

REMTELY-SENSED SUB-PROVINCE STRUCTURE RELATED TO THE
BIOGEOGRAPHIC DISTRIBUTION OF EPIBENTHIC MEGAFANA IN THE
ENGLISH CHANNEL

5.1 Introduction

In the previous chapter, the problems inherent in finding spatially cohesive data relating to the physical environment of the seabed were outlined. Moreover, a strong case was established for the link between the remotely-sensed variables and the physical variables traditionally used to characterise the distribution patterns of epibenthic fauna. The present chapter compares the spatial variability observed in a biogeographic survey of epibenthic megafauna to the structure of the sub-provinces identified from remotely-sensed properties in Chapter 3 of this thesis. It was not logistically possible to sample the epibenthic fauna of the entire study region and so the area between Portland and Lands End on the English coast was selected as a test site (figure 5.1). The area forms an ideal test site for this study as all three of the sub-provinces identified in Chapter 3 are represented within the survey area.

Prior to any comparison of the spatial distribution of epibenthic fauna with the location of sub-provinces, it was necessary to determine the fidelity of the sub-province structure at a reduced spatial scale to that of the whole English Channel area, used in previous chapters. The region between Portland and Lands End is approximately 20% of the area of the whole English Channel system: by comparing the remotely-sensed variables of sample stations within this smaller region, there is a risk that the level of description becomes too small to capture the phenomenon of interest (Goldenfeld and Kandanoff 1999). As the window through which a system is observed decreases in size, the level of variability detected in the system increases, so structure that was observed at larger spatial scales may become over-complicated with small scale idiosyncratic variability that was previously averaged out (Levin and Buttel 1987; Levin 1992; Keeling et al. 1997).
However, homogeneity between the sub-province structure observed in the analysis of the whole English Channel system and the structure observed when sample sites from within the test area are compared to one another, would confirm the sub-province classification (Levin and Buttel 1987; Keeling 1999; Levin 1999).

Figure 5.1: Map of the Lands End – Portland area of the English Channel displaying the location of the three sub-provinces.

Hence the aims of this chapter are:

i. to determine if the sub-province structure holds at a reduced spatial scale to that of the whole English Channel system;

ii. to test the hypothesis that the biogeographic distribution of epibenthic megafauna will be predicted by the remotely-sensed sub-province structure.
5.2 Validity of the sub-province structure at a reduced spatial scale

5.2.1 Methods

5.2.1.i Selection of sampling stations

Spatial re-sampling methods, that were adapted from techniques that originated in the Landscape Ecology literature (Anselin 1992; Fortin 1999) and were developed to quantitatively explore the structure of remotely-sensed ecological provinces by Hardman-Mountford et al (2006) and in Chapter 3 of this thesis, were also used to test the validity of the sub-province structure at a reduced spatial scale. To test the sub-province structure, it was necessary to re-sample the remotely-sensed data for the Lands End – Portland test area independently of that structure. This condition of independence was also required for the epibenthic sampling. Therefore, it was possible to use the same sample stations to test the validity of the sub-province structure and to sample the distribution of epibenthic fauna, facilitating a direct and objective comparison between the two factors. Owing to the limited period of time for which a research vessel could be made available for epibenthic sampling, 31 sample stations were selected. The stations were selected entirely independently from the sub-province structure by dividing the area between Portland and Lands End into four sectors:

i. Lands End to St. Austell (stations 24 – 31)
ii. St. Austell to Start Point (stations 1 – 8)
iii. Start Point to Lyme Regis (stations 9 – 16)
iv. Lyme Regis to Portland (stations 17 – 23).

The sectors were used for logistical reasons, with each sector representing a different sampling trip. The number given to each of the stations corresponds to the order in which it was sampled. Sample stations were evenly distributed within each sector: Eight stations in each, apart from the Lyme Regis to Portland sector, where there were seven stations. Each sample station was 1 km²: sea-surface for the sub-province structure validation and seabed for the epibenthic sampling. The 1 km² scale reflects the pixel resolution of the remotely-sensed images and is the smallest scale at which it was possible to sample the remotely-sensed variables. The location of each sample station is indicated by the latitude and longitude of the north-west corner of the 1 km² site (listed in Appendix A5.1).
Each sample station was then classified as belonging to one of the three sub-provinces (SPs) according to its location (table 5.1 and figure 5.2).

Table 5.1: Allocation of sample stations to sub-provinces in the Lands End – Portland test area.

<table>
<thead>
<tr>
<th>Sub-Province (SP)</th>
<th>Sample Stations Allocated to Sub-Province</th>
<th>Total Number of Sample Stations per Sub-Province</th>
</tr>
</thead>
<tbody>
<tr>
<td>SP1</td>
<td>1, 13, 15, 16, 19, 22, 31</td>
<td>7</td>
</tr>
<tr>
<td>SP2</td>
<td>2, 8, 10, 11, 12, 14, 17, 18, 20, 21, 23, 30</td>
<td>12</td>
</tr>
<tr>
<td>SP3</td>
<td>3, 4, 5, 6, 7, 9, 24, 25, 26, 27, 28, 29</td>
<td>12</td>
</tr>
</tbody>
</table>

5.2.1.ii Validation of the sub-province structure in the Lands End – Portland test area

Mean monthly data (January to December; calculated from the 1998 – 2003 time series) for the three remotely-sensed variables were extracted from the 12-month temporal mean time-series (Chapter 2), for each of the 1 km² sample stations and normalized to allow comparison between the variables. Similarity between the sample stations for the three remotely-sensed variables was quantified using Euclidean distance as the metric.

The resulting matrix was subjected to a one-way Analysis of Similarities (ANOSIM routine in PRIMER V.6) to establish whether there was a statistically significant difference between the remotely-sensed variables of sampling stations in different sub-provinces. A global test (among all three sub-provinces) and pairwise comparisons between each sub-province were conducted. The null hypothesis ($H_0$) was that no significant difference existed between the three sub-provinces, in terms of the remotely-sensed variables of the sampling stations within those sub-provinces.

The sub-province structure was based on maximum gradients of change in the remotely-sensed properties (Chapter 3). However, there were no abrupt changes from one sub-province to another. The method by which the sample stations were allocated to sub-provinces did not take account of these gradients. Therefore, it was important to examine in more detail, the relationship between the remotely-sensed properties of the sampling stations and the...
delineation of the sub-provinces. Also, an investigation of the relationship between the remotely-sensed properties of each sampling station allowed an assessment of the degree to which any increased variability, resulting from the reduced window of observation, may have affected identification of the sub-province structure. For this reason the similarity matrix for the remotely-sensed data were subjected to NMDS ordination and Hierarchical Cluster Analysis (Group Average Method with similarity profiling (SIMPROF, PRIMER V.6) at $p < 0.01$). The clusters were overlaid on the NMDS ordination to verify the mutual consistency of the two representations and the sub-province to which each sample station was allocated was indicated.

![Sample Station Indicated as belonging to: SP1 • SP2 • SP3](image)

**Figure 5.2:** Location of the $31 \times 1 \text{ km}^2$ sample stations in the Lands End – Portland test area. The remotely-sensed (SST, log(Chl-a) and $L_{yy}(555)$) of the sample stations were used to test the validity of the sub-province structure at a reduced spatial scale to that of the whole English Channel. Samples of epibenthic fauna were collected from each station in order to test the hypothesis that the macro-scale distribution of epibenthic fauna will be predicted by the structure of the remotely-sensed sub-provinces.
The monthly mean values, for each remotely-sensed variable (SST, log(Chl-a) and \(L_{Wv}(555)\)), for each of the clusters identified in the NMDS ordination and the Hierarchical Cluster analysis, were statistically compared (Pearson Correlation Coefficient) with the mean monthly values for each of the sub-provinces, calculated from the sample stations contained within each sub-province. Confidence limits (95%) were also calculated in each case. Additionally, the annual mean and range of each of the remotely-sensed variables for each of the sampling stations were compared.

### 5.2.2 Results

The global test of the one-way ANOSIM, based on the monthly mean values of the remotely-sensed properties at each sample station, indicated that the difference between the three sub-provinces was highly significant \((R = 0.528, p < 0.001)\) and the null hypothesis was rejected. The pairwise comparisons between the sub-provinces are summarized in table 5.2.

<table>
<thead>
<tr>
<th>ANOSIM Pairwise Comparisons</th>
<th>(R) value</th>
<th>(p) value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SP1 vs SP2</td>
<td>(R = 0.427)</td>
<td>(p &lt; 0.01)</td>
</tr>
<tr>
<td>SP1 vs SP3</td>
<td>(R = 0.794)</td>
<td>(p &lt; 0.001)</td>
</tr>
<tr>
<td>SP2 vs SP3</td>
<td>(R = 0.428)</td>
<td>(p &lt; 0.001)</td>
</tr>
</tbody>
</table>

Table 5.2: Pairwise comparisons (ANOSIM) to test for statistical differences between the three sub-provinces, based on the remotely-sensed properties of the sample stations in the Lands End – Portland area.

Figure 5.3 displays the NMDS ordination of the relationship between sample stations based on the monthly mean values of the remotely-sensed variables at each station. The Kruskal stress value of 0.09 indicated that the 2-D NMDS ordination was a good representation of the relationship between the surface-ocean properties of the sample stations (Clarke and Warwick 2001). Three main clusters were identified by the Hierarchical Cluster Analysis and these were overlaid on the NMDS ordination in figure 5.3. The cluster to the left-hand side of the NMDS ordination contained all of the samples allocated to SP3 and also samples 2 (between St Austell and Looe), 8 (between Bigbury Bay and Start Point) and 30 (south-west of the 136
Lizard), from SP2, and sample 1 (Whitsands Bay), from SP1. The central cluster contained
the majority of the sample stations from SP2 (all located within Lyme Bay) and also sample
station 31, located in Mounts Bay, which mapped to SP1. The third cluster to the right of the
NMDS ordination contained the remaining five sample stations from SP1 and sample station
14 from SP2: all of which were located within Lyme Bay. The cluster to the left of figure 5.3
that contained mainly SP3 sample stations, was referred to as SP3', the central cluster that
contained mostly SP2 sample stations, was referred to as SP2' and the cluster to the right that
contained mainly SP1 sample stations, was referred to as SP1'.

The Pearson Correlation Coefficient values (r), for SP1 vs. SP1', SP2 vs. SP2' and SP3 vs.
SP3', all equaled 0.99 (p < 0.01) for the monthly mean values of SST and Lw,v(555). The
monthly mean log(Chl-a) values for sub-provinces vs. clusters also displayed a high degree of
similarity: \( r = 0.86 \) (p < 0.01) for SP1 vs. SP1', \( r = 0.96 \) (p < 0.01) SP2 vs. SP2' and \( r = 0.99 \)
(p < 0.01) for SP3 vs. SP3'.

Although the monthly mean values for the clusters were extremely similar to those of the
original sub-province allocations, the cluster arrangement of sample stations did reduce the
level of variance of the monthly mean values, for all three remotely-sensed variables,
compared to that of the original sub-province arrangement. Figures 5.4 (SST), 5.5 (log(Chl-
a)) and 5.6 (Lw,v(555)) display the monthly mean values of sub-provinces and clusters with
95% confidence intervals indicated. In figure 5.4.a, the 95% confidence intervals for the
monthly mean values of SST for SP1 and SP2 overlapped between February and November.
The 95% confidence intervals of the mean monthly SST values of SP3 were clearly distinct
from those of SP1 and SP2 between January and October, but were not distinct from those of
SP1 in November or December. The 95% confidence intervals for the cluster arrangements
SP1' and SP2' (analogous to SP1 and SP2) in figure 5.4.b had smaller ranges than those for
SP1 and SP2 (figure 5.4.a). Under the cluster arrangement the 95% confidence intervals for
the SST values for SP1' and SP2' were distinct from one another from December to April and
in August and September. The confidence intervals for the mean monthly SST of SP3'
indicated that they were distinct from the confidence intervals of both SP1' and SP2' through
out the year, with the exception of December, when SP2' and SP3' differed by only 0.12 °C.
The SP1 and SP2 log(Chl-a) monthly means and corresponding 95% confidence intervals (figure 5.5.a) exhibited a high degree of variability and were only distinct from one another during January, February, August, September and December. The log(chl-a) monthly means for SP3 were distinct from those of SP1 and SP2, except for during May and August where it was not different to the mean values of SP1 and during July where there was no difference between the three sub-provinces. In the cluster arrangement of sample stations (figure 5.5.a) the SP1’ and SP2’ 95% confidence intervals indicated that the monthly mean values were distinct from one another between September and April. SP3’ was distinct from SP1’ and SP2’, except for May and September when the 95% confidence limits overlapped.
The greatest difference in the variation around the monthly mean values between the sub-province and cluster arrangement of sample stations, occurred in the $L_w(N)(555)$ monthly mean values (figures 5.6.a and b). In the original sub-province arrangement (figure 5.6.a) the monthly mean values of SP1 and SP2 were not distinct from one another between April and May, or July and September. SP3 was not distinct from SP2 between June and August or from SP1 in July. Under the cluster arrangement of sample stations, the mean monthly values and 95% confidence intervals of all three sub-provinces were significantly clearly different with the exception of SP2' and SP3' during June (figure 5.6.b).

The annual mean and mean annual range values of $\log$(Chl-a) and $L_w(N)(555)$ were highly correlated ($r = -0.834 \ (p < 0.01)$ and $r = 0.929 \ (p < 0.01)$ respectively) for the Lands End – Portland area sample stations. The corresponding SST values also displayed a significant correlation ($r = -0.433 \ (p < 0.05)$). The sub-province to which each sample station was allocated is indicated in the comparison of annual mean and annual range of each of the remotely-sensed variables (figure 5.7). Sample stations 2, 8 and 30, that were originally classed as SP2, had SST (figure 5.7.a), $\log$(Chl-a) (figure 5.7.b) and $L_w(N)(555)$ (figure 5.7.c) annual mean and annual range values more akin to those of the SP3 sample stations, than the rest of the SP2 sample stations. Sample station 14 was also originally classed as SP2, but showed a greater resemblance to the SP1 annual mean and annual range values for all three remotely-sensed variables. Sample stations 1 and 31, initially classed as SP1, both exhibited SST and $\log$(Chl-a) annual mean and annual range values closer to those observed for SP2. However, for $L_w(N)(555)$, the annual mean and annual range values of sample station 1 were clearly more in-line with those of the SP3 sample stations and sample station 31 showed a greater resemblance to the SP2 sample stations.
Figure 5.4: SST (°C) monthly means with 95% confidence intervals of each sub-province, calculated from the SST mean monthly values of each of the sample stations contained within that sub-province: a) original allocation of sample stations to sub-provinces and b) allocation of sample stations to sub-provinces as indicated by the clusters identified in the NMDS ordination in figure 5.3.
Figure 5.5: $\log(\text{Chl-a}) \ (\text{mg m}^{-3})$ monthly means with 95% confidence intervals of each sub-province, calculated from the $\log(\text{Chl-a})$ mean monthly values of each of the sample stations contained within that sub-province: a) original allocation of sample stations to sub-provinces and b) allocation of sample stations to sub-provinces as indicated by the clusters identified in the NMDS ordination in figure 5.3.
Figure 5.6: \( L_{\text{555}} \) (mW cm\(^{-2}\) \( \mu \)m\(^{-1}\) sr\(^{-1}\)) monthly means with 95% confidence intervals of each sub-province, calculated from the \( L_{\text{555}} \) mean monthly values of each of the sample stations contained within that sub-province: a) original allocation of sample stations to sub-provinces and b) allocation of sample stations to sub-provinces as indicated by the clusters identified in the NMDS ordination in figure 5.3.
Figure 5.7.a: SST (°C). Annual mean values plotted against annual range values of the remotely-sensed variables at each of the 31 x 1 km² sample stations in the Lands End – Portland test area. SST annual range vs. annual mean $r = -0.433$ ($p < 0.05$).

Figure 5.7.b: $\log(\text{Chl-a})$ (mg m⁻³). Annual mean values plotted against annual range values of the remotely-sensed variables at each of the 31 x 1 km² sample stations in the Lands End – Portland test area. $\log(\text{Chl-a})$ annual range vs. annual mean $r = -0.834$ ($p < 0.01$).
5.2.3 Discussion on the validity of sub-province structure at reduced spatial scale

The sub-province structure, based on the spatial and temporal heterogeneity of water column physical structure and associated patterns of productivity, observed at the scale of the whole English Channel system also holds at the reduced spatial scale of the Lands End – Portland test site. The gradient of change in the remotely-sensed variables from the coastal waters of SP1 to SP2 and then to the more oceanic conditions of SP3 was reflected in pairwise comparisons of the sub-provinces. Clear differences were detected between the sample stations of SP1 vs SP2 and SP2 vs SP3, but the greatest difference existed between the sample stations of SP1 vs SP3. A station by station assessment of the relationship between the remotely-sensed variables further substantiated the validity of the sub-province structure in the test site. However, six of the 31 sample stations (19.35%) were identified as having remotely-sensed properties that were typical of a different sub-province to that which they were allocated. Sample stations 2 (between St. Austell and Looe), 8 (between Bigbury Bay and Start Point) and 30 (south-west of the Lizard) were all initially allocated to SP2 but displayed surface-ocean properties that were more alike to sample stations in SP3. The sample stations...
station located in Mounts Bay (31) was initially categorized as SP1, but showed greater similarity to the other SP2 sample stations. The reverse was true for sample station 14 (Lyme Bay): initially categorized as SP2, but displayed greater similarity to the SP1 sample stations. Sample station 1 (initially classed as SP1) was located in Whitsands Bay: the region between Plymouth and Lands End which exhibited a sharp gradient from the dominant oceanic type waters of SP3 to the coastal waters of SP1.

An examination of the annual mean and range values at each sample station for each of the remotely-sensed variables, also highlighted the six stations detailed above as anomalies in the sub-province allocation. The sample stations to the west of Start Point displayed annual mean and range SST values that are typical of the more oceanic regime of SP3: higher annual mean SST and a lower annual range than shallower coastal regions. A clear divide in the sample stations to either side of Start Point also existed in the log(Chl-a) annual mean and range values. The sample stations to the west had lower annual mean and higher annual range values of log(Chl-a) than those to the east. Both the log(Chl-a) and SST observations were in agreement with observations of temperature and primary productivity in this area of the English Channel (Pingree et al. 1975; Holligan and Harbour 1977; Pingree 1980; Spooner 2001).

The region of the English Channel dominated by SP3 undergoes seasonal stratification and is more thermodynamically stable than the well-mixed regions of SP2 and SP1, which exhibited a greater annual temperature range than SP3. The high range of log(Chl-a) values observed in the SP3 sample stations was consistent with the spring and autumn blooms that are a feature of the onset and retreat of seasonal stratification (Pingree et al. 1976; Holligan and Harbour 1977; Pingree 1980). The shallower well-mixed conditions of Lyme Bay promote a higher level of primary production and exhibit much less seasonal variation than the seasonally stratified region to the west of Start Point (see Chl-a climatologies in Chapter 2 of this thesis). The distinction between the Lyme Bay sample stations and those to the west of Start Point was confirmed by the LWN(555) annual mean and annual range values. High LWN(555) values are typical of well-mixed regions and coastal regions with riverine input (IOCCG 2000; Binding et al. 2003). The SP1 sample stations were separated from the SP2 sample stations in Lyme Bay by higher annual mean LWN(555) and log(Chl-a) values and a higher annual range of SST. LWN(555) also appeared to be the distinguishing factor in separating sample station 31 (Mounts Bay) from the predominantly SP3 sample stations west of Start Point.
Under the cluster arrangement, the monthly mean values of the three sub-provinces were more distinct from one another: particularly the $L_{mR}(555)$ and $\log(\text{Chl-a})$ mean monthly values. The months when the mean monthly values of the clusters were not significantly different from each other related to particular oceanographic phenomena. For example, the SST mean monthly values of SP$1'$ and SP$2'$ were not significantly distinct between May and July or October and November. These two periods coincide with rapid heating and cooling of shallower, well-mixed regions under the peak of the net heating phase and the early rapid cooling phase of the annual heating cycle at the sea surface (Pingree 1980). The $\log(\text{Chl-a})$ mean seasonal cycle of SP$3'$ was not statistically distinct from that of SP$1'$ during May and September which coincides with the Spring and Autumn bloom events (Holligan and Harbour 1977).

The boundaries between sub-provinces are not absolute: they are based on gradients of variation in the remotely-sensed variables. Also, the sub-province structure is based on intra-annual heterogeneity in water column structure. Therefore, Platt and Sathyendranath's (1999) concept of elastic sub-province boundaries, for observations of forcing at time scales of one year or less, will apply. The six sample stations (1, 2, 8, 14, 30 and 31) whose sub-province allocation altered under the cluster arrangement of sample stations are all located directly on the boundaries between sub-provinces or in regions where maximum gradients of variation between sub-provinces exist. Therefore, variation between the initial allocation of sample stations to sub-provinces and the clusters of sample stations was primarily due to the nature of the sub-province boundaries rather than an increase in variation as a result of the decreased window of observation. The cluster arrangement of sample stations was considered to be a better representation of sub-province structure in the test area. Hence the clusters (SP$'$) were used as a revised allocation of sample stations to sub-provinces for the comparison between the distribution of epibenthic fauna and sub-province structure.

The revised allocation of sample stations to sub-provinces, under the cluster arrangement, is detailed in table 5.3 and figure 5.8 displays the geographical translation of the revised sub-province allocation.
Table 5.3: Revised allocation of sample stations to sub-provinces (cluster arrangement) in the Lands End – Portland test area.

<table>
<thead>
<tr>
<th>Sub-Provincial (SP')</th>
<th>Sample Stations Allocated to Sub-Province – Cluster Arrangement</th>
<th>Total Number of Sample Stations per Sub-Province (SP')</th>
</tr>
</thead>
<tbody>
<tr>
<td>SP1'</td>
<td>13, 14, 15, 16, 19, 22</td>
<td>6</td>
</tr>
<tr>
<td>SP2'</td>
<td>10, 11, 12, 17, 18, 20, 21, 23, 31</td>
<td>9</td>
</tr>
<tr>
<td>SP3'</td>
<td>1, 2, 3, 4, 5, 6, 7, 8, 9, 24, 25, 26, 27, 28, 29, 30</td>
<td>16</td>
</tr>
</tbody>
</table>

Figure 5.8: Geographic translation of the revised allocation of the 31 x 1km2 sample stations to sub-provinces (SP').
5.3 Predicting the biogeographic distribution of epibenthic fauna from the remotely-sensed sub-province structure.

5.3.1 Methods

5.3.1.i Sampling of epibenthic fauna

The survey of epibenthic megafauna conducted as part of this study was carried out from the R.V. Plymouth Quest (Appendix A5.2) between July and October 2004. This study concentrated on three major taxa: echinoderms, crustaceans and molluscs.

These taxa are the dominant epibenthic taxa in the majority of shelf seas (e.g. Ursin 1960; Holme 1961; 1966; Schneider et al. 1987; McClintock 1994; Kaiser et al. 1999; Rees et al. 1999; Ellis and Rogers 2000; Ellingsen 2001; Freeman and Rogers 2003; De Leo and Pires-Vanin 2006) and they include a variety of trophic groups (e.g. active-predators, scavengers, filter-feeders, grazers and detritivores).

The abundance and large size of these animals makes them suitable for collection via trawling and for identification in the field. Samples were collected using a mini-Agassiz trawl: a 1.1 m x 0.3 m steel frame with a fine inner mesh (< 10 mm) and outer 40 mm mesh cod-end (figure 5.9). Therefore, the epibenthic megafauna assessed in this study were defined as any echinoderm, crustacean or mollusc species that were collected by the mini-Agassiz trawl.

Figure 5.9: The mini-Agassiz trawl used in the macro-scale survey of mega epibenthic fauna in the Lands End – Portland test site.
The same sample stations that were used to test the validity of the sub-province structure in the Lands End – Portland test area, were also used for the survey of epibenthic fauna. The sample stations were selected \textit{a priori} of the sub-province structure. The 1 km\(^2\) sample station area was selected as this was the finest spatial scale at which the remotely-sensed variables could be sampled for comparison with the epibenthic fauna.

By selecting 1 km\(^2\) sample stations an assumption of homogeneity at 1 km\(^2\) in the spatial scale of the distribution of epibenthic megafauna in the English Channel was made. Therefore, four replicate epibenthic trawls were taken within each 1 km\(^2\) sample station in order to test the assumption of homogeneity. The sample station was divided into four equal quadrants (labeled a, b, c and d (figure 5.10)) and a randomly located trawl was taken from each quadrant.

![Figure 5.10: Schematic of the division of each 1 km\(^2\) sample station into quadrants for replicate sample collection. The cross at the top left-hand corner indicates the location reference point (latitude and longitude) for each sample station.](image)

This study focuses on macro-scale physical dynamics and their influence on the regional biogeography of benthic fauna. While there is undoubtedly spatial variation in the distribution of benthic fauna at scales of less than 1 km\(^2\), that variation is likely to be the product of biological interactions between organisms (e.g. competition or predation) (Parsons \textit{et al.} 1977; Brown 1995) or smaller-scale physico-chemical variation (e.g. Kendall and Widdicombe 1999) rather than the broad-scale physical dynamics examined in this study.
All trawls were towed at speeds of between 1.8 and 2 knots for a 10 minute period, starting with the locking of the winch when seabed contact was made and finishing with the commencement of hauling. The average area of seabed covered in each tow was 642 m² (σ = 43 m²). Morrisey et al. (1998) state that abundance data from trawls and dredges may only be considered as semi-quantitative, unless any biases involved in sampling are quantifiable and consistent. Whilst it is possible to standardize tow duration, speed and animal size class, there are other factors such as sediment type and the effect of weather conditions on sea-state that may influence the quality of the trawl sample. Despite the limitations mentioned above, trawling remains one of the most effective method of sampling epi-benthic mega-fauna over large spatial scales and can provide useful data on the types and distributions of benthic assemblages (McIntyre 1978). The four replicate trawls collected from within each sampling station will also help to eradicate biases in the trawl data (Rees et al. 1999).

The entire contents of each trawl was emptied into containers on the ship deck and processed through a 5 mm sieve. All echinoderms, molluscs and crustaceans were retained in seawater filled trays, identified to species level (where possible), counted and then returned to the sea alive to reduce the impact of trawling. If it was not possible to identify a particular species on deck, the animal was preserved in formalin (4%) and taken to Plymouth for identification. Although Holme (1961; 1966) found the analysis of dead bivalve and gastropod shells to be useful in his study of the benthic fauna of the English Channel, only live specimens were recorded in this study as the large sample volume made the analysis of dead material impractical.

Owing to adverse meteorological conditions, mechanical complications with the ship and potential encounters with sub-sea telephone cables it was not possible to obtain benthic samples from all of the intended stations. Replicate samples were collected for 20 of the 31 sample stations (figure 5.11). The allocation of these sample stations to sub-provinces (SP') is presented in table 5.4.

Sediment samples were retained at each sample station and classified according to the Folk Classification (1954) (including modifications made by the British Geological Survey (2002)). The depth (m) of each sample station was also recorded from the Medium Resolution Continental Shelf Model (MRCS) bathymetry data (see Chapter 4 for full details).
Table 5.4: Sample stations (revised sub-province allocation) in the Lands End – Portland test area where it was possible to obtain four replicates trawls of epibenthic fauna.

<table>
<thead>
<tr>
<th>Sub-Province (SP')</th>
<th>Sample Stations Allocated to Sub-Province (Revised Allocation)</th>
<th>Total Number of Sample Stations per Sub-Province</th>
</tr>
</thead>
<tbody>
<tr>
<td>SP1'</td>
<td>13, 14, 15, 16, 19, 22</td>
<td>6</td>
</tr>
<tr>
<td>SP2'</td>
<td>11, 12, 17, 18</td>
<td>4</td>
</tr>
<tr>
<td>SP3'</td>
<td>4, 5, 6, 8, 9, 24, 25, 26, 27, 29</td>
<td>10</td>
</tr>
</tbody>
</table>

Figure 5.11: Sample stations in the Lands End – Portland test area where it was possible to collect four replicate benthic trawls. The stations where it was not possible to obtain samples are indicated by white markers.
5.3.1.ii Test for similarity in epibenthic assemblages within 1 km$^2$ sample stations

By selecting 1 km$^2$ sample stations to correspond to the resolution of the remotely-sensed surface-ocean data assumptions about the distribution of the epibenthic fauna were made i.e. that the magnitude of difference in epibenthic assemblages was greater between sample stations than within each 1 km$^2$ station. The suitability of the four trawls taken within each 1 km$^2$ sample station as replicate samples for that station, was tested via the use of a one-way ANOSIM procedure (PRIMER V.6). The ANOSIM was calculated using $\sqrt{\lambda}$-transformed data. The Bray-Curtis coefficient (Bray and Curtis 1957) was used as the similarity measure (here and in all further multivariate analysis of ecological data in this Chapter) as it is considered to be the most robust coefficient for use with species data in multivariate ecological studies (Faith et al. 1987; Clarke and Warwick 2001).

5.3.1.iii Comparison of the biogeographic distribution of epibenthic fauna with the structure of the remotely-sensed sub-provinces.

Sample station mean abundance values of each species and total species richness were calculated from the four replicate trawls taken within each 1 km$^2$ station. The replicate data for each station was summarized in this way to: a) allow a direct comparison of the epibenthic data with the remotely-sensed variables on a station by station basis and b) reduce potential biases in the sampling method (trawling). Species lists for each oceanographic sub-province were also compiled and species occurring in only one of the sub-provinces and those occurring across all three sub-provinces were noted. The most suitable data transformation for sample station mean abundance values was decided after initial examination of the data and results using transformed and untransformed data were compared. As with the test for homogeneity of distribution of epibenthic fauna at 1 km$^2$, the Bray-Curtis Coefficient was used to quantify similarity.

A one-way ANOSIM (PRIMER V.6) (Clarke and Green 1988) was used to determine if there were statistically significant differences between the epibenthic fauna of the three sub-provinces. A global test among all three sub-provinces and pairwise comparisons between individual sub-provinces were conducted.

NMDS and Hierarchical Cluster Analysis (Group Average Method) were used to further examine the relationship between the 1 km$^2$ sample stations in terms of the mean abundances of epibenthic fauna. The clusters resulting from the Hierarchical Cluster Analysis were overlaid on the NMDS ordination and the sub-province, to which each sample station is
allocated, was indicated. An NMDS ordination was also created using the full set of replicate abundance data at each sample station and was compared with the NMDS ordination of station mean abundances.

NMDS ordinations of the relationship between sample stations, in terms of mean abundances of epibenthic fauna and in terms of remotely-sensed properties, were compared. Non-parametric regression analysis and the Coefficient of Determination ($R^2$) were used to assess the relationship between the underlying similarity matrices of the two ordinations (figure 5.12). Similarity in the distribution of each separate phylum (echinoderms, crustaceans and molluscs) of the epibenthos was also compared ($R^2$ values) with similarity between sample stations in terms of remotely-sensed variables.

The essential information on the multivariate structure of the species abundance matrix is summarized in the Bray-Curtis similarities between sample stations. These similarities are visualised by the NMDS and Hierarchical Cluster Analysis forming a framework within which the patterns of individuals species abundances can be interpreted (Clarke and Warwick 2001). In order to identify the species responsible for a specific facet of the multivariate picture, it is necessary to disassemble the Bray-Curtis similarities. The Similarity Percentages (SIMPER) routine in PRIMER (V.6) (Clarke and Warwick 2001) achieves this identification by assessing each species' contribution to average similarity within a group and average dissimilarity between groups. SIMPER was applied to the differences in epibenthic faunal composition between the sub-provinces. Species that had a high ratio ($> 1.5$), between the mean and the standard deviation of their dissimilarity contribution, were selected as being good discriminating species (Clarke and Warwick 2001) between the sub-provinces in question. A Bray-Curtis similarity matrix of the relationship between sample stations based on the sub-set of species identified by the SIMPER analysis was compared ($R^2$ values) to the similarity matrix based on the full set of species. The distribution and abundance of the sub-set of species identified by the SIMPER routine were then overlaid on the mean station abundance NMDS ordination and the differences in distribution and abundance between sub-provinces was discussed.
Figure 5.12: Schematic of the comparison between the two similarity matrices (non-parametric Regression Analysis and Coefficient of Determination) detailing the relationship between the sample stations in the Lands End – Portland test area in terms of a) epibenthic faunal assemblage and b) remotely-sensed variables.
The distance (km) between each sample station was calculated and the effect of spatial autocorrelation between epibenthic assemblages at the sample stations was examined using non-parametric regression analysis and the Coefficient of Determination ($R^2$). It was hypothesized that sample stations that were located close to one another would have epibenthic assemblages that were more similar than those of stations located further apart (Brown 1984).

The variation in epibenthic assemblages recorded at each sample station was additionally related to substrate type and to depth. Substrate type was classified according to the Folk Classification (1954) and depth was categorized into 10 m intervals. Both factors were overlaid separately on the NMDS ordination of epibenthic assemblages and one-way ANOSIM tests were employed to test for significant differences between the epibenthic fauna associated with each substrate type and with each 10 m depth interval.

A range of diversity measures were also employed to review the variation in epibenthic fauna. The mean and 95% confidence intervals of the following diversity measures were calculated for the total epibenthic fauna and also for each separate phyla, in each of the sub-provinces:

- Number of Individuals ($N$)
- Number of Species ($S$),
- Simpson's Index ($1 - \lambda'$) (Simpson 1949)
- Average Taxonomic Distinctness ($\Delta^*$) (Warwick and Clarke 1995)

The $1 - \lambda'$ form of Simpson's Index (equation 5.1) was selected as it is a measure of evenness, it is suitable for smaller sample sizes and is less sensitive to the degree of sampling effort (Clarke and Warwick 2001): an important consideration as the number of sample stations in each sub-province is unbalanced.

\begin{equation}
Equation 5.1: \quad 1 - \lambda' = 1 - \left\{ \frac{\sum_i N_i (N_i - 1)}{N (N - 1)} \right\}
\end{equation}
Average Taxonomic Diversity ($d^*$) was also chosen as the other diversity measures selected do not take account of phylogenetic diversity. Clarke and Warwick (2001) describe $d^*$ as:

".....the expected taxonomic distance apart of any two individuals chosen at random from the sample, provided that those two individuals are not from the same species."

and is calculated as follows (equation 5.2):

$$
\text{Equation 5.2: } d^* = \left( \frac{\sum \omega_{ij} x_i x_j}{\sum x_i x_j} \right)
$$

where $i$ and $j$ are the two species being compared, $\chi$ is the species abundance and $\omega_{ij}$ is the taxonomic distance apart, through the classification tree of species $i$ and $j$. As the average Taxonomic Distinctness is based on Simpson's Index, it also inherits the advantages of sample size independence (Clarke and Warwick 2001).
5.3.2 Results

5.3.2.i Summary of epibenthic fauna recorded
A total of 37,448 epibenthic individuals were collected, identified and counted across the 20 sample stations. 77 species were recorded: 18 were echinoderms, 19 were crustaceans and 40 were molluscs (figure 5.14). All of the 19 crustacean species recorded were decapods; the echinoderms comprised asteroids (38.89%), echinoids (22.22%), ophiuroids (33.33%) and holothuroids (5.56%). The mollusc species consisted of bivalves (50%), gastropods (42.5%), cephalopods (5%) and polyplacophorans (2.5%). All nomenclature follows the Marine Conservation Society Species Directory (MCS 1997).

5.3.2.ii Test for similarity in epibenthic assemblages within 1 km² sample stations
The global test of the one-way ANOSIM, to test the magnitude of between to within differences in epibenthic assemblage similarity was highly significant ($R = 0.873$, $p < 0.001$). As a result of this analysis, the four trawls taken within each 1 km² sample station were considered to be suitable replicate trawls for that particular sample station.

5.3.2.iii Comparison of the biogeographic distribution of epibenthic fauna with the structure of the remotely-sensed sub-provinces.
Station mean values (mean number of individuals of each species) for each species were calculated from the four replicate trawls at each sample station. The mean number of individuals ($N$) and the total number of species ($S$) for each sample station are summarised in figures 5.13 and 5.14.

The highest mean number of individual animals ($N = 3175$) was recorded at sample station 15 in SP1' and the lowest number ($N = 53.5$) were found at sample station 6 in SP3' (figure 5.13). Total number of species ($S$) ranged from $S = 34$ at sample station 24 (SP3') to $S = 10$ at sample station 13 (SP1') (figure 5.14). The maximum number of echinoderm, crustacean and mollusc species recorded at any one sample station were 10 (sample stations 4 and 27 in SP3'), 12 (sample stations 4 and 25 in SP3') and 14 (sample station 24 also in SP3') respectively. Of the 77 species identified in the survey 19.48% were found at only one station and 22.1% occurred at more than 50% of the sampling stations. *Pagurus bernhardus* and the *Macropodia spp.* were recorded at all of the sample stations in the survey.
Figure 5.13: Mean number of individuals (N) recorded at each sample station (calculated from the four replicate trawls). Standard deviations are indicated.

Figure 5.14: Total species richness (S) recorded at each sample station (calculated from the four replicate trawls).
31.2% of species were found to occur in only one of the three sub-provinces (table 5.5 and full species lists for each sub-province can be found in Appendix A5.3). The majority of these species were considered to be rare as they were only recorded at one sample station (Indicated by * in table 5.5). The only exceptions to this were Anseropoda placenta, Marthasterias glacialis, Luidia ciliaris, Jujubinus striatus and Astarte sulcata, all unique to the SP3' sample stations and Gonoplax rhomboides, Liocarcinus pusillus and Corbula gibba found only in SP1'.

Table 5.5: List of species found to occur in only one of the three sub-provinces. * Indicates that the species was recorded at only one (≤ 5%) of the sample stations.

<table>
<thead>
<tr>
<th>Phyla</th>
<th>Species observed only in SP1*</th>
<th>Species observed only in SP2*</th>
<th>Species observed only in SP3*</th>
</tr>
</thead>
<tbody>
<tr>
<td>echinodermis</td>
<td>Total = 0</td>
<td>Amphiura filiformis*</td>
<td>Anseropoda placenta</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total = 1</td>
<td>Luidia ciliaris</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Marthasterias glacialis</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Trachythone elongata*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total = 4</td>
</tr>
<tr>
<td>crustaceans</td>
<td>Apheus glaber*</td>
<td>Total = 0</td>
<td>Cancer Pagurus*</td>
</tr>
<tr>
<td></td>
<td>Ebatis cranchii*</td>
<td></td>
<td>Liocarcinus pusillus</td>
</tr>
<tr>
<td></td>
<td>Gonoplax rhomboides</td>
<td></td>
<td>Total = 2</td>
</tr>
<tr>
<td></td>
<td>Total = 3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>molluscs</td>
<td>Chlamys varia*</td>
<td>Epitonium clathrus*</td>
<td>Arctica islandica*</td>
</tr>
<tr>
<td></td>
<td>Corbula gibba</td>
<td>Total = 1</td>
<td>Astarte sulcata</td>
</tr>
<tr>
<td></td>
<td>Ocnebra sp.*</td>
<td></td>
<td>Colus jeffreysianus*</td>
</tr>
<tr>
<td></td>
<td>Phaxus pellucidus*</td>
<td></td>
<td>Erato voluta*</td>
</tr>
<tr>
<td></td>
<td>Thyasira flexuosa*</td>
<td></td>
<td>Jujubinus striatus</td>
</tr>
<tr>
<td></td>
<td>Total = 5</td>
<td></td>
<td>Scaphander lignarius*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Simnia patila*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Trivia arctica*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total = 8</td>
</tr>
</tbody>
</table>

37.66% species were recorded in all three of the oceanographic sub-provinces: 38.89% of the echinoderm species, 63.16% of the crustacean species and 25% of the mollusc species (table 5.6).
Table 5.6: List of species found in all three sub-provinces.

<table>
<thead>
<tr>
<th>Phyla</th>
<th>Echinoderms</th>
<th>Crustacea</th>
<th>Molluscs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Asterias rubens</td>
<td>Atelecyclus rotundus</td>
<td>Aequipecten opercularis</td>
</tr>
<tr>
<td></td>
<td>Astropecten irregularis</td>
<td>Crysistes cassivelaunus</td>
<td>Buccinum undatum</td>
</tr>
<tr>
<td></td>
<td>Ophiithrix fragilis</td>
<td>Ebalia tumefacita</td>
<td>Chamelea gallina</td>
</tr>
<tr>
<td></td>
<td>Ophiura affinis</td>
<td>Galathea sp.</td>
<td>Chlamys tigerina</td>
</tr>
<tr>
<td></td>
<td>Ophiura albida</td>
<td>Hyas sp.</td>
<td>Crepidula fornicata</td>
</tr>
<tr>
<td></td>
<td>Ophiura ophiura</td>
<td>Inachus sp.</td>
<td>Nassarius reticulatus</td>
</tr>
<tr>
<td></td>
<td>Psammechinus miliaris</td>
<td>Liocarcinus depurator</td>
<td>Parvicardium ovale</td>
</tr>
</tbody>
</table>

**Total = 7**

|                            | Total = 9                     |
|                            | Macropodia sp.                |
|                            | Maja squinado                 |
|                            | Pagurus bernhardus            |
|                            | Pagurus prideauxii            |
|                            | Porcellana longicornis        |

**Total = 12**

Initial examination of the mean species abundances at each sample station revealed values ranging from 0.25 (one individual of a particular species found within the four replicate trawls) to 3000 (large aggregations of certain species e.g. *Turrilelta communis*). A method of transforming the epibenthic data to down-weight the abundant species and to allow the mid-range and rarer species to exert a greater influence on the calculation of similarity was necessary. A presence/absence transformation would achieve this result. However, as one fifth of the observed species are present in varying abundances at more than 50% of the sample stations, it was decided that much important information on the distribution of epibenthic species would be lost. A $\sqrt{N}$-transformation would serve to down-weight abundant species while retaining information on the variation of species abundance and was applied to the epibenthic data.

The null hypothesis ($H_0$), that there was no significant difference between the assemblages recorded in each of the three sub-provinces was rejected; the Global multivariate test presented a highly significant result ($R = 0.515, p < 0.001$).
Table 5.7: Pairwise comparisons between sub-provinces in a one-way ANOSIM to test for statistical difference between the epibenthic faunal assemblages of those sub-provinces.

<table>
<thead>
<tr>
<th>ANOSIM Pairwise Comparisons</th>
<th>R value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SP1' vs SP2'</td>
<td>R = 0.067</td>
<td>p &lt; 0.233</td>
</tr>
<tr>
<td>SP1' vs SP3'</td>
<td>R = 0.651</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>SP2' vs SP3'</td>
<td>R = 0.536</td>
<td>p &lt; 0.002</td>
</tr>
</tbody>
</table>

The pairwise comparisons (table 5.7) revealed statistically significant differences between SP1' and SP3' and SP2' and SP3', but not between SP1' and SP2', which indicated a difference in the epibenthic assemblages of Lyme Bay and the region to the west of Start Point.

The majority of the replicates for each station were clustered tightly together in figure 5.15.b and the pattern displayed mirrors that of figure 5.15.a. Therefore, it was concluded that the use of the station mean abundance values were suitable for the comparison of the relationship between sample stations in terms of epibenthic assemblages and remotely-sensed variables.

The distinction between the epibenthic fauna of Lyme Bay (SP1' and SP2') and the region to the west of Start Point (SP3'), indicated in the ANOSIM test (table 5.7) was not immediately evident in figure 5.15.a. The SP2' sample stations were more closely allied to those in SP3' than SP1': a relationship that was also apparent in the NMDS ordination of the surface-ocean properties of each of the sample stations (figure 5.15.c). In figure 5.15.a, a gradient existed across Lyme Bay (SP1' and SP2'), from the sample stations in the western half (13 and 15 – Brixham to Exmouth) to those located more centrally (11, 14 and 16 – Start Point to Lyme Regis) and finally to stations 12, 17, 18 and 19 (across the mouth of Lyme Bay between Start Point and Portland). The SP2' stations at the mouth of Lyme Bay displayed a strong degree of similarity to the SP3' sample stations that were located to the west of Start Point. A gradient was also present between these SP2' and SP3' stations, with stations 12, 17 and 18 being more alike to the SP3' stations between Plymouth and St. Austell (4, 5, 6, 8, 9 and 24) than they were to the SP3' stations between Falmouth and the Lizard (25, 26, 27 and 29). Station 22 (SP1' - Portland Bill) was an exception to this gradient as it showed greater similarity to the SP3' stations around the Lizard peninsula than to any of the Lyme Bay stations.
Figure 5.15: Comparison of the NMDS ordinations of the relationship between the Lands End – Portland test area sampling stations in terms of a) epibenthic faunal assemblage (Bray-Curtis similarity) – Station mean abundances, b) epibenthic faunal assemblage (Bray-Curtis similarity) - All replicate samples and c) remotely-sensed variables (Euclidean distance).
Figure 5.15.c shows the NMDS ordination (results of the Hierarchical Cluster Analysis are overlaid) of the remotely-sensed variables of the 20 stations where epibenthic samples were collected. The distinction between sub-provinces was still clear, despite a 35.5% reduction in sample stations from the analysis performed in the section 5.2.2 of this chapter. The distinction between the SP3' sample stations in the Start Point to St. Austell area and those located between Falmouth Bay and the Lizard was also evident in figure 5.15.c. The change in the relationship of the SP1' sample stations to one another and to the SP2' and SP3' sample stations, was the most dramatic difference between the two ordinations. In figure 5.15.a, the ordination of the epibenthic assemblages, there was a high degree of variance amongst the SP1' sample stations, whereas in figure 5.15.c, the ordination of the remotely-sensed variables, the SP1' sample stations clustered together well. In both cases sample station 13 was something of an anomaly and stood out from the other sample stations. Sample stations 19, 16, 15 and 14, that were all closely linked in figure 5.15.c, are all centrally located in figure 5.15.a, although they were not as closely allied as they were in figure 5.15.c. In figure 5.15.c, station 22 was strongly linked to the other SP1' sample stations, but in figure 5.15.a, it was linked to the SP3' sample stations. Although it is worth noting that the relative distances of sample stations 18, 19 and 22 from one another actually varied very little between the two ordinations.

The relationship between the two similarity matrices underlying the NMDS ordinations in figures 5.15.a and c was also assessed by a means of a non-parametric regression of the remotely-sensed variables (Euclidean Distance) on epibenthic similarities (Bray-Curtis Coefficient). The regression analysis showed a positive but non-significant relationship for √Λ-transformed epibenthic data.

Figure 5.16 shows the rank value of the Euclidean distances, dissimilarity measures, plotted against the rank values of the Bray-Curtis similarities. Therefore, the relationship between the two variables appears negative when it is in fact positive. Similarity in remotely-sensed variables between sample stations predicted similarity in epibenthic megafauna (√Λ-transformed data) with $R^2 = 0.27$. Non-parametric regression analysis of similarities between sample stations in terms of the remotely-sensed variables on untransformed epibenthic similarities (Appendix A5.4) also displayed a positive but non-significant relationship with a $R^2$ value ($R^2 = 0.21$).
Figure 5.16: Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and $\sqrt{N}$-transformed epibenthic assemblages (Bray-Curtis similarities) \( (R^2 = 0.27) \)

The $R^2$ values for each phyla are summarised in table 5.8. The correlations between the distribution of echinoderms, crustaceans and mollusc species and the remotely-sensed properties of the 20 sample stations were all highly significant. All phyla exhibited positive but non-significant relationships in the regression analysis and had low $R^2$ values. The scatter plots from the regression analysis are included in Appendix A5.4.
Table 5.8: $R^2$ values for the distribution of each epibenthic phyla and the variation in remotely-sensed properties at the 20 sample stations in the Lands End – Portland test area.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Echinodermata</td>
<td>$R^2 = 0.20$</td>
</tr>
<tr>
<td>Crustacea</td>
<td>$R^2 = 0.29$</td>
</tr>
<tr>
<td>Mollusca</td>
<td>$R^2 = 0.17$</td>
</tr>
</tbody>
</table>

The average Bray-Curtis dissimilarity (table 5.9) between the epibenthic assemblages of the three sub-provinces agreed with the relationship between the sub-provinces based on their remotely-sensed properties i.e. that SP2' and SP3' were more closely related to each other than either sub-province was to SP1'. The greatest average dissimilarity occurred between SP1' and SP3' which was consistent with the notion of a gradient of change in the composition of epibenthic assemblages from SP1' to SP3'. All three pairwise combinations of sub-provinces had between 50% and 60% of their species in common.

Table 5.9: Average Bray-Curtis dissimilarity, combined species richness and number of species in common (expressed as percentage in parenthesis) for each pair of sub-provinces.

<table>
<thead>
<tr>
<th>Sub-province Comparison</th>
<th>Combined Species Number (S)</th>
<th>Number of Common Species</th>
<th>Average Bray-Curtis Dissimilarity</th>
</tr>
</thead>
<tbody>
<tr>
<td>SP1' vs. SP2'</td>
<td>63</td>
<td>36 (57.1%)</td>
<td>61.60%</td>
</tr>
<tr>
<td>SP1' vs. SP3'</td>
<td>75</td>
<td>39 (52.0%)</td>
<td>65.27%</td>
</tr>
<tr>
<td>SP2' vs. SP3'</td>
<td>69</td>
<td>36 (52.2%)</td>
<td>43.59%</td>
</tr>
</tbody>
</table>

A total of 30 species (38.96% of all the species recorded during the survey) were identified by the SIMPER routine as being the primary contributors to the difference between the three sub-provinces in terms of epibenthic fauna (table 5.10). A comparison ($R^2$) of the similarity matrices describing the relationship between sample stations using only the 30 species...
identified in the SIMPER routine and all of the 77 species recorded during the survey, showed that the subset of 30 species were a good surrogate for most of the variation between the sample stations ($R^2 = 0.97$). Most of the species (76.67%) identified by the SIMPER analysis, as being primarily responsible for the observed pattern of species distribution, were recorded in all three sub-provinces. Also, 56.66% of these species were recorded at more than 50% of the sample stations.

The distribution of each of the echinoderms species were overlaid on the NMDS ordination of the relationship between epibenthic assemblages at each sample station (figure 5.15.a) in Appendix A5.5. Appendix A5.6 shows the distribution of each of the Crustacean species and Appendix A5.7 shows the distribution of each mollusc species. The order of species in Appendices A5.5, A5.6 and A5.7 correspond to the order in table 5.10.

Table 5.10: The sub-set of 30 species identified in the SIMPER analysis of the three sub-provinces.

<table>
<thead>
<tr>
<th>Echinoderm Species</th>
<th>Crustacean Species</th>
<th>Mollusc Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Anseropoda placenta</td>
<td>a) Atelecyclus rotundus</td>
<td>a) Aequipecten opercularis</td>
</tr>
<tr>
<td>b) Asterias rubens</td>
<td>b) Ebalia tumefacta</td>
<td>b) Antalis entails</td>
</tr>
<tr>
<td>c) Astropecten irregulais</td>
<td>c) Galathea sp.</td>
<td>c) Chamelea gallina</td>
</tr>
<tr>
<td>d) Echinus esculentus</td>
<td>d) Gonoplax rhomboides</td>
<td>d) Chlamys tigera</td>
</tr>
<tr>
<td>e) Marthasterias glacialis</td>
<td>e) Hyas sp.</td>
<td>e) Crepidula fornicata</td>
</tr>
<tr>
<td>f) Ophiura albida</td>
<td>f) Inachus sp.</td>
<td>f) Nassarius reticulatus</td>
</tr>
<tr>
<td>g) Ophiura ophiura</td>
<td>g) Liocarcinus depurator</td>
<td>g) Pecten maximus</td>
</tr>
<tr>
<td>h) Ophiothrix fragilis</td>
<td>h) Macropodia sp.</td>
<td>h) Philine aperta</td>
</tr>
<tr>
<td>i) Psammechinus miliaris</td>
<td>i) Pagurus bernhardus</td>
<td>i) Turritella communis</td>
</tr>
<tr>
<td>j) Spatangus purpureus</td>
<td>j) Pagurus prideauxii</td>
<td></td>
</tr>
<tr>
<td></td>
<td>k) Porcellana longicornis</td>
<td></td>
</tr>
</tbody>
</table>

Total = 10

Total = 11

Total = 9
Six sub-groups of species were identified within the group of 30 species highlighted by the SIMPER analysis.

1) Species recorded primarily in western Lyme Bay

Four species were found only at the stations in the western half of Lyme Bay (11 (SP2'), 13, 14, 15, 16 (all SP1')):

- Gonoplax rhomboides
- Turritella communis
- Chamelea gallina
- Philine aperta

*Turritella communis* was found in very large numbers (> 1000 individuals) at stations 13 and 15 and had the greatest contribution to the dissimilarity between the SP1' and SP2' and the SP1' and SP3' sample stations. Despite the application of a $\sqrt[3]{-}$-transformation, it was clear that these high abundances of *Turritella communis* have influenced the marked separation of stations 13 and 15 from the other sample stations in figure 5.16.a.

2) Species recorded in all three sub-provinces but most prevalent in Lyme Bay (SP1' and SP2')

- Astropecten irregularis
- Ophiura albida
- Ophiura ophiura
- Nassarius reticulatus

The above species were all recorded in Lyme Bay and also at stations in SP3'. *Astropecten irregularis* occurred most frequently at stations 11 (SP2'), 14 and 16 (both SP1') and *Ophiura ophiura* was most prevalent at the central to outer Lyme Bay stations (stations 11, 14 and 16 in SP1' and the SP2' stations) with particularly high abundances recorded at stations 11 and 14 (> 100 individuals). Both *Ophiura albida* and *Nassarius reticulatus* were most commonly observed at the outer Lyme Bay stations (11, 12, 17, 18 (all SP2') and 19 (SP1')).
3) Species recorded in the central and outer Lyme Bay area (SP1' and SP2') and in SP3' but most prevalent at the outer Lyme Bay (SP2') or SP3' sample stations.

- Pagurus bernhardus
- Pagurus prideauxii
- Macropodia sp.
- Aequpecten opercularis
- Inachus sp.
- Liocarcinus depurator
- Ebalia tumefacta
- Atelecyclus rotundus
- Pecten maximus

All of the above species are widely distributed within the Lands End – Portland area. Pagurus bernhardus and Macropodia sp. were recorded at all of the sample stations.

4) Species occurring only at the outer Lyme Bay stations (SP2') and at the SP3' stations (equivalent abundances in SP2' and SP3').

- Ophiothrix fragilis
- Psammechinus miliaris
- Spatangus purpureus
- Hyas sp.
- Antalis entalis
- Chlamys tigerina
- Crepidula fornicata

5) Species occurring at the outer Lyme Bay stations (SP2') and at the SP3' stations but are most prevalent at the latter.

- Galathea sp.
- Porcellana longicornis
- Echinus esculentus
6) *Species recorded only in SP3’*

- *Anseropda placenta*
- *Marthasterias glacialis*

Spatial autocorrelation between the epibenthic assemblages of the 20 sample stations was examined and was found to have little effect. The $R^2$ value ($R^2 = 0.026$) indicated that distance between sample stations explains only 2.6% of the similarity in epibenthic assemblage.

Relating the similarity of epibenthic assemblages at the 20 sample stations to the physical variables traditionally used to determine the distribution of benthic fauna, substrate and depth, also produced weak results. Figure 5.18 displays the substrate type recorded at each sample station overlaid on the NMDS ordination of the similarities between epibenthic assemblages. Sample stations 13 and 15 had the same type of substrate (muddy-sand (mS)) and the SP3’ sample stations around the Lizard Peninsula were all classified as having a gravel (G) type substrate. The sample stations located across the mouth of Lyme Bay (12, 17, 18 (all SP2’) and 22 (SP1’)) also had a coarse substrate (gravel (G) or gravelly-sand (gS)). The groupings of sample stations detailed above showed some similarity in their epibenthic assemblages. However, there was no discernable pattern between substrate type and the gradient of variation in epibenthic assemblages identified from the NMDS ordination and SIMPER analysis (figure 5.17). The lack of relationship between substrate type and the distribution of epibenthic megafauna in the Lands End – Portland region was corroborated by an ANOSIM test. The null hypothesis, that there was no difference between the epibenthic fauna of the sample stations in terms of substrate type was accepted as $R = 0.083$ ($p < 0.233$). None of the pairwise tests between substrate types yielded significant results.

Figure 5.18 displays the depth (MRCS bathymetry data – 10 m intervals) of each sample station overlaid on the epibenthic NMDS ordination. The stations in Lyme Bay and between Start Point and Plymouth were between 60 and 80 m deep and the stations situated west of Plymouth were all greater than 80 m deep. There was a gradient of increasing depth from SP1’ to SP3’. However, the relationship between depth and the distribution of epibenthic fauna was not convincing. The ANOSIM test for difference between epibenthic assemblages with varying depth revealed only a weak relationship ($R = 0.153$, $p < 0.1$) and none of the pairwise comparisons between depth classes produced significant results.
Figure 5.17: Substrate type (Folk Classification (1954)) for each sample station overlaid on the NMDS ordination of the relationship between sample stations in terms of epibenthic assemblage.

Figure 5.18: Depth class (10 m intervals) recorded from the MRCS model bathymetry data (≈ 7.4 km x 7.4 km grid) for each sample station overlaid on the NMDS ordination of the relationship between sample stations in terms of epibenthic assemblage.
5.3.2.iii Biodiversity measures

The epibenthic faunal diversity of the three sub-provinces was compared in terms of mean numbers of individuals (N), mean number of species (S), mean Simpson's Diversity Index (1-\(\lambda'\)) and mean Taxonomic Distinctness (\(\Delta^*\)).

**Numbers of Individuals (N)**

The mean number of individuals (N) per sub-province decreased almost exponentially from 928.1 individuals per station (\(\sigma = 1191.5\)) at SP1' to 206.95 individuals per station (\(\sigma = 145.7\)) at SP3' (figure 5.19.a). However, the very large amount of variability in N at SP1' means that the sub-provinces were not statistically significant from one another. The greatest mean number of echinoderms (figure 5.19.b) and crustaceans (figure 5.19.c) occurred in SP2', whereas the difference between sub-provinces in terms of mean numbers of mollusc individuals (figure 5.19.d) mirrored the mean values for the overall N per sub-province in figure 5.20.a. In all cases, the high levels of variability resulted in a lack of statistical difference between mean values of N for each sub-province.

**Mean Number of Species (S)**

A comparison of the overall mean number of species (S) of each sub-province (figure 5.20.a) revealed greater S in SP2' and SP3' than in SP1'. The mean values of S for SP2' and SP3' were almost identical: 26 and 25.6 respectively. Both the echinoderm (figure 5.20.b) and the crustacean (figure 5.20.c) species displayed a gradient of increasing numbers of species from SP1' to SP3'. However, the greatest mean number of mollusc species (figure 5.20.d) occurred in SP2'. The mean sub-province values of S for the echinoderm species are the only values that are statistically distinct from one another: echinoderm species richness at SP1' is distinct from that at SP2' and SP3'.

171
Simpson's Index \((I - \lambda')\)

The mean values of \((I - \lambda')\) per sub-province for the echinoderm (figure 5.21.b), crustacean (figure 5.21.c) and mollusc (figure 5.21.d) species and overall (figure 5.21.a), showed a gradient of increasing epibenthic faunal diversity from SP1' to SP3'. When all of the epibenthic data was considered, the increase in diversity from SP1' to SP3' was almost linear: \((I - \lambda')\) increased by 0.224 between SP1' and SP2' and by 0.213 between SP2' and SP3'. A similar relationship is evident in the diversity of the mollusc species where there was only a 0.005 difference in the increase of \((I - \lambda')\) from SP1' to SP2' and from SP2' to SP3'. The echinoderm species showed a sharp increase in diversity \((I - \lambda')\) between SP1' and SP3' and the mean value of \((I - \lambda')\) at SP3' was statistically different from the mean values of \((I - \lambda')\) at SP1'. SP1' and SP3' were also statistically distinct in terms of crustacean diversity \((I - \lambda')\), although the greatest increase in \((I - \lambda')\) occurred between SP1' and SP2' for the crustaceans.

Taxonomic Distinctness \((\Delta^*)\)

When assessing all of the epibenthic species found in each sub-province (figure 5.22.a) \(\Delta^*\) decreased gradually from SP1' \((\Delta^* = 90.21)\) to SP3' \((\Delta^* = 75.26). The decrease in mean \(\Delta^*\) from SP1' to SP3' shown by the echinoderm species (figure 5.22.b) was very slight: \(\Delta^* = 77.3\) in SP1' and \(\Delta^* = 70.96\) in SP3'. Variation in \(\Delta^*\) in SP3' was much lower than in either SP1' or SP2'. The crustacean species (figure 5.22.c) displayed considerably lower mean values of \(\Delta^*\) \((\Delta^* < 35)\) than either the echinoderms or the molluscs (figure 5.22.d) \((\Delta^* > 70)\) and there was very little variation in crustacean \(\Delta^*\) between the three sub-provinces. The highest mean value of \(\Delta^*\) for crustaceans occurred in SP3' \((\Delta^* = 31.81)\) and the lowest mean value occurred in SP2' \((\Delta^* = 29.55)\); a maximum difference of 2.26 between sub-province means. The greatest mean \(\Delta^*\) of molluscs occurred in SP2': a 17.4\% increase in \(\Delta^*\) compared to either SP1' or SP3', which had almost identical values of \(\Delta^*\) \((\Delta^* = 79.89\) and \(\Delta^* = 79.57\) respectively).
Figure 5.19: Comparison of the mean number of individuals ($N$) of epibenthic fauna found in each sub-province for: a) the full compliment of species identified in the 2004 survey, b) echinoderm species, c) crustacean species and d) molluse species.
Figure 5.20: Comparison of the mean number of species ($S$) of epibenthic fauna found in each sub-province for:

a) the full compliment of species identified in the 2004 survey,
b) echinoderm species,
c) crustacean species and
d) Mollusc species.
Figure 5.21: Comparison of the mean value of Simpson's Index ($I - \lambda'$) for the epibenthic fauna found in each sub-province for: a) the full compliment of species identified in the 2004 survey, b) echinoderm species, c) crustacean species and d) mollusc species.
Figure 5.22: Comparison of the mean Taxonomic Distinctness ($D^*$) of epibenthic fauna found in each subprovince for: a) the full compliment of species identified in the 2004 survey, b) echinoderm species, c) crustacean species and d) mollusc species.
5.3.3 Discussion on the biogeographic distribution of epibenthic fauna

A relationship between the broad-scale distribution of epibenthic megafauna and the remotely-sensed sub-province structure in the Lands End – Portland test area was evident. Although the capacity for similarity in remotely-sensed properties to predict similarity in epibenthic community, on a station by station basis, was low (28% at best), two clear gradients of variation in the abundance of the epibenthic species were detected (figure 5.23). The first gradient was from the sheltered western side of Lyme Bay outwards towards the mouth of Lyme Bay (between Start Point and Portland) and the second gradient was from the mouth of Lyme Bay, west towards the Western Approaches. Comparisons of the epibenthic communities recorded in each sub-province (ANOSIM test) highlighted a distinction between the epibenthos of Lyme Bay (SP1’ and SP2’) and the area between Start Point and Lands End (SP3’). However, when the epibenthic communities were compared on a station by station basis (NMDS) the three SP2’ sample stations that were closest to the mouth of Lyme Bay (stations 12, 17 and 18) showed greater similarity to the SP3’ sample stations. Rather than being contradictory, these two observations substantiated the concept of the two gradients of epibenthic species distribution. Most of the SP2’ sample stations were located across the mouth of Lyme Bay and as such, were in the transition zone between the Lyme Bay gradient and the Western gradient (figure 5.23).

The Lyme Bay (SP1’ to SP2’) and Western (SP2’ to SP3’) gradients were not representative of a high turnover of species from one sub-province to another across the benthic landscape (high beta diversity). This was confirmed by the lack of statistical significance between mean diversity measures for each sub-province. The observed gradients are primarily based on changes of abundance in widely distributed epibenthic species, exceptions being the species sub-groups that were observed at the extremes of each gradient. The western Lyme Bay sub-group species (*Gonoplax rhomboides*, *Turritella communis*, *Chamelea gallina* and *Philine aperta*) were found almost exclusively at sample stations in that region and the same is true for the species recorded only in SP3’ (*Marthasterias glacialis* and *Anseropoda placenta*). The gradients observed were not a function of spatial autocorrelation, as this factor was tested in relation to the epibenthic communities recorded at the 20 sample stations, and was found to explain less than 3% of the pattern of similarity.
Figure 5.23: The two gradients of epibenthic species distribution observed in the Lands End – Portland test area:
a) The Lyme Bay gradient covering SP1' and SP2' and b) the Western gradient covering SP2' and SP3'.

Clear differences between offshore and coastally located epibenthic communities have also been observed in the North Sea (Duineveld et al. 1991; Zuhlke et al. 2001; Reiss and Kroncke 2004). In these studies of the North Sea, coastal communities were characterized by high abundances of echinoderm species, notably *Ophiura ophiura*, *O.albida* and *Asterias rubens* and the offshore communities were dominated by *Pagurus bernhardus* and *Astropecten irregularis*. These observations are in agreement with species distributions recorded during this study. *Ophiura ophiura*, *O.albida* and *P.bernhardus* were found in all three of the oceanographic sub-provinces but *O.ophiura* and *O.albida* were most abundant in SP1' and SP2' (Lyme Bay) and *P.bernhardus* was most abundant in the region of the Western gradient (SP3'). However, *A. irregularis* was found to be most abundant in SP1' and SP2' rather than the more oceanic influenced SP3' and *A.rubens* was most abundant in SP3' rather than the more coastally located SP1' and SP2'. The differences between the abundance of epibenthos found in the sub-provinces were not considered to be significant, but a general pattern of greater overall abundance of epibenthic species in SP1' and SP2' than in SP3' was observed. Reiss and Kröncke (2004) also found the species which dominated patterns of epibenthic distribution in their study to be widely distributed and that the observed pattern was primarily due to variation in abundance of those species.
Rees et al (1999) also detected a difference in the distribution of epibenthic fauna within Lyme Bay and the region west of Start Point. They concluded that the substrate type was the main structuring force: muddy sand within Lyme Bay and gravely substrate covering the rest of the western Channel between Portland and the Lands End Peninsula. This differentiation was based on only four sample stations with only one of those stations being located within Lyme Bay. Comparisons between the distribution of epibenthic fauna observed in this study and abiotic variables traditionally associated with the distribution of epibenthic fauna resulted in non-significant results for substrate type and a weak correlation ($R = 0.153, p < 0.001$) with depth. In their study linking the distribution of crustaceans and echinoderms to environmental factors in the eastern English Channel, Freeman and Rogers (2003) concluded that single factors such as substrate type and water depth are generally inadequate to describe the distribution of benthic fauna, particularly at broad scales. Basford et al (1990), Duinevald and van Noort (1990), Duineveld et al (1991) and Reiss and Kröncke (2004) also found it difficult to link the distribution of epibenthic fauna to substrate type. It was suggested by Reiss and Kröncke (2004) that in areas with large ranges of substrate type, such as the comparisons drawn between the Irish Sea, the English Channel and the North Sea by Rees et al (1999), the relationship between epibenthic fauna and substrate type is skewed by the high diversity of species found on coarser ground.

Rees et al (1999) also specified that coastal influences (e.g. proximity to large estuaries), depth, tidal current velocity and SST all help to explain the distribution of epibenthic fauna. Freeman and Rogers (2003) identified bed-stress, SST, substrate type and water depth as key factors influencing the distribution of epibenthic fauna in the eastern English Channel. Although Freeman and Rogers (2003) pinpointed certain physical factors, these factors and the corresponding distributions of echinoderms and crustaceans were not spatially translated into a geographical representation of the eastern English Channel. The physical factors identified in the two studies mentioned above are all inter-related and are all linked to the vertical structure of the water column, which can be detected using remotely sensed properties as has been demonstrated in previous sections of this study.

In his influential work of the 1960's, Holme (1961; 1966) proposed seven biogeographical regions of the English Channel based on variations in temperature and tidal velocity. There are many overlaps between Holme's biogeographical regions. For example: the “Western Species” are defined as occurring from the Western Approaches to Start Point on the English Coast, from the Western Approaches as far as Guernsey on the French coast and into the eastern English Channel in mid-Channel waters. The “West Channel Species” are defined as
occurring generally in the western English Channel but not at all in the eastern English Channel. These overlaps between regions suggest that the distribution patterns of molluscs and echinoderms observed by Holme also reflected gradual gradients of change in the abundance of widely occurring species. Some similarities between the distribution of benthic fauna observed by Holme (1961; 1966) and the distributions observed in this study exist e.g. in both studies *Marthasterias glacialis* was only recorded to the west of Plymouth. However, drawing any real comparison between the work of Holme (1961; 1966) and this thesis is greatly complicated by two factors. Firstly, Holme based his delineation of biogeographical regions on observations of epibenthic fauna at the scale of the whole English Channel whereas the benthic survey of this study dealt with only 20% of that region. Secondly, Holme sampled the benthos using a modified anchor dredge (Holme 1961) which was biased towards infauna and only sampled an average area of 1m$^2$. The present study employed a mini-Agassiz trawl which was biased towards the collection of epifauna and sampled on average a much greater area of seabed (641.76 m$^2$).

### 5.4 Conclusions

A high degree of homogeneity was detected between sub-province structure of at the scale of the whole English Channel and the structure observed when sample stations from within the Lands End – Portland test area were compared to one another. The positive outcome of this comparison confirms the validity of the sub-province classification.

This study objectively compared the structure of the remotely-sensed sub-provinces with a completely independent survey of epibenthic megafauna. The epibenthic communities of each sub-province were found to overlap but were clearly different. This difference between sub-provinces was further confirmed by the two gradients of variation in species abundances that were identified. The sub-province structure was found to explain more of the variability in the biogeographic distribution of epibenthic fauna than traditional employed physical factors such as substrate type.
CHAPTER 6

OVERALL DISCUSSION AND CONCLUSIONS

6.1 Introduction

This thesis has investigated the potential application of remotely-sensed surface-ocean data to the characterisation of biogeographic patterns in the distribution of epibenthic fauna in the English Channel. A large proportion of the text has been devoted to assessing the suitability of the remotely-sensed data for this type of study and to developing and applying a complex systems type approach to the identification of persistent patterns in the spatial and temporal heterogeneity of physical variables. The findings of each chapter are reviewed and the implications and possible future developments of this study are discussed.

6.2 Investigation of the suitability of remotely-sensed surface-ocean data as a means of describing the spatial and temporal heterogeneity of water column physical structure and associated patterns of primary productivity in the English Channel.

The balance between surface heat flux and wind and tide induced mixing is the established paradigm of water column structure in shelf-seas (Simpson and Hunter 1974; Rippeth et al. 2005). Spatial and temporal variation in the balance between these physical forcing mechanisms produces heterogeneity in water column structure. This heterogeneity can be clearly identified in the six year time series of remotely-sensed surface-ocean data for the English Channel that was used in this study.
The AVHRR SST (°C) data showed a definite distinction between the well-mixed coastal and eastern regions of the English Channel that experience a high annual temperature range and the seasonally stratified regions in the western English Channel that display greater thermal stability. The movement of the western English Channel front, east with the onset of stratification and west as stratification breaks down, is also apparent in the SST data. The spatial and temporal patterns observed in the SST data are consistent with observations of water column structure in the English Channel made by Pingree and Maddock (1977), Pingree and Griffiths (1978), Pingree (1980), Longhurst (1998b) and Spooner (2001).

The observed spatial and temporal variation in SeaWiFS Ocean Colour log(chl-a) values (mg m⁻³) corroborates the structure observed in the SST data. High log(chl-a) values are found throughout the year in the shallow, well-mixed regions of the English Channel where light and the supply of inorganic nutrients are more readily available. The log(chl-a) values in the seasonally stratified regions of the Channel concur with the observations of Holligan and Harbour (1977): low winter values followed by peaks in productivity during spring and autumn bloom events.

In shelf-seas and coastal waters (Case II waters; IOCCG 1998), the remote-sensing reflectance ratios used by the SeaWiFS Chl-a retrieval algorithm can become contaminated by the presence of suspended particulate matter (SPM) and coloured dissolved organic material (CDOM) in the water column. It was therefore necessary to compare the observed spatial and temporal variation in log(chl-a) values with the spatial and temporal variation of suspended matter, as what appeared to be high log(chl-a) values may in fact have been high values of suspended matter. Remote sensing reflectance (mW cm⁻² μm⁻¹ sr⁻¹), both in the green spectrum at 555 nm ($L_{WN}(555)$) and red spectrum at 670 nm ($L_{WN}(670)$), have been shown to be good proxies for the amount of suspended matter present in the water column (Otero and Siegel (2004) and Binding et al. (2003), respectively). A comparison of $L_{WN}(555)$ and $L_{WN}(670)$ (both SeaWiFS Ocean Colour channels) showed the two variables to be extremely similar, however, a greater signal to noise ratio was revealed in the $L_{WN}(555)$ data. Therefore, $L_{WN}(555)$ was selected in preference to $L_{WN}(670)$ as a proxy for values of suspended matter in the English Channel.
The basic pattern of heterogeneity in water column structure within the English Channel, due to spatial and temporal variation in the balance of surface heat flux and wind and tide induced mixing, could be inferred from the AVHRR SST data. The SeaWiFS Ocean Colour data ($\log(\text{chl-a})$ and $L_{\text{WN}}(555)$) added a further level of refinement to the established model of water column structure by providing information on the biological consequences of that structure and its relative stability.

The most significant mode of temporal variability in the water column structure of shelf-seas is intra-annual (Pingree 1980). Intra-annual (i.e. seasonal) variation was strongly emphasised in the time-series analysis of the six years (1998 – 2003) of remotely-sensed data. The time-series was not extensive enough to detect inter-annual variation owing to the effects of phenomena such as the NAO (Beaugrand et al. 2000; Garcia-Soto et al. 2002; Osborn 2004) and sunspot cycles (Southward et al. 1975). These phenomena influence physical conditions within the English Channel but they are driven by physical mechanisms acting on spatial and temporal scales that are beyond the scope of this thesis.

Remotely-sensed data has been previously used in conjunction with physical and biological models in studies of the English Channel (Pingree 1980; Spooner 2001). However, prior to this study no attempt to infer the physical structure of the water column and associated patterns of productivity in the English Channel, using only remotely-sensed data, had been made. Spatial and temporal analysis of the six year time-series of the remotely-sensed variables (SST, $\log(\text{chl-a})$ and $L_{\text{WN}}(555)$) for the English Channel region clearly showed that it is possible to utilise this data to describe the documented patterns of variation in water column structure and productivity. Therefore, it was concluded that the available SST, $\log(\text{chl-a})$ and $L_{\text{WN}}(555)$ data incorporated the appropriate level of spatial and temporal variability (geometric dimensionality) to describe the phenomenon of interest (geophysical dimensionality) (Gallaudet and Simpson 1994; Goldenfeld and Kandanoff 1999). Establishing whether a data set meets the specified geometric and geophysical dimensionality of the system under investigation is a critical prerequisite to the application of any kind of variance partitioning technique. Patterns in the spatial and temporal heterogeneity of a complex system are an emergent property of that system (Levin 1999; Wu and Marceau 2002) and variance partitioning techniques, such as Principle Components Analysis (PCA), are methods of detecting and describing those patterns.
6.3 Application of remote-sensing to the identification of persistent spatial structure (sub-provinces) within the spatial and temporal heterogeneity of physical water column structure and associated patterns of productivity in the English Channel.

T-mode Principle Components Analysis (PCA), a method designed for measuring how spatial pattern varies in time, was used to extract the dominant underlying patterns or gradients of variation in the spatial and temporal heterogeneity of the three remotely-sensed variables (SST, log(Chl-a) and $L_{\text{WN}}(555)$). In the case of each variable, the dominant spatial pattern was found to persist throughout the 12 month time-series of monthly mean images, indicating a degree of permanent structure. These observations are commensurate with Hutchinson’s (1953) definition of pattern as a steady state phenomenon rather than as a product of thermodynamic equilibrium and with Platt and Sathyendranath’s (1999) approach to defining functional units in the ocean. The persistent structures identified in each of the remotely-sensed variables could also be clearly explained in terms of the variation in physical water column structure and associated patterns of productivity that were observed in the first stage of this study (Chapter 2).

The dominant, persistent structures identified for each remotely-sensed variable were compared and three distinct areas within the English Channel were defined using an unsupervised classification routine. These areas are termed “sub-provinces” following Longhurst’s (1998a; 1998c) characterization of oceanographic biomes and provinces. The scale of investigation in this study is at a finer scale than that of Longhurst’s provinces (1998c), hence the areas are referred to as sub-provinces. The sub-province structure was corroborated via the use of spatial analysis re-sampling methods similar to those advocated by Fortin (1999) and Anselin (1992) and by further exploratory multivariate statistical analysis.

Sub-province 1 (SP1) encompasses the well-mixed coastal regions of the English Channel and is characterized by a high annual range of SST (°C), high values of $L_{\text{WN}}(555)$ (mW cm$^{-2}$ µm$^{-1}$ sr$^{-1}$) and high values of log(Chl-a) (mg m$^{-3}$). Owing to the high values of $L_{\text{WN}}(555)$, the log(Chl-a) values were interpreted with care. Sub-province 2 (SP2) is predominantly located in the eastern basin of the English Channel and like SP1, it remains well-mixed throughout the year. The annual temperature range for this sub-province is lower than for SP1, as are the recorded values of $L_{\text{WN}}(555)$. Sub-province 3 (SP3) dominates the western English Channel.
This western region is seasonally stratified and therefore experiences a lower annual temperature range than either SPI or SP2. Although peaks of productivity occur with the spring and autumn blooms, productivity and hence $\log(\text{chl-a})$ values, are generally lower than in the other two sub-provinces. $L_{\text{W455}}$ values are also at their lowest in SP3.

Sub-province boundaries are elastic rather than absolute (Platt and Sathyendranath 1999). The sub-province classification is based on gradients of variation in the remotely-sensed variables and is defined in terms of the concept of pattern as a steady state phenomenon (Hutchinson 1953) and as an emergent property of a complex system (Levin 1999; Levin 2002; Wu and Marceau 2002). This definition necessitates that the sub-provinces must be thermodynamically open systems, i.e. the values of the variables that specify the sub-province are not fixed, but the integrity of the sub-province structure endures. The concept of elastic boundaries was highlighted in the comparisons of intra-annual variation between each sub-province, for each of the remotely-sensed variables. In all three cases (SST, $\log(\text{Chl-a})$ and $L_{\text{W455}}$) the sub-provinces were found to be least distinct from one another during summer and most distinct during winter.

Although T-mode PCA has been widely employed in oceanographic remote sensing studies (e.g. Paden et al. 1991; Fang and Hsieh 1993) as a method of assessing spatial and temporal variability, it has only recently been applied as a means of defining ecological provinces (Hardman-Mountford 2000; Hardman-Mountford and McGlade 2002; Hardman-Mountford et al. 2006). This study is the first attempt to apply the methodology, with the aim of province identification, to a shelf sea region and it is also the first attempt at combining SST, Chl-a and $L_{\text{W455}}$ data for this aim. Additionally, the methods of spatial re-sampling and analysis employed to corroborate the sub-province structure have been newly adapted for use in this type of remote-sensing study have been in part developed via this thesis.
6.4 The relationship between the sub-province structure detected from remotely-sensed data and the spatial variation in seabed physical variables used to describe the distribution of benthic fauna in existing studies.

The difficulties in finding broad-scale, spatially cohesive data relating to physical conditions on the seabed were highlighted. Additionally, the link between water column structure and physical variables (bed-stress and depth) that have been related to the distribution of epibenthic fauna in existing studies was discussed. Bed-stress \( T_B \) is directly linked to the spatial variation of substrate type and is also proportional to the dissipation of tidal energy \( D \) (Pingree and Maddock 1977; Pingree 1980). The ratio between the dissipation of tidal energy \( D \) and water depth \( h \) forms the basis of Simpson and Hunter's (1974) stratification parameter \( S \). The tendency of the water column to stratify is central to the established paradigm of water column structure in shelf seas (Pingree and Griffiths 1978; Pingree 1980; Rippeth et al. 2005) and the spatial and temporal heterogeneity created by variation in water column structure can be detected using surface-ocean remotely-sensed data.

The observed structure of the remotely-sensed data was compared with bathymetric data extracted from the MRCS model (Holt and James 2001) and with estimates of bed-stress from Pingree and Maddock's (1977) model of tidal residuals in the English Channel. The bed-stress estimates were found to be positively correlated with \( \log(\text{Chl-a}) \) and \( L_w(555) \) annual mean values. Depth was positively correlated with SST and negatively correlated with \( \log(\text{Chl-a}) \). These comparisons indicated that the relationship between seabed physical conditions and water column structure holds at the scale of the whole English Channel. However, as the bed-stress data were only estimates, this relationship could not be considered as a robust assessment of the link between environmental heterogeneity on the seabed and the structure detected in the remotely-sensed data.
6.5 Predicting the biogeographic distribution of epibenthic megafauna in the English Channel from the structure of the remotely-sensed sub-provinces.

The epibenthic megafauna of the western English Channel (Land End to Portland) were surveyed between July and October 2004 as part of this study. It was not logistically possible to survey the whole study area and so a smaller test area between Portland and Lands End was selected. This test area encompassed all three of the sub-provinces identified in Chapter 3 of this thesis. Before any comparisons between the remotely-sensed sub-province structure and the distribution of epibenthic fauna could be made, it was necessary to test whether or not the sub-province structure held at the reduced spatial scale of the test area. Spatial re-sampling and analysis techniques were employed to assess whether the sub-province structure could be detected, when samples of the remotely-sensed variables taken within the test area were compared. The sub-province structure observed within the Lands End – Portland test area showed homogeneity with the structure observed at the scale of the whole English Channel. The fidelity of the sub-province classification is confirmed by its persistence when examined via a smaller window of observation (Levin and Buttel 1987; Keeling 1999; Levin 1999). The same sample stations were used for the survey of epibenthic fauna as were used for the re-sampling of the remotely-sensed data. The location of the sample stations was selected completely independently from the location of the proposed sub-provinces.

Literature detailing the distribution of epibenthic megafauna in this region of the western English Channel is extremely limited. Ford's (1923) benthic survey was restricted to the Plymouth region. Holme (1961; 1966) collected numerous samples of benthic megafauna in the study area but the sample size was limited to approximately 1 m². Rees et al (1999) also surveyed epibenthic fauna in the western English channel as part of a larger study however, their inferences regarding the distribution of epibenthic fauna in this area were based on only four sample stations. Although only 20 stations were eventually sampled in this study, four replicate samples were collected at each of those stations and each replicate sample covered approximately 640 m² of seabed. Therefore this study represents a considerable advance, in terms of area sampled, density of samples collected and rigour of experimental design, to the existing surveys of epibenthic megafauna in the western English Channel region.
On a station by station basis, the capacity of the remotely-sensed variables to predict the distribution of epibenthic fauna was limited to less than 30%. However, when the epibenthic communities of each sub-province were compared, a stronger relationship emerged. The epibenthic communities of the three sub-provinces were shown to be overlapping but clearly different: a pattern that was consistent with the gradients of variation in the remotely-sensed variables that formed the basis of the sub-province classification. Two primary gradients of change in the epibenthic fauna were detected. The first gradient was between the western side of Lyme Bay (SP1') and the mouth of Lyme Bay (SP2') and the second was between the mouth of Lyme Bay (SP2') and Lands End (SP3'). The observed gradients of epibenthic faunal distribution in the study area were dominated by 30 species (10 echinoderm, 11 crustacean and 9 mollusc species). Most of these species were generalists (in terms of spatial distribution and habitat selection (Holt et al. 1997)): they were recorded in all three sub-provinces and at a high proportion of the sample stations. Variation in the abundance of these 30 key species underpinned the observed gradients of change in the epibenthic communities of the three sub-provinces. Additionally, the distribution of epibenthic fauna observed in this study was not spatially autocorrelated, displayed a very weak correlation with depth and no correlation at all with substrate type.

The link between the distribution of epibenthic fauna and variation in water column structure is not a new concept (e.g. Jennings et al. 1999b). However an investigation of that link, utilising the extensive spatial and temporal cohesion and resolution of remotely-sensed data coupled with a complex systems type approach, had not been attempted prior to this thesis.

6.6 Additional factors influencing the spatial distribution of epibenthic fauna in the English Channel.

Within the confines of the data set used in this study, the remotely-sensed sub-province structure explained a greater proportion of the variation in the distribution of epibenthic megafauna than substrate type, depth or spatial autocorrelation. The question of which additional factors may also influence the spatial distribution of epibenthic fauna at the scale of the English Channel is then raised?
Important detail in the distribution of fauna may have been averaged out because the scale of sampling was too coarse (Levin 1992; Keeling et al. 1997). Generalist species dominate the observed pattern of distribution: is this because they are the most abundant species and that detail of the distribution of rarer species has been lost? The epibenthic data were $\sqrt{\cdot}$-transformed prior to analysis: a procedure that severely down-weights the more abundant species and allows rarer species to exert a greater influence.

Most of the epibenthic fauna identified in this study have biogeographic ranges that extend well beyond the boundaries of the English Channel e.g. the brittlestar, *Ophiura ophiura*, is found from northern Norway to Madiera (Mortensen 1927; Picton 1993; Hayward and Ryland 1995). The niche of these epibenthic fauna, defined as the multidimensional combination of abiotic and biotic variables required for a population to persist (Hutchinson 1957), is not constrained to the English Channel. Based on the observations of epibenthic fauna made in this study and on the work of Reiss and Kröncke (2004) in the North Sea, it is suggested that regional scale (i.e. the English Channel) variation in water column structure and associated patterns of productivity does not set the regional scale species pool for epibenthic fauna. Instead, water column structure appears to create either optimal or suboptimal conditions for the epibenthos, with high abundances of a particular species coinciding with optimal conditions and low abundances with suboptimal conditions. Hence the gradients of variation in the abundance of dominant epibenthic species observed in this study and by Reiss and Kröncke (2004) in the North Sea. The observed distribution of the dominant epibenthic species concurs with the observations made by Holt (1997) regarding the effects of landscape heterogeneity on local community composition. A species will persist and be widely distributed in a heterogeneous environment if it can colonize patches of neighboring sub-provinces (habitat types) without reducing its rate of colonization of patches in the original sub-province (habitat type).

The large body size and level of mobility of epibenthic megafauna may also mean that density dependent population dynamics amongst these species have played a role in producing the observed gradients of variation. Seasonal variation in epibenthic communities has been observed by Frauenheim et al. (1989) and Reiss and Kröncke (2004) in the North Sea and German Bight. These authors found seasonal variation in the abundance of the dominant, widely distributed epibenthic fauna but not in their spatial distribution. Migration of adult epibenthic species has been found to be triggered by fluctuations in temperature and is thought to be the most important process behind these seasonal fluctuations in epibenthic populations (Freeman et al. 2001; Hinz et al. 2004; Reiss and Kroncke 2004). The
The distribution of epibenthic fauna recorded in this study is a summer distribution as the epibenthic survey was conducted between July and August (2004): the peak of the annual net heating cycle, when temperatures were at their highest. The summer months were also the time when the three sub-provinces were least distinct from one another in terms of intra-annual variation in the remotely-sensed variables. It is possible that gradients of variation in abundance, and possibly distribution, of the dominant epibenthic species observed in this study would be different if the survey was repeated during the winter months, as some of the epifauna may migrate offshore in search of warmer winter temperatures (Freeman et al. 2001). However, this hypothesized migration is likely to still correlate with the gradients of variation in remotely-sensed properties, from SP1' to SP2' and from SP2' to SP3', as these gradients reflect intra-annual variation in temperature. SP1' and SP2' have higher summer temperatures than SP3' owing to the fact that they are well-mixed. SP3' undergoes a much smaller annual temperature range and is warmer than both SP1' and SP2' during the winter months. SP1' and SP2' also displayed higher log(Chl-a) values than SP3' during the summer months. The increased solar irradiation during this period and the nutrient supply afforded by the well-mixed environment of SP1' and SP2' serves to enhance primary productivity in these sub-provinces. Although primary productivity in the seasonally stratified waters of SP3' peaks with the spring and autumn blooms there is a marked dip in productivity during in mid-summer as the nutrients in the surface mixed layer are depleted. Hyperbenthic species were shown to actively migrate into areas with high primary productivity by Hamerlynck and Mees (1991) however Reiss and Kröncke (2004) found that the seasonal variation of epibenthic fauna in the southern North Sea had no significant relationship with levels of Chl-a in seabed sediment. The three sub-provinces defined in this study were found to be more distinct from one another during the winter months; therefore the distinction between the epibenthic communities of the sub-provinces may also be more distinct during winter. However, at this stage, information on the intra-annual variation of epibenthic communities, over a broad spatial scale in the western English Channel, does not exist. Hypotheses regarding potential relationships between sub-province structure and intra-annual variation in epibenthic fauna are can only be considered as conjecture.

Although the 20 sample stations in the Lands End – Portland test area encompassed all three sub-provinces they were also all located relatively close to the English coast. Headland and peninsula structures in coastal morphology cause tidal current shear, which frequently results in the formation of eddies. Eddies are generally associated with high levels of turbulence and bed-stress. There are known eddy structures around Portland Bill and the Lizard peninsula (Pingree and Maddock 1977; Pingree 1980) and the epibenthic communities of the sample
stations at these locations were found to be similar. However, the combined effect of coastal morphology and tidal velocity was shown to be reflected in the remotely-sensed sub-province structure at the scale of the whole English Channel (Chapter 4). Therefore, in theory, similarities between the Portland Bill sample station (22) and the Lizard peninsula sample stations (25, 26, 27 and 29) should also have been detected in the remotely-sensed data, but this was not the case.

Anthropogenic factors may also have a significant influence on the distribution of epibenthic fauna, e.g. fishing, pollutants from riverine input and shipping (the English Channel is one of the busiest shipping lanes in the world) (OSPAR 2000). There is no doubt that commercial fishing will influence the distribution of epibenthic fauna. The effects of trawling on benthic communities have been well-documented (Kaiser and Spencer 1995; Kaiser 1996; Kaiser et al. 1998; Thrush et al. 1998; Jennings et al. 2001a; Jennings et al. 2001b; Thrush et al. 2001; Thrush and Dayton 2002; De Biasi 2004; Lewinson et al. 2004; Kaiser et al. 2005). Short term effects of fishing on the epibenthos include increased mortality of epifauna and also an increase in scavenging species as their food supply is enriched by discards from trawling (Kaiser and Spencer 1994; Reiss and Kroncke 2004). Long term effects include shifts in community structure, e.g. domination by species that are most resilient to the effects of trawling such as echinoderms (Kaiser and Spencer 1995; Kaiser 1996). Two of the UK's largest trawler ports, Brixham and Newlyn, are situated in the study region (Pawson et al. 2002) and in 1995 more than 2,200,000 hours of fishing effort (trawling) were recorded for the ICES box that contains the English Channel (Jennings et al. 1999a). Quantifying the effects of fishing effort is extremely difficult as it is not evenly distributed and data recorded per ICES box can at best give only an estimate of the rate of disturbance of the epibenthic fauna (Jennings et al. 1999a).
6.7 Implications and final conclusions

Levin (1992) and Goldenfeld and Kadanoff's (1999) central tenet, regarding the use of the correct scale of description for the phenomenon of interest, is key to successful adaptive management of the marine environment at the ecosystem or regional seas scale. It is essential to understand physical and biological patterns of variability at an equivalent scale to that at which the environment is being managed. However, the way in which processes interact to produce these patterns of variability, at the whole ecosystem scale, is highly complex and frequently confounded by anthropogenic factors (Hardman-Mountford et al. 2005).

The epibenthic fauna of shelf seas are important in terms of nutrient cycling, detrital decomposition and in their role as a food source for higher trophic levels (Pearson 2001; Reiss and Kroncke 2004). A multitude of environmental variables have been associated with the broad-scale distribution of epibenthic fauna, including seabed and sea-surface temperature, bed-stress, productivity and substrate type. All of these physical variables are linked to variations in tidal velocity, which has been shown to be fundamental to the variation in water column structure of shelf seas (Simpson and Hunter 1974; Simpson et al. 1977; Pingree 1980; Rippeth 2005). This thesis has demonstrated that the essential spatial and temporal variability of water column structure in the English Channel region can be identified solely from the use of remotely-sensed images of the sea-surface. The utilisation of remote-sensing in ecology is a relatively recent but critical development (Kerr and Ostrovsky 2003; Turner et al. 2003). Remotely-sensed data offer the opportunity to compare spatial and temporal variation in environmental variables to variation in species distributions with an unparalleled level of cohesion and resolution. The novel application of a complex systems type approach to the detection of emergent pattern in the remotely-sensed spatial and temporal variability of water column structure has resulted in the identification of three sub-provinces within the English Channel. The sub-provinces encapsulate spatial structure in the intra-annual variation of temperature, productivity and tidal mixing and this structure has been shown to be related to spatial variation in depth and bed-stress. Most existing studies have attempted to relate the biogeographic distribution of epibenthic fauna to a myriad of what are essentially autocorrelated variables at the regional seas scale. This study, via the identification of the sub-provinces, has developed a simple framework that embraces the complexity of, and the interactions between, these physical variables and reduces the number of assumptions that need to be made when combining disparate data sources. The sub-
provinces also incorporate a level of spatial and temporal coverage that has previously not been applied to studies of the biogeographic distribution of epibenthic fauna. The patterns that emerge from complex systems, such as ecosystems, do not always require complex explanations (Goldenfeld and Kadanoff 1999; Levin 1999).

Current schemes for relating patterns of benthic species distribution and physical variables combine physical and biological information within nested scales and are based on observations made at relatively small spatial scales (e.g. Connor et al. 1997a; Connor et al. 1997b). These hybrid classification schemes have been used to relate benthic species distributions to biogeographic physical variables in UK shelf-seas (e.g. Connor et al. 2006). Although the hybrid classifications have been successfully applied to, pragmatic, conservation-based mapping in the inter-tidal zone (e.g. Foster-Smith et al. 2001; Roff et al. 2003), the validity of employing these schemes to characterise the distribution of benthic species at a regional seas scale has not been tested. The scale of description at which the relationship between benthic species and their environment were originally characterised is not necessarily an appropriate scale for the phenomenon of interest: in this case regional sea scale dynamics. The sub-province structure identified in this thesis allowed simple and objective comparisons to be made between patterns of distribution of epibenthic fauna and physical dynamics at the scale of regional seas management, i.e. the English Channel. A key feature of the sub-province structure is that it also incorporated temporal variability in physical factors as well as spatial variability. This is an important point overlooked by static studies, e.g. those where physical data are contemporary with the biological information and annual variability is overlooked. The results of this study indicated that dominant patterns of epibenthic species distribution, in the English Channel, were gradients of abundance in generalist species and that these gradients of abundance were related to variations in water column structure. The level of correlation achieved between the structure of the remotely-sensed sub-provinces and the biogeographic distribution of epibenthic fauna, in an area of shelf-sea where fishing disturbance will clearly confound any perfect relationship between non-anthropogenic environmental factors and distribution patterns of fauna, is very encouraging. The potential application of this method to the adaptive management in the marine environment should be further investigated.
6.8 Suggestions for further work

Owing to the limited area in which the relationship between sub-province structure and the distribution of epibenthic species could be tested, it is essential to test this relationship more extensively. It is suggested that the Lands End – Portland test area be extended further east towards the Isle of Wight and further offshore from the English Coast. At least two other test sites should also be assessed: ideally one should be located near the French coast and another in the eastern basin of the English Channel.

In view of the work of Reiss and Kröncke (2004), seasonal variation in the distribution of epibenthic fauna should be investigated. The relationship to sub-province structure established in this thesis was based on summer distributions of the epibenthic fauna and many of the dominant species have been shown to migrate (Freeman et al. 2001; Hinz et al. 2004; Reiss and Kroncke 2004). Additionally, the summer months are the period when the sub-province structure is least distinct. The sub-provinces are most distinct from one another during the winter months and therefore comparisons with winter distributions of epibenthic fauna may produce a more definite relationship.

A comparison of epibenthic species distributions with fishing effort may help to separate natural variation (i.e. that encapsulated in the sub-province classification) from the effects of direct anthropogenic influences. Fishing effort data is only available on a very coarse scale and so quantifying the spatial variation in trawling effort at the regional seas scale could prove difficult. Another option could be to focus on the distribution of echinoderm species as these species have been shown to be resilient to trawling damage. The echinoderms could be useful indicators of environmental change resulting from indirect anthropogenic influence, e.g. climate change. Information on the feeding guilds and reproductive strategies (i.e. whether or not they have a planktonic lifecycle stage) of the dominant epibenthic species may help to explain the gradients of abundance in the distribution of these species.

If sub-province structure was found to consistently exhibit a clear relationship with the distribution of epibenthic fauna, then the sub-provinces could be used as the first stage in a hierarchical decomposition of a temperate shelf-sea ecosystem (Wu and David 2002). Spatial and temporal variation of physical and biological factors within each sub-province would need to be investigated.
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214


A3.1 Selection PC/eigenvector modes $\log(\text{Chl-a})$

Figure A3.1.a: $\log(\text{Chl-a})$. The Guttman Criterion: The $\log(\text{Chl-a})$ data is normalised therefore each variable has unit standard deviation. Any individual PC/eigenvector mode should account for the variance of at least a single variable if it is to be retained for interpretation. Only PC/eigenvector modes with an eigenvalue of $\geq 1$ are retained.

Figure A3.1.b: $\log(\text{Chl-a})$. Logarithmic Eigenvalue Curve (LEV): PC/eigenvector modes that lie above the straight line drawn through the higher number roots are retained. Farmer (1971) demonstrated that a PCA of random data produces a straight line LEV graph therefore PC/eigenvector modes that lie above the line were retained, as these were considered to be non-random.
Figure A3.1.c: log(Chl-a). North et al. (1982) Rule of thumb for testing uniqueness of PC/eigenvector modes. Adjacent PC/eigenvector modes with eigenvalues of similar magnitude can become mixed, forming "degenerate multiplets". An eigenvalue must be separated from its adjacent eigenvalue by more than its sampling error (indicated by error bars in above plot) in order for it to be considered separate and not part of a degenerate multiplet. The cut off point for retaining PC/eigenvector modes should not fall in the middle of a multiplet.

A3.2 Selection PC/eigenvector modes $L_{WN}(555)$

Figure A3.2.a: $L_{WN}(555)$. The Guttman Criterion: The $L_{WN}(555)$ data is normalised therefore each variable has unit standard deviation. Any individual PC/eigenvector mode should account for the variance of at least a single variable if it is to be retained for interpretation. Only PC/eigenvector modes with an eigenvalue of $\geq 1$ are retained.
Figure A3.2.b: $L_{NM}(555)$. Logarithmic Eigenvalue Curve (LEV): PC/eigenvector modes that lie above the straight line drawn through the higher number roots are retained. Farmer (1971) demonstrated that a PCA of random data produces a straight line LEV graph therefore PC/eigenvector modes that lie above the line were retained, as these were considered to be non-random.

Figure A3.2.c: $L_{NM}(555)$. North et al (1982) Rule of thumb for testing uniqueness of PC/eigenvector modes. Adjacent PC/eigenvector modes with eigenvalues of similar magnitude can become mixed, forming "degenerate multiplets". An eigenvalue must be separated from its adjacent eigenvalue by more than its sampling error (indicated by error bars in above plot) in order for it to be considered separate and not part of a degenerate multiplet. The cut off point for retaining PC/eigenvector modes should not fall in the middle of a multiplet.
A5.1 Location of sample stations (latitude and longitude) in the Lands End – Portland test area

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Figure A5.1: “The Plymouth Quest” berthed at Sutton Harbour Marina in Plymouth’s Barbican area. “Quest” is a 21.5 m L.O.A. wet fish stern trawler.
A5.3 Full list of species found in each sub-province

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A5.4 Regression analysis plots for the relationship between sample stations in terms of similarity of remotely-sensed variables vs. similarity of epibenthic fauna (untransformed data for all epibenthic species and $\sqrt{\cdot}$-transformed data for each separate phyla).

Figure A5.4.a: Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and untransformed epibenthic assemblages (Bray-Curtis similarities).
Figure A5.4.b: Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and $\sqrt{\cdot}$-transformed echinoderm assemblages (Bray-Curtis similarities).

Figure A5.4.c: Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and $\sqrt{\cdot}$-transformed crustacean assemblages (Bray-Curtis similarities).
Figure A5.4.d: Non-parametric regression of the relationship between sample stations in terms of remotely-sensed variables (Euclidean distance) and $\sqrt{\chi^2}$-transformed crustacean assemblages (Bray-Curtis similarities).
A5.5 Distribution of Echinoderm species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages

**Anseropoda placenta**

**Astropecten irregularis**

**Asterias rubens**

**Echinus esculentus**
Figure A5.5 (a-j): Distribution of each of the 10 Echinoderm species identified in the SIMPER analysis (PRIMER-E) analysis as being primary contributors to the dissimilarity between the three oceanographic sub-provinces in terms of epibenthic megafauna. The distribution of each species is overlaid on the NMDS ordination of the relationship between sample stations in terms of epibenthic mega-faunal assemblage and abundances are indicated.
A5.6 Distribution of Crustacean species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages

### Atelecyclus rotundus

### Galathea sp.

### Ebalia tumefacta

### Gonoplax rhomboides
Figure A5.6 (a-k): Distribution of each of the 10 Crustacean species identified in the SIMPER analysis (PRIMER-E) analysis as being primary contributors to the dissimilarity between the three oceanographic sub-provinces in terms of epibenthic megafauna. The distribution of each species is overlaid on the NMDS ordination of the relationship between sample stations in terms of epibenthic mega-faunal assemblage and abundances are indicated.
A5.7 Distribution of Mollusc species identified in SIMPER analysis overlaid on NMDS ordination of relationship between sample stations in terms of epibenthic faunal assemblages

**Aequipecten opercularis**

**Stress: 0.06**

**Chamelea gallina**

**Stress: 0.00**

**Antalis entalis**

**Stress: 0.06**

**Chlamys tigerina**

**Stress: 0.00**
Crepidula fornicata

Stress: 0.00

16(0.25) 11(0.75) 14(0) 17(0) 12(0.75) 10(0.25) 8(0) 5(0) 4(0.25) 26(0) 22(0.25)

15(0.25) 13(0) 6(0) 19(0)

Nassarius reticulatus

Stress: 0.00

16(0) 11(0) 5(0) 14(0) 15(0) 13(0) 19(0) 6(0) 22(0.25)

Pecten maximus

Stress: 0.00

16(0) 11(0.5) 14(0) 17(0) 12(0.25) 10(0) 8(0) 5(0) 4(0) 26(0) 22(0)

15(0) 13(0) 6(0) 19(0)

Philine aperta

Stress: 0.00

16(0) 11(0.25) 14(0) 17(0) 18(0) 27(0) 22(0) 19(0) 26(0)

13(0.25) 6(0) 22(0)

h)
Figure A5.7(a-i): Distribution of each of the 10 Mollusc species identified in the SIMPER analysis (PRIMER-E) analysis as being primary contributors to the dissimilarity between the three oceanographic sub-provinces in terms of epibenthic megafauna. The distribution of each species is overlaid on the NMDS ordination of the relationship between sample stations in terms of epibenthic mega-faunal assemblage and abundances are indicated.