UNIVERSITY OF SOUTHAMPTON

EFFECTS OF OCEANOGRAPHIC FACTORS ON THE MESOZOOPLANKTONIC COMMUNITIES OF THE EAST SOLENT AND OUTER APPROACHES

By

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Thesis submitted in partial fulfilment of the requirements for the Degree of
Doctor of Philosophy

School of Ocean and Earth Sciences
Faculty of Science
January 2000

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

SCHOOL OF OCEAN AND EARTH SCIENCES

Doctor of Philosophy

EFFECTS OF OCEANOGRAPHIC FACTORS ON THE MESOZOOPLANKTONIC COMMUNITIES OF THE EAST SOLENT AND OUTER APPROACHES

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A series of oceanographic surveys was carried out between June and August 1995 in the East Solent and its outer approaches, covering an area including the East Solent up to Calshot, and extending to Selsey Bill to the East and St Catherine's point to the South. The hydrographic and hydrodynamic characteristics of the physical environment, and the spatial and seasonal dynamics of local mesozooplankton communities were assessed, using a range of *in situ* and remote sensing techniques. Zooplankton samples were taken during the course of four surveys, concurrently with physical oceanographic measurements. A high-frequency Ocean Surface Current Radar was deployed in June 1995 and 1996, which resolved the smaller-scale surface current field.

Radar measurements and the results from a 2-D hydrodynamic revealed that the predominant summer tidal residual flow takes the form of an anticyclonic gyre of approximately 15-20 km in diameter, situated off Bracklesham Bay. Overall, the mesozooplankton community was found to be predominantly euryhaline-marine, and dominated by *Acartia* spp., *Centropages hamatus*, *Temora longicornis*, and meroplanktonic taxa such as larvae of *Crepidula fornicata*, barnacle and decapod larvae. The community showed pronounced shifts in abundances in time and space. The holoplankton and meroplankton compartments were apprehended together and as separate sub-communities, and in the light of a prior benthic survey, which established the distribution of subtidal communities of the area. The two subgroups showed marked differences in their dynamics.

Three station groups were identified through multivariate analyses, corresponding essentially to Solent, Bracklesham Bay and southern stations. These had marked fluctuations in their component taxa, but as a whole were found to be strongly constrained by environmental variables, notably temperature, salinity and chlorophyll (measured by fluorescence). The southern group of stations was clearly defined in terms of lower abundances, whereas the near-shore groups were relatively homogeneous. It is hypothesised that the coastal/sea separation resulted predominantly from a hydrographic separation, possibly reinforced by tidal effects, whilst the Solent/Eastern distribution could result from the influence of hydrodynamic factors, such as recirculation within the gyre. Given these patterns, the potential for dispersal or retention of mesozooplanktonic organisms in the Solent area was assessed using a 2-D hydrodynamic model. The results are discussed in the light of benthic-pelagic coupling through larvae, and of the medium-term variability of coastal ecosystems.

Table of Contents

List of Tables

List of Figures

Acknowledgements

I would like to thank my supervisors, Dr J. A. Williams and Dr. M. Sheader, for their support and for giving me the opportunity and freedom to undertake this project. I am also grateful to the University of Southampton for providing me with a studentship.

Dr. Eric Thiébaut (Université Paris VI) initiated this project whilst on an EC fellowship at the then Department of Oceanography, University of Southampton. I cannot thank him enough for the part he has played then and since. He has been an inspiration and a good friend.

The skipper of M/V *Mary Lisa* and M/V *Scimitar*, Dave Burden, was instrumental in the success of the fieldwork, and is gratefully acknowledged here.

The EC-MAST *Fluxmanche* program must be thanked for the many contributions made to the present work; in particular Dr. Simon Boxall for his collaboration at many levels, Ms Sarah Chaddock for running OSCR, Dr. J-C. Salomon for allowing the use of his model, and Dr. Pascal Bailly-du-Bois for his help, and supplying RECALMER. Ms Virginie Hart must be especially thanked for her enthusiasm and participation in the design, organisation, and running of the field work.

Several people made important contributions at various stages: Ms Céline Ellien for essential help with the model, and helpful discussions and advice; Magnus Axelsson for his hard and thorough identification work; Dr. Jonathan Sharples for reviewing chapter 2; Ms Jill Schwarz for help with MATLAB and the CCA figures; and Dr. Leonie Dransfeld for her help in the final stages. I thank the many others that helped at one stage or other, some of which are acknowledged in the relevant sections.

My particular gratitude goes to Pr. Paul Tyler for his encouragement, to Dr. Alex Rogers and Dr. Richard Lampitt, and to my colleagues and friends from the Molecular Ecology Research Group. Ems Magnus, Glen Kendall, and Pierre & Thérèse Remande played a special part and helped more than I can say.

Finally, I would like to thank Elisabeth Remande-Guyard, my family in its widest possible sense, and the very special friends that all were of great support.

This work is dedicated to Suzanne Burdon, Rachel Florens and Jérémy Guyard.

Who can say of a particular sea that it is old?
Distilled by the sun, kneaded by the moon,
it is renewed in a year, in a day, or in an hour.

Thomas Hardy: *The Return of the Native*

Chapter 1: Introduction

The composition and abundance of ecological communities of the English Channel are subject to important spatial and temporal variations in time and space (Dauvin, 1997). These changes are predominantly driven by climate (Le Fèvre-Lehöerff *et al.*, 1983) *via* hydrography, phytoplankton production and water currents (Robinson *et al.*, 1986; *e.g.* Brylinski, *et al.*, 1988; Brylinski & Aelbrecht, 1993). They change at the scale of global climate cycles (Southward, 1983), of cycles of a few years (3-8; Robinson & Hunt, 1986; Fromentin & Ibanez, 1994), over one year (Robinson *et al.*, 1986), with the diurnal cycle (*e.g.* Zouhiri & Dauvin, 1996), or over a tidal cycle (*e.g.* Dauvin *et al.*, 1998). Furthermore, this variability is influenced by local environmental factors such as topography and background sedimentology, freshwater and nutrient inputs, and others (*e.g.* Le Fèvre-Lehöerff *et al.*, 1983, Fromentin & Ibanez, 1994), which combine with intrinsically biological factors to create the local dynamics of ecosystems. A prime objective for oceanographers is to describe and understand this variability and the mechanisms that lie behind it.

The present work addresses the local and one-season scale of variability of the mesozooplanktonic communities of the East Solent and Outer Approaches. A particular focus is placed on the interaction of these communities with their physical and biological environment: hydrography, hydrodynamics, and the relationship, through meroplankton, with benthic populations. The precise aims and structure of the thesis are stated in section 1.C, after a description of the environmental background of the English Channel, and of the study area.

1.A. The Coastal Environment

The coastal environment includes the coastal zone (river, estuary, coastal boundary layer), the shelf proper and the shelf break (Alongi, 1998). Its upper limit is the zone of uppermost tidal influence and is fixed; the coastal boundary layer, often a tidal front, changes with season, tidal mixing, freshwater input and weather conditions. These characteristics of diversity and variability are reflected in the range and diversity of ecological communities found in the coastal ocean. However it also represents a dynamic environment which is being impinged on increasingly, and is being integrated into economic, transport or leisure activities. On a global scale continental margins represent about 8% of the total surface area and 0.5% of the volume of the world ocean, but 30% of total productivity and 90% of the total fish catch. It acts as the interface between land and ocean, yet its complexity has meant that we still understand little of its underlying mechanisms.

For the past three or four decades the development of fast and/or synoptic instrumentation and data processors has allowed research to move on to a more wide-ranging approach. Oceanographers now look at different compartments together (biology, physics, chemistry...), and integrate them in a more general framework. This, together with an increasing use of modelling, has driven a readjustment of our temporal and spatial scales of observation. By definition, marine ecosystems are multi-dimensional in terms of their component species and their environment, and show both temporal and spatial variations. As such they necessitate adequate sampling methods and appropriate statistical tools to extract their structuring mechanisms. There is now a growing trend to apply these methods, thus expanding our knowledge of ecosystem function: including wider spatial and temporal scales, distinguishing new compartments and processes within the food web, and separating life cycle stages of organisms to understand population regulation (McArdle *et al.*, 1997; Jumars, 1993, chapter 5). In recent years there has been an increasing awareness of the importance of physical-biological interactions, at all spatial and temporal scales, highlighting their importance (*e.g.* Legendre & Demers, 1984; Mann & Lazier, 1991; Jumars, 1993). This approach is now finding its way from theory to experimental and field testing. Coastal areas, such as the English Channel, are of particular interest in this respect, since they are rich and diverse in their biota. They are often shallow, subject to intense tidal, wind-driven or density currents, and large environmental fluctuations on short time scales to which organisms must respond and adapt.

1.B. Environmental Background

1.B.1. The English Channel

The English Channel has benefited from a long history of oceanographic research from several countries. It is a shallow shelf sea (<200m), and regionally fits within the framework of the North Atlantic circulation. As such it is influenced by long term changes such as the North Atlantic Oscillation, as reflected in changes in wind and current circulation, and the consequent Russell cycle, seen for example in drastic changes in fish stocks over decadal time scales (Southward, 1983).

On shorter time scales, and as most coastal seas, it is dynamically driven by a strong oscillatory tidal motion. Instantaneous tidal currents reach ~ 2 knots for an average tide, and in general are associated with a residual, non-oscillatory component. These currents tend to be weak, typically one or two orders of magnitude lower than the tidal streams; however they are permanent (if variable with the Spring/Neap cycle), and thus may be of greater significance for medium- and long-term transport, relatively to stronger but erratic wind-driven flows, or currents linked to density or pressure gradients (Salomon & Breton, 1993). They have been shown to influence the long term transport of dissolved substances in the Channel (Guéguéniat *et al.*, 1993; Fluxmanche II, 1998). This takes the form of a west to east flow, and in many areas of the Channel generate closed recirculation cells, or 'gyres', associated with topographical features (Zimmerman, 1981; Salomon & Breton, 1991, 1993; figure 1.1). The increasing evidence for the ubiquity of these gyres in coastal waters has led to an interest in a theoretical treatment of their underlying physical forces. They arise as a result of the interaction of tidal currents and the local geomorphology of an area, generating a transfer of vorticity from the tidally oscillating to the residual field (see I. S. Robinson 1981, 1983 and Zimmerman, 1981, for a physical treatment). Modelling has shown their potential for acting as retention zones for particles (Salomon, 1990), but until now their effects have not been observed *in situ*.

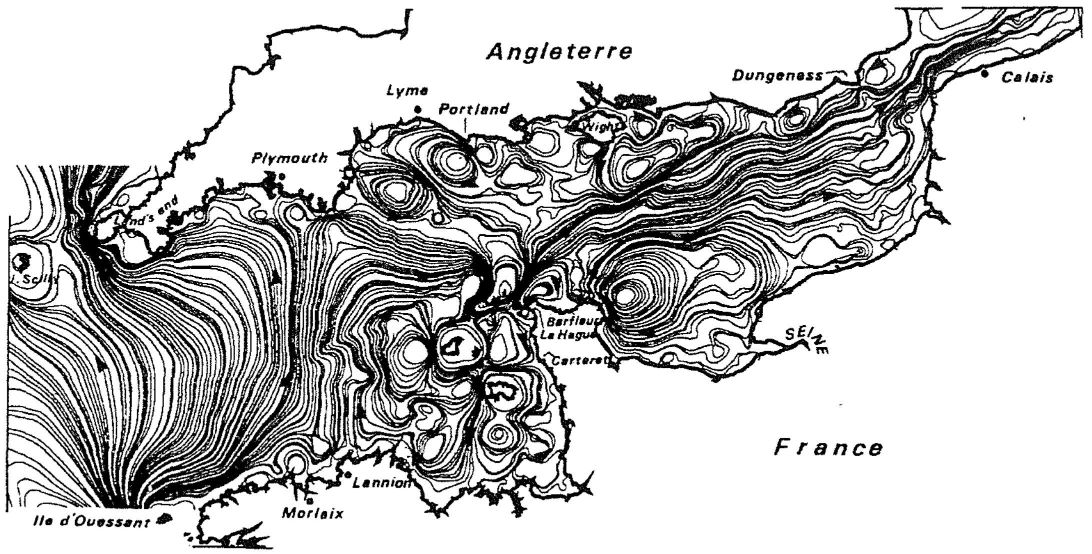

Figure 1.1: Long term trajectories of water movement as calculated by a 2-D hydrodynamic model in a situation of no wind (from Salomon & Breton, 1993).

Wind-driven currents in the Channel are of smaller magnitude than instantaneous tidal currents, but can be greater than tidal residuals and therefore may play an important role in modulating their effects, particularly as they may act to disrupt recirculation patterns. Locally, their long term importance will therefore depend on the relative magnitudes of these two effects, and on their variability in speed and direction, since there is a time lag between their onset and the transmission of momentum to deeper layers of the water column. The overall 'response time' of the Channel/North Sea system is though to be 4 days (Salomon & Breton, 1993). Wind-induced currents can also act to occasionally 'flush out' areas that otherwise show long residence times (*e.g.* Geyer, 1997).

Density currents are not thought to be significant overall in the English Channel, because of strong tidal mixing (Salomon & Breton, 1991). They can however become significant locally (Prandle, 1991), such as in the Baie de Seine, where high freshwater inputs are found (400 $m^3.s^{-1}$ on average), or along the coast of Northern France where a band of relatively freshwater, close to the coast, displays particular physico-chemical and biological characteristics (the 'Fleuve Côtier': *e.g.* Brylinski & Aelbrecht, 1993).

There is a separation between the eastern and western sections of the English Channel, principally linked to the relationship between depth and current strengths (Simpson & Hunter, 1974), such that stratification occurs in the deeper western section during the summer (Pingree, 1975). This has important consequences for primary production (Pingree *et al.*, 1978): the spring bloom occurs earlier in stratified and shallow areas compared with deeper well-mixed regions (Hoch & Garreau, 1998). Locally, the decay of production is then more-or-less marked according to stratification and mixing levels or nutrient inputs from rivers, and important differences can be observed between different localities (Le Fèvre-Lehöerff *et al.*, 1993).

1.B.2. The Solent

The Solent area is situated midway along the English Channel, on the Hampshire and Sussex coasts (figure 1.2). Geographically it includes Southampton Water, the East and West arms of the Solent, Spithead, and the natural harbours of Portsmouth, Langstone and Chichester, with the Isle of Wight as a southern boundary. In the present context the 'Solent Area' will extend to the outer approaches of the Solent, *i.e.* an area approximately delimited by Selsey Bill to the east, and by S^t Catherine's Point to the south.

As a whole, and given its area, the Solent includes a wide range of terrestrial and marine habitats, which harbour a range of communities. Many of these are of conservation or scientific interest, such as mudflats, mixed and *Spartina* marshes, intertidal rocky shores, chalk cliffs, or saline lagoons. The region has been the subject of many changes both in the recent geological past, and more recently through industrialisation, urbanisation, and coastline development. The area to the east and north of Calshot is an important regional centre of industrialisation, and is densely populated. This has brought with it domestic sewage and industrial effluent outlets, and an increased nutrient and pollutant load from rivers. Southampton and Portsmouth harbour are centres of international shipping, and the Solent is subject to a permanent activity of tankers, container ships and other commercial or military vessels, as well as being an important area for recreational sailing and water sports. It supports commercial oyster, clam and bass fisheries, and in parts is subject to intensive dredging. There is also some activity linked to the semi-commercial or recreational fishing of cod, mackerel, plaice, and, in the Test estuary, salmon. In addition, several areas are used for gravel and sand extraction. It is therefore an area where natural resource management and development plays a vital role, and where it is crucial to understand its ecology (Lockwood, 1986; Clark & Gurnell, 1987).

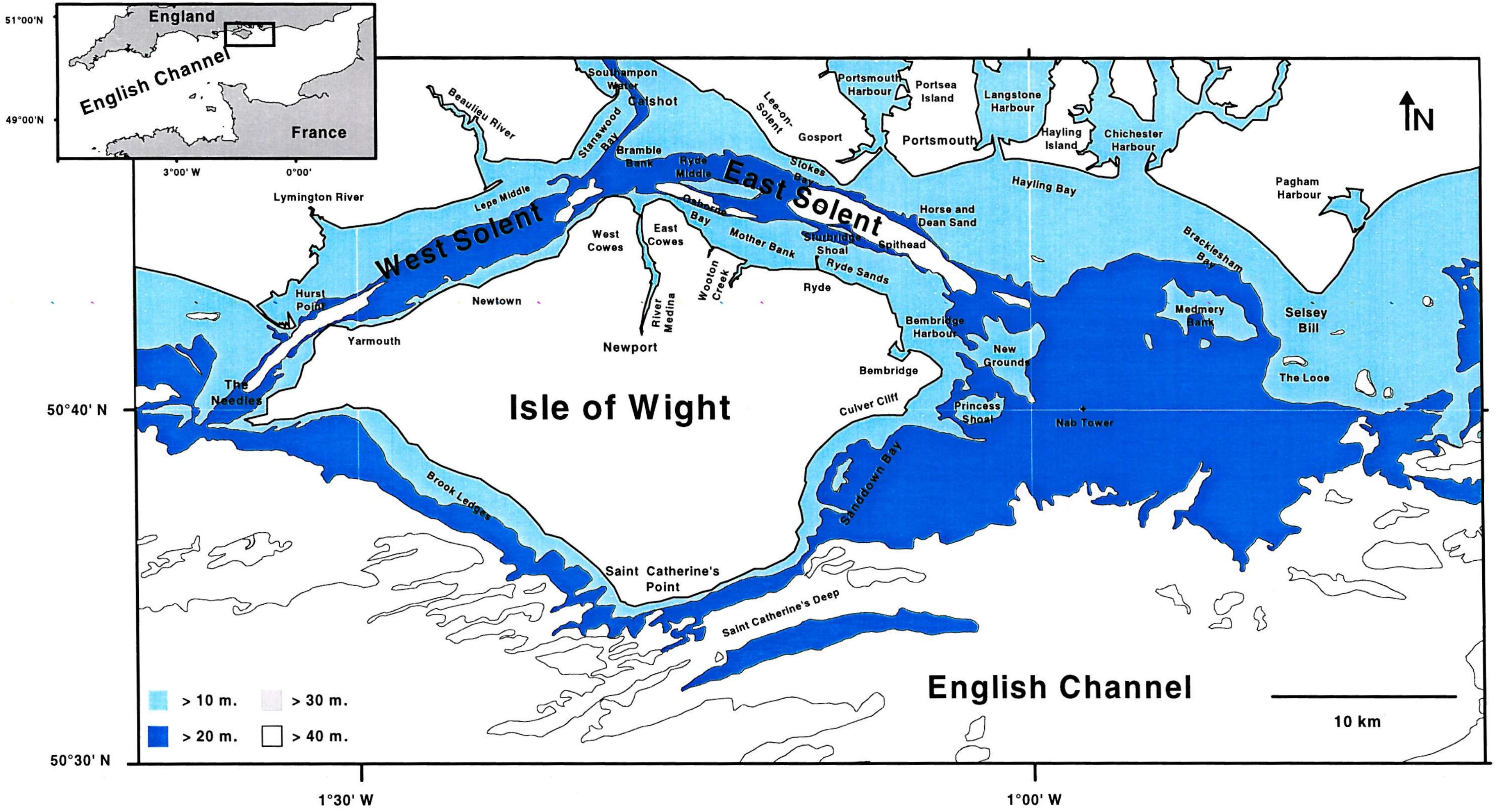

Figure 1. 2: Situation map of the Solent area. Coastline and bathymetry digitised from Admiralty chart n. 2045.

1.C. Aims of the Study and Thesis Structure.

The aim of this study was to determine the local/spatial and short-term/temporal organisation of the mesozooplanktonic communities of the East Solent and Outer Approaches, over the summer of 1995, and, further, to investigate:

1. The role of physical factors, particularly hydrodynamic processes, and specifically tidal residual currents, in the transport of mesozooplanktonic populations.
2. The differential effects of these factors on the two sub-communities of the mesozooplankton: holo- and meroplankton.

In order to address these aims, a multidisciplinary approach was necessary, involved the following:

1. A characterisation of the physical environment, hydrographic and hydrodynamic.
2. Determining the background benthic populations, as a source of meroplankton.
3. Quantifying the mesozooplanktonic populations:
    i. as they relate to the physical environment
    ii. as they can be understood in terms of the holo- and meroplanktonic sub-communities.

The principle hypotheses to be tested were:

1. Biological-physical interactions such as export and retention can account for the spatial and temporal variations in mesozooplanktonic populations.
2. Holoplanktonic and meroplanktonic sub-compartments are subject to different constraints, and therefore exhibit different dynamics; *i.e.* meroplankton will be more closely bound by hydrodynamic processes, being dependent on transport from relatively fixed adult populations, while holoplankton will be more closely associated with hydrographic factors of temperature and salinity.

The structure of the thesis is divided into two parts, A and B. Part A deals with the 'environment', which in this context is both physical and biological: Chapter 2 describes the physical oceanography of the area, as observed using a range of methods during the summer of 1995; and the benthic communities of the East Solent (chapter 3), sampled in February 1995, which form the background against which the permanent and temporary components of the mesozooplankton will be looked at. Part B then reviews the forcing factors of mesozooplanktonic communities in the marine environment, particularly hydrodynamical (Introduction to Part B), after which chapter 4 presents the results of a series of surveys describing the spatial and temporal trends of mesozooplanktonic communities of the Solent area, as sampled in June-August 1995, and with particular reference to mero- and holoplanktonic subcommunities. Chapter 5 then discusses the results of simulations performed using a 2-dimensional hydrodynamic model, which characterise the interactions between circulation patterns, winds, and zooplankton transport, and examine their possible long-term variations. The assessment of this series of results is done within each chapter, with a synthesis and further discussion in chapter 6 (General Discussion).

Part A: The Environment

Chapter 2: Physical Oceanography of the Solent Area

2.A. Introduction

Part of the reason for the development of industrial, shipping and marine activities in the Solent area is its particular configuration and oceanographic characteristics: the shelter it affords over much of its area from the predominantly southwesterly winds, and its particular tidal regime, characterised by a double high water stand. The present knowledge of the oceanography of the region is reviewed in the next sections, followed by the results of: 1) 5 oceanographic cruises carried out in June-August 1995, and 2) the deployment of the Ocean Surface Current Radar (OSCR) in June-July 1995 and 1996. These are then compared with the output of a 2-D hydrodynamic model of the long-term residual circulation of the study area.

2.A.1. Wind and wave climate

The wind climate of the Solent area is influenced locally by topography, but follows that of the English Channel in having a dominance of WSW to SW winds, reinforced by the main axes of the Solent channels. The wave climate is much less documented, with regular measurements having been taken only on the hovercraft slipway at Lee-on-Solent, between 1968 and 1975. Hydraulics Research (1993) have reviewed the available data and modelled the wave climate. Wave action is predominantly from the SW, which makes most of the area sheltered to a greater-or-lesser extent by the Isle of Wight. In the outer approaches, diffraction effects redirect waves to the north, and therefore the exposure of *e.g.* Hayling Island is greater than would be expected otherwise. The area West of Portsmouth/Bembridge is the most sheltered, with an increasing degree of exposure Eastwards. Waves greater than 2 m are expected to occur less than 1% of the time within the East Solent, whereas northwest of the Selsey Bill/S^t Catherine's Point axis, waves of 2.75 m are predicted to occur at the same frequency, reaching 3.25 m to the SW. Wave climate has been shown to be associated in certain areas with sediment movement (Hydraulics Research, 1993).

2.A.2. Tidal regime

The Solent area has been recognised for a long time for its particular tidal regime (Webber, 1980), part of the complex English Channel tidal dynamics. At the scale of the

Channel, there is a degree of resonance of the basin with the semi-diurnal oceanic tide, with the Coriolis effect and frictional losses of tidal energy causing higher tidal ranges on French coasts. Within the Solent area, this resonance leads to a predominance of the semi-diurnal tide, with tidal range increasing from west to east and doubling over a distance of 80 km. The majority of this change occurs in the Solent, over a distance of 16 km, both at Spring and Neap tides. High and low water tend to occur slightly in advance in the West Solent, relative to the East Solent and Southampton Water. The proximity of the M_2 amphidrome, the particular configuration and shallowness of the area and the Isle of Wight/Cherbourg constriction of the Channel, create a singular tidal pattern whereby Southampton Water and the West Solent have a double high water, and the rest of the area sees a prolonged period of high water (figure 2.1). Concurrently there is a long tidal rise (7 hours, compared with 5.5 hours of tidal fall) both at Springs and Neaps, and a reversal of currents slightly before high and low water.

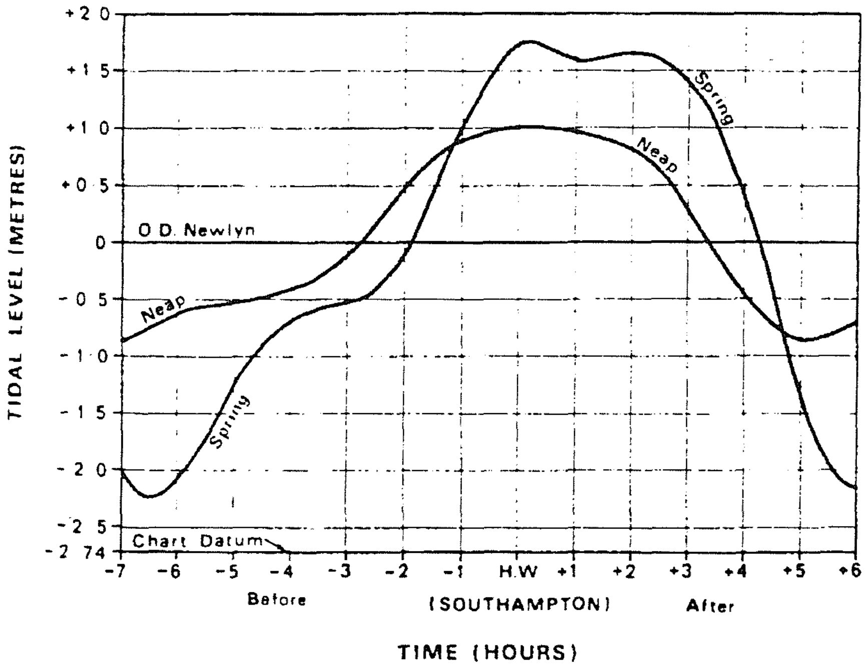

Figure 2.1: Typical tidal curves for Southampton Water (from Webber, 1980).

2.A.3. Tidal volumes

The tidal prism of the Solent system (*i.e.* East, West Solent and Southampton Water) has been estimated at 540×10^6 m^3 at Springs and 270×10^6 m^3 at Neaps (Blain, 1980), with

Southampton Water accounting for about 20%. Throughput has been estimated for the West Solent at 900×10^3 m^3 (Springs) and 550×10^3 m^3 (Neaps) (Blain, 1980). The corresponding volumes for the East Solent are 650×10^6 m^3 and 430×10^6 m^3. This gives a flushing rate of c. 6 ¼ days, with a minimal contribution from riverine input (< 2% of the mean neap tidal prism), most of which comes from Southampton Water. The proportion of 'new water' entering the system is estimated at one fifth to one third of the total flood prism.

2.A.4. Tidal currents

Currents are dominated by tidal movement, and data for the area are limited to admiralty charts. The East Solent has slower currents than most areas of the region, with an average at Springs of 2.0-2.4 knots. These can be much faster in the West Solent with Springs averaging 3.0-3.5 knots, and up to 4.5 knots in the Hurst Narrows. Strong currents are also found south of St. Catherine's point with average Springs up to 4 knots (all these data from Admiralty chart 2045). These current velocities are probably underestimates of surface currents, since they are based on averages taken at 9 m depth.

2.A.5. Residual currents

There is little information available on residual currents (Clarck & Gurnell, 1987). Current directions are generally along the axis of the channel in the West Solent, except where estuaries occur. The pattern in the East Solent is more complex and variable due to the greater channel width and the occurrence of banks. The general axis is still parallel to that of the East Solent, but locally small eddies (Osborne Bay, Stokes Bay) or estuarine flows are thought to occur (Medina Estuary, Wooton Creek, Southampton Water and Portsmouth Harbour). Very little data is available for the area East of the Isle of Wight. Overall, the ebb currents tend to be stronger than flood currents due to the asymmetrical tidal profile, and there is a change in tidal range and phasing of high and low water from West (earlier) to East (later), leading to a time lag in the onset of flood and ebb, and in the occurrence of peak currents. In the West Solent, Dyer & King (1975) have calculated, from moored flow meter data, that the residual current was in general small, and influenced by meteorological effects. It flows generally from east to west, particularly at Springs. Dyer and King also found some correlation between easterly winds and westerly residual flow, and between westerly winds and easterly flow, presumably from atmospheric pressure effects.

Recently there has been some evidence for the existence of a tidal residual gyre in the region of the outer approaches to the East Solent. It comes from two sources: the first is the model by Salomon & Breton (1991, 1993; figure 1.1), which showed a wind-sensitive residual gyre in the area. The second source has been reported in Boxall & Robinson (1987) and consists of several surveys. The results are summarised chronologically below:

- May 1980: Coastal Zone Colour Scanner images (4 dates in April/May). These revealed a dark area east of the Isle of Wight and a high reflectance area to the south, probably from chalk cliff erosion. The permanence of these features was interpreted as inhibition of cross tidal mixing, and the development of a westward residual flow close to the coast. Water in the gyre area was then thought to be advected and mixed to the south, as revealed by fringes similar to Pingree *et al.*'s (1985) observations around the Channel Islands. Other CZCS images of the Solent area (May 1981, 1984, 1985) indicated similar patterns.
- May 1984: From the Ministry of Agriculture, Food and Fisheries (MAFF) surface drifters were deployed at two sites, one in the centre of the 'gyre' area (A), and the other south of the Isle of Wight (B). The first returns of drifters released at A came from the area between Selsey Bill and St. Catherine's point; *i.e.*: the Solent. None were recovered from the east of Selsey Bill on this side of the English Channel. Other returns were from France 57 days later. No drifters from B were recovered from the English coast, and the others were returned 27 days later from France.
- May 1985: MAFF current meter, south of the Isle of Wight. Measurements showed a tidal excursion of c. 20 km at that point (predominantly E-W), with a southward residual tidal flow of c. 3 km/tidal cycle (~ 7 cm.s^{-1}), which was of the same order as the separation between the fringe elements observed previously.
- May 1986: CZCS images. These were obscured by cloud cover over the region of interest. However, for other parts of the Channel, the images were similar to March/April, not May) images taken other years.
- May 1986: Sea surface drifters, bottom drifters, and parachute drogues. These three experiments showed a general residual flow to the east/ north-east for the whole area. This, together with the CZCS, was interpreted as wind effects breaking up the pattern of tidal residual circulation. In 1986, the climate for Northwest Europe was over six weeks behind average.
- Mid June 1986: Drift cards (again two sites). These were deployed six weeks after the May experiments to test hypothesis of a seasonal westward circulation. The results

were similar to the May 1984 MAFF surveys, *i.e.* a pattern of retention east of the Isle of Wight.

These results point towards the presence of a near shore westward residual flow, culminating in a recirculation residual cell in the area of the outer approaches, east of the Isle of Wight and North of St. Catherine's Point. To the south of the outer approaches the apparent residual circulation was southward, then eastward. This pattern was observed to be seasonal and not seen before April/May, when winds presumably disrupted the average tidal flow, and the residual flow was towards the coast following the dominant southwesterly winds. These results are summarised in figure 2.2.

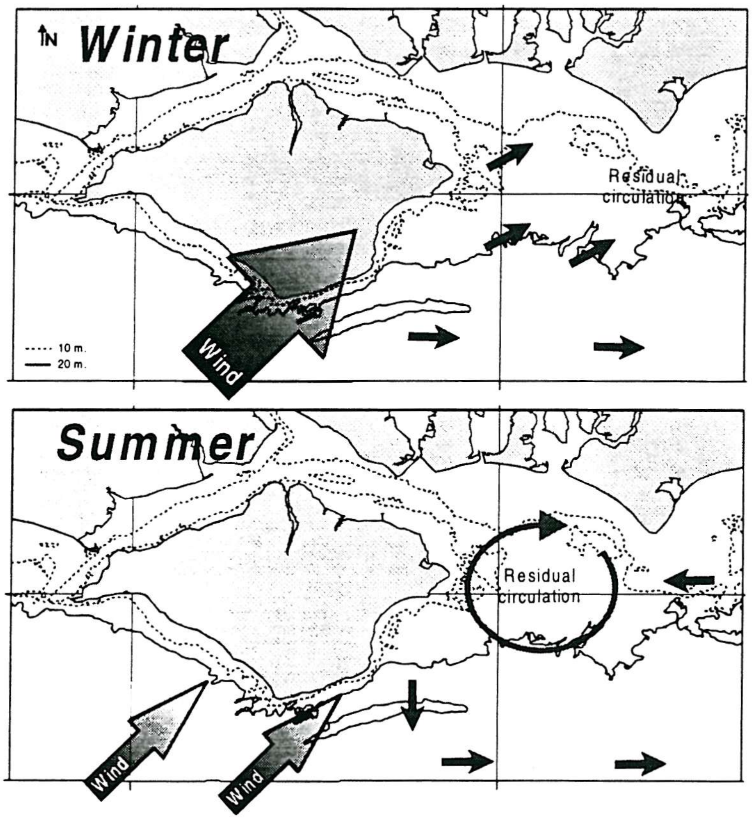

Figure 2.2: Schematic diagram of the possible interaction of wind and residual currents in the Solent area: in winter, circulation is principally wind-driven, and directed onshore and to the east; in summer, tidal residual circulation dominates and takes the form of an anticyclonic recirculation cell to the east of the Isle of Wight, with westerly circulation further east, and a southerly flow to the south, where it rejoins the general easterly circulation of the English Channel.

2.A.6. Hydrography

The average yearly near-surface salinity[1] for the Southampton Water/East & West Solent system has been approximated at S = 34.4 (Phillips, 1980), with winter levels poorly represented. From Southampton Water to the East Solent (around Horse & Dean Sands), Castro-Longoria (1998) recorded in 1995 seasonal variations of ~ 4 salinity units, from S = 32 (February) to just below S = 35 (August), and a steady increase and decrease in-between. There was no evidence of stratification outside of Southampton Water. A gradient was seen between the top of Southampton Water and the Solent, from ~3-4 units in April to ~1.5-2 units in August. Water temperature reached a minimum of 8.2°C in March 1995 and a maximum of 20.6°C in August.

Castro-Longoria (1998) also found low values of chlorophyll *a* in the Solent, compared with her measurements in Southampton Water, and with a decreasing seaward gradient.

It had two seasonal maxima, one in May-June, with values ranging from 11.0 $\mu g.l^{-1}$ in the West Solent, 14.3 $\mu g.l^{-1}$ at Calshot, 6.6 $\mu g.l^{-1}$ off Gosport and 3.4 $\mu g.l^{-1}$ off Portsmouth. The other peak occurred in July with ~1.3 $\mu g.l^{-1}$ in most of the Solent, and 2.8 $\mu g.l^{-1}$ at Calshot. This places the Solent in the lower-than-average bracket for Channel coastal sites (*e.g.* Le Fèvre-Lehoërff *et al.*, 1993). Although the Solent area was not sampled, autumn-winter values for Southampton Water were around 0.1-0.3 $\mu g.l^{-1}$, and started rising around April-March. Hoch (1998) has modelled the primary production for the English Channel, and found values of <150 $gC.m^{-2}.yr^{-1}$ for the Solent area, which places it at the lower end of values for the English Channel, close to values found further West.

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[1] In this and later sections, salinity measurements are given following UNESCO (1981).

2.B. Methods

The following sections describe the physical oceanographic environment of the sampling area, as characterised by the physical variables measured during the time of study. To this end a three-tiered approach was taken: hydrographic sampling, hydrodynamic remote sensing of surface currents by HF Radar, and hydrodynamic modelling of tidal residual currents.

2.B.1. Hydrography

The sampling strategy was designed so as to find a compromise between sampling over a large area and retaining a sufficiently small interval between sample stations. Given the boat speed, and the fact that a shortest possible time between beginning and end of sampling had to be kept, a star-shaped, 3-transect sampling pattern was chosen over a grid pattern, as in Hill *et al.* (1994). This enabled the survey to cover a wide area, kept stations close to each other, and gave a 'reference point' in the centre (station 5) which was sampled at each transect for comparison. The sampling strategy and station names are illustrated in figure 2.3(A). 39 stations were planned for each cruise, 30 along the three main transects, and 9 in the Solent: West Lepe, North East Lepe, Lepe, South East Lepe, Calshot, East Ryde, North Sturbridge, Sturbridge, and South Sturbridge. The transects are in order of station numbers: transect 1 (NW-SE): stations 1-11; transect 2 (SW-NE): stations 12-21; transect 3 (N-S): stations 22-29 (there is no station 25). Station 5 was sampled three times as 5-1, 5-2 and 5-3 on each transect. Transect stations are 1.5 nm apart and their positions were determined by GPS. Sampling lasted approx. 10 min, with an interval of ~30 min. between stations.

The same idea of sampling at several scales was used in the time domain: 5 surveys were spaced so as to include weekly, monthly and seasonal scales, beginning in the spring and ending at the end of the summer. Weekly, bi-weekly, monthly and two-and three-monthly time intervals are represented in figure 2.3(B):

Although planned, two other surveys for the autumn and winter could not be carried out.

At each station a Conductivity-Temperature-Depth (CTD) probe was cast, fitted with a Chelsea Instruments Aquatrack fluorometer, tuned for chlorophyll fluorescence, and a 25 cm path length SeaTech transmissometer. The chemistry of the water column (nutrients and heavy metals), chlorophyll *a* and suspended particulate matter (SPM), and calibration samples were to be taken from 11 rosette samples. These samples proved however to be for the most part either unavailable or unusable. As a result, calibration was available only for

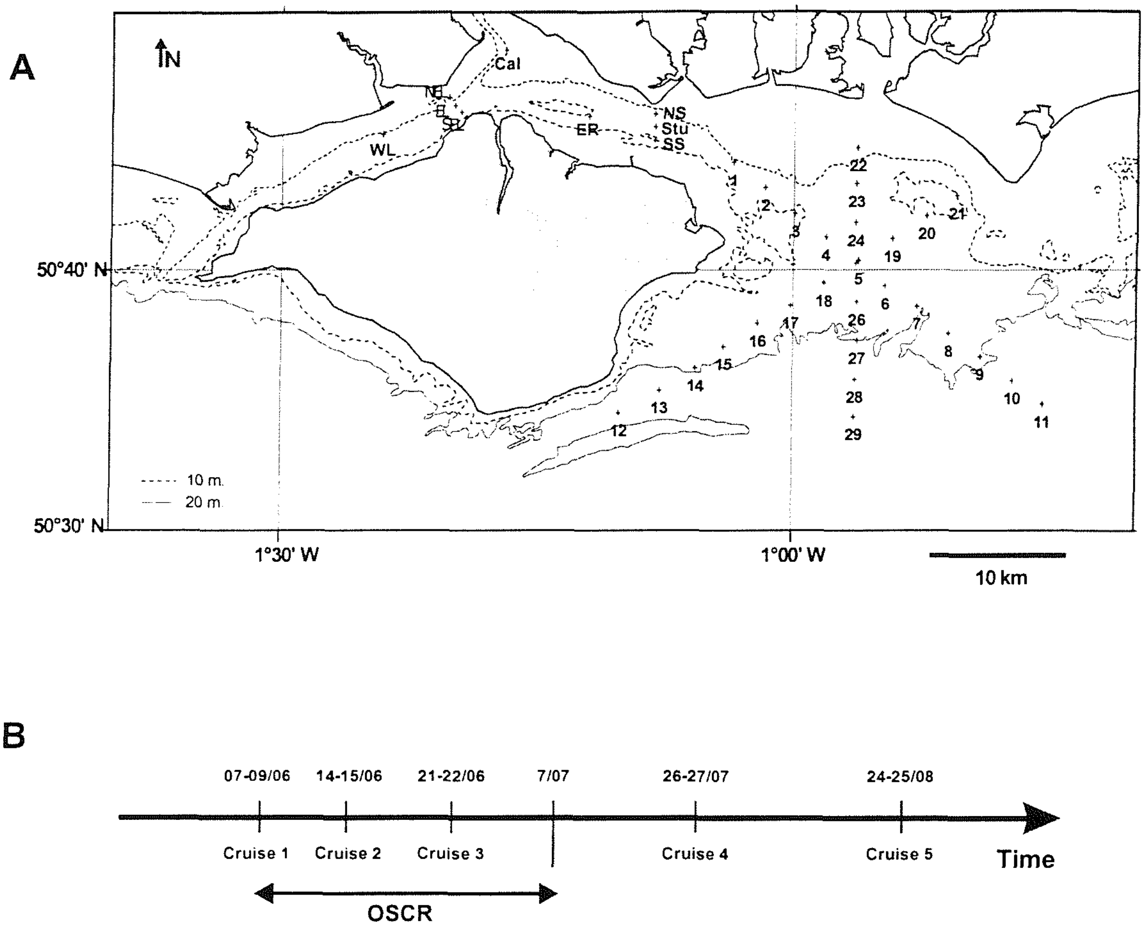

Figure 2.3: Sampling strategy (A) and sampling time line (B): WL = West Lepe; EL, NEL, SEL = East, North East and South East Lepe; Cal = Calshot; ER = East Ryde; Stu, SS, NS = Sturbridge, South Sturbridge, North Sturbridge; station 5 is sampled three times as 5-1, 5-2 and 5-3.

salinity measurements; chlorophyll *a* (fluorescence) and suspended particulate matter (transmissometry) results are therefore displayed in volts (sections 2.C *et seq.*).

2.B.2. Water column stability

As a measure of water column stability, the potential energy anomaly ϕ (*e.g.* Simpson & Sharples, 1991) was calculated at each station. This is a measure of the energy required to mix the water column and is calculated as:

$$\phi = \frac{1}{h}\int_0^h [\bar{\rho} - \rho(z)]\, gz\mathrm{d}z; \quad \bar{\rho} = \frac{1}{h}\int_0^h \rho(z)\,\mathrm{d}z \qquad (2.1)$$

where h is water depth, ρ density and g the gravitational acceleration. The z-axis (depth) is positive downwards.

2.B.3. Tidal correction

Aliasing and pseudoreplication have always been a problem for ecologists, albeit often hidden within the statistical design of field experiments (Hurlbert, 1984). In the marine context, one aspect of this is the tidal correction of oceanographic measurements, the bases of which were set out by Defant (1950).

In tidal environments, a single ship sampling consecutive station positions will be sampling each station at a different state of the tide. The resulting spatial pattern will show an artefactual periodicity of measured values, linked to tidal oscillation. To avoid this, either all samples have to be taken at the same time, or they have to be sampled at the same tidal state (*e.g.* high tide on consecutive days). Both these solutions are impractical even for small surveys, and in effect the researcher has to compromise between two requirements: the need for a synoptic view (stations sampled at the same time), and the need to achieve a sufficient spatial cover (number, spread and distance between stations).

Tidal correction attempts to solve this problem, resulting in *quasi*-synoptic sampling. It involves bringing back all positions of a given survey to a given uniform reference time. For this, tidal current directions and speed have to be integrated from the time of sampling to the reference time, correcting positions accordingly. This has been formalised by Brockmann & Dippner (1987):

If **a** is the geographical position of a sampling point, t_0 the actual time of measurement, then the fluid element position to be corrected can be identified by its position **x** which depends on the initial coordinates **a** and the elapsed time t-t_0. Thus:

$$x = x(a, t-t_0); \quad x(a, 0) = a \qquad (2.2)$$

The Lagrangian velocity u is defined as:

$$\frac{d}{dt} x(a, t-t_0) = u(a, t-t_0) \qquad (2.3)$$

So that:

$$x - a = \int_{t0}^{t} u(a, t-t_0)\, dt \qquad (2.4)$$

The connection between the Lagrangian and the Eulerian velocity **U** is given by:

$$u(a, t-t_0) = U(x(a, t-t_0), t-t_0) \qquad (2.5)$$

And hence:

$$x - a = \int_{t0}^{t} U(x(a, t-t_0))\, dt \qquad (2.6)$$

This method involves a Lagrangian/Eulerian 'switch', in order to change the frame of reference. There are a number of problems with the application of this method, especially regarding the Eulerian velocities needed for the calculations. In a varying environment, such as the East Solent, these need to be known at a scale equal to or smaller than that of the sampling effort, or somehow interpolated in an appropriate way between data points. It assumes horizontal uniformity of u at the scale of the observations. The finer the resolution at which current vectors are known, the better local effects such as small eddies, which are likely to influence the area in question, can be resolved. It also does not take into account the residual component of the current, since it is the instantaneous velocity field that is used in integration, however this can be ignored over short time scales (<< one tidal cycle). It also ignores diffusion, which in some cases can be an important factor; again the magnitude of this error will depend to a large extent on the integration time.

Here, the program 'RECALMER', developed by Pascal Bailly-Dubois and Karine Thoral, of the Laboratoire de Radioécologie Marine de l'IPSN (Institut de Protection et de Sûreté Nucléaire) was used. It uses instantaneous current vectors from the *Fluxmanche* hydrodynamic model (Salomon & Breton, 1991, 1993), which has a spatial resolution of 1 nm and a time step of 12 minutes; thus it does not resolve small scale effects. Three tidal states are included in the database of the RECALMER program corresponding to Springs, Neaps and average tides, equivalent to tidal coefficients of 95, 70 and 45, as defined by the Service Hydrographique et Océanographique de la Marine (SHOM), which, theoretically, may vary from 20 (maximum Neaps) to 120 (maximum Springs), with 70 being an average tide. For any given tidal state the values are then interpolated between these three databases. Wind-driven currents are not taken into account. The times and tidal coefficients are from SHOM, and the integration time step in RECALMER is of one minute. The baseline used is the time of high tide at Brest.

2.B.4. Radar measurements: Ocean Surface Current Radar

2.B.4.a. *General*

The rapid development of remote sensing in its wider sense has in recent years opened many new possibilities in most sub-disciplines of oceanography. This has been achieved through the development of new instrumentation such as satellites, airborne sensors, Sonars, Acoustic Doppler Current Profilers, or high frequency (HF) Radars, such as the Ocean Surface Current Radar (OSCR). These HF Radars have been in use for over two decades now, and their acceptance as non-invasive, long-term synoptic current measurement tools is growing (*e.g.* Paduan & Graber, 1997).

2.B.4.b. *Principle*

Radar has been in use in marine science for several decades; the first observation that the 'clutter' that obscured the return from ships or aircraft could be a useful signal in itself is due to Crombie (1955). He observed that returned HF signals (3-30 MHz) recorded near the sea showed a Doppler shift of a fraction of a hertz above and below the transmitted frequency. This was due to Bragg scattering by ocean waves (see below), travelling radially towards or away from the signal source, and of half the radar wavelength. The principle behind these observations, and the success of HF radar systems, depends on the interpretation of returned electromagnetic signals from the water surface. Because of the complex nature of the sea surface, the reflection of electromagnetic energy from an emitting source will send back a modified backscatter spectrum, even from a single original frequency. It is the interpretation of these spectral returns for different transmit frequencies which conveys information on sea surface variables, mainly currents, but also wind and wave measurements.

Many instruments rely for these measurements on Bragg scattering, a resonance phenomenon of the transmitted signal returned by sea surface waves of exactly half the Radar emitted wavelength. This causes strong peaks in the return signal at these particular frequencies. For HF systems the target waves are 'short' gravity waves with wavelengths of the order of 10 m. Apart from very shallow areas, these can be assumed to be travelling as deep-water waves and thus their speed is given by $c = \sqrt{(g/\lambda 4\pi)}$, where λ is the wavelength of the transmitted signal and g is the gravitational acceleration. The difference between the total Doppler shift of the returned signal and that expected from the gravity waves as calculated above is assumed to be the due to the underlying surface currents. Because of the reliance on these gravity waves, HF radar can only resolve currents which affect them, *i.e.* in the top few metres, and with a further depth limit (d) given by the radar wavelength such that ~d = $\lambda/8\pi$. This relationship also allows, when used with different wavelengths, to measure current shear in the first 2 metres of the water column.

The operational frequencies of HF systems lie in the range of 3 to 30 MHz, with wavelengths of 10-100 m (as opposed to Radar proper, where wavelengths lie in the microwave band of ~1 mm-1 cm). The Doppler shift measured is due to the components of the currents that are 'away' or 'towards' the emitting station only, and thus two or more sites must be combined to form vector surface current estimates, with radials crossing at between 30° and 150° in order to resolve the current vectors satisfactorily. Thus four main measurements are necessary: the range (distance) to the target (a patch of water), the direction of the target as referred to a given azimuth, the Doppler frequency of the target, and the power of the return signal (which is linked to the accuracy of the measurements, section 2.B.4.c below).

Although they share the same operating principles, there are several possible types of HF radar configurations, each with a different capacity to resolve the measurements mentioned above. Typically the range can be anywhere between 1 and 150 km, at a resolution of c. 0.3-3 km along a radial beam, with azimuthal resolutions of c. 5°, approximately representing between 0.5 km near the coast and a cell width of 10 km at a range of 100 km. The precision of the velocity measurements is limited by the resolution of the Doppler spectrum, and is typically 2-5 $cm.s^{-1}$.

2.B.4.c. *Distance measurement*

Distance is calculated as $ct/2$, where c is the velocity of light in a vacuum (3.10^8 $m.s^{-1}$) and t the pulse width (= return time) in seconds. The accuracy of the measurement is linked to the pulse width, itself a decreasing function of power. Thus the greater the power the smaller the signal-to-noise ratio and accuracy.

2.B.4.d. *Doppler measurement*

Doppler measurements are done by repeating the range measurements at a regular rate and performing a time series analysis on the samples obtained from each of the individual range measurements. The frequency resolution is given approximately by $\Delta f = 1/T$ Hz, where T is the coherent integration time (s). The velocity resolution is then $\Delta v = \lambda \, \Delta f/2$ ($m.s^{-1}$), where λ is the radar wavelength in metres.

2.B.4.e. *Azimuth angle measurement*

The returned pulse covers an area which is divided by OSCR into sectors, within which distance and Doppler measurements are made. To do this, the phased array system is used, *i.e.* the difference in phase of the returned signal between each of the antennas is compared. The precision of the angle separation depends on the aperture of the antenna (its area on the ground), and the wavelength.

2.B.4.f. *Harmonic analysis*

From the series of measured instantaneous current measurements, harmonic analyses can be performed at each cell position to determine the tidal constituents and the residual current, which together explain the observed currents measured by OSCR. The minimum period of measurement necessary to resolve closely spaced tidal constituents (the synobic period) is given by the related beat frequency (the so-called Rayleigh criterion), *i.e.* 15 days for the two largest constituents M_2 and S_2. However the signal to noise ratio for OSCR measurements is such that periods of 30 days are recommended. Figure 2.4 and table 2.1 summarise the time and extent of OSCR measurements in 1995 and 1996. Harmonic analyses were performed using a least squares regression, by the program TIRA (Tidal Institute Recursive Analysis), developed at the Proudman Oceanographic Laboratory and modified subsequently at the Department of Oceanography, University of Southampton. TIRA identifies 39 constituents, including residual currents.

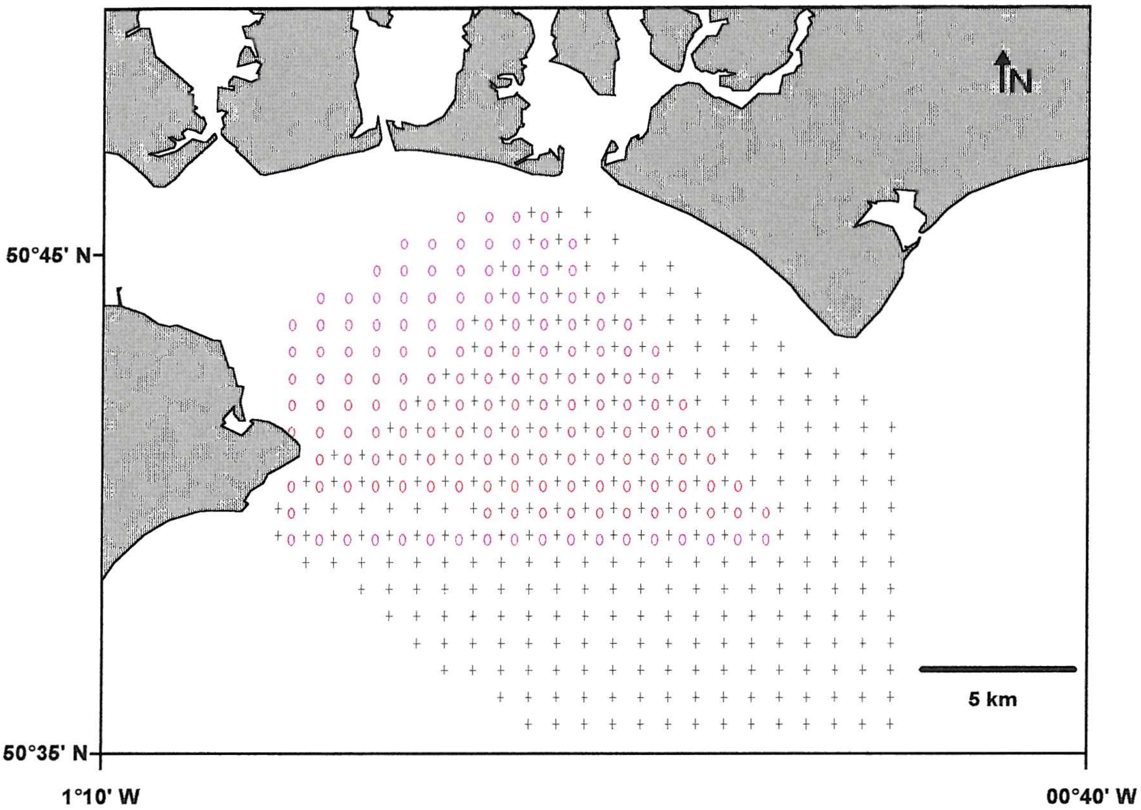

Figure 2.4: Ocean Surface Current Radar cells positions: 1995 (o) and 1996 (+)

	1995	*1996*
Approximate surface covered (km^2)	175	280
Approximate geographical range	01°05' - 00°50' W 50°40' - 50°45' N	01°05' - 00°46' W 50°35' - 50°45' N
Start and end dates	7/06 - 7/07	27/06 - 27-07

Table 2.1 Ocean Surface Current Radar deployment summary for 1995 and 1996.

2.B.5. Physical Hydrodynamic Modelling of Residual Currents

2.B.5.a. *General*

Long term tidal residual currents in various tidal and wind conditions were calculated using a finite-difference 2-D hydrodynamic model, developed, as part of the EC-MAST *Fluxmanche* program, by Jean-Claude Salomon and co-workers (Salomon & Breton, 1991, 1993) at IFREMER Brest (Institut Français de Recherche pour l'Exploitation de la Mer), initially for the whole of the northwest European continental shelf (boundary conditions are from Schwiderski, 1983). In its present configuration it is limited geographically to 48°18' N - 51°20' N and 6°28' W - 3°00' E, divided into 367 × 184 cells (resolution: 1 nm).

2.B.5.b. *Principle*

First the instantaneous currents for each cell are calculated by solving the depth-integrated equation of motion in its classic form, for a variety of tidal and wind conditions (Salomon & Breton, 1993):

$$\frac{\partial V}{\partial t} + V.\nabla\varsigma + 2\,\Omega \wedge V = -\,g\nabla\zeta - \frac{gV|V|}{Kr^2\ H^{4/3}} + \varepsilon\nabla^2 V \qquad (2.7)$$

where V is the depth-averaged velocity, ζ is the surface slope, g is the gravitational acceleration, H is the depth of the water column, Kr is Strickler's friction coefficient, ε is the horizontal viscosity coefficient, and Ω is the angular velocity of the Earth's rotation.

For each departure position $\mathbf{x}_0$ and departure time t_0 these instantaneous currents are integrated in space and time over a tidal cycle, and the resultant residual velocities are calculated. For each $\mathbf{x}_0$ there are as many trajectories and residual velocities as there are t_0 departure times.

Instead of averaging these vectors over time and assigning the result to each $\mathbf{x}_0$, the Lagrangian residual velocity is assigned to the averaged position of the trajectory over a tidal cycle (the "barycentre" = "centre of gravity"). This amounts to a change of co-ordinate system, and allows a single trajectory to be assigned to each point of the model (as opposed to one for each t_0).

The model has been calibrated and verified extensively within Fluxmanche, notably in the Baie de Seine and the straits of Dover against OSCR, current meters, drifting buoys and radionuclide tracing (*e.g.* Broche *et al.*, 1986, Guéguéniat *et al.*, 1993, Orbi & Salomon, 1988, Salomon *et al.*, 1988, Salomon *et al.*, 1993).

2.C. Results

Results are displayed in four sections: sampling and tidal correction; hydrographic results; OSCR; and hydrodynamic modelling.

2.C.1. Sampling and tidal correction

The stations sampled on each cruise and their repositioning with RECALMER are displayed on figures 2.5 and 2.6; Table A.2.1 (appendix A) displays the dates, tidal states and starting times for each cruise, and for each transect within cruises. For all cruises, transects 1, from the Solent to station 11, and 2, from stations 12 to 21, are relatively unaffected by repositioning, although there is a stretching out around St. Catherine's Point of the outermost stations of transect 2, and there is an important westward shift of the first transect on cruise 5 (figure 2.6). Most affected are the stations of the second transect (22-29), which are consistently shifted to the West. The greatest displacement relatively to geographic space is that of station 29 in cruise 4, by ~14 nm. Since there is no consistency between sampling times and the state of the tidal cycle (table A.2.1), and given the dominant currents patterns of the area, this is likely to be a reflection of these prevailing currents rather than sampling strategy. Of the stations displayed in figures 2.5 and 2.6, those where the CTD failed or where no zooplankton was collected are displayed in table A.2.2 (appendix A).

Overall the repositioning of stations has an important impact on the placement of stations. It reduces the regularity of the sampling interval, and in particular it effects the extent of spatial coverage, and leaves gaps in the spatial coverage, particularly to the S and SE of the area.

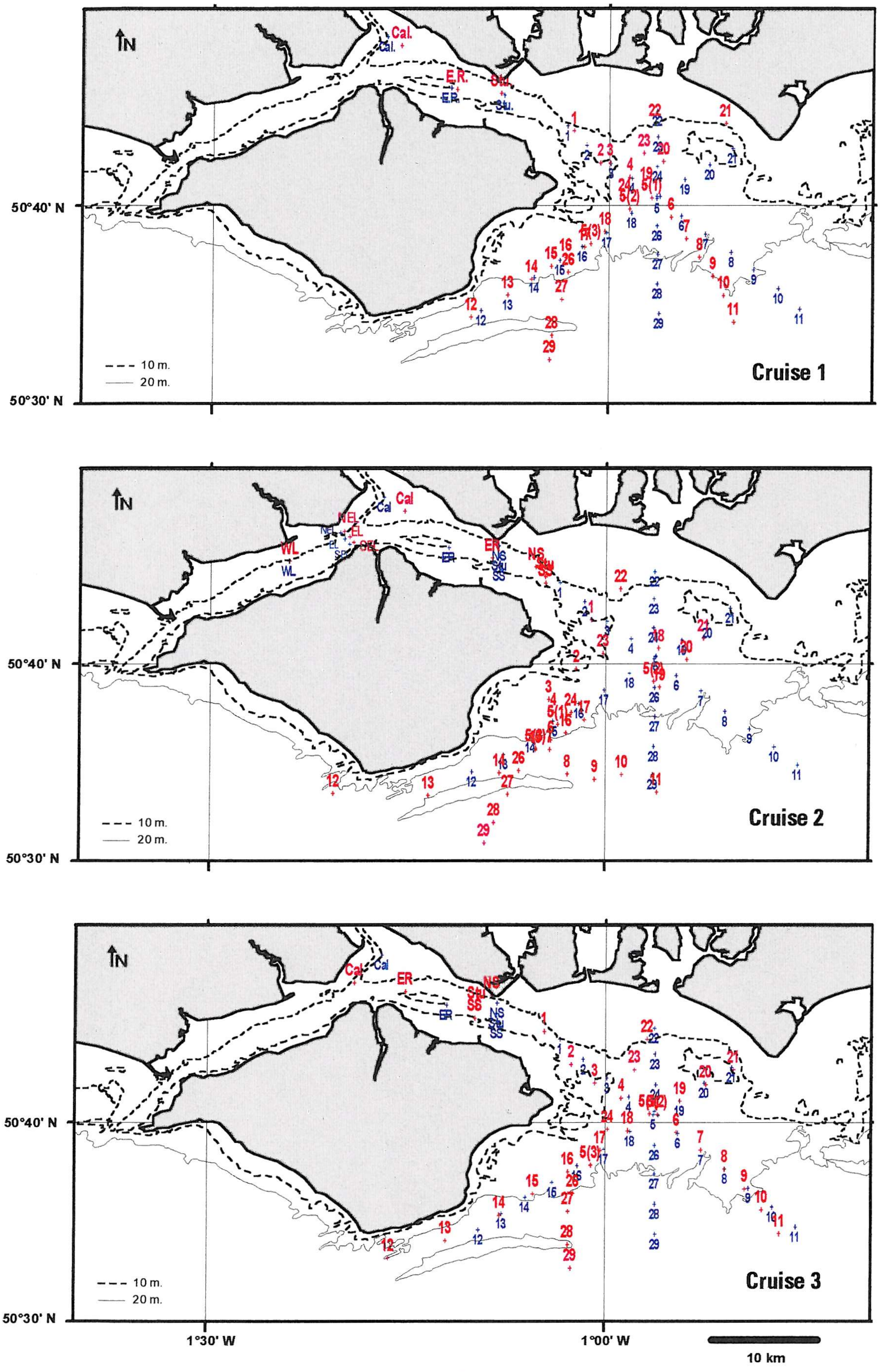

Figure 2.5: Sampled (✚) and repositioned (✚) positions for cruises 1 (7-9/06/1995), 2 (14-15/06/1995), and 3 (21-22/06/1995).

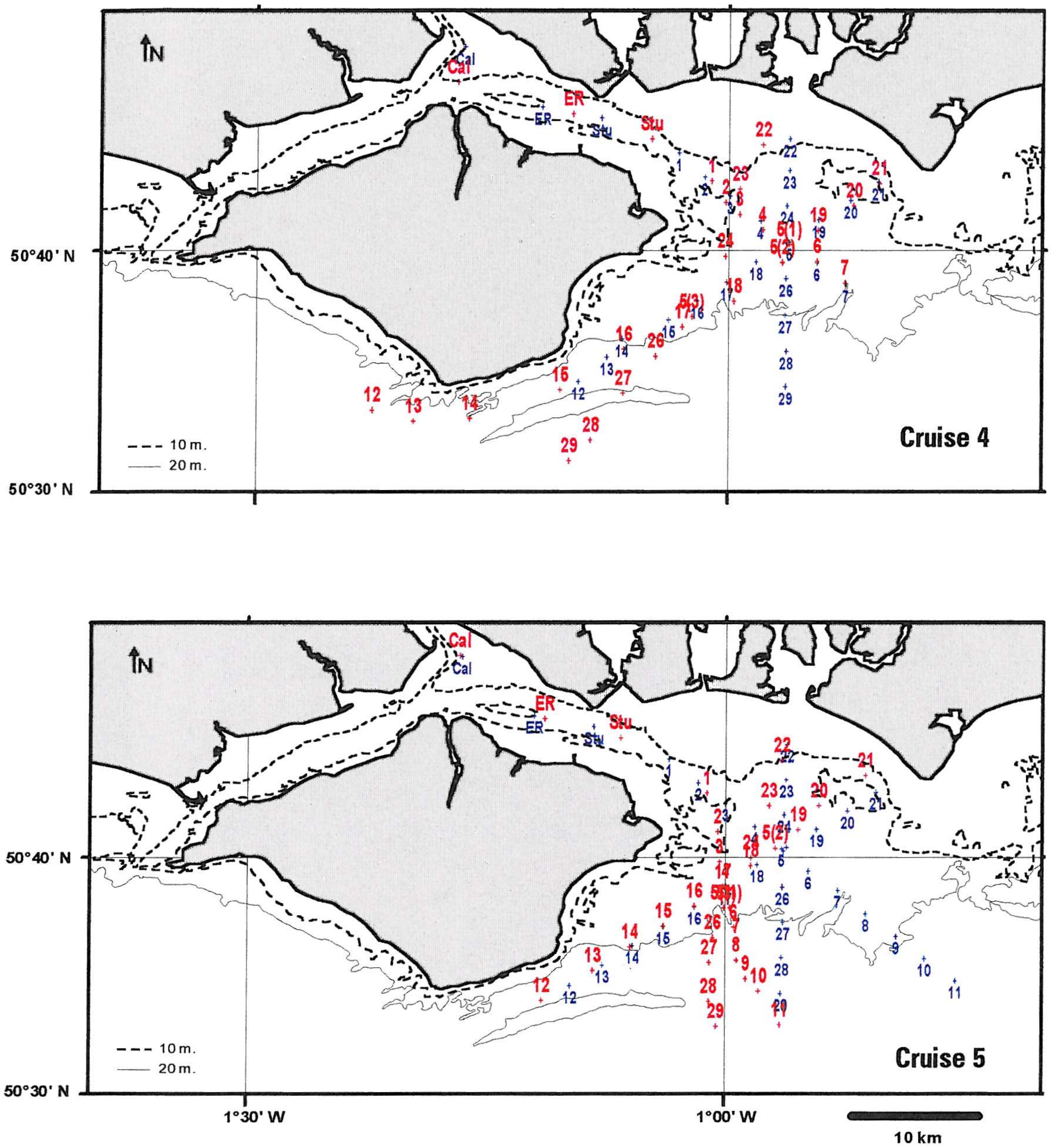

Figure 2.6: Sampled (✚) and repositioned (✚) positions for cruises 4 (27-28/07/1995) and 5 (23-24/08/1995).

2.C.2. Hydrography

2.C.2.a. *Temperature and Salinity*

The results of the CTD data are displayed in figures 2.7 to 2.11, and T-S diagrams in figures 2.12 and 2.13. For the maps of figures 2.7-2.11, physical measurements were interpolated over the area by krigging, using the Surfer package (Golden Software), with an anisotropy of 1.5 in the north-south direction to compensate for the displacement of the second transect. At some stations there was evidence of slightly decreased salinity values at depth, independently of the algorithm used for salinity calculations, and of the order of 0.01 salinity units. This was indistinguishable on vertical CTD plots, and represents ~1/20th to 1/30th of the average range of values. There is little evidence of stratification, with only a slight increase in surface temperature and decrease in salinity found in Solent stations in cruise 3. A few examples of CTD vertical plots are displayed in figure A.2.1 (Appendix A).

The correlation between physical factors (together with total zooplankton abundance, *c.f.* chapter 4) is displayed in table A.2.3 (appendix A). Average temperature, salinity and density for each cruise are displayed in table 2.2 together with their maxima and minima:

Cruise	**Temperature (min/max, °C)**	**Salinity (min/max, PSS78)**	**σ_{t-g} (min/max, kgm^{-3})**
1	14.3 (13.6/15.1)	34.4 (33.1/34.7)	26.0 (24.8/26.3)
2	14.3 (13.1/15.0)	34.4 (33.4/34.7)	26.0 (25.0/26.5)
3	15.4 (13.8/16.5)	34.4 (33.7/34.7)	25.8 (24.9/26.3)
4	19.3 (18.2/20.4)	34.6 (33.8/34.7)	24.8 (23.9/25.2)
5	20.7 (19.9/21.6)	34.8 (33.8/35.0)	24.6 (23.5/24.9)

Table 2.2: Average, minima and maxima of temperature, salinity and σ_{t-g} for cruises 2-5. Cruise 1: 7-9/06; Cruise 2: 14-15/06; Cruise 3: 21-22/06; Cruise 4: 27-28/07; Cruise 5: 23-24/08.

Cruises 4 and 5 are characterised by increased temperature and salinity, from ~ 14-15°C/34.4 for June cruises, to ~19-20°C/34.6-34.8 for July and August (reflected also

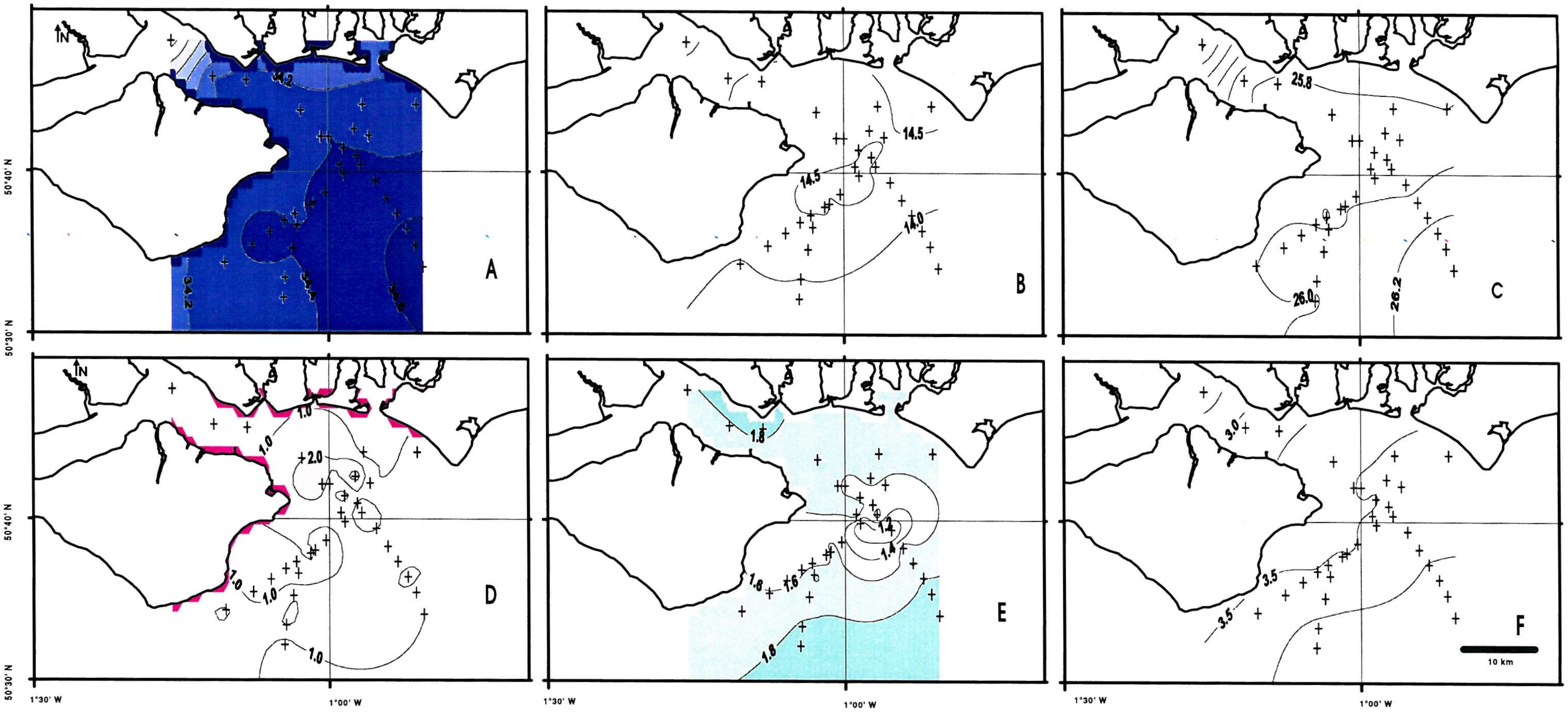

Figure 2.7: Cruise 1 (7-9/06/1995): Salinity (A), temperature (B; °C), $\sigma_{t\text{-}g}$ (C; kg.m^{-3}), Potential energy anomaly (D), Fluorescence (E; Volts), beam attenuance (F; Volts). All measurements averages between 1.5 and 4.5 m. depth.

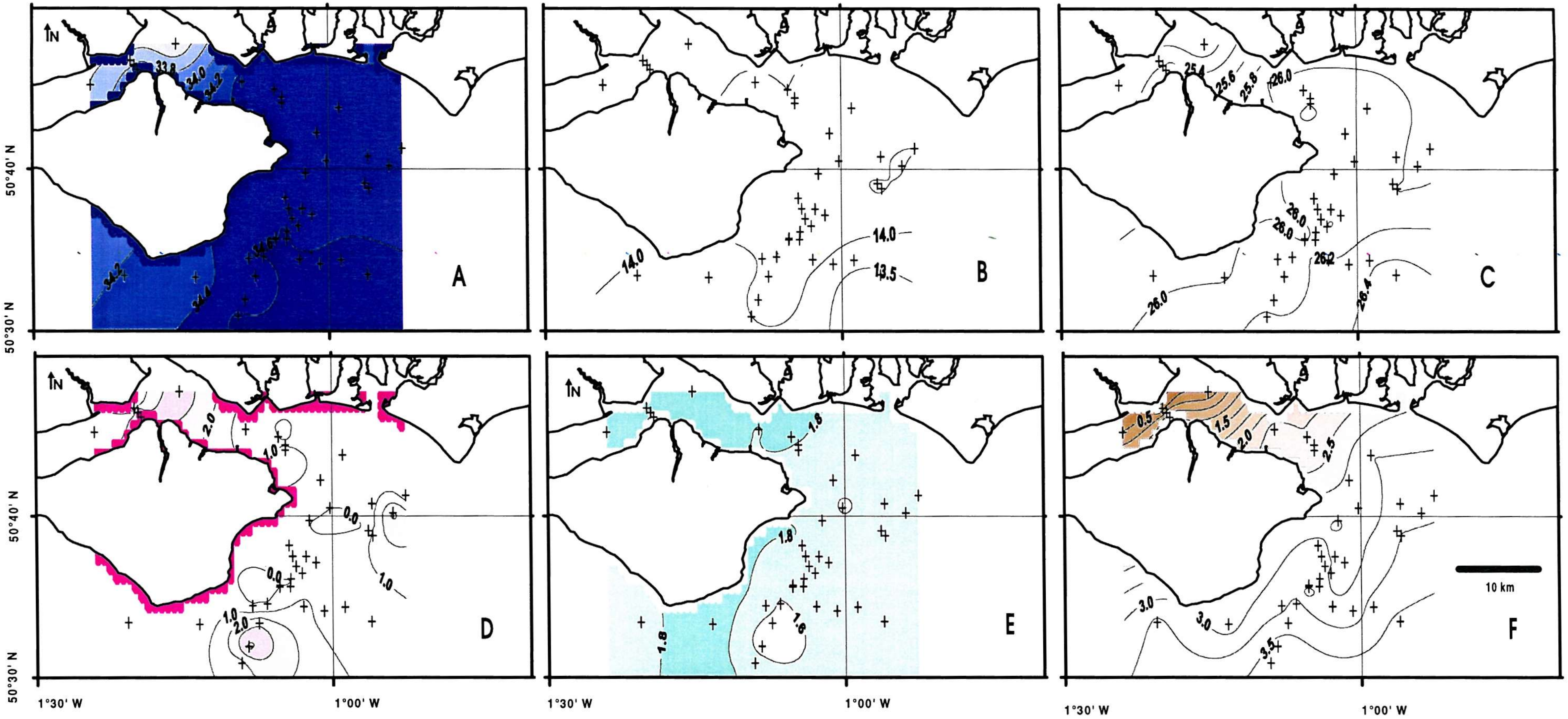

Figure 2.8: Cruise 2 (14-15/06/1995): Salinity (A), temperature (B; °C), $\sigma_{t\text{-}g}$ (C; kg.m^{-3}), Potential energy anomaly (D), Fluorescence (E; Volts), beam attenuance (F; Volts). All measurements averages between 1.5 and 4.5 m. depth.

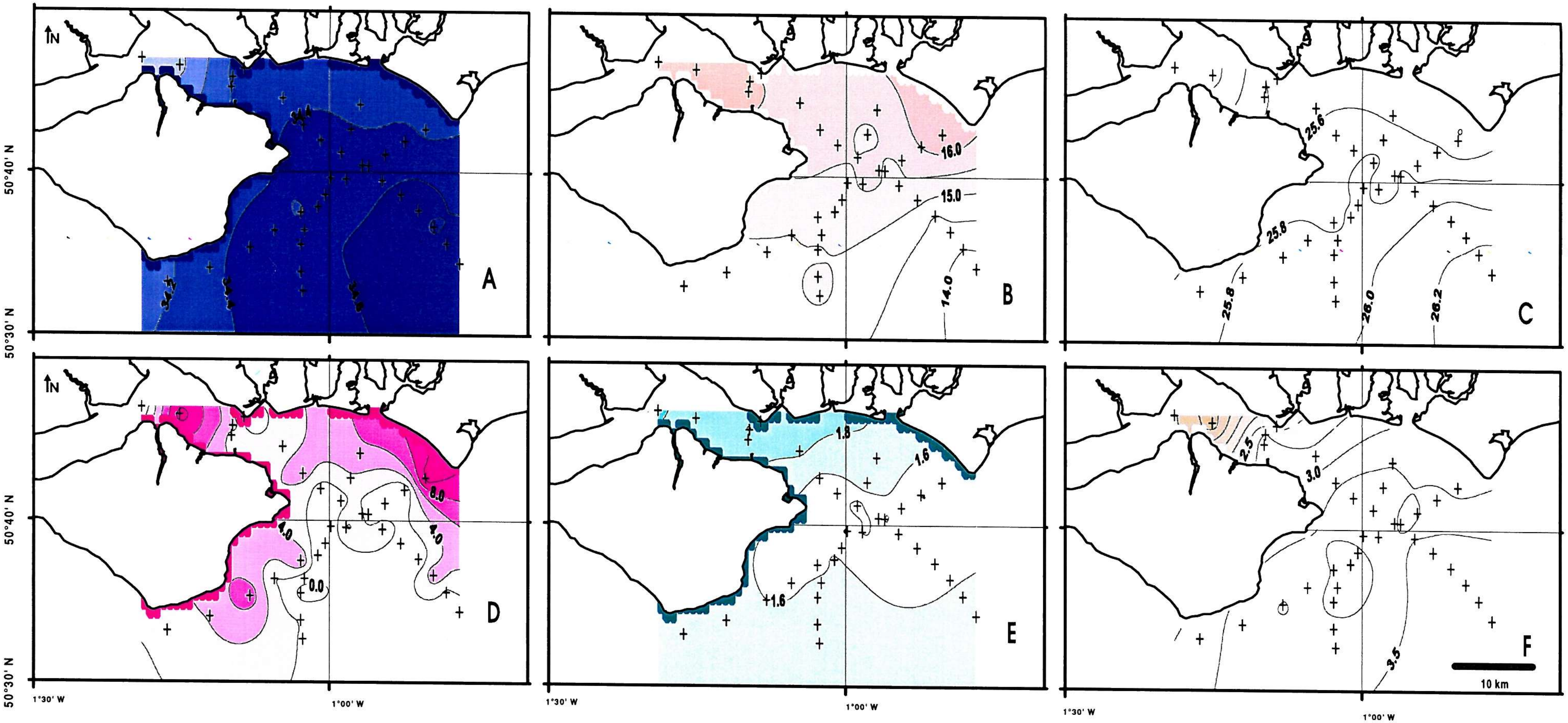

Figure 2.9: Cruise 3 (21-22/06/1995): Salinity (A), temperature (B; °C), σ_{t-g} (C; kg.m^{-3}), Potential energy anomaly (D), Fluorescence (E; Volts), beam attenuance (F; Volts). All measurements averages between 1.5 and 4.5 m. depth.

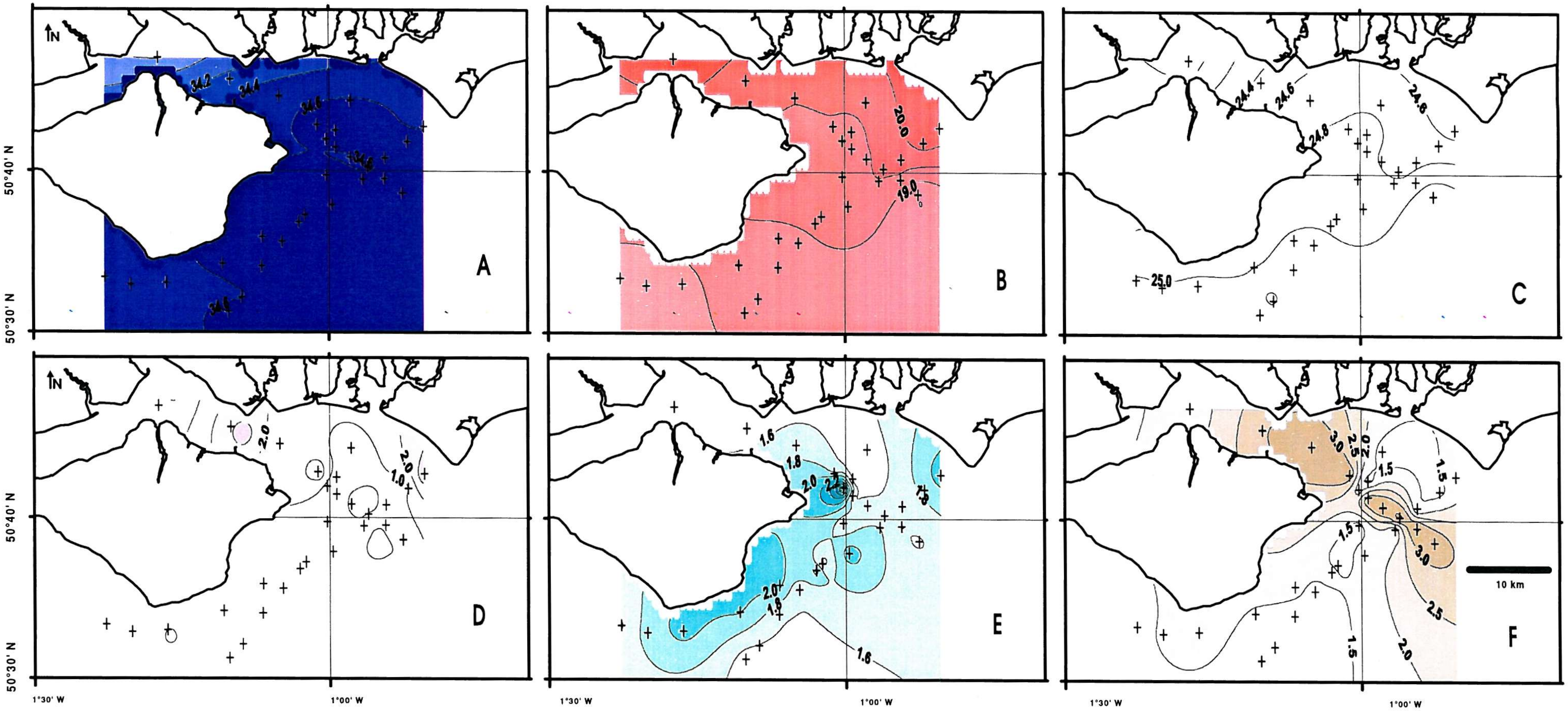

Figure 2.10: Cruise 4 (27-28/07/1995): Salinity (A), temperature (B; °C), $\sigma_{t\text{-}g}$ (C; kg.m^{-3}), Potential energy anomaly (D), Fluorescence (E; Volts), beam attenuance (F; Volts). All measurements averages between 1.5 and 4.5 m. depth.

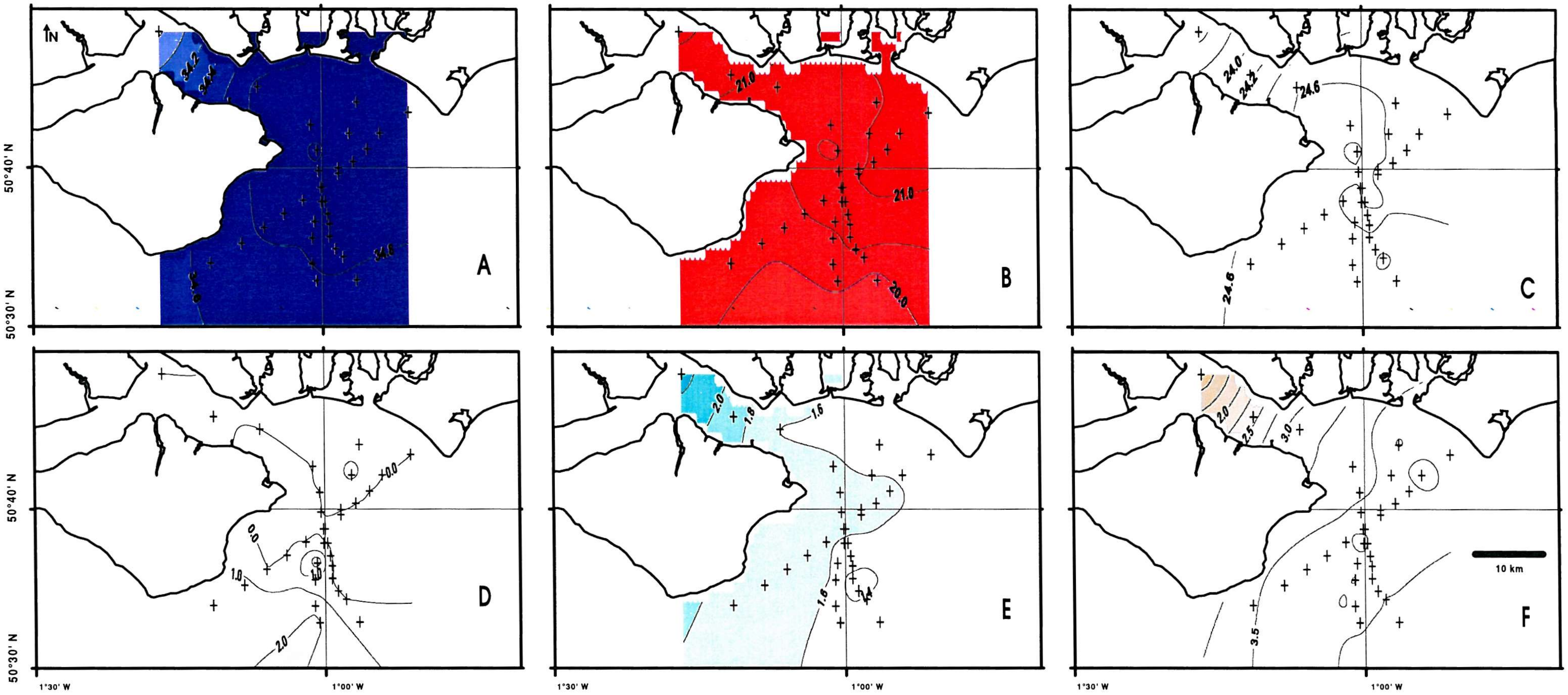

Figure 2.11: Cruise 5 (23-24/08/1995): Salinity (A), temperature (B; °C), $\sigma_{t\text{-}g}$ (C; kg.m^{-3}), Potential energy anomaly (D), Fluorescence (E; Volts), beam attenuance (F; Volts). All measurements averages between 1.5 and 4.5 m. depth.

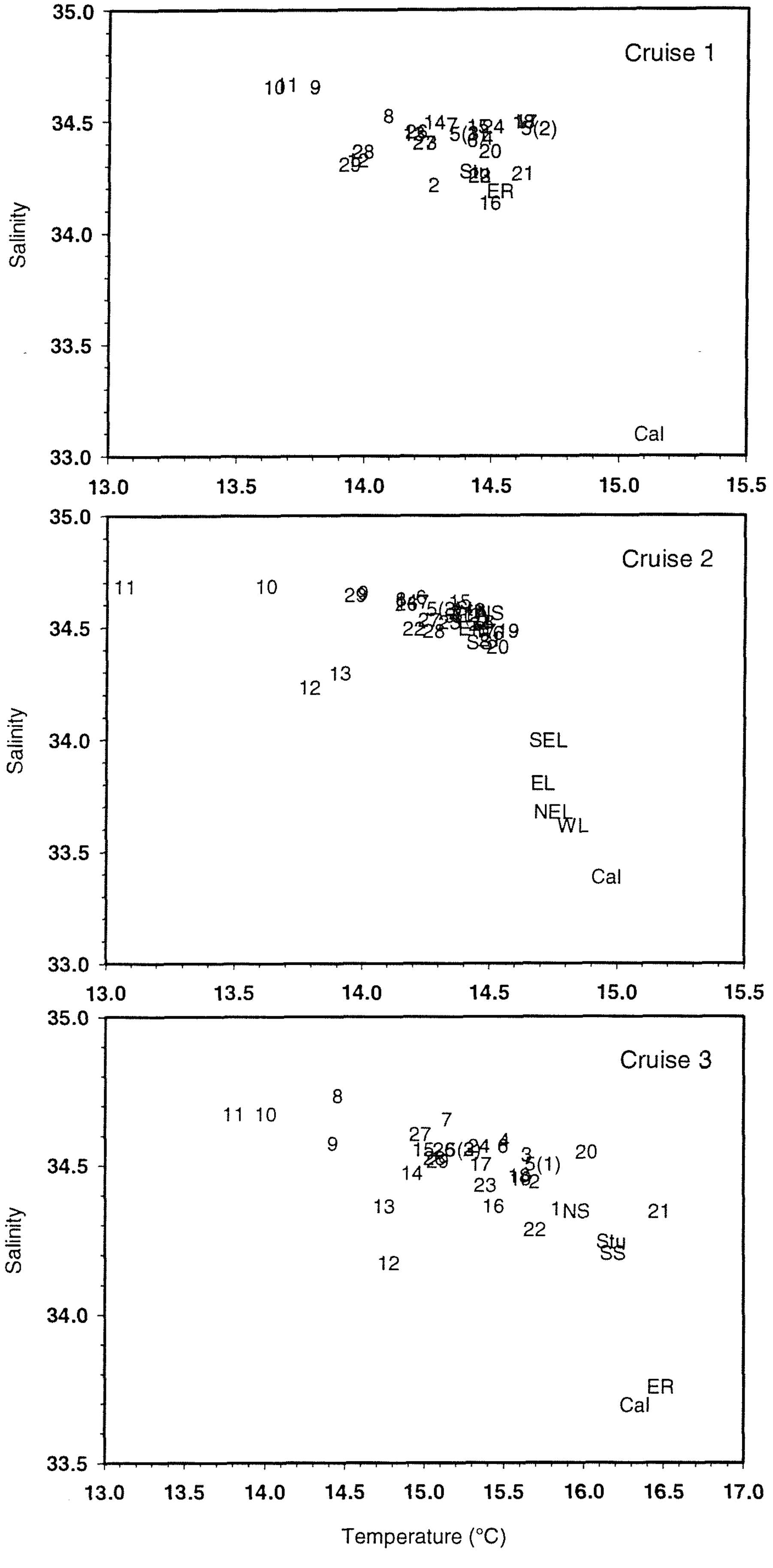

Figure 2.12: Temperature-Salinity diagrams for cruises 1-3.

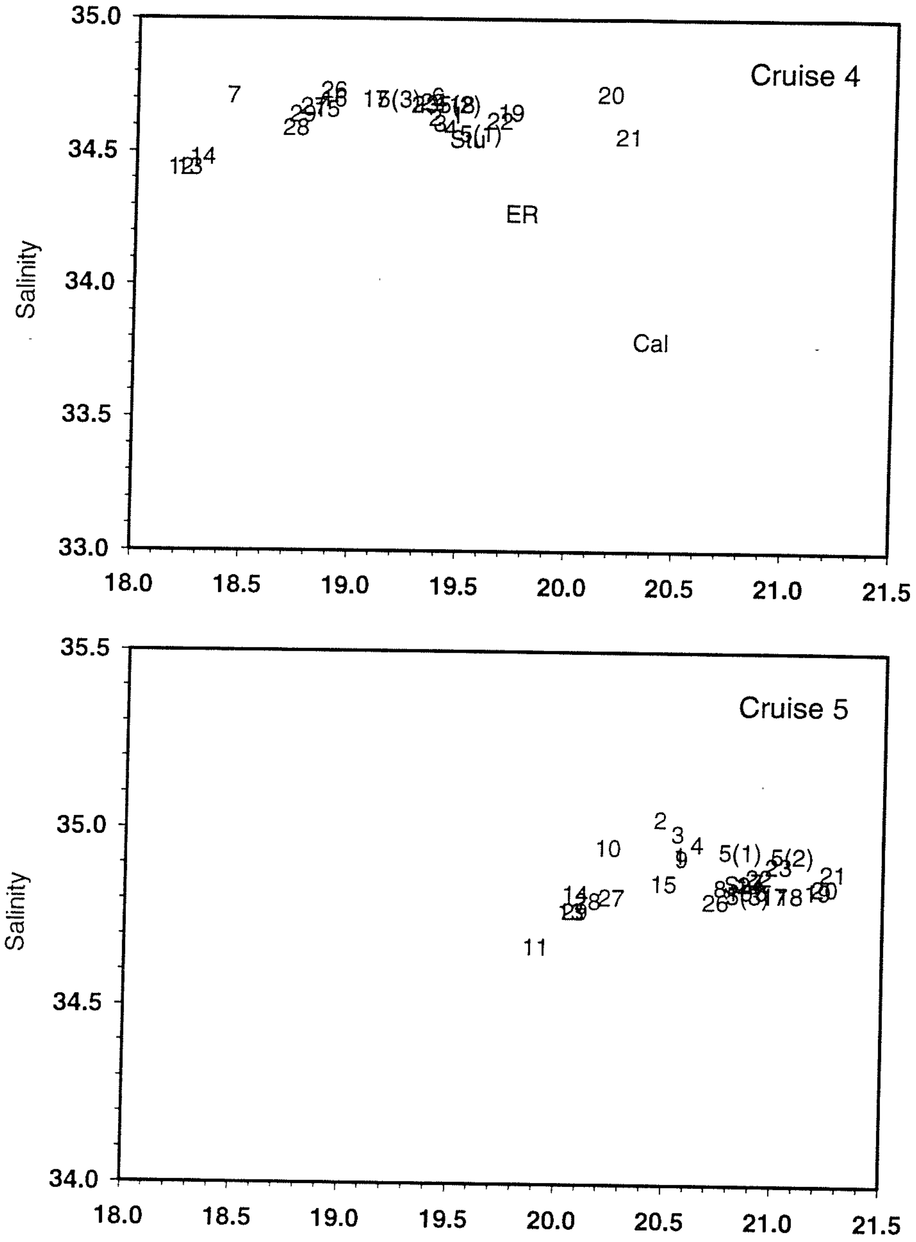

Figure 2.13: Temperature-Salinity diagrams for cruises 4 & 5.

in the decreasing density values). One-way Analyses of Variance (ANOVA) followed by *post-hoc* Studentised Newman-Keuls tests (SNK) reveal significant differences in average salinity between June, July and August, but not within June cruises ($F_{4,157} = 16.67$, $P < 0.01$). For temperature the pattern is similar, but cruise 3 is significantly different from cruises 1 and 2 ($F_{4,157} = 1227.52$, $P < 0.01$). The very large F ratio reflects the high increase in temperature between cruises, relatively to the within-date variability, particularly between June and July/August.

Spatially, the pattern for salinity varies little from date to date, with decreasing NW/SE values and little freshwater influence beyond the East Solent. Maximum values remain at $S = 34.7$, except in cruise 5 where it reaches $S = 35.0$. Minimum values increase from $S = 33.1$ to $S = 33.8$. There is no apparent strong frontal structure, and little evidence of tidal influence, indicating that the freshwater influence is limited to the upper reaches of the East Solent, and to some extent close to the harbours. There is a consistent W-E gradient of salinity to the south of the sampling area, with intermediate salinities S-SW of the Isle of Wight (see stations 12-13-28-29 on T-S diagrams, figures 2.12 and 2.13), which show little variation across the season, and higher salinities to the SE. There is also the influence of freshwater coming out of Portsmouth-Chichester-Langstone harbours, evident in the band of lower salinities outside of these harbours and towards Selsey Bill.

The temperature distribution is also coherent, with no discernible influence of tidal state, indicating a probable link to topography. This can also be seen in the higher temperature over banks (see figure 1.2). Given average salinity levels, the low inputs of freshwater and the consistency of the pattern between dates, this is unlikely to be linked to inputs of warmer freshwater. The gradient is of decreasing temperature north to south with isopleths slightly closer together to the south of the area (cruises 1, 2, 5) or the west (cruises 3, 4). A patch of warmer water is present to the north-east, in the shallow area off Bracklesham Bay (possibly associated with Medmery Bank) in cruises 1, 3 and 5, which include this area. Unlike salinity, the stations to the south of the Isle of Wight do not show a particular signature.

These features are reflected in the density distribution with a gradient increasing NW to SE, two patches of lower density water in the NE and SW stations, and no marked frontal area.

The T-S diagrams (figures 2.12 and 2.13) show that, in terms of segregating stations, emphasis shifts from both temperature and salinity being important (cruises 1-3) to temperature being the dominant factor (note the change in scale on the x axis in cruises 4 and 5). The estuarine-marine gradient is clearly defined, corresponding to transect 1, with stations 10-11 at the marine end (St. 7 in cruise 4), and the East Solent stations at the other. In cruise 2, Calshot is at the estuarine end and the West Solent stations appear as intermediate. South-western stations (12-13) come out towards the low end of the salinity axis, but also towards lower temperatures, closer to marine stations. Stations 20-21, at the top end of transect 2, are of average salinity but higher temperature. Intermediate stations are distributed over a narrow range of salinity values, although temperature becomes important in separating stations as early as cruise 3.

2.C.2.b. *Stratification*

The potential energy anomaly ϕ shows no clear spatial pattern in cruises 2 and 3. In cruises 4 and 5 it shows a similar distribution of higher stratification in shallower areas of the Solent and Bracklesham Bay/ Medmery Bank, associated with the higher temperatures of these areas. Cruise 3 has higher levels of average potential energy, and indeed the ANOVA/SNK tests show significant differences only between cruise 3 and all others ($F_{4,157} = 8.63$, $P < 0.01$). This variability could possibly be interpreted as rapid short-term changes of the water column stability, possibly linked to the state of the tide.

2.C.2.c. *Chlorophyll Fluorescence*

Fluorescence exhibits a far more 'patchy' distribution than purely physical parameters (figures 2.7-2.11). One-way ANOVA shows a significant difference between cruises ($F_{4,157} = 5.04$, $P < 0.01$), with maximum average values in July, minima in August and June as intermediate. Variance between cruises is however small, as is the F ratio, indicating large within-cruise variance. The SNK test finds cruise 4 to be significantly different from cruises 1, 3 and 5, and cruise 2 from cruise 5 ($P<0.01$). Spatial patterns are not clear-cut, but higher levels are found close to shore, and June sees a tendency towards lower levels in the central and south-western parts of the sampling area. Cruise 4 has a pronounced patchiness, whilst cruise 5 shows a decreasing NW to SE gradient. Fluorescence was found to be negatively correlated with temperature in cruise 1 (-0.38, table A.2.3), and salinity and beam attenuance in cruise 3 (0.58 and –0.64). To put these patterns in perspective, Castro-Longoria (1998), sampling the same year close to Sturbridge, found chlorophyll *a* values of 1.2 $\mu g.l^{-1}$ in June, 1.1 $\mu g.l^{-1}$ in July and 1.0 $\mu g.l^{-1}$ in August. This can be compared with Fluxmanche II (1998) results, which show values for May 1995 of ~5.5 $\mu g.l^{-1}$ at station FX7 (close to Nab Tower), down to less than 1 $\mu g.l^{-1}$ in September.

2.C.2.d. *Beam Attenuance*

Beam attenuance does not follow a consistent increase, which could be linked to decreasing input from river flow as could be expected, indicating possible resuspension or advection processes. Maximum particulate load is found in July, minimum in cruise 1 (but cruise 5 is close), and intermediate values in cruises 2 and 3, with relatively low variance within dates. All cruises are found to be significantly different from each other except cruises 1 and 3, and 1 and 5. Fluorescence and beam attenuance are correlated at the $\alpha = 0.05$ level only for cruises 3, with $r = -0.64$, however there are clear similarities in the spatial distribution of both in cruise 5. The spatial distribution is stable, with a decreasing gradient from Southampton Water to the SE, reflecting a predominantly conservative behaviour and no discernible input from the harbours of Portsmouth, Langstone or Chichester. In cruise 4 however (figure 2.10) we see much lower values (*i.e.* high particulate load) in the East Solent area, down to station 7. This may reflect an exceptional input from these harbours, but there is no increase in values towards the Solent and off Chichester Harbour, as would be expected from increased precipitation. This cruise was interrupted because of bad weather, and it is therefore probable that we see the resupension of sediment from wave/wind action. There is also no correlation with fluorescence in this cruise. Because these high values are tied to transect 1, it is probable that we see a transient effect, since it is not picked up on the other two transects done the next day. From Fluxmanche II (1998) results, it appears that total SPM values decreased from <24.0 $mg.l^{-1}$ in May 1995 at Nab Tower to, <6.0 $mg.l^{-1}$ in September, with a strong negative coast-Channel gradient.

2.C.3. Ocean Surface Current Radar

2.C.3.a. *Tidal constituents*

Table A.2.4 shows the average amplitudes of the 15 constituents that showed the greatest values for 1995 and 1996. The amplitude values were calculated using averages over all cells. The differences in geographical ranges between the two years may explain some of the discrepancy between years, but for most constituents, particularly M_4, S_2, and N_2, the agreement between years is good. The expected dominance of the M_2 tide is evident, being greater by two-thirds than the next constituent (~60 $cm.s^{-1}$). However the M_4 harmonic has a low average amplitude, comparable to N_2 (~ 10 $cm.s^{-1}$); S_2 is important (~ 18 $cm.s^{-1}$). Spatially M_2 and S_2 follow each other closely (Paphitis, 1997), with a similar pattern of greater eccentricities in the southern half of the area decreasing closer to shore until they become close to rectilinear. This trend is reversed for the (topographically linked) M_4 constituent.

2.C.3.b. *Residual currents*

Residual currents, Z_0, as measured by OSCR, are displayed in figure 2.14. They range from 0 to 16 cm.s^{-1} (1995) and from 1 to 23 cm.s^{-1} (1996), with averages of the order of 5 cm.s^{-1} and 2 cm.s^{-1} respectively, reflecting sampling during strong NW currents off Selsey Bill in 1996. This ranks them amongst the weaker tidal constituents, all with similar amplitudes, so slight differences in accuracy or those due to the difference in geographical range of measurements may easily alter the ranking order of table A.2.4. These values are however well in the range of those commonly observed around the UK (10-20 cm.s^{-1} according to Prandle, 1997). The current field is coherent for both years and areas of overlap are similar. Wind data from Havant Borough Council (figure A.2.2, appendix A) shows that for the most part wind directions are similar for both years, making it difficult to deduce the influence of wind on the residual currents as measured here. However the occurrence of northerly winds (absent in 1996), could be linked to the variation of weak currents around the area of New Grounds, which are NW in 1995 and north/NE in 1996.
Generally the mean flow field can be separated into:

- Strong currents to the W and E;
- A band of weaker currents south of Hayling Bay;
- A band of stronger currents south of Bracklesham Bay.

Whilst the circulation pattern can be described as:

- A general NE direction over the sampling area;
- Currents coming in to the area mainly from the East Solent and the E (southwards);
- A boundary of strong southward currents to the W;

Several re-circulatory gyres, the main one centred around weak currents to the south-east of the area (around Medmery Bank), but also two smaller ones, one at the mouth of Chichester harbour (not sampled in 1995), the other just westward (not sampled in 1996). Although 1996 does not show this, given both maps it is also possible that currents coming from the East Solent that are then deviated northwards (as in 1996), can in turn be re-circulated (as in 1995) around New Grounds.

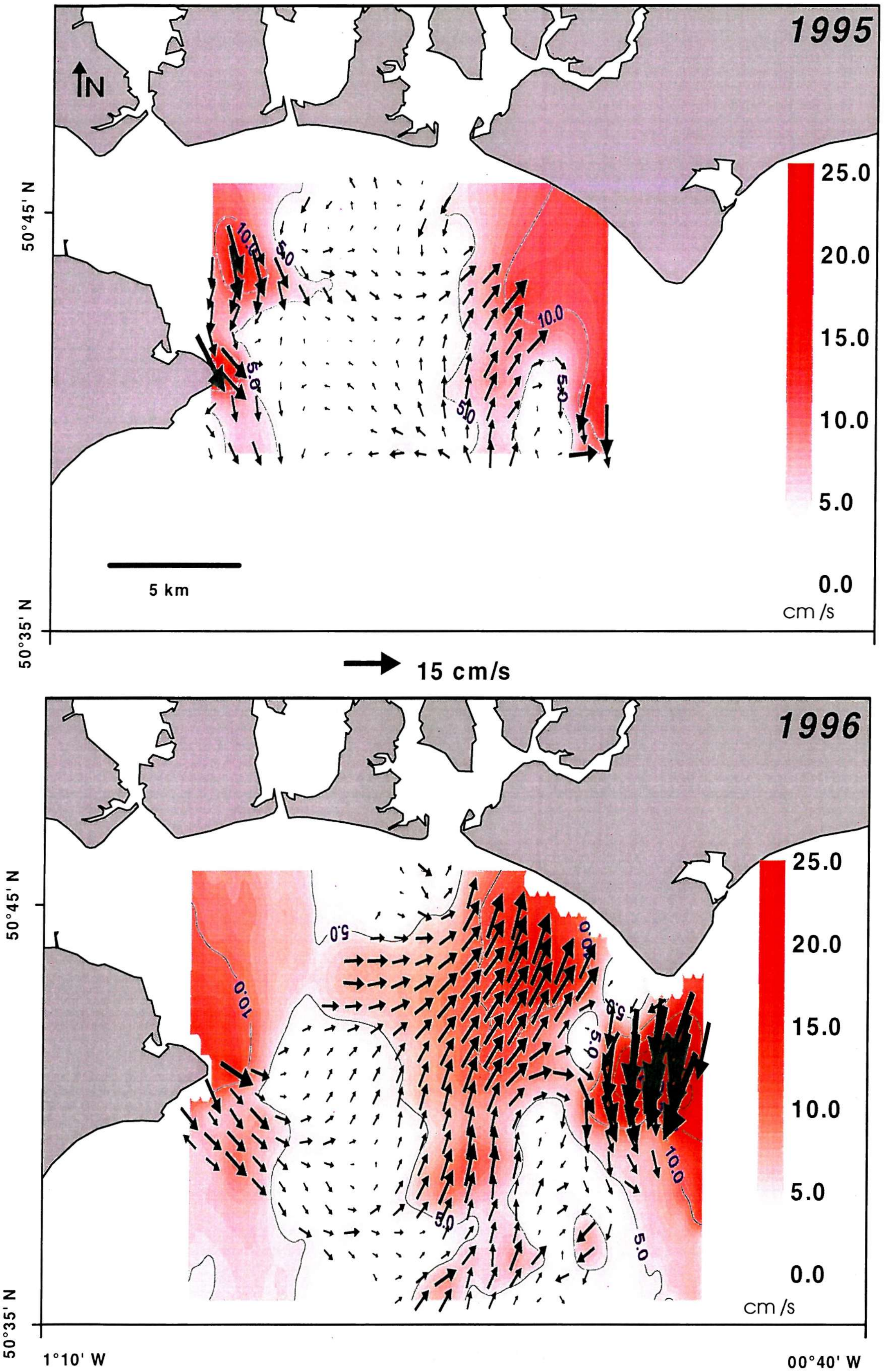

Figure 2.14: Instantaneous surface residual currents as measured by OSCR from 07/06 to 07/07/1995 (top) and from 27/06 to 27/07/1996 (bottom). Contours represents current speed isolines (cm.s^{-1}).

2.C.3.c. Pseudo-*Lagrangian Particle Tracking*

Given the instantaneous surface currents measured by OSCR, the TIRA software can simulate the tracking of water particles. For this it uses an interpolation method between the four closest cells to the particle at any given time, resulting in *pseudo*-Lagrangian particle tracking. Due to gaps within the data, only a limited number of simulations were possible. Four simulations were done corresponding to releases at high and low water on Spring and Neap tides, all from a cell close in position to the centre of the study area (Nab Tower), as shown in figure 2.15, and table 2.3. Wind conditions were southwesterly in most cases, but generally variable. Runs from other cell positions showed similar patterns. In all four situations, the retention in the area is strong, and releasing the particle at high or low water makes no appreciable difference to the outcome. However there is a marked difference between Spring and Neap tide situations: in the first case the water particle is brought north-eastwards (to shore) after only a few tidal cycles (about two days). In the second the particle stays in the general vicinity for over a week (table 2.3), but with no strong shoreward transport, before leaving the measurement area, possibly staying trapped in the recirculation cell off Bracklesham Bay. The variability of the ellipses followed by the track could suggest a possible effect of wind forcing on the trajectory of the surface current, with apparently little effect on the transport out of the area. There is also little difference between runs despite different wind conditions.

Figure	Date (Time) of start and end of simulation	Tidal situation	Wind Situation
2.14 A	01/07 (11:00) - 03/07 (12:20)	High Water Springs	SW, 6-8 m.s^{-1}
2.14 B	27/06 (08:20) - 29/06 (19:20)	Low Water Springs	Variable
2.14 C	08/07 - (04:20)-16/07 (02:00)	Low Water Neaps	SW, 2-6 m.s^{-1}
2.14 D	08/07 (10:00) - 16/07 (02:00)	High Water Neaps	SW, 2-6 m.s^{-1}

Table 2.3: Conditions of *pseudo*-Lagrangian particle tracking simulations.

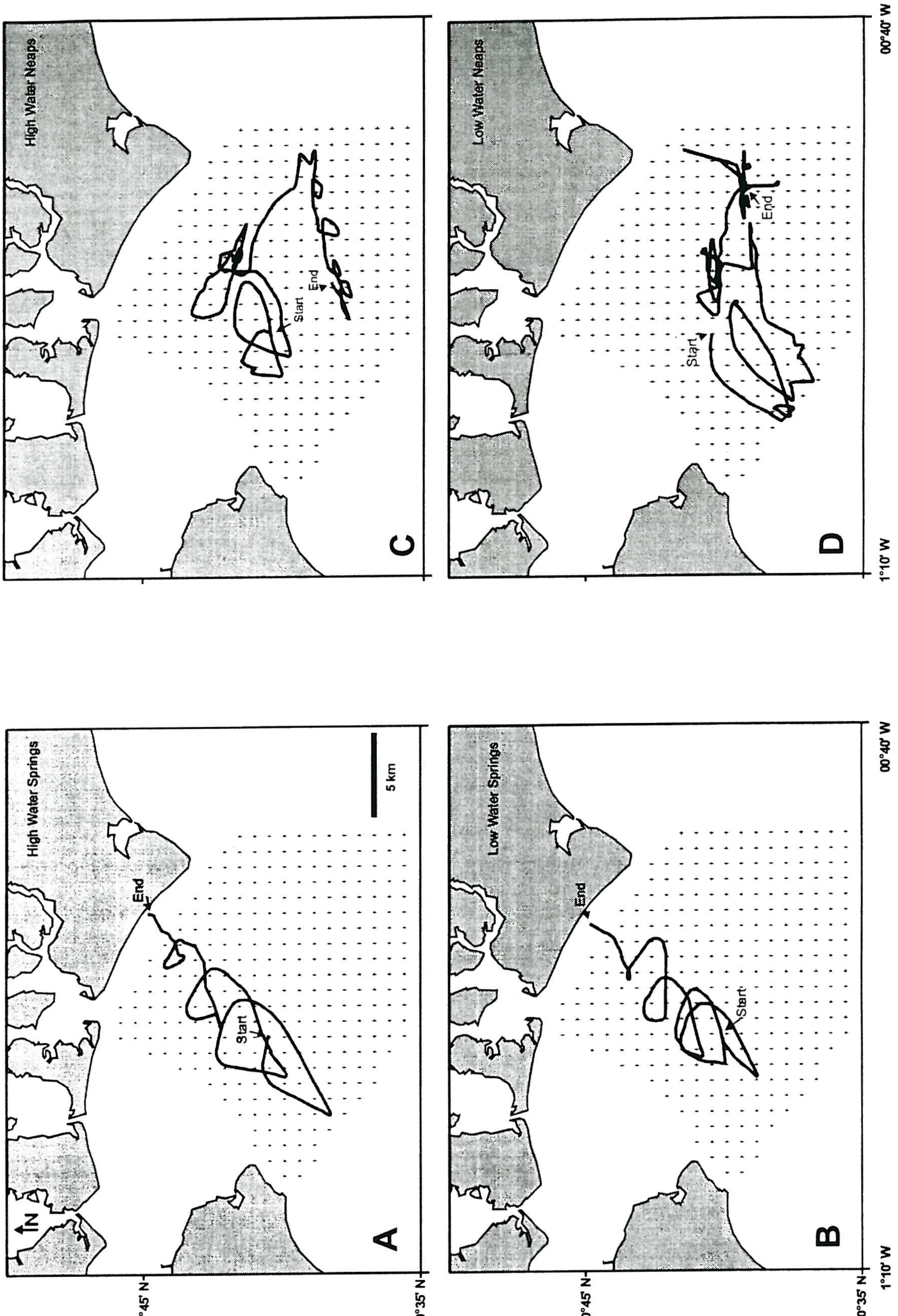

Figure 2.15: Simulated trajectories of water particles by *pseudo*-Lagrangian tracking, from instantaneous surface current measurements by OSCR (1996): A) High Water Springs (01/07 -11:00 to 03/07 -12:20); B) Low Water Springs (27/06 - 08:20 to 29/06 -19:20); C) High Water Neaps (08/07 - 04:20 to 16/07 - 02:00) D) Low Water Neaps (08/07 -10:00 to 16/07 - 02:00). See also table 2.3.

2.C.4. Hydrodynamic Modelling

2.C.4.a. *Model results*

Figure 2.16 shows the residual currents of the area, as calculated by the model, in a situation with no wind. Spatially, the model shows a number of recirculation cells in the area, most notably to the east of the Isle of Wight, but also two to the south of the study area, one to the west, one to the southwest of the Isle of Wight, and one off the Needles (western tip of the Isle of Wight). The whole area to the south of the study area can be considered as a cyclonic recirculation cell, constituted of several smaller sub-cells (some of it, further south, is not visible on figure 2.16).

The areas of stronger currents are associated with shallower regions such as the east of the Isle of Wight, and/or with headlands such as off Selsey Bill or St Catherine's Point. Although they are not shown here, simulations in various conditions of wind strength and directions show these patterns to be stable, changing the intensity and the relative importance of different recirculation cells, but not their overall pattern. In particular, the 'central gyre' to the east of the Isle of Wight remains in most situations. The exception is for SW winds of 6.0 $m.s^{-1}$ or more. In this case the flow is W to E over practically the whole area (figure 2.17). Wind data from Havant Borough Council has averages for SW, WSW and SSW winds of 5.45 ms^{-1} in June-July 1995 and 4.26 $m.s^{-1}$ in June-August 1996, and only one instance each year of such winds over 3 consecutive days (see also figure A.2.2). The model configuration available for this study does not allow for an in-depth study of the effects of winds and tides on the patterns of residual circulation *per se*, and the reader is referred to the works of Salomon and co-workers (Salomon *et al.*, 1988, Salomon, 1989, Salomon & Breton, 1991, 1993, Salomon *et al.*, 1993). However, the effects on the transport of particles can be looked at, and this together with a more detailed account of wind and tide interactions will be given in chapter 5.

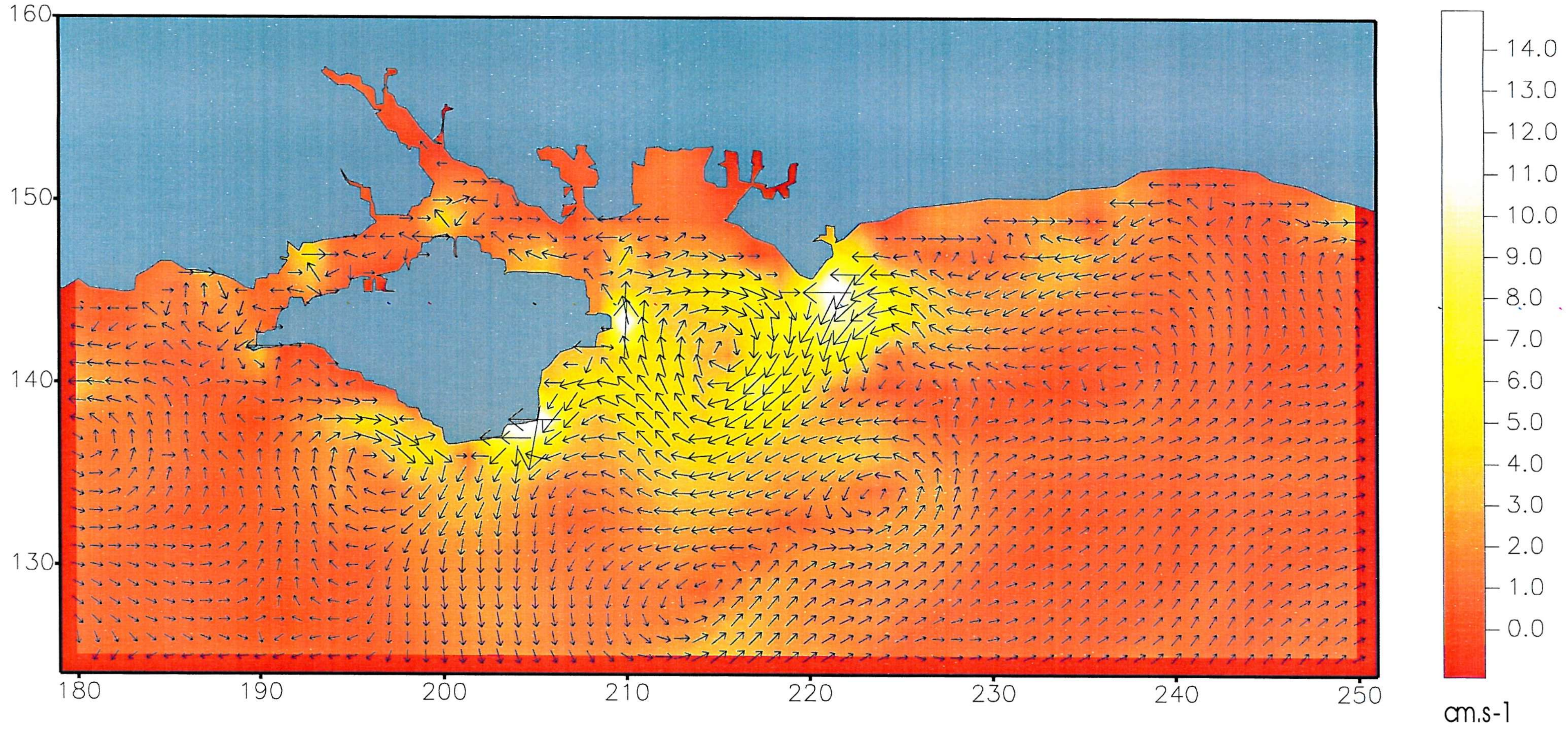

Figure 2.16: Modelled long-term depth-integrated tidal residual currents calculated in conditions of no wind (cm.s^{-1}). Coordinates are as used by model (Salomon & Breton, 1991, 1993).

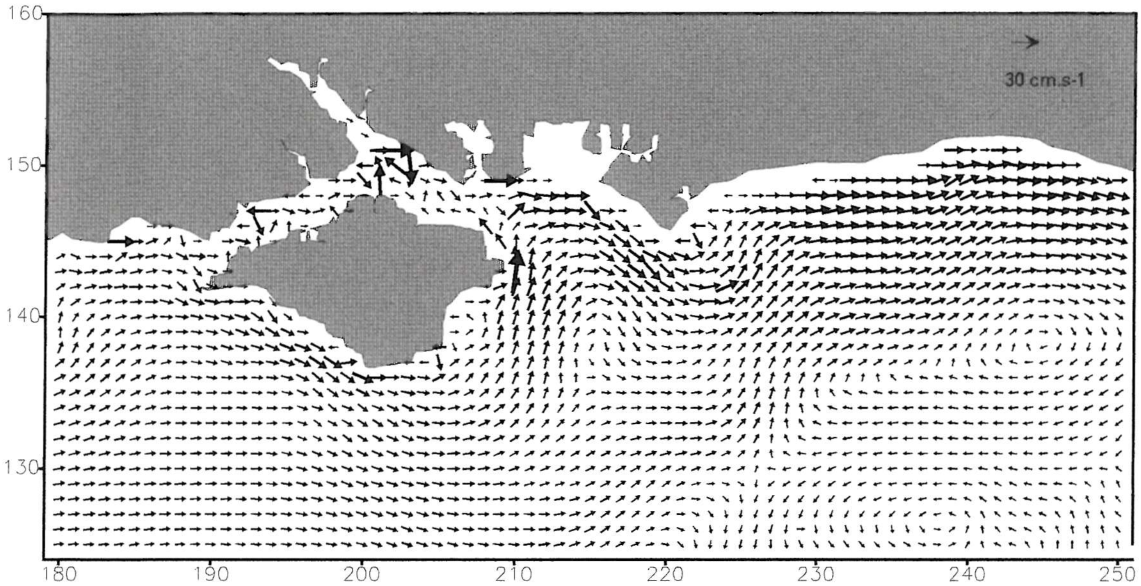

Figure 2.17: Modelled tidal residual currents (cm.s^{-1}) in conditions of a south-westerly 6 m.s^{-1} winds. Coordinates are as used by model.

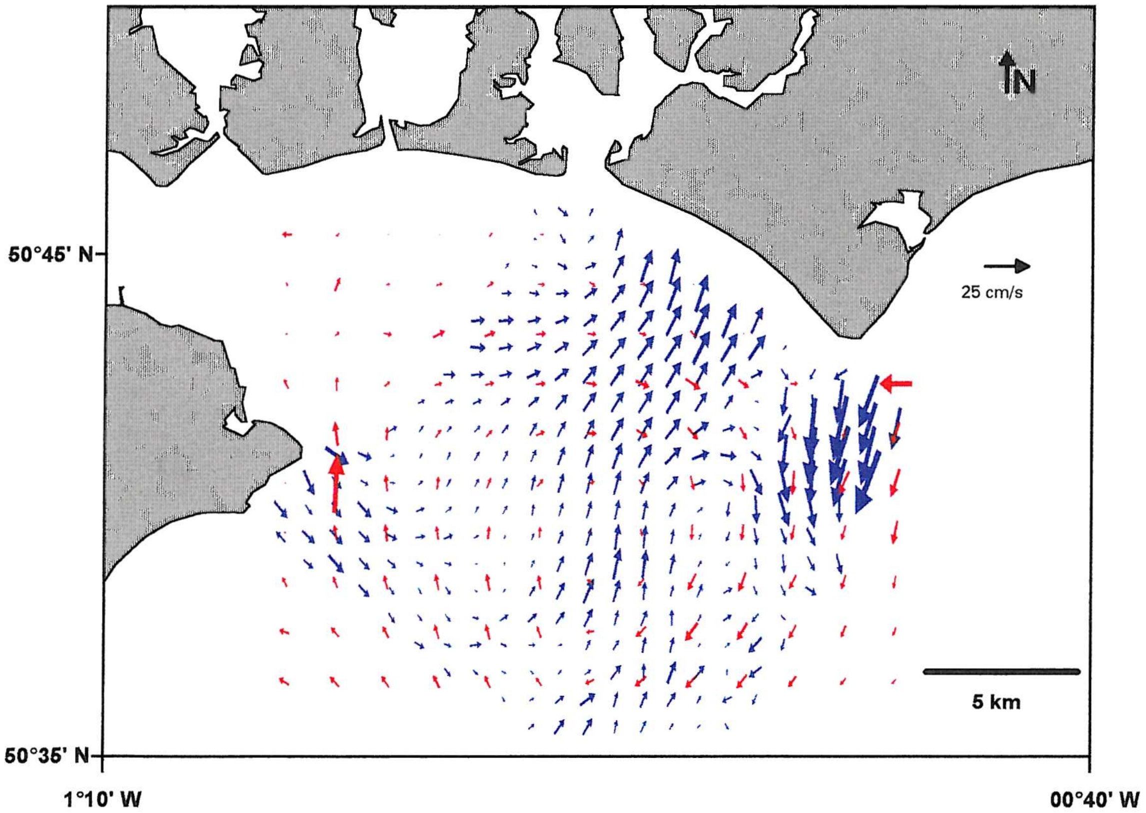

Figure 2.18: Comparison between OSCR (blue) and model (red; no wind) residual currents for the area covered by OSCR in 1996.

2.C.4.b. *OSCR/Model comparisons*

Figure 2.18 compares residual currents as calculated by the model (with no wind) and those measured by OSCR over the 1996 OSCR field of measurement (which is the most extended spatially). There is general agreement as to the flow pattern, and in particular in resolving the main anticyclonic gyre. Discrepancies concern weaker velocities as calculated by the model, especially to the north-west (Bracklesham Bay); in the south-western area (New Grounds, Princess Shoal...) circulation is opposite that measured. When averaged over an area roughly equivalent to that of the OSCR sampling area, the average is lower by about 30% (4.6 cm.s^{-1}, compared with 6.6 cm.s^{-1}), with similar ranges (1.2-23.7 cm.s^{-1} for OSCR, 0.2-19.6 cm.s^{-1} for the model). Model velocities are depth-averaged, which could partly explain why OSCR velocities, which are surface values, are larger. These discrepancies may also be the result of wind-driven currents in OSCR measurements or, as has been observed by Prandle (1991), a residual circulation due to density gradients.

2.D. Discussion

2.D.1. Tidal Correction

When the tidal excursion is large relative to the distance between stations, and/or the time between sampling is large relatively to a tidal cycle, it becomes imperative to work in a coordinate system independent of time, where the relative positions of sampling stations are fixed. This is clearly seen in the results of the repositioning, which show the strong influence of the tide, and the potential for aliasing it represents if not taken into account. Although stations were ~1 nm apart when sampled, when repositioned some where displaced relatively by up to over 6 or 7 nm (*e.g.* station 29 on most cruises, figures 2.5 & 2.6). This change in configuration contradicts the original star-shaped sampling strategy, but is necessary in order to resolve the 'true' relative positions of stations.

The accuracy of the repositioning depends on the accuracy and precision of the instantaneous currents used for the integration and, therefore, given a certain imprecision, also on the time over which the integration takes place. Their accuracy will affect the result inasmuch as local effects such as small gyres may be influential. A longer time of integration will also tend to bias the result if it is on a scale where residual currents or diffusion processes become significant.

In this case, the instantaneous currents are from a model developed for the English Channel, which has not been thoroughly tested in this particular area. It has been extensively validated in several others (*e.g.* Broche *et al.*, 1986, Guéguéniat *et al.*, 1993, Orbi & Salomon, 1988, Salomon *et al.*, 1988, Salomon *et al.*, 1993). In an undergraduate project, Stevens (1997) found that for the Solent area covered by OSCR, there was good agreement between instantaneous currents as calculated by the model and those measured by OSCR, especially with little wind influence. However this author found a phase lag of ~2 h, the model being ahead of the measurements.

RECALMER seldom integrates over more than half a tidal cycle and the average integration time for each cruise is 2-3 hours, with maxima at 5-6 h. This represents average displacements of 3-6 nm. Cruise 2 is most affected with an average of 6 hours integration, a maximum displacement of ~14 nm, and an average of ~5 nm. To put these figures in context, 6 hours represents a displacement of ~1300 m for a residual current of 6 $cm.s^{-1}$, such as measured by OSCR. If one assumes a surface current of 3% of wind speed, for a wind of 6 $m.s^{-1}$, this implies a 3.9 km displacement, *i.e.* a distance far less than one transect, but equivalent to 2-3 stations. These values are exaggerated, since tidal residuals will not be constant in direction over such time scales. Surface current velocity is greater than the depth-integrated velocity, and at depth the intensity of instantaneous tidal currents in the area is such that wind effects are assumed to be slight. Thus the true picture of water movement in the area is likely to be more complex than that depicted by repositioning, but the error is probably reasonable.

2.D.2. Hydrography

Ultimately the test of the repositioning method is whether the physical measurements are spatially coherent. Salinity, temperature and beam attenuance show unity of structure between all five cruises. This is despite both repositioning and interpolation (krigging) between non-regularly spaced points, in itself a potential source of error (Akima, 1978).

The beam attenuance data in particular shows the most consistent spatial distribution, acting as 'control' and lending support to the repositioning. It is poorly correlated with fluorescence, and thus can be considered as a *quasi*-conservative tracer, except in cruise 4, where in all probability resupension events occurred during the sampling. Cruise 2 shows no deviation from the general picture and thus the longer integration times does not seem to have been a major source of error.

This clear patterning, despite the irregular grid, also reflects a degree of homogeneity across the different zones of the area, and therefore quite a low level of structure: there are no apparent strong gradients or frontal zones, no stratification of significance outside of the upper East Solent, and the main evolution from one cruise to the next is that of increasing salinity, with a greater homogeneity across the region. Within cruises, temperature is the principal source of variation between stations. This can be linked to bathymetry, and the trend is reinforced during the season, with 4-5°C increase between June and July. The warming of the area appears also between June cruises, especially between cruises 2 and 3. The 14.6°C isopleth moves from within the East Solent during cruise 2, to the South of the sampling area in cruise 3, though this could well be linked to the lesser influence of tidal mixing. Salinity values show a maxima to the SE, and thus the area to the South of the Isle of Wight may see some freshwater influence, possibly from Southampton Water and the estuaries of the West Solent coming round S^t Catherine's Point, since there are no important freshwater influences to the West. The salinity maps show the influence of central English Channel waters, intruding from the SE and which reach their maximum influence in August. Nevertheless, the 35.5 isopleth varies little in position, remaining mostly between East Ryde and Bembridge Harbour. It is furthest offshore during cruise 3, where the tide is also weakest (table A.2.2, appendix A).

2.D.3. OSCR

OSCR measures currents integrated over the first two metres of the water column, averaged over about 1 km^2 spatially and 20 min temporally. Caution should therefore be extended when interpreting these results, and when comparing the measurements with *in situ* measurements or hydrodynamic models. A considerable effort has been put into validating OSCR measurements against drogues, near-surface moored current metres, ship-borne ADCPs, and hydrodynamic or tidal models (Prandle, 1991, Aldridge, 1997), with the conclusions that the current field is close to the "true" surface current field when spatial variability over the cell area is accounted for (Paduan & Graber, 1997, Prandle, 1991), and the error for instantaneous currents is of the order of 7-8 $cm.s^{-1}$ (Chapman & Graber, 1997). This is small compared with average instantaneous currents of the Solent. The concordance of OSCR results between 1995 and 1996, despite a change in range and position of the radar, together with the internal (spatial) coherence of the results, are indications of the reliability of the measurements in the present context. This is found also in the tidal ellipses for most tidal components and indeed, to a degree, in the average amplitudes of the constituents, which show clear spatial patterns and for the most part can be tied to topography (see also Paphitis, 1997).

The general picture is that of a complex structure, stable between the two years of observation, with at least one strong recirculation cell of c.20 km diameter. There is no apparent strong export zone from the area, in terms of surface currents. There is a great range of amplitudes (1.2 to 23.7 $cm.s^{-1}$ in 1996), weaker currents also being more variable between years. This would indicate firstly, that the observed residuals are tidally- rather than wind-driven, and secondly, that wind effects are probably small or too variable, and that averaged over a Spring/Neap cycle, they do not modify the overall residual circulation pattern.

The pseudo-Lagrangian tracks calculated by TIRA show the importance of tidal state on the particles trajectories. They are rapidly brought to shore at Springs, but stay in the Bracklesham Bay area at Neaps for over two weeks. From this data, the fate of a water particle cannot be deduced beyond the points of exit, and at Springs for example, the fate of the particles in a real situation is unknown, *i.e.* whether it is then deflected westwards, or to the east, where it could either be kept in the area, or advected out of the system to the east or south. The difference in trajectories would indicate however, when compared with the residual currents integrated over a whole tidal cycle, that the actual path of water particles is likely to vary according to the Spring/Neap cycle, and that residual currents averaged over long periods may be misguiding when it comes to determining the fate of particles on short time scales.

2.D.4. Hydrodynamic Modelling

From the model, it appears that recirculation cells are a feature at the regional scale (figure 2.16). At the scale of the survey, the model output reveals less of the fine structure of the current field than does OSCR (figure 2.18), although both are broadly in agreement as to the flow pattern. Nevertheless, despite the somewhat different resolutions, and certain discrepancies, there is a degree of concordance between OSCR and the model over the area of overlap, in that both indicate a degree of recirculation in the area: the model does not resolve small scale features, and the recirculation cell is general to the area East of the Isle of Wight; for OSCR the pattern is more detailed, and the recirculation is mostly off Bracklesham Bay, also anticyclonic. This general agreement also confirms the idea that wind effects may be weak, since the model run was done with no wind included. This may prove to be limiting when these do become significant, since there is no long time series such as OSCR to compare with directly.

The main discrepancy between OSCR and model is not the pattern of circulation, but the current velocities, which are greater in the Radar-measured current field. The most likely explanation for this difference that of an 'overestimation' of the currents by OSCR, since it measures surface currents, whereas the model is depth integrated, and thus the surface current speeds will not be an accurate description of the flow when integrated over the whole water column. Other factors may also be of significance, in particular density currents, since these may act to reinforce the residual circulation. Prandle (1991) argues that this is the case for OSCR measurements of surface residual currents observed in Morecambe Bay and elsewhere, and that significant residual currents can be caused by density gradients as small as 0.05 km^{-1}. As mentioned previously, wind effects may also explain the discrepancy, since model runs are made with no wind included. However this would tend to disrupt the residual circulation, rather than reinforce it as is the case here (especially for SW winds, which were dominant at the time). In any case it may be that, in the Solent area, the model underestimates residual transport, though the actual pattern is of general recirculation. The pattern of flow under strong SW winds could possibly indicate the fate of particles released at Neaps in the OSCR simulation, which may be entrained around Selsey Bill and towards the east if wind effects are strong enough. The assumption is that the strong winds last for at least four days, since this is though to correspond to the 'response time' of the Channel system; it is unclear how sensitive the residual tidal patterns will be to more variable wind conditions.

2.E. Summary

- The repositioning of stations shows that tidal movement is important and a potential source of error through aliasing, if not corrected. It creates a westward shift of most stations, compared with the original positions, particularly those of transect 2 (N-S), and reduces the resolution of the sampling to the SE.
- The hydrography of the area shows relatively small gradients of temperature and salinity. There is no appreciable stratification beyond the upper East Solent, and the potential energy anomaly shows no clear spatial or seasonal pattern, except a small link to temperature, possibly a sign that this parameter undergoes rapid temporal changes which are not resolved by the survey.
- Salinity increases from the upper Solent to SE stations, with a group of intermediate salinity stations to the SW of the sampling area. The gradient diminishes with season. Temperature sees a greater seasonal variation, including within June cruises, and is influenced by bathymetry. High temperatures occur towards Bracklesham Bay.
- There is little variation in beam attenuance values, which are not significantly correlated with fluorescence. They show a clear Solent-SE gradient, except in cruise 4, probably from resupension events.
- fluorescence values show a high variance within cruises but little variation between dates, except in July when they are significantly above average.
- The hydrodynamic modelling and radar measurements of surface currents are broadly in agreement as to the residual flow pattern, but show stronger residual flows for the latter. Both show the occurrence of a recirculation cell off Bracklesham Bay. OSCR results show that the pattern of instantaneous circulation in surface waters varies significantly with the Spring/Neap cycle. Wind effects are potentially important if maintained over long periods (>4 days), but the OSCR results tend to indicate low winds over the OSCR sampling period (June 1995 and 1996).

Chapter 3: Benthic Communities

3.A. Introduction

3.A.1. Benthic Communities of the English Channel

The benthic communities of the English Channel often show clear distribution patterns, as a result of the interaction of strong West-East gradients in climatic factors (Crisp & Southard, 1958, Holme, 1961, 1966), and marked sedimentary patterns (Cabioch *et al.*, 1977). This gives rise to a decrease in the number of sessile and soft-sediment species towards the Eastern Channel (Cabioch *et al.*, 1977; Dauvin *et al.*, 1994), with in some cases clear distribution limits separating eastern and western species (Holme, 1961, 1966; review in Hiscock, 1998; see also the introduction in Hayward & Ryland, 1995). Thus several types of species can be distinguished according to their distribution:

- Those with a general distribution, for which presence or absence is little influenced by climatic gradients or substrate conditions, at this scale of observation (*e.g. Halecium halecinum, Hydrallmania falcata, Alcyonidium gelatinosum, Dendrodoa grossularia,* and *Sabellaria spinulosa*).
- Species limited by climatic factors: these show distribution limits tied to temperature gradients and include *e.g.* 'western' species, 'cornubian' and 'western Channel' species, which reach their eastern limit at some point in the Channel, or 'northern/eastern' species, limited to the Eastern part (Holme, 1961, 1966; Cabioch *et al.*, 1977 make several other distinctions along the same lines).
- Species limited by sedimentary factors: these are restricted to certain areas where suitable conditions occur (*e.g. Alcyonidium mytili, Dysidea fragilis, Botryllus shlosseri*)
- Species limited by both sedimentary and climatic factors. These can be divided into eastern and western species, the first itself divided into several subgroups (Cabioch *et al.*, 1977). Examples of eastern species are *Balanus crenatus*, *Modiolus modiolus, Buccinum undatum,* and *Flustra foliacea*. There is also a group of 'central Channel' species limited both eastwards and westwards.
- Species which have localised distribution patterns and do not fit within the above classifications. These tend to have fragmented or very localised populations in the Channel.

Holme (1966) points out that climate-related distributions show diminishing densities at the limit of their range, rather than abrupt boundaries, as can be seen in sediment-dependent distributions. Nevertheless, he also singles out Start Point and S^t Alban's Head as the eastern or western limits for several species: the first as the limit of 'Cornubian' (southern) species, at the limit of their northern distributions, the second as a separation between western and eastern Channel species. The differences in stratification between East and West Channel provide a fairly clear and regular distinction between the two halves of the Channel (corresponding approximately to the 60m isobath), and can account for certain abrupt biogeographical changes. Similarly, reviewing the literature on biogeographical provinces of the British Isles, Hiscock (1998) draws the separation between the boreal-lusitanean and boreal provinces at the Isle of Wight on the British side, and between the Lusitanean-boreal and boreal on the French side, at the Cotentin peninsula. From the above sources, the Poole Bay - Beachy Head area (for the British side) appears as an area of transition where a number of western/southern species reach their eastern/northern distribution limits. This is also confirmed by Rees *et al.* (1999), who sampled around the coast of the UK and in the North Sea, and who define an eastern Channel/east coast gravely community, with *Vesicularia spinosa* and *Alcyonidium diaphanum* as indicator species, with its eastern limit at the Thames estuary, and its western limit west of the Isle of Wight. The most common taxa were *Hydrallmania falcata*, Paguridae, *Macropodia rostrata*, *Alcyonidium diaphanum, Vesicularia spinosa, Flustra foliacea* and Gobidae.

3.A.2. Bathymetry and Sediment Distributions of the Solent Area

Geologically, a distinction can also be made such that the line running from the Isle of Wight to the Cotentin peninsula divides the Eastern Channel, characterised by gravel and sand, from the Western Channel, where the substrate is predominantly of bioclastic origin (Larsonneur *et al.*, 1982). In the Solent, as in other bays and estuaries, are found fine sediments, which in this case result from the flooding of the 'Solent River' system after the last ice age (Dyer, 1980). The majority of sediments are thus of recent origin (mainly shingle), with rare outcrops of hard rock in the intertidal (*e.g.* Bembridge ledges), or, subtidally, of clay and limestone. It is shallow, lying mostly above the 20 m isobath. Surficial sediment distributions have been described by several authors (*e.g.* Dyer, 1980; Hydraulics Research, 1991; Algan *et al.*, 1994), as illustrated in figure 3.1. The West Solent, where tidal currents are strongest, is dominated by coarse sediments (gravel, cobbles, boulders), except at the mouth of estuaries, where sediments range from sand to mud. Like Southampton Water, the East Solent proper, with calmer conditions, is covered for the most part by recent sediments, mainly mud or sandy mud, with a maximum thickness of c. 2 m and clayey or sandy patches in certain areas. It is approx. 5.5 km wide and characterised by a number of banks (*e.g.* Bramble Bank, Ryde Middle Bank), with a maximum depth of 20 m but an average depth closer to 10 m. Finer sediments are also found in the natural harbours of Portsmouth, Langstone and Chichester: mainly muds and sand, which can also be found at their mouths, and can extend southward in small banks. Further south and east (outer approaches), sand and gravel or muddy gravel dominate, in a complex pattern where limits between types may be variable, and not always as clear as those on figure 3.1. Sand accumulation zones occur to the south of Bracklesham Bay, and in Sandown Bay (Hydraulics Research, 1993) - the former possibly as a result of the recirculating residual circulation observed in chapter 1 (see also Paphitis, 1997). Gravel and cobbles, more typical of the central English Channel, are found further out.

3.A.3. Animal Communities of the Solent Area

Subtidally, the most conspicuous feature of the benthic communities of the Solent is the presence of dense beds of the American slipper limpet, *Crepidula fornicata* (*'Crepidula'* hereafter). These occur at high densities (though precise figures seem not to have been established), especially in the East Solent, and form a particular community (Barnes *et al.*, 1973; 'BEA73' hereafter). Nevertheless, there are a number of community types present, which can be broadly separated into the following geographical areas (compiled from BEA73; Dixon & Moore, 1987, Collins & Mallinson, 1983, Collins, *et al.*, 1989, Hiscock, 1998; Thorp, 1980).

- Southampton Water. *Crepidula* occurs throughout the estuary, but in higher numbers towards its southern end, where it is associated with a community similar to that found in the East Solent (*see below*), but with certain species lacking (*e.g. Flustra foliacea*), and others thought to be more typical of Southampton Water (*e.g. Idotea linearis, Carcinus maenas, Tealia felina*). For most of its area, the dominant bivalve is *Cerastoderma*

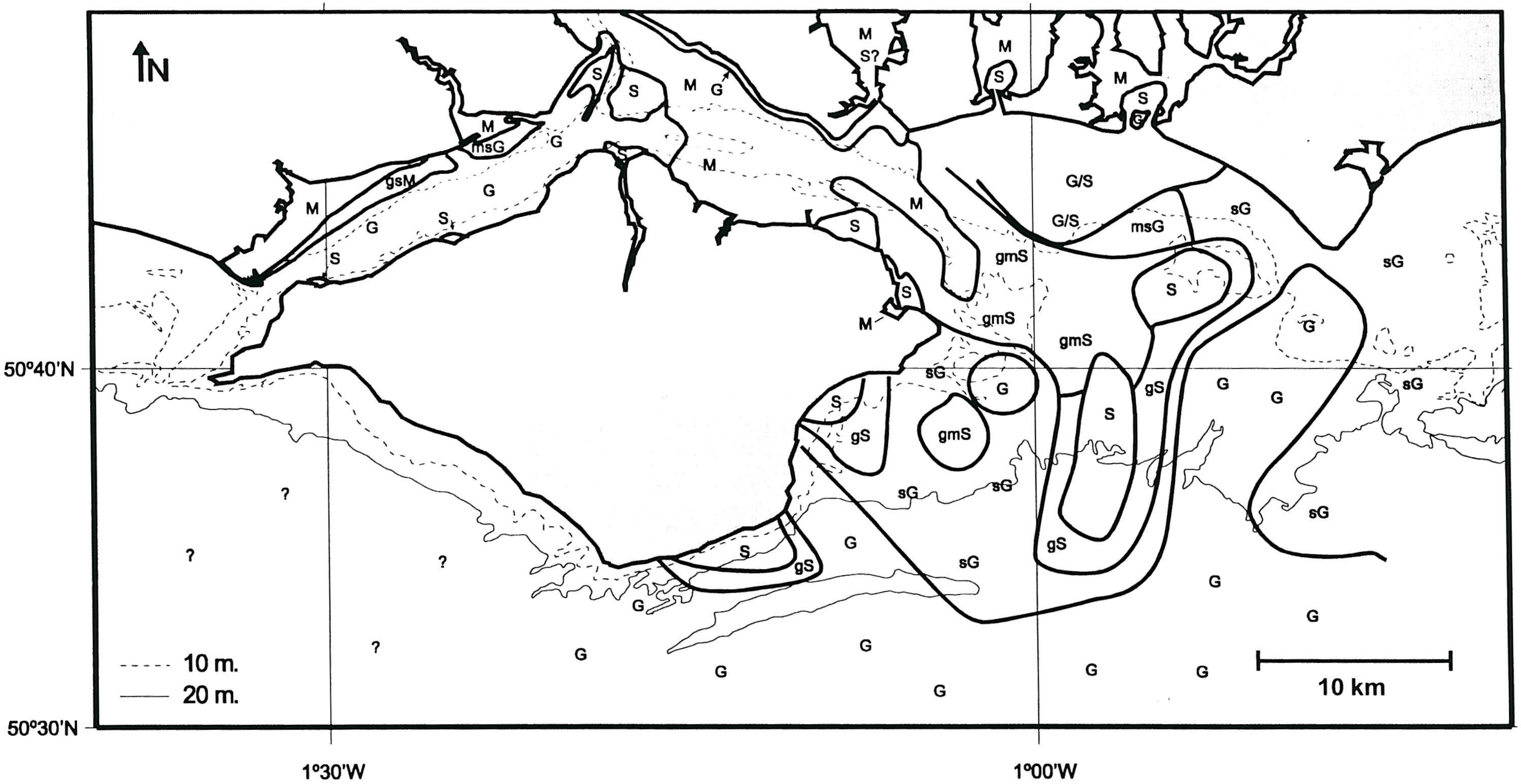

Figure 3.1: Distribution of lithological types of surficial sediment in the Solent area, compiled from Hydraulics Research (1993) and Dyer (1980). Sediment classification based on Folk (1980): M = muds; S = sands; G = gravels; sG = sandy gravel; msG = muddy sandy gravel; gmS = gravelly muddy sand; gS = gravelly sand.

edule, although the *Mercenaria mercenaria* population, no longer abundant, is currently on the increase. Cirratulid polychaetes are common (*Caulleriella* spp., *Cirriformia* spp. and *Aphelochaeta marioni*). The more polluted western side is dominated in areas by *Capitella capitata* and *Nereis diversicolor*, the latter also occurring towards the more estuarine areas, together with *Streblospio shrubsolii*, oligochaetes such as *Tubificoides* spp., and *Carcinus maenas*, *Cyathura carinata* or *Melita palmata.* BEA73 also report the presence of a species-poor *Abra/Nephtys* association near the mouth of the estuary, on a "glutinous, black, sulphurous mud substratum" with *Crepidula* absent and a small number of *Abra nitida, Nephtys hombergii, Cerastoderma edule, Pagurus* spp., *Carcinus maenas* and *Buccinum undatum*. Calshot spit also harbours a community on the cobble-strewn intertidal flats (Holme & Bishop, 1980, cited in Dixon & Moore, 1987), dominated with *Littorina littorea* and *Semibalanus balanoides,* with also frequent occurrences of encrusting algae, *Littorina saxatilis,* and *Nassarius reticulatus*, similar to subtidal communities of the area.

- The West Solent is subject to intense tidal currents, and is, for the most part, muddy sand covered with cobbles, *Crepidula* shells, or pebbles. It supports a sparse community, dominated by *Crepidula*, with fewer numbers compared with the East Solent, especially in the zones of fastest currents. A large proportion is composed of ubiquitous sessile epifaunal species: *Balanus crenatus, Pomatoceros triqueter* and *P. lamarcki, Flustra foliacea*, *Dendrodoa grossularia* and the sponge *Halicondria panicea*, and *Hydrallmania falcata.* A native population of *Ostrea edulis* also occurs in Stanswood Bay. In more sheltered areas, mainly on the North side are found *e.g. Liocarcinus* spp., *Pagurus bernhardus, Pilumnus hirtellus, Gibbula cineraria, Nucula nucleus, Sagartia troglodytes*, *Styela clava*, or *Buccinum undatum*. In the more sandy areas close to estuaries are polychaetes, such as *Lanice conchilega* or *Sabellaria* sp., and the rare clay outcrops include mainly *Pholas dactylus.* Taxa which occur with the *Crepidula* community but were found to be typical of the West Solent are *e.g. Pisa* sp., and *Ocenebra erinacea.* Whilst found in the Solent as a whole, *Ostrea edulis*, *Pilumnus hirtellus*, *Gibbula* sp., *Nucula* spp., or *Buccinum undatum* were found to be more abundant.
- The East Solent supports a similar community to that of the West Solent described above, with a higher mud content, and higher numbers of *Crepidula*. BEA73 attribute a proportion of the silt present in the *Crepidula* beds to the faeces and pseudofaeces of

the gastropod itself. The area tends to see an increase in diversity (compared with the West Solent), with higher numbers of *Alcyonidium gelatinosum* and fewer *Flustra foliacea* and *Hydrallmania falcata*. BEA73 characterised the *Crepidula* community as being typified by suspension feeding organisms and scavengers. In terms of total percentage abundance (from dredge sampling), they found the most abundant animals to be (after *Crepidula*): *Pagurus bernhardus*, *Styela clava*, *Porcellana (Pisidia) longicornis*, *Dendrodoa grossularia*, *Buccinum undatum*, *Alcyonidium gelatinosum*, *Hydrallmania falcata*, *Ascidiella aspersa*, Aphroditidae (mainly *Harmothoe* spp.), hydroids, *Halicondria panicea*, *Flustra foliacea*, and *Gibbula cineraria*. This association was found in most of the area, but in lower numbers in shallower areas (<17m) where macroalgae were found (*Griffithsia flosculosa* and *Laminaria saccharina*), together with their associated fauna.

- Harbours. The natural harbours of Portsmouth, Langstone and Chichester are particular in presenting large areas of fully saline mudflats, characterised by *Nereis* spp., *Streblospio benedicti* in their upper reaches, and *Abra tenuis*, *Cerastoderma edule*, *Nephtys hombergii* and cirratulids closer to the entrances of the harbours. They also present areas of clean, fairly exposed sand at their mouths. Withers & Thorp (1978) surveyed the fauna present in the sands of Langstone harbour, concluding that their species composition related to disturbance levels (as tidal movements). The two most abundant species were *Scoloplos armiger* and *Bathyporeia sarsi*, which occurred together with *Urothoe brevicornis* and *Nephtys hombergii*. *Arenicola marina* was present in more muddy sites, together with *Corophium arenarium*. Other species found were *Glycera convulata* (= *G. tridactyla*) and *Pygospio elegans* for polychaetes (*Lanice conchilega* also occurs in the intertidal - pers. obs.). *Macoma balthica*, *C. edule*, and *A. tenuis* were amongst the few bivalves found.
- The outer approaches. This area has been considerably less studied. Collins & Mallinson (1983) carried out a diver survey of the fauna from Selsey Bill to the Isle of Wight and around Bembridge. They distinguished 6 types of environments: sand, gravel, cobble, boulder, clay bedrock and limestone bedrock. Sand was found to be mobile and species-poor, with as main species *Buccinum undatum*, *Pagurus bernhardus*, and *Nassarius reticulatus*. *Lanice conchilega* and *Amphitrite* sp. were also found in deeper, more stable areas. Gravel was found to be the most common type of substrate, often mixed with sand, where *Lanice conchilega*, *Amphitrite* sp., *Cerianthus lloydii* and *Mya truncata* are reported as common. *Crepidula* was found

over most of the area, with however *Mytilus edulis* replacing it some eastern areas, south of Selsey Bill. Other common species include *Urticina felina, Alcyonidium gelatinosum,* and *Flustra foliacea.* Cobbles were found as raised mounds over the sea bed, with a dense associated epifauna and an associated small mobile fauna: *Halicondria panicea*, *Hydrallmania falcata*, *Obelia* sp., *Alcyonidium gelatinosum, Flustra foliacea, Nemertesia antennina, Halecium halecinum*, *Sabellaria* sp., and *Galathea squamifera, Bugula turbinata, Epistomia bursaria,* and *Dendrodoa grossularia.* This was similar to that found around limestone and hard sandstone boulders observed. These were also raised, and carried a rich epifauna of similar species. Clay bedrock was found to be unstable, partly because of the boring by *Pholas dactylus*; it carried few species, mainly *Urticina felina*, *Galathea squamifera* and *Dysidea fragilis*. However the limestone bedrock was found to be the most diverse of substrates, especially in shallow areas. These were colonised by kelps and other macroalgae, were bored by *Barnea* sp. and *Hiatella* sp., and supported various sponges (*e.g. Dysidea fragilis, Halicondria* spp., *Axinella polyploides, Hemimycale columella*), hydroids, bryozoans and anemones, together with polychaetes (the sabellid *Bispira volutacornis, Pomatoceros triqueter, Sabellaria* sp., *Amphitrite* sp.), echinoderms (*Cucumaria* sp., *Thyone* sp. - probably *Thyone fusus*, *Ophiotrix fragilis*), barnacles (*Balanus* sp.), and others.

- The chalk cliffs which occur at Culver Cliff, between Bembridge and Sandown (also to the SW of the Isle of Wight, but these have not been surveyed) are dominated subtidally by algae (*e.g. Laminaria* spp., *Halidrys* sp.), and at depth (where algae are less dense) support mainly hydroids (*Tubularia indivisa*, *Kirchenpauria pinnata*), sponges (*Dysidea fragilis, Halicondria panicea*, *Amphilectus fucorum*) and hydrozoans (*Anemonia viridis*, *Urticina felina*, *Cereus pedunculatus*). Dixon & Moore (1987) also report *Semibalanus balanoides, Littorina littorea* and the patchy occurrence of *Nucella lapillus* as being common in the intertidal. Deeper Limestone outcrops off Bembridge (Nab, Princess and Culver shoals) were also found to have fewer algae, and the presence of the hydroids *Nemertesia antennina* and *Tubularia indivisa*, bryozoans (*Flustra foliacea, Bugula* spp.), a diverse but sparse number of sponges (*Dysidea fragilis*, *Halicondria panicea*), and the soft coral *Alcyonium digitatum.* In areas of strong currents were dense blankets of *Dendrodoa grossularia*, together with *Polycarpa rustica.*

3.A.4. *Crepidula fornicata*

The American slipper limpet, of the family Calyptraeidae, originates from the East coast of the USA. It was introduced in Europe at the end of the last century, amongst oysters (*Crassostrea virginica*), brought to boost European populations after overfishing of local populations. Since then it has spread successfully to the whole of Western Europe, and a number of locations around the World (Blanchard, 1997). It is euryhaline and eurythermal, and therefore can colonise a variety of environments, with recorded densities of up to 500 m^{-2}. It develops mainly amongst oyster beds, on the coastal infralittoral zone, in sheltered environments such as bays and estuaries. It is most abundant in shallow, protected and muddy sublittoral environments, but can be found in dense patches also on rocky, gravely or sandy bottoms (Hamon & Blanchard, 1994; Blanchard, 1997). It has developed massive populations in the Thames estuary and the Solent, in the Norman Gulf and Marennes Bay in France, and in the Scheld estuaries in the Netherlands. Its success can be attributed to several factors:

1. Its dispersal abilities, linked to its ciliated larva and a relatively long larval life: 1 to 2 weeks according to Marteil (1963), 3 weeks according to Blanchard (1997). Laboratory work by Pechenik (1984) and Pechenik & Lima (1984) has shown the influence of temperature (and diet): for example, most larvae underwent metamorphosis spontaneously between 9-15 days at 25°C, and between 24 and 31 days at 15°C (Pechenik & Lima, 1984). *Crepidula* larvae have also been found on mobile animals such as crustaceans (crabs, spider crabs, lobsters) or molluscs, *e.g. Pecten maximus* or *Buccinum undatum*, and it has been observed on flotsam, fouling on ship hulls, or in ship ballast water.
2. Its association with oyster beds, and its transport with these oysters through human activity, as stocks are moved around. Its geographical distribution follows that of oyster farms, and its spread is quicker where oyster beds are numerous.
3. Its colonising potential: it is able to settle on bottles or other debris, on most substrates, and under a wide range of environmental conditions. For example its first appearance in the Bay of St Brieuc (Brittany) was in 1976, on scallop shells (*Pecten maximus*; Dupouy & Latrouite, 1979). In 1979 it was estimated to 'parasitise' ~10% of scallops. It then forms chains of up to 10 individuals, which further increases the potential for other individuals to settle.
4. The lack of specific predators, compared with North American populations (where it is endemic).

5. Competitive exclusion. This acts on three levels:
    - spatial exclusion, linked to its ability to colonise different substrates, to the smothering of the substrate by the accumulation of the shells of dead individuals, with the consequent modification of the ecosystem, for example by modification of the boundary-layer flow which, will alter the rate of food supply (Fréchette & Butman, 1989), or sedimentary and settlement processes (Butman, 1986; Turner *et al.*, 1994); the accumulation of faeces/pseudofaeces may also render the substrate unsuitable for certain species.
    - Trophic competition. Once the dense populations of *Crepidula* are established, they may compete for food resources.
    - Removal of larvae of other species from the water column.

According to Marteil (1963), the female has between 10×10^3 and 25×10^3 eggs in 60 to 80 spherical egg-sacs, which are protected by the shell during the incubation period (2 to 4 weeks). In Brittany, the reproduction period was seen to last from February-March to September-October. After settling, the juvenile may roam freely until it attaches to the substrate or to a colony of conspecifics. *Crepidula* is protrandric: young individuals tend to be male, and may inseminate several females further down the colony. Its lifetime is of the order of 10 years, with recruitment of 1 or 2 males per colony, which therefore usually consist of up to ~10 individuals, though juveniles may settle in the middle of the chain, initiating branching. Chains are often broken by the dredges of oyster fishermen, though whether this is detrimental or a benefit to the population (by increasing the 'settling space' for new recruits) is unknown.

3.A.5. Objectives

Since Barnes *et al.*'s (1973) survey of the bottom fauna of the Solent, there have been no comprehensive studies of the East Solent benthic communities. This chapter will determine the spatial distribution of the bottom fauna of the East Solent. It was hypothesised that *Crepidula fornicata* would have a major impact on these benthic communities, as very high densities have been shown to be present in previous studies. The importance of this species will be assessed in relation to its distribution, and known environmental conditions prevailing in the area.

3.B. Methods

3.B.1. Sample Collection & Identification

The data presented here represents the results of a subset of 19 stations, out of a total of 49, taken from R/V *Mary Lisa*, on 28th of February 1995 (3 stations) and between the 10th and 14th of March 1995 (16 stations; figure 3.2). These dates were chosen so as to limit the occurrence of juveniles, and therefore the results presented should reflect adult population distributions. Samples were taken using a cockle dredge of 0.6 m diameter, lined with sacking of ~1mm mesh size. This was preferred over other methods of collection because of the wide variety of substrate types and the predominance of areas of shells, pebbles, cobbles, boulders or bedrock, were a grab would have been inoperative. Dredging lasted 10 minutes at each station, at a speed of 2 knots. On one occasion (station 23), where very little fauna and no sediment were collected, a pipe dredge was used to confirm the sample. Dredge contents were sieved on board through a 1 mm sieve, using the deckwash. The sieve contents were then stored in labelled 5 l plastic buckets, in 10% buffered formalin solution stained with rose bengal.

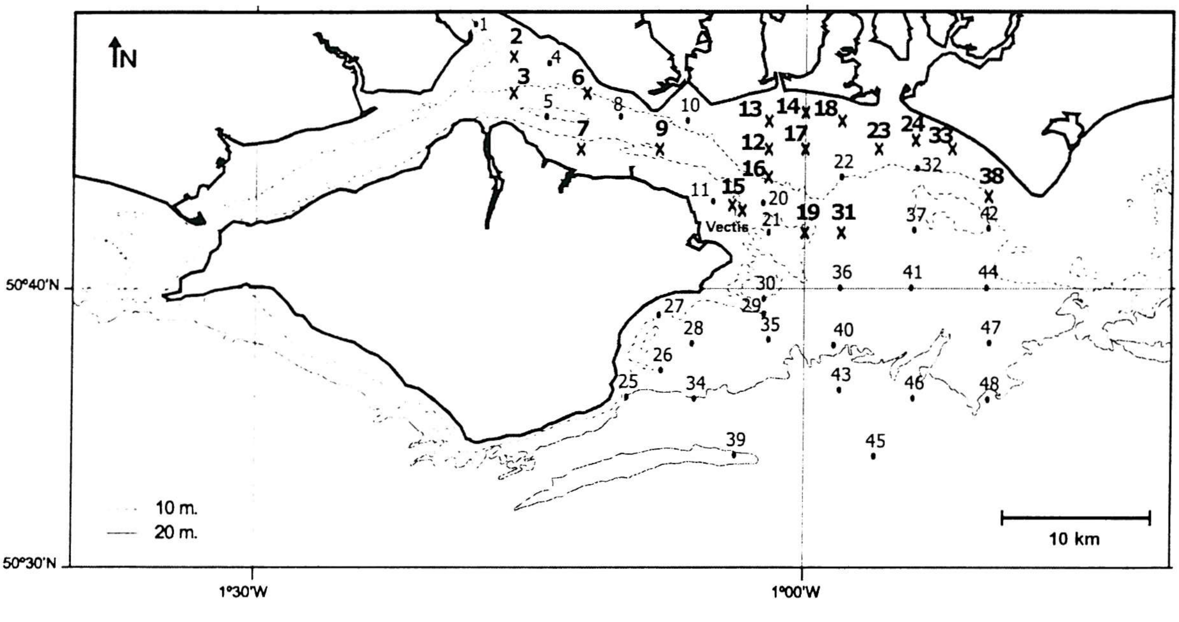

Figure 3.2: Sampling stations for benthic survey (**x**: fauna identified).

In the laboratory, animals were sorted from the sediment that remained and placed according to phyla, in separate containers and in stained buffered 5% formalin solution.

Identification was done by M. Axelsson, as part of a B.Sc. project (Axelsson, 1996), under a binocular or high power microscope, down to species level when possible. Identifications were checked by M. Sheader (Southampton Oceanography Centre). Species identification keys used were: George & Hartmann-Schröder (1985, Polychaeta: Eunicida), Graham (1971, Prosobranchia), Hayward & Ryland (1990a,b), Hayward & Ryland (1995), Ingle (1983, Decapoda: Macroura), Jones & Baxter (1987, Mollusca: Polyplacophora), Jones (1976, Cumacea), King (1974, Pycnogonida), Lincoln (1979, Amphipoda: Gammaridea), Naylor (1972, Isopoda), Pleijel & Dales (1991, Phyllodocoidea), Sheader (unpublished, Polychaeta), Smaldon (1979, Reptantia), Thomson (1988, Opistobranchia) and Thomson & Brown (1976, Opistobranchia).

3.B.2. Data Treatment

Two types of species were excluded from the statistical analyses: the colonial epifauna, which could not be individualised (Bryozoa, Hydrozoa, Porifera), or which were found mainly attached to pebbles or boulders (Cirripedia, Serpulidae). Sabellariidae (*Sabellaria spinulosa*) were included in this category, as they occurred in reefs which may have been inadequately sampled. The other type are species which were likely to exhibit avoidance behaviours: fish, mysids, shrimps and prawns (Crangonidae, Hyppolytidae, Pandalidae, Processidae, Alpheidae), although the mobile crustaceans were counted and identified when they occurred. Counts of individuals were then $\log_{10}(x+1)$ transformed to normalise the data, and the resulting figure given a score on an abundance scale ranging from 0 to 5, corresponding to abundances of <2, <5, <20, <100, <500, <2500 individuals per sample. These correspond to back-transformed intervals of log(2500)/5, the maximum abundance per taxon being 2177. At some stations, where numbers were too great, not all *Crepidula* individuals were kept, and these were given a maximum abundance score of 5. The Bray-Curtis semi-metric distance between samples was then calculated as (Legendre & Legendre, 1998):

$$D(x_1,x_2) = \frac{\sum_{i=1}^{n} |y_{i1} - y_{i2}|}{\sum_{i=1}^{n} (y_{i1} + y_{i2})} \qquad (3.1)$$

where for all taxa y, $D(x_1,x_2)$ is the distance between samples x_1 and x_2, and y_{i1} and y_{i2} are the abundances of taxa y_i in samples x_1 and x_2. This distance does not take double negative values into account, and tends to lay the same weight on rare and abundant species, since it is the differences that are summed (assuming variance is independent of mean). Cluster analysis was then performed on the resulting distance matrix, and a dendrogram of station groupings produced. The (unweighted) pair-group average linkage rule was used (=UPGMA, Sneath & Sokal, 1973). This is the most common method of agglomerative clustering (Gauch, 1982) and most adequate for samples which show clear discontinuities. Stations were then ordinated using Multidimensional Scaling (MDS). MDS is complementary to the cluster analysis in that it allows a visualisation of the configuration of distances between stations, since different arrangements can result in the same cluster analysis results (Manly, 1994). Furthermore, ordination allows an interpretation of the axes in terms of faunistic composition. The theory and computations behind MDS can be found in Kruskal (1964a, 1964b), Kruskal & Wish (1978), Torgerson (1952), and Gower (1987). To summarise, MDS finds a 'map' of stations in a reduced number of dimensions, where the rank ordering of distances in the new configuration is as close as possible to the original ordering of (Bray-Curtis) distances, computed from multi-species data. MDS does not rely on an underlying model of distribution (*e.g.* Gaussian or monotonic), which makes it appropriate for semi-quantitative data or presence/absence data. The correlation between new and old distances is measured as 'stress' and can be seen as a measure of the goodness-of-fit of the ordination.

Computationally, MDS is an iterative procedure, in five steps (Manly, 1994):

1. A set of more-or-less arbitrary coordinates in the reduced n number of dimensions of the analysis is given to stations (usually, as in this case, from scores obtained from an initial factor analysis).
2. Euclidean distances between objects are calculated on these coordinates, with d_{ij} the distance between objects i and j.
3. The distances d_{ij} are regressed on the original (Bray-Curtis) distances δ_{ij}, the regression being monotonic/nonmetric, and a new set of distances between objects ('disparities') is obtained from the regression
4. The goodness of fit between the disparities and the original distances is assessed by a measure of stress.
5. The coordinates are changed slightly in such a way that stress is reduced.

These steps are repeated until stress cannot be reduced further. The solution is then a set of coordinates in n dimensions which are the best representation of the objects in the reduced number of dimensions. Stations can then be plotted in the first two (or three) dimensions of the MDS on an ordination diagram.

The resulting quality of the ordination can be assessed by a 'Shepard diagram', where Bray-Curtis distances are plotted against the new set of distances. The regressed input distances can also be displayed as a step-function, and deviations from the step-line indicate lack of fit.

Following the cluster analysis, the station groups were compared using:

1. A measure of diversity: the Shannon-Weaver diversity index was calculated as:

   $$H' = -\sum^{s} p_i \ln p_i$$

   Where s is the number of taxa and p_i the proportion of individuals belonging to taxa i. H' takes into account both the number of taxa and the distribution of individuals across taxa. To maintain consistency with other statistics, H' was calculated using the categorised abundance scores (rather than raw counts) and thus only comparisons within the present survey are meaningful.

2. The information statistic test (Field *et al.*, 1982). This allows a ranking of the characteristic species for each station group. Thus to compare station groups A and B for species i, the statistic $2\Delta I_l$ is calculated as:

   $2\,\Delta\, I_i = 2\ (I_{ti} - I_{1i} - I_{2i})$ (3.2)

   Where $I_{ti} = N_t \log N_t - A_{ti} \log A_{ti} - (N_t - A_{ti}) \log (N_t - A_{ti})$; N_t is the total number of samples in groups A and B and A_{ti} is the number of samples where species i is present; I_{l1} and I_{l2} are calculated similarly. This index takes into account presence/absence data only. Species can then be ranked according to $2\Delta I_l$ to assess the contribution to group differences. $2\Delta I_l$ approximately follows the χ^2 distribution and can be tested against a given α level with d.f.=1; however the assumptions of the χ^2 test are not met and probability levels are better considered as indices of group separation (Field *et al.*, 1982). Here a value of $2\Delta I_l = 3.84$ was used as an arbitrary cut-off point to distinguish characteristic from ubiquitous species (this corresponds to $P = 0.05$ at d.f.=1).

Following the analysis on stations, a reverse analysis on species was performed. For this the station × species matrix is inverted and standardised such that the new values are the percentage of occurrence of each species (abundance of species i at station j / the total abundance of species i). Bray-Curtis distances, cluster analysis and MDS were then computed as above.

3.C. Results

3.C.I. Community Composition

3.C.1.a. *Taxonomic composition*

The number of species identified totals 175, which can be compared with work by Rees *et al.* (1999), who report 414 species identified from ~200 trawl and grab samples around the UK coast. A complete species list is shown in table A.3.1. Crustaceans are by far the largest group in terms of number of species (table 3.1; figure 3.3), with 73 species (98 if all species found are included), which represents overall 49% of the total. Amphipods are the most diverse group within this phylum, with 34 species (23%), in 16 families, the most diverse being the Ampeliscidae (6 species of *Ampelisca*). Next are the brachiuran crabs (19 species, 13%) in 8 families (mostly Portunidae and Majidae). Although not included in table 3.3, mysids and carideans each represent 12 species. 41 species of polychaetes were counted (27%), divided in 18 families; the largest are the Aphroditidae (9 species), followed by the Phyllodocidae and the Terebellidae (4 each). Bivalves also account for 12 species (8%), in 5 orders and 8 families. Prosobranchs include 7% of species (11) in 9 families. These 5 groups represent together 85% of all species. If the parasitic copepod is excluded (*Sphaeronella* sp., found on *Atylus guttatus*), the smallest group are the echinoderms, with two species (*Ophiotrix fragilis* and *Amphipholis squamata*).

3.C.1.b. *Dominance patterns*

Numerically, the communities sampled are dominated by *Crepidula*, which has the highest average score on the abundance scale (table 3.2). There is an abundance of mobile crustacean species: *Pagurus bernhardus, Idotea linearis, Schistomysis* spp., *Crangon crangon, Macropodia rostrata, Pontophilus trispinosus, Paramysis arenosa,* and others (the more mobile of these will not be sampled efficiently by dredge but their counts are included as being indicative; if anything, they will be underestimated), or molluscs (*Nassarius reticulatus*, *Buccinum undatum*). The infauna is not very numerous or diverse, but is dominated by *Nucula nitidosa*, and there are a number of small infaunal species found amongst muddy heterogeneous sediments or shells, such as the amphipods *Ampelisca diadema, A. brevicornis* and *Atylus guttatus,* or the Aphroditidae *Gattyana cirrosa* and *Lepidonotus squamatus.* Except for the species mentioned, polychaetes are

						Group (% categorised abundance)			
Phylum	**Class (subclass)**	**Order (suborder)**	Total % categorised abundance	n. of species	% n. of species	A	B	C	Vectis
Annelida	Polychaeta		24.3	41	27.3	32.5	14.6	8.4	43.3
Crustacea	Malacostraca	Cumacea	2.5	8	5.3	1.8	0.5	9.6	3.3
		Isopoda	4.3	4	2.7	2.7	8.3	2.4	0.0
		Amphipoda	20.9	34	22.7	18.4	20.9	25.3	36.7
		Decapoda (Anomoura)	8.6	8	5.3	6.3	11.2	13.3	3.3
		Decapoda (Brachiura)	9.8	19	12.7	8.4	13.1	10.8	0.0
Pycnogonida			1.7	4	2.7	2.7	0.5	1.2	0.0
Mollusca	Polyplacophora		1.5	4	2.7	1.8	1.9	0.0	0.0
	Gastropoda (Prosobranchia)	Archeogastropoda Mesogastropoda Neogastropoda	15.7	11	7.3	13.0	21.8	15.7	3.3
	Gastropoda (Opistobranchia)	Nudibranchia	1.4	3	2.0	1.5	1.9	0.0	0.0
	Pelecypoda	Myoida Mytiloida Nuculoida Pterioida Veneroida	8.6	12	8.0	9.6	4.9	13.3	10.0
Echinodermata	Ophiuroidea		0.8	2	1.3	1.2	0.5	0.0	0.0

Table 3.1: Summary statistics for benthic samples by main taxonomic categories. Copepoda, Caridea, Mysidacea, Sabellariidae and Serpulidae are excluded from these calculations: % total categorised abundance; n. of species; % total number of species; % categorised abundance per groups (as defined by cluster analysis).

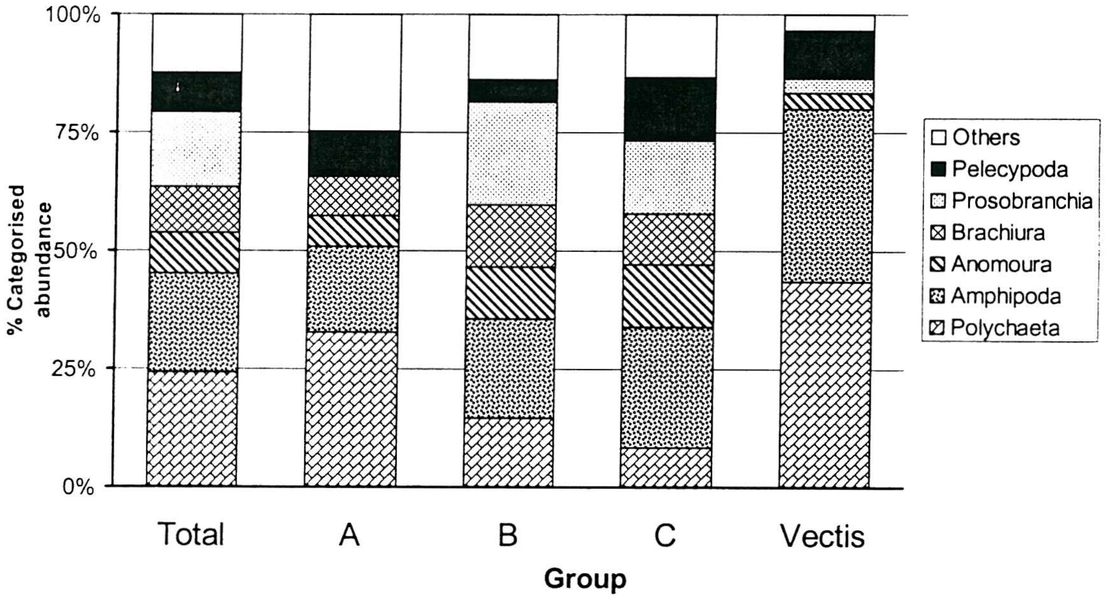

Figure 3.3: Proportion of main taxonomic categories for benthic samples (as % of categorised abundance, >5%, from table 3.2). Total: whole data set; groups as defined by cluster analysis.

A/(B+C)		B/(A+C)		C/(A+B)	
A. acutifrons	**4.96**	*A. acutifrons*	2.91	***D. pugilator***	**5.09**
C. bioculata	**4.96**	*C. bioculata*	2.91	***C. cassivelaunus***	**4.12**
A. brevicornis	**4.96**	*A. brevicornis*	2.91	*G. cirrosa*	2.45
P. hirtellus	**4.61**	*N. nitidosa*	2.56	*B. undatum*	1.74
G. cirrosa	**4.11**	*P. hirtellus*	1.85	*C. fornicata*	1.70
L. squamatus	3.40	*N. hombergi*	1.14	*P. altamarinus*	1.51
N. hombergi	2.93	*M. othonis*	1.14	*L. squamatus*	1.45
M. othonis	2.93	*A. diadema*	0.94	*A. diadema*	1.45
C. cassivelaunus	2.16	*L. squamatus*	0.94	*A. guttatus*	1.18
N. nitidosa	1.85	*P. bernhardus*	0.63	*P. hirtellus*	1.18
P. altamarinus	1.65	*C. fornicata*	0.63	*N. hombergi*	0.94
D. pugilator	1.65	*D. pugilator*	0.58	*I. linearis*	0.94
P. bernhardus	1.01	*G. cirrosa*	0.39	*M. othonis*	0.94
I. linearis	0.93	*B. undatum*	0.39	*A. acutifrons*	0.73
A. guttatus	0.48	*H. reticulata*	0.18	*C. bioculata*	0.73
C. fornicata	0.36	*C. cassivelaunus*	0.12	*A. brevicornis*	0.73
L. pusillus	0.27	*I. linearis*	0.12	*L. pusillus*	0.73
M. rostrata	0.20	*P. altamarinus*	0.00	*H. reticulata*	0.52
A. diadema	0.05	*L. pusillus*	0.00	*M. rostrata*	0.31
B. undatum	0.05	*M. rostrata*	0.00	*N. nitidosa*	0.18
H. reticulata	0.00	*A. guttatus*	0.00	*P. bernhardus*	0.16

Table 3.2: Dominant species of the East Solent area as found in the present survey. Left column: species with an average score per station >0.4; right column: species with maximum score >2. Scores correspond to: 0: <2; 1: <5; 2 <20; 3: <100; 4: <500; 5 <2500 individuals per sample. Values for sessile and vagile epifaunal species are included but should be considered as indicative only.

relatively underrepresented, mostly by *Nephtys hombergii, Caulleriella bioculata, Eupolymnia nebulosa,* and the sessile *Sabellaria spinulosa* and *Pomatoceros triqueter.*

Most of the species abundant over the whole survey area are also those most abundant locally; however there are exceptions: *Achelia echinata* (Pycnogonida), *Atylus guttatus, Eupolymnia nebulosa, Nassarius reticulatus, Macropodia rostrata,* and *Pontophilus trispinosus* have high average scores but do not reach very high abundances locally. Conversely *Ampelisca tenuicornis, Ampithoe rubricata, Nephtys* sp., *Nucula nucleus, Onchidoris bilamellata* and *Pagurus cuanensis* reach high abundances locally but are not abundant across the whole area.

In terms of taxonomic groups, crustaceans come out as being most abundant (table 3.1), mainly from the numbers of amphipods (esp. *Ampelisca diadema*, *A. brevicornis*, *Atylus guttatus*) and decapods (*Pagurus bernhardus*, *Macropodia rostrata*, *Pilumnus hirtellus*). Although they are not included in table 3.1, carideans and mysids were very numerous in some samples (*Crangon crangon*, *Pontophilus trispinosus*, *Thoralus cranchii* / *Schistomysis spiritus*, *S. kervielli*, *Paramysis arenosa, Gastrosaccus spinifer*. They are followed by polychaetes (*Gattyana cirrosa*, *Nephtys hombergii*, *Lepidonotus squamatus*) and gastropods (*Crepidula*, *Nassarius reticulatus*, *Buccinum undatum*). Bivalves are well represented, mainly because of the high numbers of *Nucula nitidosa*, and to a lesser extent of *N. nucleus* and *Ostrea edulis*.

3.C.2. Station groupings

3.C.2.a. *Cluster analysis and MDS*

The cluster analysis divides the stations into three groups, with station Vectis as outlier (figure 3.4). These clusters are good representations of station separation, as demonstrated by the MDS ordination (figure 3.5), which separates the clusters along dimension 1 and 2 (three dimensions were necessary in the MDS, and the resulting stress is 0.066, indicating a close fit to the original data; see figure A.3.1, appendix A). Spatially the station groups follow an E-W disposition (figure 3.6), corresponding to group A: stations of the East Solent; group B: stations off Portsmouth-Langstone-Chichester harbours; and group C: stations of Bracklesham Bay. There is no appreciable difference in depth between groups

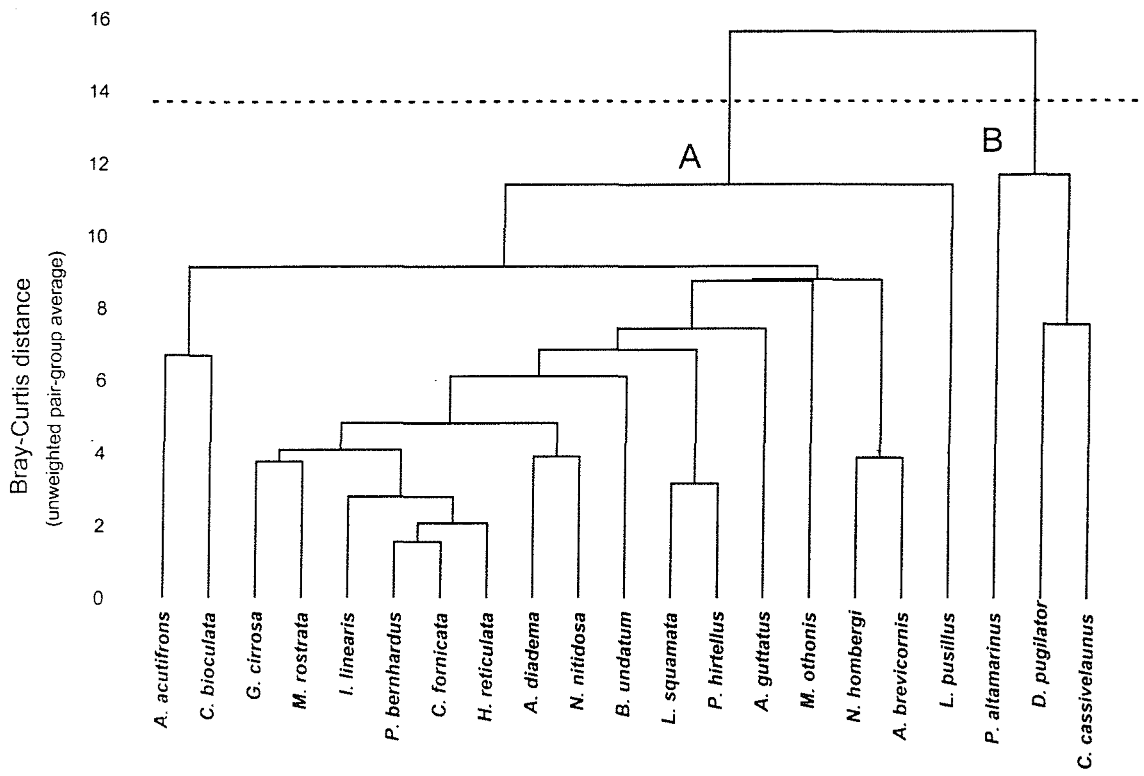

Figure 3.4: Dendrogram of East Solent semi-quantitative dredge samples (Bray-Curtis distance, unweighted pair-group average linkage rule).

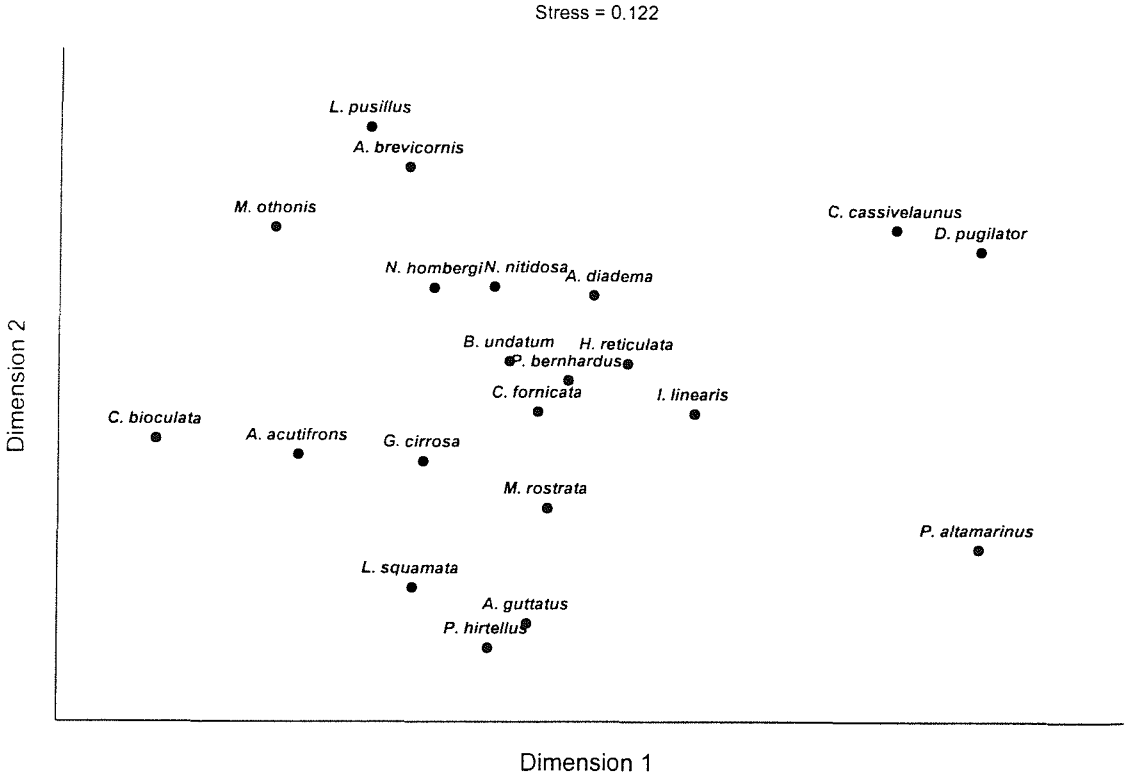

Figure 3.5: MDS on Bray-Curtis distance matrix for East Solent semi-quantitative dredge samples (dimensions 1 and 2 out of 3). Groupings are as defined by the cluster analysis.

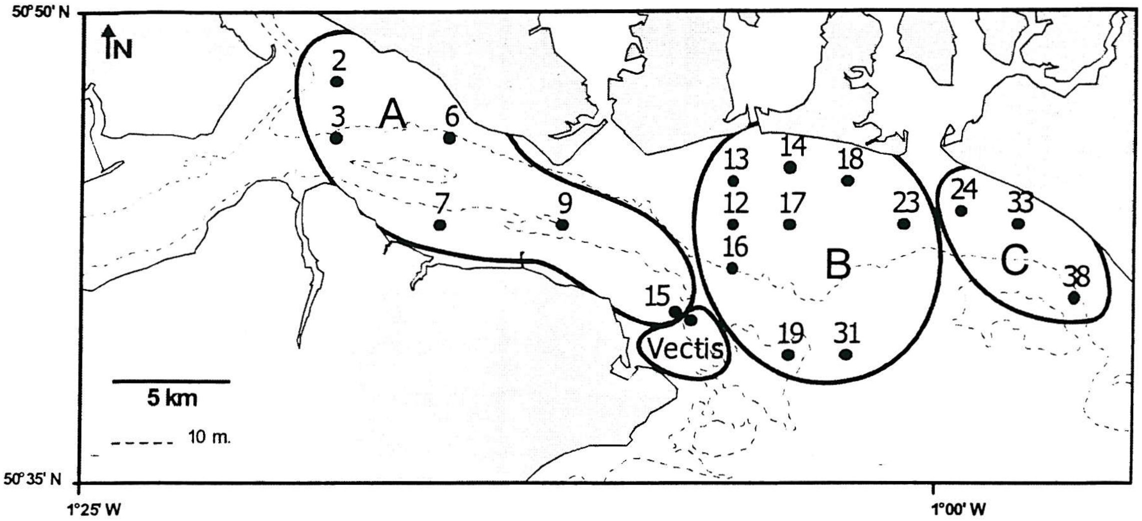

Figure 3.6: Spatial distribution of benthic station groupings as defined by the cluster analysis.

A/(B+C)		B/(A+C)		C/(A+B)	
A. acutifrons	**4.96**	*A. acutifrons*	2.91	***D. pugilator***	**5.09**
C. bioculata	**4.96**	*C. bioculata*	2.91	***C. cassivelaunus***	**4.12**
A. brevicornis	**4.96**	*A. brevicornis*	2.91	*G. cirrosa*	2.45
P. hirtellus	**4.61**	*N. nitidosa*	2.56	*B. undatum*	1.74
G. cirrosa	**4.11**	*P. hirtellus*	1.85	*C. fornicata*	1.70
L. squamatus	3.40	*N. hombergi*	1.14	*P. altamarinus*	1.51
N. hombergi	2.93	*M. othonis*	1.14	*L. squamatus*	1.45
M. othonis	2.93	*A. diadema*	0.94	*A. diadema*	1.45
C. cassivelaunus	2.16	*L. squamatus*	0.94	*A. guttatus*	1.18
N. nitidosa	1.85	*P. bernhardus*	0.63	*P. hirtellus*	1.18
P. altamarinus	1.65	*C. fornicata*	0.63	*N. hombergi*	0.94
D. pugilator	1.65	*D. pugilator*	0.58	*I. linearis*	0.94
P. bernhardus	1.01	*G. cirrosa*	0.39	*M. othonis*	0.94
I. linearis	0.93	*B. undatum*	0.39	*A. acutifrons*	0.73
A. guttatus	0.48	*H. reticulata*	0.18	*C. bioculata*	0.73
C. fornicata	0.36	*C. cassivelaunus*	0.12	*A. brevicornis*	0.73
L. pusillus	0.27	*I. linearis*	0.12	*L. pusillus*	0.73
M. rostrata	0.20	*P. altamarinus*	0.00	*H. reticulata*	0.52
A. diadema	0.05	*L. pusillus*	0.00	*M. rostrata*	0.31
B. undatum	0.05	*M. rostrata*	0.00	*N. nitidosa*	0.18
H. reticulata	0.00	*A. guttatus*	0.00	*P. bernhardus*	0.16

Table 3.3: Information statistic (2 I_i) between station groupings calculated for each species included in the statistical analyses. In bold are values of 2 I_i which correspond to a ^{2} of P< 0.05; above the dashed line are values corresponding to P< 0.1. Probability values are indicative only since assumptions of the ^{2} test are not met.

(one-way analysis of variance, α=0.05; averages are group A: 11.0 m; group B: 7.0 m; group C: 8.8 m). However the sediment in these groups is distinctive, as can be seen in table 3.4. Group A is dominated by fine sediments, mud and/or sand, and empty *Crepidula* shells. Group B has fewer *Crepidula* shells, and the sediment is coarser (gravel and/or sand). Group C is made up of fine sand, and Vectis muddy sand.

Group	Station	Sediment type
A	2	Crepidula shells; Muddy
	3	Crepidula shells; No sediment in dredge (fine sand?)
	6	Crepidula shells; Fine sand
	7	Crepidula shells; Muddy
	9	Oyster bed
	15	Muddy gravel
B	12	gravel
	13	gravel/sand
	14	sand
	16	fine sand
	17	gravel
	18	gravel
	19	gravel/pebbles
	23	fine sand
	31	Crepidula shells/gravel/sand
C	24	fine sand
	33	fine sand
	38	fine sand
	Vectis	muddy sand

Table 3.4: Sediment type encountered in benthic station groups.

3.C.2.b. *Characteristic Species*

The higher-level taxonomic make-up of each group and of the whole community can be seen in table 3.1, and characteristic species in table 3.3 (above), and figure 3.3 (above). For Vectis (not shown), it is clearly distinguished by the high proportions of infaunal species, mainly polychaetes and amphipods: *Gattyana cirrosa*, *Nephtys hombergii*, *Lepidonotus squamatus*, *Ampharete acutifrons*, *Caulleriella bioculata;* and *Ampelisca diadema, A. brevicornis, Atylus guttatus, Harpinia pectinata,* and *Maera othonis.*

Ampelisca spp., particularly *A. tenuicornis,* are known to occur in great densities and form tube beds at the Vectis site (M. Sheader and S. Suhr, Southampton Oceanography Centre, pers. comm.). In this particular case it is probable that the sample was taken at the margins of the sediment patch, which is restricted, explaining the majority of *A. diadema,* usually found in more gravely substrates. The third largest group is the Pelecypoda, with high numbers of *Nucula nitidosa*.

Differences between groups A-C are best looked at in terms of component species, but in general group A has a higher proportion of polychaetes (*Gattyana cirrosa*, *Lepidonotus squamatus, Nephtys hombergii, Caulleriella bioculata*), and a lower proportion of anomourans; group B sees a higher percentage of prosobranchs (*Crepidula, Nassarius*) and fewer bivalves; and group C has higher share of amphipods (*Ampelisca diadema*, *Atylus svammerdami*), bivalves (*Nucula nitidosa*) and anomourans (*Pagurus bernhardus*, *Diogenes pugilator*). Average diversity (H') values for groups A, B, C and Vectis are 3.4, 2.8, 3.0 and 2.7 (differences between means of groups A-C are significant at $P<0.05$, $F_{2,15}=3.96$) - although comparisons can only be made with caution since in effect the sampling is different between groups because of the different sediment types. The specific richness of each group is perhaps more significant in this case, with values of 40.2, 22.6, 24.7 and 19 ($P<0.05$; $F_{2,15}=4.00$). The station groups are of different sizes and again this limits comparisons since the number of species is generally linked to the number of samples. Nevertheless the largest group (B) has also the smallest average number of species after Vectis; thus, given the present sampling methods, the community of the East Solent is the most diverse of the area, despite the dominance of *Crepidula*.

In terms of characteristic species (Table 3.4 above), group A is well characterised with 5 species, mainly infaunal, which show marked differences in abundances between group A on one hand and groups B and C on the other (for $P<0.05$). Three of these are infaunal polychaetes (*Ampharete acutifrons*, *Caulleriella bioculata, Gattyana cirrosa*), to which can be added *Lepidonotus squamatus* and *Nephtys hombergii*, if values of $P<0.1$ are included. There is also *Ampelisca brevicornis* (+ *Maera othonis*) and *Pilumnus hirtellus*. The similarities between the distribution of these species is clear (figure 3.7) and these species are clearly indicative of this station group. Group B is less well defined, with no species included for $P<0.05$ and three for $P<0.1$; these are the same as the first three of group A, and they all occur in station group B only in station 14. In general group B has low abundance values; figure 3.6 reveals that no species is limited solely to this group, and that those that occur in high numbers are mobile species (except the ubiquitous *Crepidula*), and occur across the whole area: *Crepidula*, *Buccinum, Pagurus bernhardus*, *Macropodia rostrata, Nassarius reticulatus*, and *Idotea linearis.* Therefore they will not be picked up by the presence/absence measurement of the information statistic; nevertheless this does single out group B as a 'true' entity and not an artefact of the cluster analysis. As for group

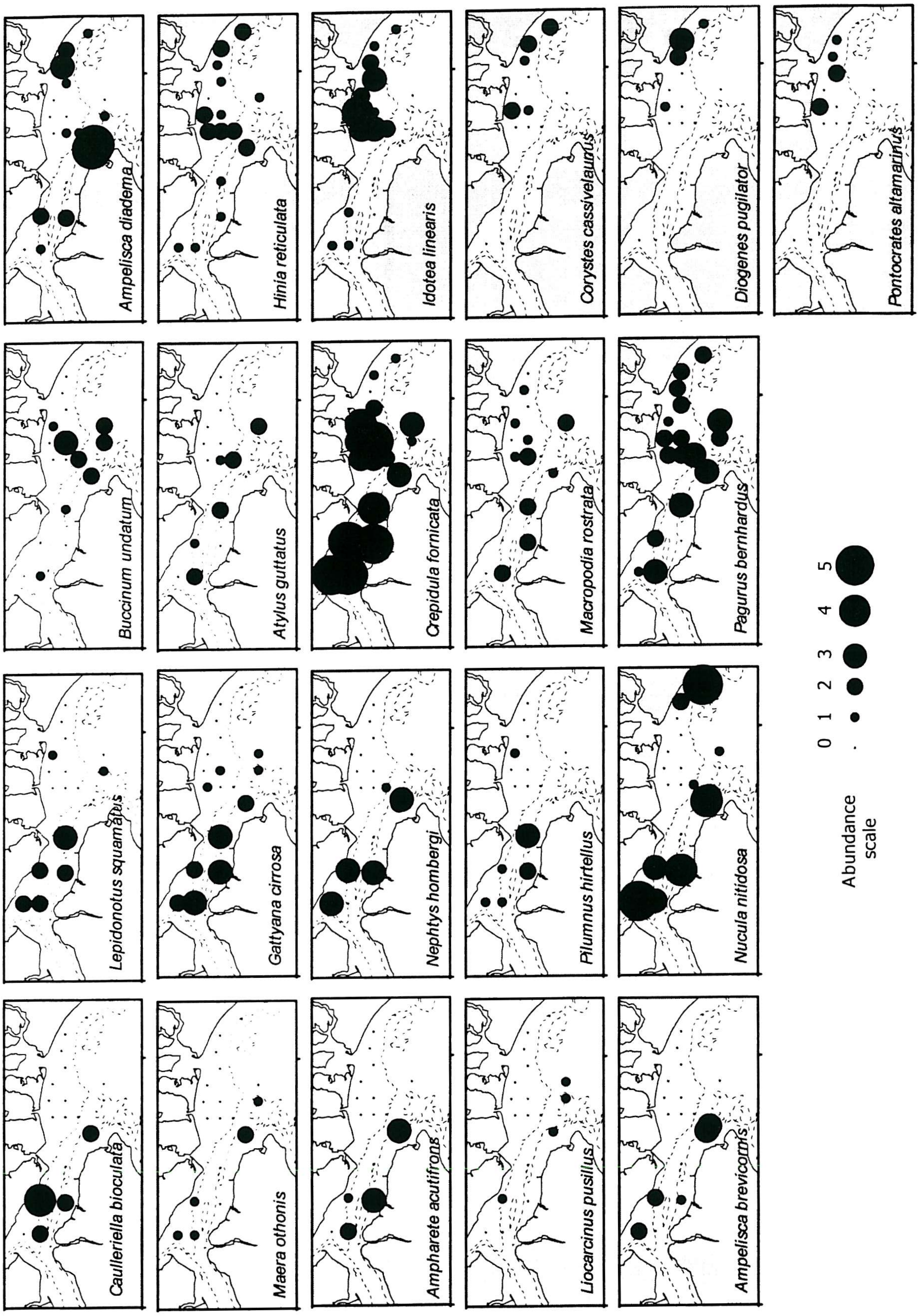

Figure 3.7: Spatial distributions of selected taxa, arranged by coordinate on inverse MDS dimension 1 (top to bottom & left to right). Abundance classes correspond to numbers/sample of: 0: absent; 1: <5; 2: <20; 3: <100; 4:<500; 5: <2500.

C it is distinguished by the decapods *Diogenes pugilator* and the sand-burrowing masked crab *Corystes cassivelaunus*.

The inverse cluster analysis (on standardised abundances) does not separate species into three groups, but in two (A and B on figure 3.8). The level of separation was kept at ~85% of the maximum cluster distance, to maintain consistency with the station groupings. Group A is composed of the majority of species, with *Liocarcinus pusillus* as a direct outlier within the cluster, possibly because of its limited distribution. *Ampharete acutifrons* and *Caulleriella bioculata* are close together, and these are the main characteristic species of station group A. the faunistic group B is made up of the crustaceans *Pontocrates altamarinus*, *Diogenes pugilator* and *Corystes cassivelaunus*; the last two being characteristic of station group C; *P. altamarinus* however displays a very similar distribution. This confirms the results of table 3.2, in that station group B is poorly defined and the main separation is between groups A and C; but the species described as characteristic of group B, in terms of abundance, do cluster closely together (also with *Gattyana cirrosa*, abundant in group A but present in 4 stations of group B). The inverse MDS analysis (figure 3.9 above; the inverse MDS Shepard diagram is displayed on figure A.3.2), which like the cluster analysis takes the abundance scores into account, makes the separation between species more explicit: dimension 1, the dimension of greatest distance, separates species characteristic of group A to the left, from species from group C to the right (table 3.4; figure 3.9). This becomes obvious in figure 3.7, where the distribution maps are arranged in order of their coordinate on the MDS dimension 1. Here there is a clear trend from East Solent species (*Caulleriella bioculata* to *Nucula nitidosa*) to group B species (*Buccinum undatum-Idotea linearis*) and group C species (*Corystes cassivelaunus-Diogenes pugilator*), with intermediate species at the limits of these separations. Thus the MDS segregates most clearly the different distribution types. In parallel we see a change in habitat: first infaunal species (except *Liocarcinus pusillus* and *Pilumnus hirtellus*; the former is usually associated with gravel or rock bottoms, and given its small abundance it is probably misallocated), until *Crepidula*, then mobile epifauna (*Buccinum undatum-Diogenes pugilator*), or species typically associated with sand (*Idotea linearis*, *Corystes cassivelaunus* and *Pontocrates altamarinus*).

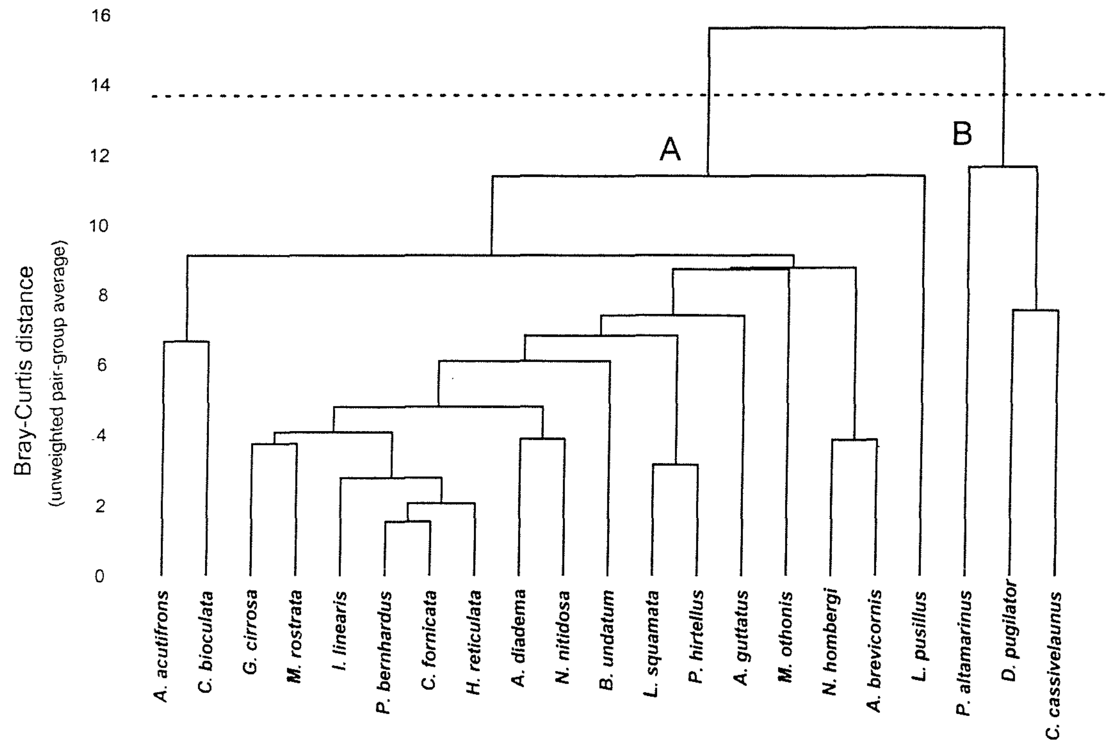

Figure 3.8: Dendrogram of Species (Bray-Curtis distance, unweighted pair-group average linkage rule).

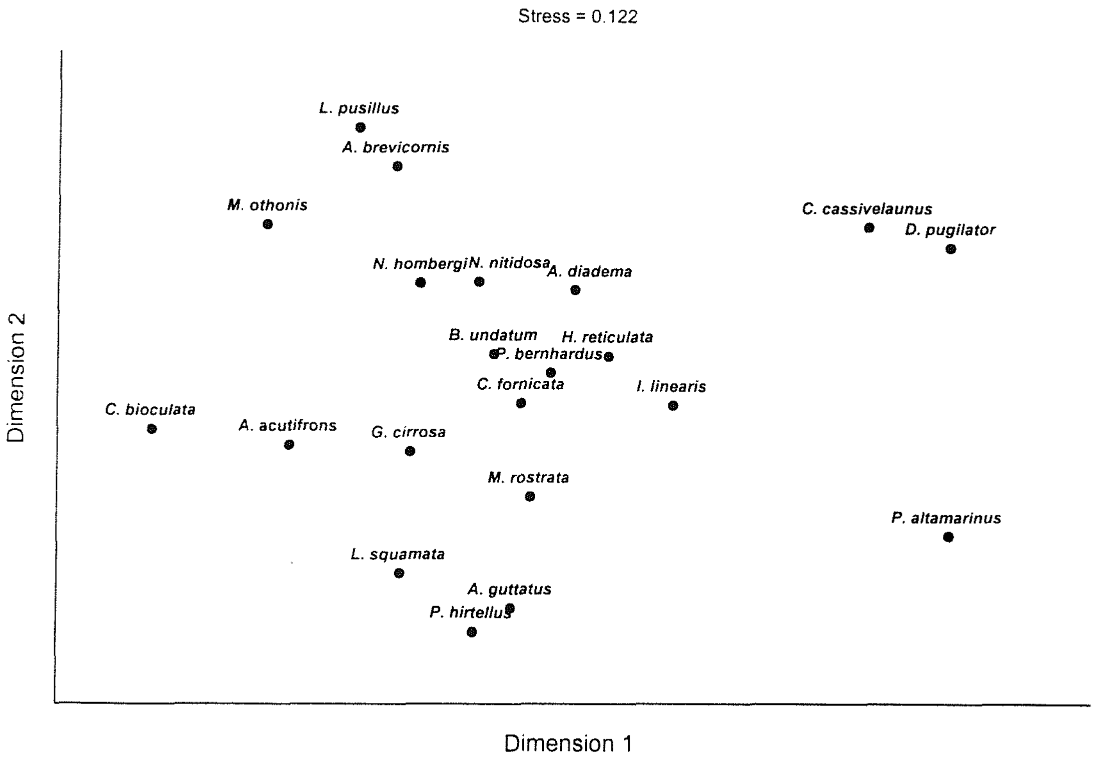

Figure 3.9: MDS on Bray-Curtis distance matrix for species included in analysis (dimensions 1 and 2 out of 3).

3.C.3. Benthic Communities of the Solent Area

Using the survey log (table A.3.2, appendix A), and compiling results from other surveys, the communities of the Solent area have been schematically summarised in figure 3.10, which should be seen as a summary of the different communities; the boundaries between them are not clear cut and each covers more variety than is apparent from this diagram. Clay patches for example occur throughout the area; only one is displayed in figure 3.10 since it is the only one that could be placed with relative precision. Similarly oyster beds are numerous and somewhat mobile, but the three indicated on figure 3.10 were sampled during this survey.

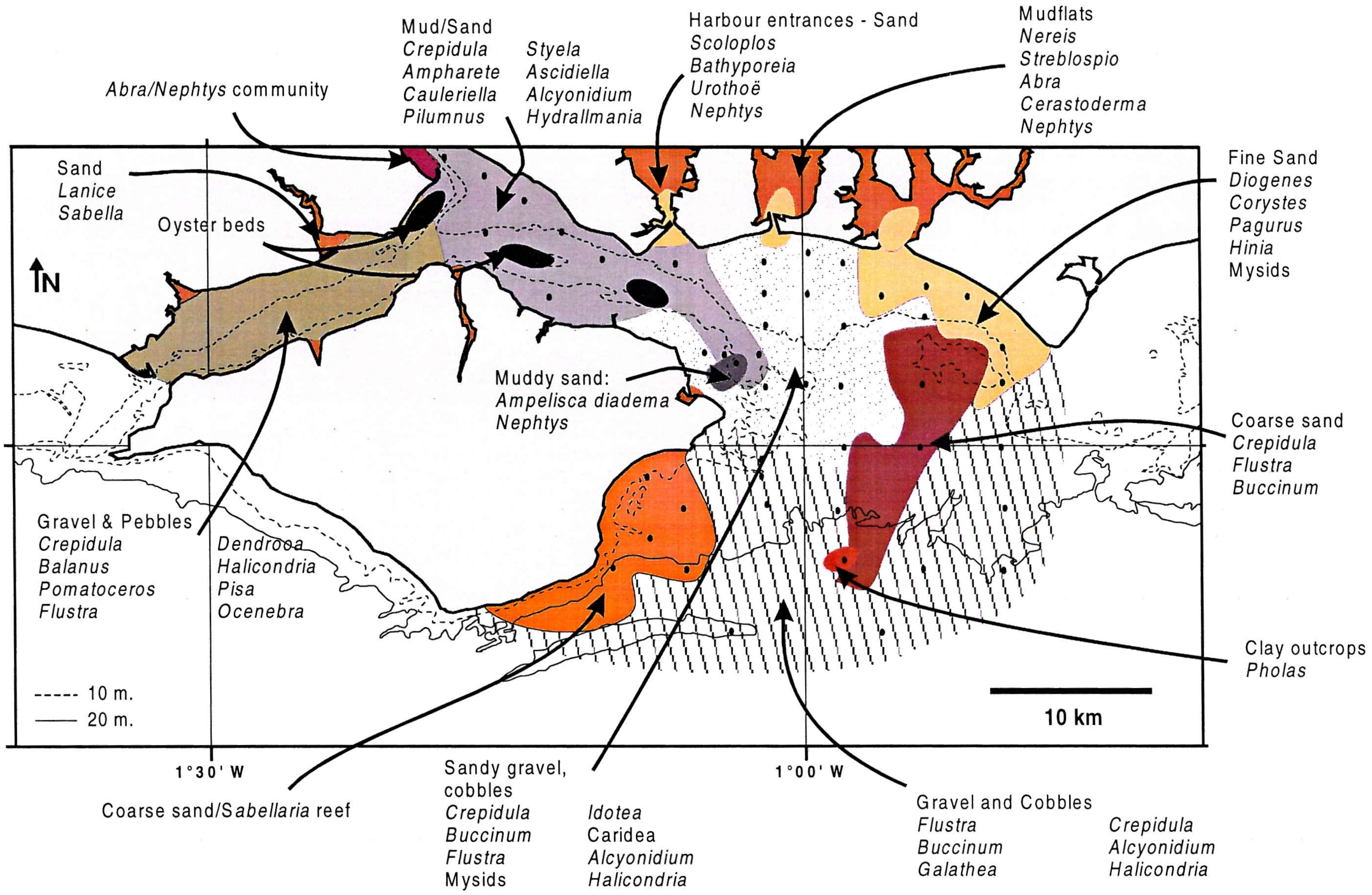

Figure 3.10: Schematic diagram of the distributions of benthic populations of the Solent area, compiled from: this study; Barnes *et al.*(1973), Dixon & Moore, (1987), Collins & Mallinson (1983); Hydraulics Research (1993). Intertidal populations are not included in this diagram.

3.D. Discussion

The community sampled shares many similarities with previous studies, notably that of BEA73, who used similar methods, albeit restricted to the East Solent proper. There are some discrepancies, such as the presence, amongst the dominant species of the former study, of *Gibbula cineraria*, *Macropipus arcuatus* and *Thelepus cincinnatus* ; these are absent from the present survey, as are most echinoderms (*Solaster papposus*, *Henricia sanguinolenta*, *Asterias rubens*, *Psammechinus miliaris* and *Thyone fusus*); however the rarity of this last group was already noted by BAE73, who suggested that the lack of food sources - *i.e.* bivalves - may be the cause of their low numbers (rather than low salinities). Similarly *Nucula nitidosa*, *Ampelisca diadema*, *Caulleriella bioculata,* and *Gattyana cirrosa,* important numerically in the present survey, do not appear in the species list of BEA73. Nor do these authors list amphipods or mysids. This can be attributed in part to the wider mesh size of 38 mm of the dredge used by BEA73, and/or possibly by a seasonal difference (the 1973 study was in September-October), as well as the 'stochastic variation' of populations, over the 1/4 of a century that separates the two studies. Nevertheless, given these differences and this time span, the community seems to have been remarkably stable in its composition, indicating that it has probably reached some state of equilibrium, and that recruitment has been stable. This is probably the case since 1962-63, date of a severe winter, and after which followed an important *Ostrea edulis* settlement - probably the last important shift in the community (Holme, 1967). It is harder to compare with the study by Collins & Mallinson (1983) since their (summer) survey, corresponding roughly to station groups B and C, used very different methods (SCUBA diving). As a result much of the species reported are sessile epifaunal taxa, or large mobile species. For others, qualitatively at least, the descriptions concord; for example in identifying *Buccinum undatum*, *Nassarius reticulatus* and *Corystes cassivelaunus* as typical of sandy sediments, although they include *Lanice conchilega*, whereas only one individual was found in this survey. *L. conchilega* can retract deep in its burrow and it is likely that a dredge will undersample this species were it does not penetrate the sediment sufficiently. Collins & Mallinson (1983) also found a more diverse set of echinoderms (*e.g.* *Asterias rubens*, *Crossaster paposus*, *Ophiura* sp.).

Faunistic surveys of the area have unfortunately not included environmental factors directly, although the sedimentary environment has been relatively well covered by geologists (section 3.A.2). The present results indicate a fairly marked link of fauna and sediment type, since there are relatively few species which occur throughout the area, and the 3 groups identified show marked boundaries - if only by the absence of a number of species, as for group B. It may be surprising however not to find dense populations of *Crepidula* more widespread, since this gastropod it is ubiquitous across the area, and therefore not heavily constrained by sediment type; BEA73 point out that, given a small initial hard area such as debris or dead shells, *Crepidula* can settle on a wide variety of sediments, and once the first chains are in place, further colonisation can continue until the whole substrate is covered in *Crepidula* chains, dead shells, and their associated community. Dense populations of *Crepidula* occur on sandy and gravely patches which occur in the East Solent, but not further East, towards Selsey Bill. Thus it is probable that other factors must be at work in regulating the distribution of the *Crepidula* community. Although it may take many forms, several authors have studied or hinted at the importance of exposure in shaping and controlling subtidal benthic communities (*e.g.* Eleftheriou & Nicholson, 1975). Often this is linked indirectly to tidal stress or wave action (the latter being more unpredictable and therefore potentially more damaging). Withers & Thorp (1978) thus relate the distribution of infaunal species in Langstone Harbour to different degrees of exposure (as current shear), with fewer sessile or bivalve species in more exposed areas, where fast-moving or fast-burrowing species are at an advantage. Hydraulics Research (1993) and Paphitis (1997), amongst others, have studied the mobility of sediments in the area: it was found to be limited to the Northern part of the survey area, *i.e.* where fine sediments are present, and where - as elsewhere - tidal currents are strong, but also where the shallowness of the area makes wave action potentially significant, *e.g.* off Bracklesham Bay (chapter 2, section 2.A.2). These occur predominantly from the SW (Hydraulics Research, 1993), and thus the Isle of Wight provides some shelter; however refraction effects divert them towards the (East) Solent channel, with Hayling Island still experiencing significant wave action. Furthermore, winds from the S, SE or E can also occur, though infrequently because of the predominant wind patterns and the small 'fetch' from those directions. Thus overall the pattern is of a gradient of decreasing wave action from the inner Solent towards the east and southeast (Hydraulics Research, 1993). Instantaneous tidal currents are strongest in the West Solent, in parts of the Outer Approaches (Outside of the harbours, and particularly south of the Bembridge-Selsey Bill axis); intermediate values occur off Bracklesham Bay. The interaction of these two effects results in a gradient of sediment mobility increasing East to West (under most conditions; Hydraulics Research, 1993). These different factors can be tied to the three subcommunities identified in this study as station groups A, B and C. East Solent/Group A in the most sheltered/average tide/low sediment movement area, group B in the strong tide/medium wave exposure/average sediment movement, and group C in weak tide/maximum wave exposure/strongest sediment movement. Associated with these gradients is the dominance of *Crepidula*, which despite its ubiquitous presence, only develop dense beds in the East Solent, where presumably sediment mobility is limited and where it can settle and develop chains. Group B sees relatively high numbers of *Crepidula,* but less than the East Solent and is also more exposed, with less fine sediments and a predominance of sandy gravel. Group C however is mainly sandy, has the most mobility and seems incompatible with the *Crepidula* association.

Where *Crepidula* occurs *en masse*, it modifies the sedimentary regime of deposition and accumulation of the areas it colonises, biotic factors take hold, and therefore its influence on the community cannot be separated from environmental factors directly. Like *Sabellaria* spp., *Pygospio elegans* (Morgan, 1997), and other species, *Crepidula* can modify profoundly its environment, and a positive feedback process may occur once an area that is sufficiently protected to allow settlement, fixation of initial colonies and feeding is colonised - *i.e.* a stable substrate but also a relatively unperturbed environment. The ability of *Crepidula* to form chains, and of covering the substrate with dead shells, allows it to colonise areas of muddy sediments in densities unattainable by other filter feeders such as bivalves.

Nevertheless, *Crepidula* is absent or in lower numbers in certain sheltered areas, such as the Vectis site, where presumably a combination of depositional processes, fine sediment resuspension, and sediment movement inhibit filter feeding or settlement. Here the number of species is lower, consisting mainly of infaunal species such as polychaetes and amphipods, particularly *A. diadema* and other ampeliscids. Thus despite smothering the sediment surface and excluding certain species, *Crepidula,* in effect, may well enhance the 'niche space' of the community by creating new surface areas, and by the presumably large biomass now fixed from the water column. Although it has few predators, its faeces and pseudofaeces are presumably important inputs of organic matter, since ecological transfer rates for filter feeding organisms are thought to be between 5 and 20% (Chardy, 1987), and *Crepidula* is responsible for at least a part of the fine particle fraction accumulated in the assemblage. The quantity and diversity of crustacean and gastropod scavengers and predators in the *Crepidula* community is testimony to the availability of food material. It is tempting to attribute the higher diversity of the *Crepidula* association to the gastropod itself, because of the higher organic matter fixation and the increased availability of substrate on which to settle, or find shelter and food, especially for sessile species such as *Alcyonidium gelatinosum*, *Hydrallmania falcata*, *Halicondria panicea*, or *Styela clava*, which are abundant in the East Solent, and smaller species such as *Galathea squamifera*, *Pisidia longicornis* or Aphroditidae which can take advantage of the shelter afforded by the epifauna and empty shells. Nevertheless the relative effect of reduced levels of disturbance from wave action or tidal scouring, favourable to the development of the slipper limpet, are unknown. It is also possible that the differences in diversity between the station groups are due to an artefact of the sampling method, since the efficiency of the dredge is very different in the *Crepidula* association than it is in the sandy area of group C; however from comparisons with the studies of BEA73, or Collins & Mallinson (1983), this would not seem to be the case. Thus it is not possible in our present state of knowledge to separate the abiotic factors from *Crepidula* in shaping the communities of the area. There are no pre-*Crepidula* records, and the different communities differ markedly in their environmental conditions. The strong association of *Crepidula* with the East Solent, and the particular conditions that are found there - moderate currents, shelter, shallowness and substrate, would indicate that there are strong constraints on its distribution. The case of the Vectis site is interesting, in that this area is within the East Solent, but has very few *Crepidula* associated with it. The muddy-sand sediment is characteristic, and its geographical restriction would indicate a particular hydrodynamic regime which favours depositional processes, and/or is the site of frequent sediment movement. These would probably not be a major constraint on the predominant *Ampelisca* spp. since there are several example of *Ampelisca* spp. migrating at night into the water column (*e.g.* Dauvin & Zouhiri, 1996). However the precise mechanics of the constitution of this *Ampelisca* community are unknown.

Sediment distributions are known to determine the large-scale distribution of organisms in the Channel (Cabioch *et al.*, 1977; Hiscock, 1998; Rees *et al.*, 1999), and BEA73 lay great weight on the influence of sediment distributions (and macroalgal abundance) in determining the level of presence of *Crepidula*. This, when tied to apparent stability of the community, would imply a stable climatic and sedimentary biotope, and/or a resilient community. For other (soft sediment) sites of the English Channel, Fromentin *et al.* (1997) have shown that local conditions could be important in moderating long term climatic effects (1978-1992) and carried a high proportion of variance (see also Fromentin & Ibanez, 1994). Thus in the present case the resilience of the ecosystem may be due to locally stable environmental conditions, amongst which are food inputs (benthic systems of the Channel rely to a great extent on allochtonous inputs of organic matter; Chardy, 1987), disturbance levels, winter temperatures and flow regime predictability, and/or the resilience of the community (*e.g.* regular recruitment or rapid recolonisation). Holme (1983) remarks that, at the scale of the Channel, hydrographically variable areas are likely to experience more variation than those that are hydrodynamically dominated; this is likely to be the case here, were temperature and salinity gradients are limited but tidal currents are strong. This would act at several levels: on the distribution of sediments and adults, but also through the production, distribution or supply of phytoplankton, and for species with a pelagic larval phase, through the dispersal and recruitment of larvae, which would benefit from the shelter from wind currents (*e.g.* Bertness *et al.*, 1996; Commito *et al.*, 1995), and/or from a semi-closed circulation system, such as hypothesised in chapter 2. Such a pattern has been hypothesised to occur by Thiébaut *et al.* (1997) for a muddy-fine sand community of the Bay de Seine, which also displays a degree of long-term persistence, together with mechanisms for larval retention (biotic and abiotic). The *Crepidula* population of the Solent is most likely isolated, with the closest area of dense beds being found in the Essex estuaries (BEA73), and there is no evidence of spreading of this species through larval dispersal along the Channel coast. It is therefore very likely that it is dependent on self-recruitment, which given its two-to-three week larval phase, implies some degree of retention in the area. Elsewhere in the Channel, working on a 15 year time series, Davoult *et al.* (1998) have shown that a community dominated by dense beds of (filter feeding) *Mytilus edulis* showed marked changes in community structure (*e.g.* loss of diversity), which were tied to the variability in recruitment of the bivalve. Thus it may be that in the Solent the interaction of local oceanographic conditions and the presence of *Crepidula* has led to a rich, diverse and stable community since the introduction of this gastropod.

The Solent area as a whole can be seen to include a number of restricted communities, such as the *Sabellaria* beds, sand patches, clay and chalk outcrops or the Vectis site. The long term variability of these areas is unfortunately unknown, as this could have led to a comparison with the *Crepidula*-dominated areas, and an assessment of the role of this species in promoting stability.

3.E. Summary

- The Solent area as a whole can be seen as a diverse mosaic of communities. Over the survey area, *Crepidula fornicata* was found in dense beds, and it is thought to be an important structuring agent for the benthic communities of the East Solent, probably influencing sediment deposition, settlement patterns, food inputs and other processes.
- The subtidal communities of the East Solent sampled were separated into three groups according to their taxonomic composition, which could be linked to their sedimentary environments:
  - A mud *Crepidula* community, which covers a majority of the area of the East Solent. It was characterised principally by *Crepidula fornicata*, *Caulleriella bioculata*, *Ampelisca diadema*, *Pilumnus hirtellus* and *Gattyana cirrosa.*
  - A coarse sand & gravel community off Hayling Island, with a majority of ubiquitous species; the most characteristic were *Ampharete acutifrons*, *Caulleriella bioculata* and *Ampelisca brevicornis.*
  - A fine sand community off Bracklesham Bay, characterised by *Diogenes pugilator* and *Corystes cassivelaunus*.
  - A muddy-sand community at the Vectis site, characterised by *Ampelisca diadema*, *A. brevicornis*, *Nucula nitidosa* and *Nephtys hombergii.*
- Three factors are though to influence faunistic distributions: the presence/absence of *Crepidula*, sediment deposition and mobility, and wave action.
- The community of the East Solent is though to have been relatively stable for at least 3 decades, possibly from stable local environmental conditions, combined with a resilience of the community, and regular recruitment.

Part B: The Mesozooplanktonic Community

B.1. Forcing Factors of Zooplanktonic Communities

In the English Channel, long term trends in the evolution of zooplanktonic communities are thought to be influenced by global climatic factors (Southward, 1983). This is illustrated by the Russell cycle, which is linked to dramatic shifts in the planktonic community, first observed in the mid-1920s: the decline of several fish species, and of zooplankton, by an order of magnitude; the replacement of *Sagitta setosa* by *Sagitta elegans*; the increase of pilchard by several orders of magnitude, and other phenomena, including the spread of warmer-water benthic species (Southard, 1983; Mann & Lazier, 1991, chapter 9). Most of these trends were reversed in the 1960s, and this cycle is though to be linked to global North Atlantic weather patterns, *i.e.* the North Atlantic Oscillation (NAO). Such changes can be brought about in part by the changes in the patterns of phytoplankton production: increased winds over the eastern North Atlantic in the 1950-1980 period, linked to the NAO, have been followed in the North Sea by a shift in the onset of the spring bloom, a decrease in overall production and a reduction in zooplankton biomass. Thus even for long-term trends the principal forcing factor of mesozooplanktonic communities is primary production. At the seasonal level, patterns of growth and reproduction are also correlated to phytoplankton patterns, themselves dependent on the physico-chemical properties and dynamics of the water column. Seasonally these vary in relatively predictable ways, which has led to a classification of the types of seasonal production patterns according to the evolution of the physical environment (Colebrook & Robinson, 1965). In coastal waters, strong tidal and wind currents often prevent stratification, leading to a seasonal pattern of primary production, the so-called 'coastal cycle', with an early spring bloom and relatively high, if variable, biomass throughout the summer. The high phytoplankton growth rates are not followed by a proportional increase in zooplankton growth rates, and a large fraction of the primary production is exported to the benthos. This pattern is typical of the southern North Sea and the Eastern English Channel. In deeper areas, where stratification can occur, production is characterised by a double peak in production in Spring and Autumn, with relatively low biomass in between (the 'shelf cycle', typical of the western English Channel).

Thus ultimately, the processes governing both phytoplanktonic production and zooplanktonic populations are the dynamics of the water column. Within each 'cycle' and as spatial scales get smaller, attention shifts from global rates of production, to local processes of mixing and transport of populations. Thus the relationship between hydrodynamic factors and planktonic communities has become an accepted part of most marine ecological studies, and according to Legendre & Demers (1984), may be "the driving force of aquatic ecosystems", either directly, or through the interaction with lower trophic levels, and ultimately with primary producers. These biological-physical interactions take on many forms, and act at all scales, from the ocean basin to the molecular level (Denman & Powell, 1984; Mann & Lazier, 1991; Svendsen, 1997). Concerning the distribution of zooplankton, these processes can be summarised as (Legendre & Demers, 1984):

- Biogeographic structures, resulting from basin-wide circulation.
- 100-1000 km patches associated with oceanic currents (*e.g.* Gulf Stream).
- 1-100 km (mesoscale) structures associated with *e.g.* upwelling (tied to phytoplanktonic production, but also circulation patterns) or mesoscale circulation (eddies, local wind forcing; Rand & Hinch, 1998).
- 1m-1km: hydrodynamic features such coastal fronts (Wolanski & Hamner, 1988), internal waves or tides.

As the scale of observation gets smaller, biological effects such as vertical migration or aggregative behaviours also become more visible, though the major forcing factor of patchiness above ~10 m are still considered to be hydrodynamics (Fasham *et al.*, 1974). Legendre & Demers (1984) also argue that even at small scales, a strong correlation to phytoplankton will not remove the effects of hydrodynamic factors, but that "phytoplankton will become the vector through which hydrodynamically induced heterogeneity is transferred to higher trophic levels". In coastal waters, several studies show that tidal advection may be one of the dominant factors for phytoplankton distributions (Denman & Powell, 1984). An example is that of the western Irish Sea, where Dickey-Collas *et al.* (1996) argue that differences in tidal currents and water depth separate seasonal hydrographic areas, with different associated 'cycles', as described above (and including different zooplanktonic communities separated by frontal areas; Burkart *et al.*, 1995). Zooplankton production was found to be correlated to these patterns, but also to currents, in particular the establishment of a summer cyclonic gyre, which acted as a retention area (as discussed by Hill, 1994, Hill *et al.*, 1996, 1997; section B.2.e.2 below).

The following chapters will study the temporal dynamics of the mesozooplankton communities of the Solent area during June-August 1995. It is perhaps appropriate to review the first hydrodynamic processes affecting the distribution of zooplankton populations in coastal waters, and their interaction with biological factors.

B.2. Zooplankton Transport In the Marine Environment

B.2.a. General

Oceanographic factors relevant to plankton transport are wind-, tide- and density-driven circulation (Denman & Powell, 1984; Shanks, 1995), sometimes resulting in complex patterns, such as aggregation along fronts (Eggleston *et al.*, 1998), by Langmuir cells (Shanks, 1995), internal waves (Shanks, 1995), or internal tidal bores (Pineda, 1999). From the point of view of the biological oceanographer, it can also be seen as the result of the interaction between the passive and active processes of physical transport and (biological) movement. The scale of observation determines to some extent which of these processes is observed. Rather than list the various oceanographic phenomena involved in transport (as in Shanks, 1995), this review will follow another distinction drawn in the literature of separating active (biological) and passive (physical) processes (*e.g.* Boicourt, 1988). Because larvae are often associated with commercially exploitable species, and because their emission source is often better known than for holoplankton, the literature concerned with transport in coastal waters is biased towards larval transport, and this will be reflected in this review; however the processes are applicable to both holo- and meroplankton.

B.2.b. Passive Physical Transport

When considered as passive particles, zooplanktonic organisms are entrained by diffusion and advection (Scheltema, 1986; Okubo, 1994). Diffusion is the dispersion of propagules resulting from turbulent flow. It can be measured as an increase in average distance between propagules (Scheltema, 1986). It is a small-scale process compared with advection, so that their relative importance will vary according to the scales of observation involved, with diffusion important at short time and space scales (*i.e.* for larvae that spend only a very short time in the water column, such as *Spirorbis* sp., *Arenicola marina*), and advection of major importance for zooplankton with long generation times, teleplanic larvae or generally for larvae spending a significant amount of time in the water column. Assessing the importance of diffusion in the field is however difficult due to the overriding influence of other factors, which drown its signal; its importance at other than very short distances is still elusive (Scheltema, 1986).

Advection is a horizontal transport that can be related to a defined current regime. In the present context, it entails estuarine, coastal or oceanic circulation, and these are often complex. Richards *et al.* (1995), for example, have shown that modelling using even the simplest parameters of advection, diffusion and mortality could create unpredictable patterns of dispersal along straight coastlines, when tidally oscillating currents were taken into account. Other authors demonstrate, again through modelling, how local oceanographic conditions can favour either retention close to an emission source, or a loss, depending on the prevailing current and wind regimes. This is the case for Salomon (1990), who applied the 2-dimensional model of the English Channel described in Chapter 2 to the advection/ diffusion of larvae, 'seeding' his model at nine different sites. His results, expressed as proportion of larvae retained to larvae emitted, show the variability between different areas. Some are modelled as being particularly favourable to retention (Lyme Bay, Plymouth Sound, Baie de St Brieuc, Baie de Seine, Channel Islands), due to low residual currents and/or eddy effects, others particularly favourable to export (central Channel, Baie de Somme, Dover Straits). Salomon (1990) interprets his results in the light of the distribution of benthic communities in the Channel, explaining the apparent differences in faunal composition between the British and French coasts noted by Holme (1961, 1966).

Environmental variations can also cause variability at particular sites. This was modelled for blue crab larval dispersal in Chesapeake Bay by Johnson & Hess (1990). Their model, verified against drift buoys, attempted to separate the relative effects of wind, fresh water flow and density differences on the transport of larvae. They showed that wind was the most important factor, but that it could both favour or inhibit retention within the Bay. On average however 13% of larvae were kept within the Bay, while 87% were exported. Interestingly, a large proportion (29%) where then re-imported. Black *et al.* (1991) have also used modelling (2- and 3-D advection/diffusion models) to simulate larval dispersal around coral reefs. Their results show how the interaction between local topography, current regime and larval life-span can create complex patterns, which may favour self-seeding even in isolated islands. These patterns promoted much longer residence times than were expected otherwise. Dippner (1993) went a step further, and compared field data with his own modelling results of the German Bight circulation pattern. His results predict that under particular wind regimes, the normal circulation breaks down, promoting the formation of eddy fields. Comparing this data with previous work, Dippner (1993) infers that these eddies favour the retention of sprat larvae (*Sprattus sprattus*), and increase their survival index.

Such models consider zooplankton as passive particles, and this is sometimes borne out by field studies. Many of the above emphasise the role of physical processes on dispersal, and Sewell & Watson (1993), for example, describe the retention by these alone of asteroid larvae (*Pisaster ochraceus, Pycnoppodia heliantoides* and *Dermasterias imbricata*), close to parent populations in Nootka Sound, British Columbia, resulting in what these authors believe to be a closed community. In practice however most larva are active, and we find in nature a continuum between situations where patterns of larval distributions can be explained solely by advection and dispersion of passive particles, and situations where zooplankton movement alone is sufficient. Where each situation lies on the continuum depends on the species involved. According to Butman (1987), it is also to some extent arbitrary, and will depend on the scale at which the phenomenon is observed.

B.2.c Horizontal Swimming

The first active potential mechanism of dispersal is through horizontal swimming (Shanks, 1995). Swimming is common in vertebrate and invertebrate larvae (Chia & Bucklands-Nicks, 1984; Young, 1995), and indeed also found in macrophyte spores (*e.g.* Frederiksen *et al.*, 1995). Two modes of locomotion are available: either cilia (generally in smaller larvae), or muscular movements, with the two sometimes being combined (Chia & Bucklands-Nicks, 1984). Horizontal dispersal ability through swimming will depend on the ratio of water current to swimming speeds; thus organisms which rely solely on ciliary movements, or small zooplankton/early larvae which use muscular movement can reach speeds on the order of a few mm.s^{-1} to a few cm.s^{-1}. This can be compared with the average coastal current, of the order of 10s of cm.s^{-1} (Shanks, 1995). For fast swimming organisms this could be sufficient to counteract medium term residual currents - that is, if the swimming is directed. Both Epifanio (1988) and Shanks (1995) cite studies where directional swimming may be important in certain decapods (*e.g. Homarus americanus*), with as cues sun compass, magnetic compass, wave direction, chemical cues or sound of surf. However both consider that the evidence for active dispersal in this sense is very scarce, and that it does not appear a good candidate for crab larvae, and *a fortiori* for the majority of invertebrate species, including holoplankton (Castel & Veiga, 1990).

B.2.c. Active Vertical Migration

The vertical migration of planktonic organism, as relevant to transport, can take three forms: 1) Ontogenetic migration; 2) Tide-synchronised migration; and 3) Diel vertical migration. These have different consequences when interacting with oceanographic factors.

B.2.c.1. *Ontogenetic Migration*

Bryant *et al.* (1998) show how, for *Calanus finmarchicus,* a fixed ontogenetic change in depth can lead to stable areas of recruitment, when interacting with general, basin-scale circulation. This was modelled to occur for periods of over 10 years, despite long and complex transport routes. However the area where such interactions have perhaps been the most commonly reported are estuaries. They vary from highly stratified to vertically homogeneous, and thus represent different problems for the planktonic organisms inhabiting them (Scheltema, 1986). Stratified estuaries, because of their two-layer circulation pattern provide an opportunity for larval retention mechanisms when they are combined with an ontogenetic migration.

Research has especially concentrated on decapod species (especially *Uca* spp., *Callinectes sapidus* and *Pagurus* spp.), as reviewed by McConaugha (1992). A typical pattern would be that after export out of estuaries, larvae concentrate in the lower parts of the water column, with movement towards or away from the estuary regulated by vertical migration. This pattern diminishes with ontological development, resulting eventually in recruitment of larvae close to the parent populations. Thiébaut *et al.* (1992), in one of the rare studies dealing with non-decapod larvae (Stancyk & Feller, 1986), showed how larvae of the polychaete *Owenia fusiformis* were retained within the baie de Seine estuary. Early larvae (stage 1 of 4) tended to be found in surface waters, resulting in a net seaward export within the Seine river plume. As larvae get older they are found on average in greater numbers in deeper more saline waters (stage 2 just above the level of no-motion, stages 3 and 4 below), resulting in net landward transport. This pattern varied according to the stratification of the water column, suggesting an effect both of physical and behavioural processes. Similar patterns have also been shown to occur for different phyla (*e.g.* Scheltema, 1986; Stancyk & Feller, 1986; Boicourt, 1988), and have also revealed the importance of ontogenetic migration in shelf waters.

B.2.c.2. *Tide-Synchronised Vertical Migration*

This pattern of behaviour is probably the most widely reported in the literature, and again a large proportion is concerned with decapod larvae (particularly the blue crab *C. sapidus*: Blanton *et al.*, 1995, Epifanio, 1995, Garvine *et al.*, 1997, Olmi & Orth, 1995), though it is also common in other taxa. (*e.g.* Garrison & Morgan, 1999; review in Stancyk & Feller, 1986). The use of vertical migration in relation to tidal currents to promote directional transport has been termed 'Selective Tidal Stream Transport' (STST, *e.g.* Hill, 1994). For decapod larvae of the southeastern coast of the U.S., Blanton *et al.* (1995), for example, suggest that larval behaviour can produce a regular recruitment pattern, despite variable oceanographic conditions. Using a model of the cross-shelf circulation, the authors show how prevailing winds can be responsible for either upwelling or downwelling current regimes. This can be reconciled with the regular recruitment patterns that occur, only if larvae are not greatly affected by the circulation patterns, or if vertical migration can adapt itself to each situation to effect shoreward transport. The evidence goes both ways: Zeng & Naylor (1996) have experimental and field evidence showing that vertical migration patterns are endogenous in three populations of *Carcinus maenas* in North Wales. The pattern of vertical migration is linked to the tidal period, with ascent occurring during expected ebb tide. This would tend to favour retention close to shore, however the authors found that this pattern was similar at three different sites despite varying tidal conditions. This would suggest that at least in this species, retention or export are by-products of a fixed behaviour which globally tends to promote retention. This would imply that the presence or absence of a zooplanktonic species in any particular area could be a function of its 'compatibility' with prevailing current patterns; for example the work of Bryant *et al.* (1998) mentioned above showed that the distribution of *Calanus* in the northwest Atlantic could be explained solely by the interaction of the prevailing current regime and a fixed (ontogenetic) pattern of migration behaviour. The same may apply to STST, and the directiveness implied in 'selective' is perhaps unfortunate. This idea can be reinforced by Epifanio (1995), who reviews transport modes of the blue crab to estuaries of the Southeastern coast of the U.S., and finds a 'stochastic' variation linked to prevailing wind patterns. This is also the case for modelling by Johnson & Hess (1990) who found that, for similar situations, the most important factor was wind forcing. The other side of the argument is brought forth by Morgan (1996), who showed that hatching rhythms of *Uca pugilator* were different in different environments, and that transplanted crabs could switch to the pattern of the local population.

Rowe & Epifanio (1994a,b) show data in which weakfish larvae (*Cynoscion regalis*), in Delaware Bay, showed STST patterns which could explain larval fluxes landward, and effect retention in the estuary. This species showed a vertical migration pattern which correlated with the semidiurnal tide signal, leading to a net flux towards the inside of the Bay. The observed pattern was also ontogenetic in that it was present only in later stage larvae, with the cues being probably some aspect of flow rather than salinity or temperature. However, in his review of decapod larvae dispersal, mortality and ecology, McConaugha (1992) describes how *C. sapidus* larvae do not realise their "dispersal potential", through an interaction between variable oceanographic conditions and biological patterns of vertical migration. *C. sapidus* hatches close to the mouth of estuaries, resulting in export to shelf waters where subsequent development takes place. This is not the case at his particular study site, where wind forcing establishes a 2-layer flow pattern (current and counter current). The vertical migration of *C. sapidus* larvae interacts with these processes which results, together with Eckman forcing, in larval retention at the mouth of the estuary. Here again physical factors are a major forcing factor: the pattern described above is dependent on wind effects and thus may or may not occur each year. McConaugha (1992) cites a number of other studies where decapod larvae are retained close to their parent populations in analogue ways.

B.2.c.3. *Diel Migration*

In a special case of the above patterns, Hill (1991a, 1991c, 1994) has modelled the interactions between the S_2 (solar) component of the tide and diel vertical migration of zooplankton. He found that this coupling can lead either retention or transport of zooplankton out of a particular area. In Hill's model this depended on the phase of the S_2 tidal current relative to the diel migration pattern, both of which are Sun-synchronised. Hill (1994) shows maps of some expected areas of divergence, convergence and retention of diel-migrating organisms around the coast of the British Isles. Theoretical displacements of 4 km.day^{-1} were calculated as being possible. Similarly, Smith & Stoner (1993) have modelled the potential transport of diel-migrating organisms through tidal channels, averaging over a whole year. They found this time very little transport overall in most cases, concluding that turbulent mixing acted to limit the significance of vertical migration; there is as yet little evidence to decide either way, but it is likely that differences in local conditions will be important.

B.2.d. Other Patterns

B.2.d.1. *Biological and Local Variability*

In practice each area will have its oceanographic and biological specificities, which leads to a wide range of dispersal modes, both between and within specific areas. Anger *et al.* (1994) show how, in the same locality (a coastal brackish lagoon in Argentina), certain species would experience dispersal and others retention according to their respective "needs" (Anger *et al.*, 1994). For two grabsid crab species (*Cyrtograpsus angulatus* and *Chasmagnatus granulata*) the coupling of larval hatching rhythms, tidal state and the day/night cycle favoured an export of zoeae stages from the lagoon to the open sea. They found that the larvae of these species occurred more often at flood tides and at night than on ebb tides during the day. For the caridean shrimp *Palaemonetes argentinus*, retention was predominant, probably through diel vertical migration of the animals. These larvae prefer low salinity (lagoon) waters, and were found more often during daytime than at night in oligohaline areas of the lagoon. The authors conclude that export and retention in these species is a by product of selection for osmoregulation (shrimp) and predator avoidance (crab).

In contrast, two differing larval strategies can result in similar dispersal patterns if the environmental conditions are favourable: Bhaud & Grehan (1990) argue that for the terrebellids *Eupolemnia nebulosa* and *Lanice conchilega*, their two different development modes both result in retention close to the parent populations. *E. nebulosa* is limited by dispersal capabilities (this polychaete produces egg masses which use macroalgae as nursery areas, rather than planktonic larvae), whilst *L. conchilega*, despite its long (6 wks) larval life, is retained through local oceanographic conditions. Thus contrasting life-cycle strategies are not a guarantee of differences in transport patterns, as even long pelagic larval phases can lead to local recruitment (as mentioned earlier for *Calanus* in the northwest Atlantic)

As noted before in the case of *C. sapidus,* and for Dippner's (1993) modelling results, -but probably true for most situations- a particular pattern of retention or dispersal can also vary for a single species at a given locality. Arcachon Bay (France) is separated from coastal waters by a shallow ground-sill which, despite important water fluxes, limits larval exchange between the two water masses to the surface layer. The horizontal distribution of larvae is thus controlled by their vertical distribution, in turn a function of larval age (Mathivat-Lallier & Cazaux, 1990). This was found to be the case for the larvae of *Lanice conchilega*, who tend to be found deeper as they advance in their pelagic development, implying a different export rate for young and old larvae. Periods of high winds/swell were found to be of importance for the rate of exchange, implying that variability in recruitment within the bay could be a factor of 'mortality' at the younger larval stages, itself related to meteorological conditions. A similar case is reported by Falkenhaug *et al.* (1995), working in a Norwegian fjord system where circulation is also prevented by a sill. It was found that the zooplanktonic community was strongly influenced by the rate of advection, and that inputs from outside the fjord were often higher than the local production of copepods. They also found that transport was dependent on the vertical position of zooplanktonic organisms, which changed seasonally, but that the rate of exchange was highly dependent on prevailing meteorological conditions. In contrast, Thiébaut *et al.* (1994) argue from their data on *Owenia fusiformis* larvae in the Baie de Seine, that variability induced by wind conditions affect the distribution of larvae only at small spatial scales. General dispersal within the bay was found to be dependent mainly on the tidal circulation of the area, itself permanent.

B.2.d.2. *Gyres*[1]

Dispersal along straight coasts or within estuaries are by now fairly well described phenomena. There are however types of coastal circulations such as residual gyres, for which the influence on transport, or indeed their physical oceanography, have still to be understood in detail. Gyres can be seen as closed circulation systems, potentially favouring aggregation or retention of particles (sediments, phyto-, zoo- and ichthyoplankton; Denman & Powell, 1984), and increasing residence times in particular localities. The increased turbulence associated with their periphery may also have a wide range of effects on planktonic communities (Margalef, 1997; Petersen, 1998; Raby, 1994; Salas-de-Leon, 1998; Sundby, 1997; Svendsen, 1997), or they can be associated with upwelling of nutrients and enhanced productivity (Salas-de-Leon, 1998, Pinot *et al.*, 1995). There is increasing evidence that residual gyres are a common feature of neritic waters: modelling by Salomon & Breton (Salomon, 1989; Salomon & Breton, 1991, 1993), and modelling and/or observations by Tyler (1976), Tyler & Banner (1977), Pingree & Maddock, (1985), Zimmerman (1981), Nichols *et al.* (1982), Dippner (1993), Hill (1993), Hill *et al.* (1994), Boxall & Robinson (1987), or Hill *et al.*, (1996) have shown their ubiquity in the seas of the northwest European Shelf. There are three types of gyres commonly reported from coastal waters: baroclinic seasonal gyres (Hill, 1993), gyres formed by topographical rectification of ocean currents such as oceanic 'rings' or neritic circulation eddies, on the scale of 100-200 km. (*e.g.* Lee *et al.*, 1992, 1994), or tidal residual gyres (A. R. Robinson, 1983). The latter are generated by the interaction of tidal currents and local topography (Zimmerman, 1981; Pingree & Maddock, 1985). All have the potential to aggregate particles at their centre (clockwise gyres in the northern Hemisphere - Shanks, 1995) or at their edge (counterclockwise in the northern Hemisphere). Yet the study of such phenomena remains rare - perhaps because of its logistical difficulty: their time scale is much larger and their signal usually smaller, relatively to the tidal period and short-term wind effects.

Gyres cover a number of different phenomena (both physical and biological) which occur at different scales. Rather than review the physical oceanography of each, it is more convenient for the purposes of this review to look at the literature concerned with

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[1] A more appropriate term would be 'eddy' since 'gyre' usually defines ocean-scale circulation (Baretta-Bekker *et al.*, 1992); however the use of 'gyre' to describe mesoscale recirculation cells is widely applied in the literature. Both terms are used here, independently of scale (see also the introduction in Robinson, 1983).

zooplankton transport only. The reader is referred to texts such as Loder (1980), Zimmerman (1981), I. S. Robinson (1983), Apel (1987), Wolanski & Hamner (1988), Visser *et al.* (1990), Mann & Lazier (1991), Hill (1993), Hill *et al.* (1994), or Wolanski *et al.* (1996), for more details.

If we exclude the now considerable literature on basin-scale oceanic gyres (A. R. Robinson, 1983; Joyce & Wiebe, 1992) and research on other biological effects in coastal areas (*e.g.* primary production, for example Pinot *et al.*, 1995), the effects of coastal gyres on transport are still relatively unexplored. An exception to this rule is the influence of the gyres generated by the Florida current. These have been well defined by a series of authors (Criales & McGowan, 1994; Lee *et al.*, 1992, 1994; and others). They describe a cold cyclonic gyre, formed by the meandering of the Florida current off the Florida Keys. The spatio-temporal scale of the gyre is c.100 km and 1-2 months and it occurs regularly over the Pourtales Terrace, between Key Largo and Key West. Circulation velocities reach 20 to 50 $cm.s^{-1}$ (Lee *et al.*, 1992). The influence of this gyre is seen particularly in the upwelling of nutrient-rich water at its centre (2 $m.day^{-1}$), and the retention and shoreward transport of fish and lobster larvae (from prevailing winds and Eckman transport). These benefit from the enhanced productivity from the raising of the nutricline, which increases the concentration of copepod nauplii, a possible food supply of the larvae. The analysis of Lee *et al.* (1994) is that the effect of the Pourtales gyre will be different according to the relation between the duration of the planktonic period and the lifetime of the gyre. The slipper lobster (*Scylarus* sp.), grouper and snapper larvae are likely to be affected most, having a planktonic period on the order of 1 month, while species such as *Panulirus* sp. (spiny lobster) with a larval period of up to 12 months would be affected quite differently (Lee *et al.*, 1994; see also Criales *et al.*, 1994 for other crustaceans). Mesoscale processes such as the Pourtales gyre have also been described around oceanic islands: Lobel & Robinson (1986) have studied circulation patterns around Hawaiian waters, and found that the eddy fields formed around them could act as nursery areas for larval fish, keeping cohort groups together. They followed a cyclonic eddy which remained in the vicinity of the same area for c. 60 days, a duration on the same order as that of development for several species of reef fish; using drogues, they showed that material at the centre of the gyre could remain there for almost two months. This type of study has been popular (*e.g.* Wolanski *et al.*, 1996, Black, 1991) because of the importance of the question of self-seeding *versus* connectivity between reefs.

Hill (1993) and Hill *et al.* (1994, 1996, 1997) have documented the case of a seasonal baroclinic gyre in the Western Irish Sea, caused by a lens of cold water trapped in a depression below the thermocline, and above which develops a cyclonic circulation. This pattern is highly seasonal (because of its dependence on stratification); it occurs above a patch of muddy sediment harbouring populations of the Norway lobster *Nephrops norvegicus*, which occur in isolated populations, but also have a long larval life (~50 days); the gyre has the potential of favouring the maintenance of the population if hatching and stratification coincide. Dickey-Collas *et al.* (1996) have also discussed the importance of this gyre in retaining early stage fish larvae in summer, through advection and/or the higher zooplanktonic production associated with the gyre (Burkart *et al.*, 1995). Hill (1993) discusses the potential for the occurrence of such gyres elsewhere on the northwest European shelf, and cite six other locations, including the German Bight, where modelling by Dippner (1993) reveals a series of deeper-water, topographically-induced eddies which would retain larvae in deeper waters of the German Bight, while individuals higher in the water column are advected shoreward by Eckman transport. Both results would explain the apparent positive relationship between increasing westerly wind, and increased survival of sprat larvae. Nichols *et al.* (1982) report the advection of a patch of young zoeae of *Cancer pagurus* off the coast of Northumberland. They interpret this in the light of previous studies which report the presence of a residual gyre in the area. This gyre retains young larvae during the summer months, but disappears in the Autumn and is replaced by a southerly drift, entraining with it later-staged larvae. Tyler (1976) and Tyler & Banner (1977) have linked the effects of a coastal gyre with benthic populations (mainly ophiuroids) in Oxwich Bay (Bristol Channel). They relate tidal and wave action, sediment distributions and adult echinoderm distributions, and conclude from the poor correlation between sediment parameters and adult distributions, that the patterns observed are due to differential settlement rates induced by the trapping of larvae. Tremblay *et al.* (1994) have looked at the biological implications of a residual gyre in the Georges Bank area. Using high resolution 3-D modelling, they describe the possible dispersal patterns of scallop larvae (*Placopecten magellanicus*) according to several factors: prevailing hydrodynamic conditions (gyre intensity), larval origin (three main input patches), and planktonic development length (short, base case and long development). The gyre over Georges Bank reaches maximum intensity in early Autumn, which corresponds to the peak of spawning in scallops. Tremblay *et al.* (1994) find that according to their model the gyre will retain larvae in the area for most populations, resulting in mixing between populations and self-seeding overall. However the fate of the larvae is very dependent on initial conditions and varies significantly according to the position of release, the average depth of the larval 'cloud', and the duration of the larval period. Hannah *et al.* (1997) have also modelled the Gulf of Maine and Georges Bank area, this time in the context of *Calanus* supply, and show that the patterns of abundance of this copepod could be dependent on the hydrographic structure of the area, mainly regulated by the interaction of wind stress and the topographic gyre over Georges Bank; vertical positioning (whether active or passive) was also found to be important in determining the fate of modelled populations; this is also confirmed by Lynch *et al.* (1998), who emphasise the interaction between hydro- and population-dynamics for *Calanus* (see also Davis, 1984). The effect of gyres on holoplankton however are usually more difficult to assess in field studies, since these tend to act more on the distribution of densities of otherwise ubiquitous species, rather than trap distinct populations, and the source populations are usually poorly known (except when there are clear distribution differences between stages, *e.g.* Boucher, 1988; Bryant *et al.*, 1998). Pinca & Dallot (1995), for example, report the occurrence of an eddy in the Ligurian Sea associated with higher concentrations of chlorophyll *a,* and several copepod species. Through their analysis, the correspondence between faunistic and station groupings (through Q- and R- mode MDS and classification) were found to coincide only partially. However others have applied similar multivariate analyses with a degree of success in revealing distinct community patterns. Thus certain gyres may be considered as separate biotopes (*sensu* Van der Spoel, 1994). Murdoch (1989) reports the occurrence of an eddy off Otago peninsula (New Zealand). The circulation and hydrographic structure observed were tied to several permanent species groups: although the component species changed with season, clustering and MDS analysis extracted three assemblages linked to hydrographic factors: outer-shelf, mid-shelf and neritic. The latter was linked to the eddy, which showed a particular community composition, entrained oceanic species inshore and seemed to retain larvae of benthic crustaceans and certain fish eggs. In the Bay of Campeche (Mexico), Salas-de-Leon *et al.* (1998) showed the marked influence of a cyclonic, upwelling-forming gyre on the zooplankton. This was observed to be a seasonal phenomenon, and caused increased nutrient inputs and zooplanktonic abundances; it also acted to maintain the 'oceanic community' out of the Bay.

Several features stand out of these studies, notably the complex links between hydrography, hydrodynamics, and behaviour or the length of time spent in the water column, which interact to produce observed patterns of zooplanktonic distributions. In the main, gyres appear as distinct but variable environments, which may act to define biogeographical separations at a scale where these are otherwise though to be rare (Van der Spoel, 1994); and few studies fail to emphasise the role of variability, particularly linked to wind effects.

Chapter 4: Mesozooplanktonic Communities of the East Solent and other approaches.

4.A. Introduction

This chapter reports the results of mesozooplanktonic surveys taken concurrently with the physical oceanography data, on the four latter cruises described in chapter 2. After a summary of previous mesozooplanktonic studies carried out in the area (section 4.A.1), the aims and strategy will be set out in section 4.A.2.

4.A.1. Previous Work

The temporal dynamics of the phyto- and zooplankton of Southampton Water have been well studied, *e.g.* Antai (1989, bacterioplankton and microflagellates), Conover (1957, *Acartia* succession), Crawford *et al.* (1985, *Mesodinium* blooms), Dunn (1987, phytoplankton distributions), Hirst (1996, zooplankton production), Iriarte, (1991) and Iriarte & Purdie (1994, picophytoplankton), Kifle (1992, primary production), Kifle & Purdie (1993, *Mesodinium* blooms), Lucas (1993), Lucas & Williams (1994, 1995, gelatinous predators), Raymont & Carrie, (1964, zooplankton production), Savage (1965, phytoplankton), De Souza-Lima & Williams (1978, oxygen consumption), Williams (1980, phytoplankton), Zinger (1989; zooplankton community structure). To summarise, a single phytoplankton bloom of varying length occurs in late spring / early summer, with chlorophyll *a* values ranging from 1-2 $\mu g.l^{-1}$ in winter to 10-20 $\mu g.l^{-1}$ in summer, and up to 100-150 $\mu g.l^{-1}$ during *Mesodinium* blooms in June/July. The phytoplankton species succession varies according to site but generally is diatom-dominated in winter-spring and dinoflagellate-dominated in the summer (esp. by *Mesodinium*). Towards Calshot the bloom is dominated by the diatoms *Schroederella delicatula* and *Thalassiosira* sp. (in June; chlorophyll *a* values can reach 7.5 $\mu g.l^{-1}$), and *Chaetoceros* sp. (August; Kifle, 1992). Zooplankton is dominated by calanoid copepods: particularly *Acartia* spp., but also *Centropages hamatus, Paracalanus parvus, Pseudocalanus elongatus* and *Temora longicornis.* Towards Calshot, barnacle nauplii, gastropod eggs and larvae, *Oikopleura* spp., and *Pleurobrachia pileus* have been found to be more abundant.

The zooplanktonic population dynamics of the Solent and its outer approaches have been much less well covered, with the only published study to date, that of Castro-Longoria (1998; 'CL98' hereafter), which describes the seasonal dynamics of the main mesozooplanktonic taxa, from April 1995 to April 1996 (for the Solent). The survey area included several stations in Southampton Water, and stations in the West Solent, Calshot, and in the East Solent off Gosport and Portsmouth (close to the 'Sturbridge' station - *c.f.* results section). The main results are:

- In the Solent, the mesozooplankton community is dominated by calanoid copepods: *Acartia* spp., *C. hamatus*, *Paracalanus parvus*, *Pseudocalanus elongatus* and *T. longicornis*. Other important taxa include barnacle nauplii, *Oikopleura* sp., chaetognaths, larvae of gastropods, *Pisidia longicornis*, and bryozoan larvae.
- Clear differences were found between Southampton Water and the Solent, in terms of the relative abundances of species. Southampton Water is estuarine in essence, and this is reflected in the abundance of species such as *Acartia tonsa, A. margalefi,* ascidian larvae, *Eurytemora affinis,* the mysid *Mesopodopsis slabberi*, and *Oithona nana.* Greater Solent abundances were found for total meroplankton, the calanoids *Anomalocera patersoni, C. hamatus, Isias clavipes, Labidocera wollastoni, Paracalanus parvus, Parapontella brevicornis, Pseudocalanus elongatus, T. longicornis,* the harpacticoids *Stephos minor, S. scotti,* and larvae of cirripedes (nauplii), bryozoans, decapods, and gastropods.
- Differences in abundances between the East and West Solent were found despite the apparent absence of hydrographic gradients, for example *Oikopleura* sp. and *Euterpina acutifrons,* more abundant in the West Solent.
- A double peak in abundance was observed, corresponding to increases in different species. The first peak occurred in April-May (max. 12000 ind.m^{-3} near Calshot, 14000 ind.m^{-3} in the Solent), with calanoids in general and *Acartia* spp. in particular as important components. After a decrease to ~400 ind.m^{-3} in June, numbers rose up too 1000-2000 ind.m^{-3} in early autumn. Most species followed this pattern but had one peak which dominated clearly. 'spring' species were *e.g. Pseudocalanus elongatus, T. longicornis, E. affinis, Calanus helgolandicus,* barnacle nauplii and *Oikopleura* sp. 'August-September' species were *e.g. C. hamatus, P. parvus, P. brevicornis.* Some taxa peaked in July, such as *Euterpina acutifrons,* decapod and gastropod larvae, and *Oithona nana.* These patterns can be linked to increases in temperature, and chlorophyll *a* levels which also peaked in May, and, for meroplanktonic taxa, to spawning events. The absence of a second zooplankton peak in late summer but not of phytoplankton can be seen as an indication of high grazing rates.

4.A.2. Aims & Strategy

A detailed description of the spatio-temporal dynamics of the mesozooplanktonic communities of the study area has not previously been carried out. This chapter presents the results of a series of four cruises conducted in June-August 1995, and, specifically, two hypotheses will be addressed concerning the spatial and temporal changes in community composition over the period of investigation:

1. The holo- and mero-planktonic sub-compartments of the mesozooplanktonic community display different spatio-temporal patterns and dynamics.
2. These differences can be related to the different constraints that act upon the two sub-compartments; *i.e.* distance from adult populations and transport processes for meroplankton, and more direct hydrographic factors for holoplankton.

The following methods of data analysis were applied:

1. Expressing global trends of the data with univariate measures.
2. Extracting the underlying structure of the community using ordination.
3. Dividing stations and taxa into groups, and placing these into a spatial context, using cluster analysis.
4. Assessing the contribution of individual taxa to these groups, using analysis of variance tests.
5. Determining the role of holo-and meroplankton sub-components in producing these patterns, by similar analyses (ordination and clustering).
6. Assessing the role of environmental factors, using a constrained ordination method.

4.B. Methods

4.B.1. Sampling

The general sampling strategy has been described in chapter 1. For plankton, cruise 1 (07-09/06/95) was considered a pilot survey, and although plankton samples were taken, a smaller net was used. Comparisons with identical tows with the WP-2 nets used subsequently showed major qualitative differences in net efficiencies and it was decided not to use the samples quantitatively.

Whereas 3 transverse stations were sampled for physical oceanographic data at East Ryde and Sturbridge, only central ones were sampled for plankton (table A.2.2; see also figures 2.4, and 2.5 for station positions). No zooplankton samples were taken in the West Solent.

At each station a 200 µm WP-2 net of 0.25 m^2 aperture was deployed (UNESCO, 1968), fitted with a TSK (Tsurumi-Seiko Kosakusho) flowmeter. A horizontal tow at 3 m depth was chosen over a vertical tow as most appropriate, given practical limitations: shallowness of many sampling stations, size of nets and the configuration of the research vessels. A well-mixed water column was assumed *a priori,* given previous work in the Solent (*e.g.* Phillips, 1980), and the strength of currents relative to depth and freshwater input in most areas. All samples were taken by day. The depth of sampling was ensured by weighing down the net at its mouth with led weights, and attaching it to a floating surface buoy *via* a chain. Tows lasted 5 minutes, at a speed of ~1 knot, after which samples were transferred to 1 litre plastic containers and fixed immediately in ~5% buffered formalin solution. These were then filtered down in the lab, and placed in 300 ml plastic jars in 5% buffered formalin solution for preservation.

In the laboratory, stations were sub-sampled using a Folsom plankton splitter (Van Guelpen *et al.*, 1982), until a manageable amount of plankton was obtained, and the whole subsample was counted: on average this represented about 20% of the total sample for cruise 2, 40% for cruise 3, 7% for cruise 4 and 4% for cruise 5. This represents subsamples of 20, 38, 5 and 3 m^3, out of averages of respectively (± standard errors) 105±5.0, 93±1.9, 75±4.2 and 77±3.0 m^3 total sample volumes. On average 4766 individuals were counted and identified per sample (121 samples in total), to the lowest practical taxonomic unit, under a binocular microscope and using a Bogorov chamber. Results were arranged in a stations × taxa matrix.

4.B.2. Diversity Indices

From the data obtained two indices of diversity were calculated. The Shannon-Weaver diversity index was calculated as:

$$H' = -\sum^{s} p_i \ln p_i$$

Where s is the number of taxa and p_i the proportion of individuals belong to taxa i. H' takes into account both the number of taxa and the distribution of individuals across taxa. The equitability index J' was calculated for each sample as:

$$J' = \frac{H'}{\log(\mathit{number\ of\ species})}$$

and is a measure of the equitability of the distribution of individuals across taxa.

4.B.3. Correspondence Analysis (CA)

For multi-station/species analyses, marine ecologists in this country usually follow a school of thought that uses preferably either Factor Analysis in the form of Principal Component Analysis (PCA), or Multi-Dimensional Scaling (MDS). Terrestrial (particularly plant) ecologists and workers in other countries, mainly continental Europe, often use Correspondence Analysis (CA). PCA, MDS and CA rely on different underlying models of species distributions ("response models") and therefore have different uses (Jongman *et al.*, 1995). PCA assumes a linear response and therefore is best suited for classifying, *e.g.* sites according to their 'environmental variables composition'. CA on the other hand, assumes a unimodal response, which makes it suitable for analysing multispecies data, each having presumably a unimodal response to underlying environmental factors.

CA originated independently in several countries, mainly through the work of Benzecri (1973), Hirschfeld (1935) and Fisher (1940) (Manly, 1994). Its first application to ecological work was done under the name 'Weighted Averaging' by Whittaker (1967). This multiplicity of approaches is reflected in the variety of algorithms and indeed names for the technique (*e.g.* Contingency Table Analysis, RQ-Technique, Optimal Scaling, Dual Scaling, Reciprocal Averaging, Optimal Scoring, Quantification Method, Homogeneity Analysis. In French-speaking countries it is known as Analyse Factorielle des Correspondances, and is sometimes translated as 'Factorial Correspondence Analysis', or 'FCA'). This method of ordination was chosen for this work.

CA is an exploratory tool inasmuch as it has no statistical significance associated with it; as such it is strictly an ordination method. Stations and samples are placed in the same ordination space, and in other words CA answers the question: "What is the optimal ordination such that stations can be characterised by their faunistic composition and taxa can be characterised by their distributions across stations?" It seeks the correspondence between groups of stations and species, or how groups of one can be characterised by groups of the other. Algorithmically there are two ways of answering this, one by iteration ('Reciprocal Averaging') and the other by matrix algebra, by extraction of the eigenvalues and associated eigenvectors of a distance matrix, similarly to PCA (*e.g.* Jongman *et al.*, 1995; Legendre & Legendre, 1998). Both find a unique (identical), optimal solution for a given data set, and are objective, inasmuch as they are independent of any *a priori* classification of taxa or stations, although of course still relying on the underlying 'unimodal response' model, unlike (*e.g.*) MDS. The computation for CA can be found in *e.g.* Legendre & Legendre (1998), and involves in its matrix form a classical eigenanalysis, but using the Pearson χ^2 distance between expected and observed frequencies of the station × taxa matrix (there is therefore no distinction between Q- or R-modes of analysis). This distance is relatively insensitive to absolute abundances, but will pick up the distribution of variance across rows and columns. It also ignores double-negatives. The contribution of a point (station or taxa) to total χ^2 of the data set is its mass. The proportion of total inertia explained by a point is its relative inertia; its correlation with a dimension is the quality of the representation of that point for a given ordination (also termed 'cosine^2').

CAs were computed with the STATISTICA package (StatSoft, inc.) and checked for consistency with the CANOCO program (Ter Braak, 1988). To remove the effect of rare taxa, for each cruise, only those which occurred in over 1% abundance at any given station were kept for the analysis (*n.b.*: these occurred also in over 5% of stations). Because zooplankton samples are often distributed log-normally, the CAs were performed on the $\log_{10}(x+1)$ abundances (Cassie, 1968). The number of dimensions used in the CA was chosen using the 'scree test' (Catell, 1966), by looking for a break in the curve of decreasing eigenvalues. Where no clear break was present, or in cases where overall quality values were inappropriately low, species or stations with the greatest absolute inertia were sequentially removed until a satisfactory solution was obtained. They were then added as supplementary points in the analysis. Although they do not contribute to χ^2, quality values for a given representation (their correlation with the CA dimensions) can still be computed, and these supplementary points can be displayed in the ordination plots.

4.B.4. Clustering

Modifying a method followed by several authors, *e.g.* Bachelet & Dauvin (1993), stations and species were grouped using a hierarchical agglomerative cluster analysis on the CA coordinates in the first few dimensions of the CA. The number of dimensions was chosen so as to explain 90% of the variance (usually 5-7 axes). This includes the information of several axes in the final groupings, with the potential disadvantage of including more 'noise' than with fewer axes, however preliminary tests showed that increasing the number of dimensions made little difference to the outcome of the analysis. Stations and taxa were clustered simultaneously, rather than separately as in PCA or other types of factor analysis, where R-mode or Q-mode algorithms differ. This is unlike the usual method of separating stations and taxa in the cluster analysis following an ordination, and thus does not apprehend 'faunistic groupings' explicitly: the analysis is aimed directly at extracting the correspondence between stations and taxa as found through the CA. This has the advantage of resulting in a one-to-one correspondence between station and faunistic groups and represents them as they occur in the ordination space. To this end the Euclidean distance was used in the cluster analysis, and the standardisation in the CA was such that row coordinates were computed based on the row profiles, and *vice-versa*: distances between rows or columns in the CA can therefore be interpreted directly[1]. After preliminary tests the complete linkage agglomeration rule was chosen (Manly, 1994).

4.B.5. Multivariate Analyse of Variance and the post-hoc Studentised Newman-Keuls Test.

To assess statistically how groups differ in terms of the distribution of taxa abundances within and between them, a Multivariate Analysis of Variance (MANOVA) was performed on the abundances per taxa, within station and taxa groups. Thus the differences in abundance are compared between station groupings, for each taxa group. This is analogous to the method used by Grioche *et al.* (1999), with two important differences:

1. The analysis is not used to 'discover' which taxa group correspond to which station groups, since this is already given by the CA/clustering method.
2. Station groupings are compared between each other, for each taxa group as a whole and for each taxon within these groups.

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[1] In fact, with this standardisation, the squared Euclidean distance between points in the CA dimensions approximates a weighted χ^2 distance (Hoffman and Franke, 1986); *n.b.:* station points cannot be compared with taxa points.

MANOVA allows each taxon to be compared across groups with individual *F* tests, in addition to an overall comparison between groups, so the contribution of each taxon to the overall statistic can be analysed. Specifically, MANOVA tests the effect of a treatment (in this case station groupings) on several dependent variables (taxa abundances) concurrently. The logic and nature are the same the univariate ANOVA, but the covariance between dependent variables is taken into account in the final statistic (Wilk's Lambda, analogous to the *F* statistic). Following a significant probability of detecting differences in abundance between station groups, at the chosen α-level, individual *F* tests for each taxa are looked at; although they carry a P-value, they are not interpreted as carrying a significance, but rather as a share of the contribution to the multivariate statistic (Green & Vascotto, 1978; see also Green *et al.*, 1993). The Newman-Keuls test (also called the Student, or Studentised, Newman-Keuls test, SNK) is then applied between groups, to identify which taxon contributes the most to the *F* statistic (Grioche *et al.*, 1999).

Basing the comparisons between groups on taxa which were used to determine these groups in the first place violates the assumption of independence, *i.e.* the independent variable is not truly independent, and therefore the significance testing is biased towards rejecting H_0 (=finding differences between groups). Thus results of the MANOVA, *F* and SNK tests do not represent unbiased probabilities. The purpose however is to detect *which* taxa contribute to these differences once they have been established by CA and clustering, and ANOVA is generally robust to such violations. Furthermore, to reduce the effect of departures from normality, abundances were first $\log_{10}(x+1)$ transformed (Cassie, 1968).

4.B.6. Canonical Correspondence Analysis (CCA)

Canonical Correspondence Analysis (CCA) was used to relate patterns of faunistic composition and distribution to environmental variables. CCA is a method of restricting the CA axes to be linear combinations of environmental variables. The algorithm used is similar to CA: for a given dimension each iteration calculates alternatively the site scores given the species scores, and the species scores given the site scores. It includes at each iteration a weighted multiple regression of the site scores on the environmental variables, using the station totals as weights. The station scores used in the next step are the fitted values of the regression at the previous step (here R- and Q- modes differ). Thus CCA is a constrained form of CA, and the ratio of the CA inertia to that of the CCA is the proportion of variance in the data set explained by the environmental variables chosen. The final regression coefficients are called canonical coefficients, which define the axes of the CCA, and the final multiple correlation coefficient is the species-environment correlation, which is a measure of the fit between the axes of the ordination and the environmental variables (Ter Braak, 1986; Jongman *et al.*, 1995). The resulting scores can then be plotted in an ordination diagram.

As for CAs, analyses were done on $\log_{10}(x+1)$ abundances to normalise the data, and the environmental variables were first standardised to equal mean and variance 1, so as to minimise the effect of using different units. The number of environmental variables used in the analyses were chosen using the forward selection method of CANOCO (Ter Braak, 1988), which tests the significance of the additional variance explained by an environmental variable, based on a Monte Carlo permutation distribution. Here a critical α of 0.05 was chosen and 9999 permutations were performed each time. After calculating the CCA ordinations, environmental variables can be displayed as arrows placed on the ordination diagram, with their origin at the centroid (Ter Braak, 1988). The length of the arrow is related to the canonical coefficient and can be interpreted as the rate of change of species composition along that environmental variable. The projection of the tip of the arrow on a given dimension is relative to the correlation between the variable and the specific dimension. The perpendicular projection of species points on the axes of the arrows represents the 'centre of gravity', or optimum, of that species along the environmental gradient. The ordination and environmental variables axes are not proportional, so only the relative lengths and directions of the arrows are relevant.

4.C. Results

4.C.1. General & Taxa Identified

The stations sampled for plankton can be seen in figures 2.5 and 2.6 (Chapter 2) in conjunction with tables A.2.1 and A.2.2 (Appendix A). Over the sampling period, 47 taxa were counted and identified (for each cruise: 41, 39, 41, 44 respectively). When there was uncertainty as to their identification, certain taxa were amalgamated together in the final counts; as a rule, intra-cruise resolution was maximised at the expense of between-cruise comparisons.

Calanoids copepods were separated into *Acartia* spp., *Calanus helgolandicus, Centropages hamatus,* copepod nauplii, *Eurytemora affinis, Isias clavipes, Labidocera wollastoni, Para/Pseudocalanus* spp., *Parapontella brevicornis, Temora longicornis,* and 'unidentified copepods' (mainly copepodite stages). For *Acartia* congeners, CL98 reports the presence of *Acartia bifilosa* (see also Hirst & Castro-Longoria, 1998), *A. margalefi* (Castro-Longoria & Williams, 1996), *A. discaudata, A. clausi* and *A. tonsa,* in the Solent-Southampton Water area. According to CL98, *A. margalefi, A. tonsa* and *A. bifilosa* show low numbers beyond Southampton Water after April. *A. discaudata* was present in the Solent in July (438 ind.m^{-3} at 10 m depth) and August (280 ind.m^{-3}); *A. clausi* in June (5 ind.m^{-3}), July (74 ind.m^{-3}), and August (229 ind.m^{-3}).

The *Para/Pseudocalanus* spp. counts include *Paracalanus parvus* and *Pseudocalanus elongatus*, the second of which occurred in small numbers and mainly at copepodite stages. The harpacticoid *Euterpina acutifrons* was counted separately, as was the cyclopoid *Oithona nana*. Other copepods were separated into Monstrilloidae (very few individuals) and other harpacticoid and cyclopoid copepods, which include a small number of the latter and were amalgamated as 'other harpacticoids'. Other crustacean groups are: amphipoda, barnacle cyprids, barnacle nauplii, cumaceans, insecta (sea mites and *Anurida* sp. (?)), isopoda, mysidacea and ostracoda. For cruises 2, 4 and 5, The group 'decapod larvae' does not include caridean larvae and decapod megalopae, which were.

Bivalve larvae were not speciated and probably represent several species, with probably an important proportion of *Ostrea/Crassostrea* spp. Gastropods were separated into four morphotypes, which represent distinct taxa at least at the generic level: *Littorina* spp. larvae, 'gastropods 1', identified by Prof. P. Bouchet (Muséum National d'Histoire Naturelle, Paris) as larvae of *Crepidula fornicata*; and 'gastropods 2' and 'gastropods 3', unidentified but distinct. Gastropods 2 were amalgamated with *Crepidula* larvae in cruise 3.

Polychaetes were separated into the holoplanktonic Syllidae, and meroplanktonic taxa: spionid larvae, *Lanice conchilega* larvae, 'other polychaete larvae' and 'polychaete post-larvae', most of which are probably Nephtyidae metatrochophore larvae. *Nephtys* spp. eggs (identified by E. Castro-Longoria, Southampton Oceanography Centre) were also counted when they occurred in cruises 4 and 5.

Other groups were: ascidian larvae, bryozoan (cyphonaute) larvae, identified as *Membranipora membranicea* by Prof. J.-L. D'Hondt (Muséum National d'Histoire Naturelle, Paris), unidentified echinoderm larvae (all ophiopluteid larvae), fish eggs and fish larvae, medusae (= hydromedusae), *Oikopleura* sp. (probably *O. dioica*), Pycnogonida, and *Sagitta* sp. Both *Sagitta setosa* and *Sagitta elegans* occur in the English Channel, but within Southampton Water Lucas (1993) reports only *Sagitta setosa* during 1989-1991.

4.C.2. Univariate Measures

Table 4.1 displays the basic statistics of planktonic abundance and diversity for each cruise. The spatial distributions of total abundances are displayed in figure 4.1. For reference, the spatial distributions of certain taxa are displayed in figure A.4.1 to A.4.4.

4.C.2.a. *Numerical Abundance*

Cruises 2 and 3 can be clearly separated from cruises 4 and 5 both in terms of overall numbers and the spatial distribution of densities: For the former (June) cruises, abundances are ~350 ind.m^{-3} (table 4.1), compared with average numbers of ~1700 and ~2900 ind.m^{-3} per station in July and August. This still represents an average difference of 1200 ind.m^{-3} between the latter two, but the differences between cruises 2 and 3 and between 4 and 5 are not statistically significant at $\alpha = 0.05$, though the high intra-cruise variance may influence this result. In June, high densities are found to the SE, and to some extent in the East Solent. The latter are due mainly to meroplanktonic taxa, particularly decapod and *Crepidula* larvae in cruise 2 (East Ryde, Sturbridge, stations 1 and 2), and barnacle nauplii and *Crepidula* larvae in cruise 3 (Calshot, East Ryde, and station 1). Those to the SE can be linked to high numbers of holoplanktonic taxa such as *Acartia* spp., *T. longicornis*, *C. hamatus*, but also caridean larvae and other decapod larvae, and decapod megalopae in cruise 2; and in cruise 3 those same taxa plus *Oikopleura* sp., *Para/Pseudocalanus* spp., and *E. acutifrons*.

		Cruise 2 (14-15/06/1995)		Cruise 3 (21-22/06/1995)		Cruise 4 (26-27/07/1995)		Cruise 5 (24-25/08/1995)	
Number of stations		31		33		25		32	
Specific Richness		**30.4**	*0.53*	**27.2**	*0.46*	**27.3**	*0.56*	**30.3**	*0.41*
Min. - max. number of taxa per station		22	35	23	34	22	33	26	35
H'* *(diversity index)		**2.24**	*0.054*	**2.09**	*0.067*	**2.04**	*0.050*	**2.04**	*0.036*
J'* *(equitability index)		**1.51**	*0.036*	**1.46**	*0.046*	**1.43**	*0.035*	**1.38**	*0.024*
n.m^{-3}/taxa		**10.4**	*2.05*	**14.3**	*2.55*	**62.5**	*8.11*	**95.6**	*8.35*
Total n.m^{-3}		**322.0**	*64.90*	**389.2**	*118.43*	**1861.28**	*361.37*	**2894.1**	*186.50*
of which:	Holoplankton	**175.7**	*53.91*	**300.7**	*113.28*	**1343.2**	*262.60*	**2413.3**	*156.88*
	Meroplankton	**146.3**	*24.15*	**88.5**	*22.51*	**518.0**	*108.82*	**480.8**	*56.97*

Table 4.1: Summary statistics for cruises 2-5 (**averages** and *standard errors*): Number of stations sampled; Specific richness; min. and max. number of taxa; *H'*; *J'*; density of individuals per species; total density (ind.m^{-3}).

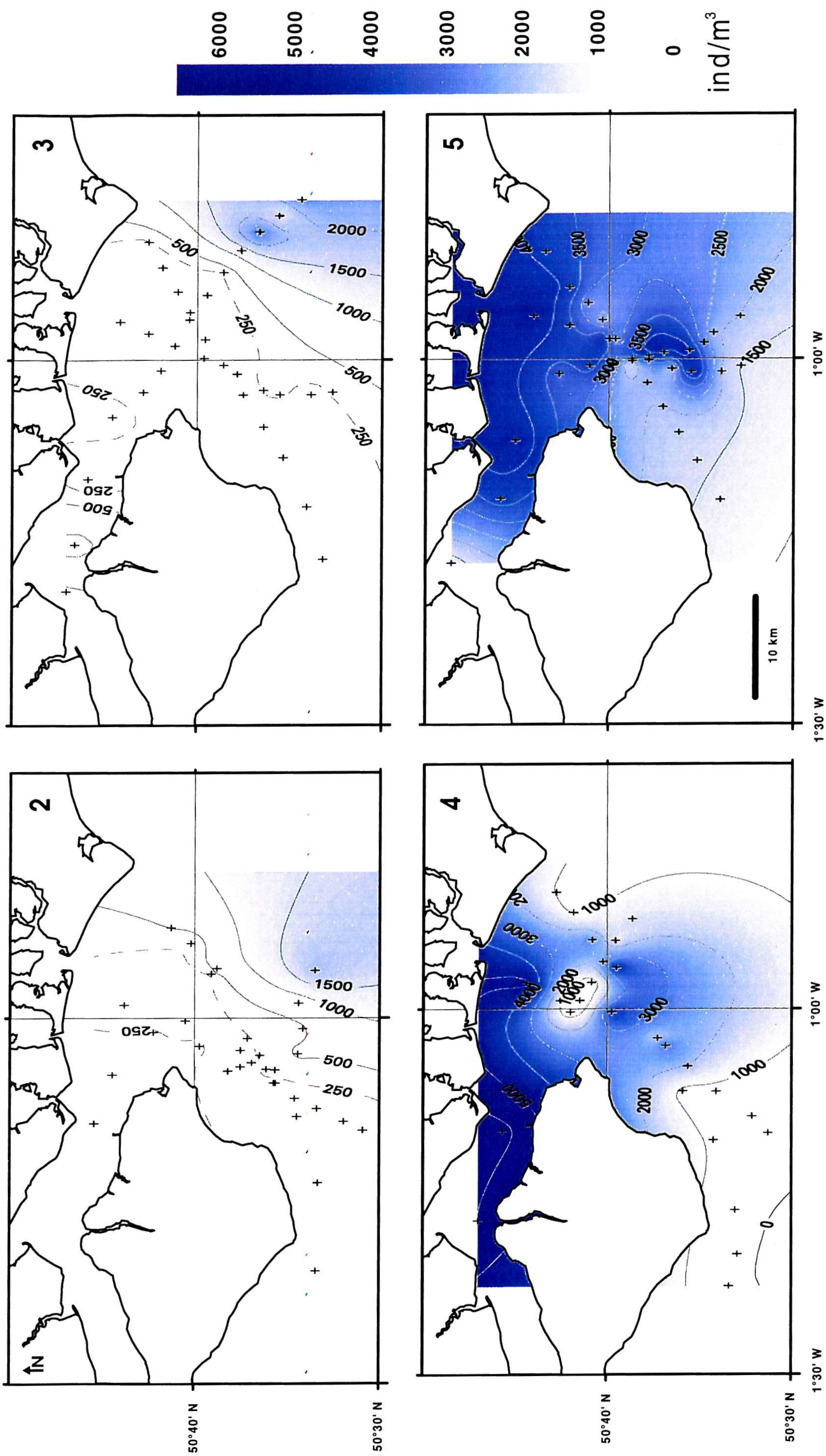


Figure 4.1: Density distribution of mesozooplankton for cruises 2-5 (ind.m^{-3}).

In July and August, higher densities are found close to shore, down to Sandown Bay, and towards Selsey Bill; densities decrease further out down to around 200 ind.m^{-3}. There is also a small patch of low densities around stations 2, 3 and 4 in cruise 4 (140 to 440 ind.m^{-3}), untypical of the surrounding stations, and with relatively low numbers of *T. longicornis, Acartia* spp. and *Oikopleura* sp.

These patterns of density distributions are reflected in the correlation between total mesozooplankton density and temperature (table A.2.3): a negative correlation in June (though not significant in cruise 2), positive in July and August. There is also a positive correlation with fluorescence in June, and with salinity in cruises 2 and 5. These significance levels should be treated with caution as the influence of autocorrelation was not assessed (Sokal & Rohlf, 1995).

Distinguishing more specifically between holo- and meroplankton (figure 4.2), the break in abundances between June and July-August is seen in both. For meroplankton average abundances decrease between cruises 2 and 3, from 146 to 88 ind.m^{-3}, and between cruises 4 and 5, from 518 to 480 ind.m^{-3} (neither are significant at $\alpha = 0.05$). The meroplankton is in higher numbers close to shore in all 4 cruises (the higher numbers to the East in cruise 2 are due to the extrapolation of very high densities of *Crepidula* larvae in stations 19-21). Holoplankton follows the bimodal distribution apparent in the total density distributions of figure 4.1, and higher numbers in the Solent are principally from *Acartia* spp. individuals. Higher meroplankton values are principally due to the following taxa, detailed in order of decreasing average numerical abundances (numbers are **maxima** per cruise):

- Cruise 2: *Crepidula* larvae (478 ind.m^{-3}, station 19); decapod larvae (114 ind.m^{-3}, East Ryde).
- Cruise 3: barnacle nauplii (476 ind.m^{-3}, East Ryde); *Crepidula* larvae (118 ind.m^{-3} st. 21)
- Cruise 4: *Crepidula* larvae (1555 ind.m^{-3}, st. 22); decapod larvae (248 ind.m^{-3}, st. 8); barnacle nauplii (806 ind.m^{-3}, Calshot).
- Cruise 5 *Crepidula* larvae (1104 ind.m^{-3}, st. 22), 'gastropods 2' (497, ind.m^{-3}, st. 2); barnacle nauplii (605, ind.m^{-3}, Calshot).

Out of all taxa, 4 have their maxima in cruise 2 (*Littorina* spp. larvae, *Eurytemora affinis,* fish larvae and amphipods) and 5 in cruise 3 (ascidian larvae, *C. helgolandicus*, echinoderm larvae, isopods, and pycnogonids). 11 show a maximum in July (*e.g. T. longicornis*, caridean and other decapod larvae, isopods, *Crepidula* larvae and

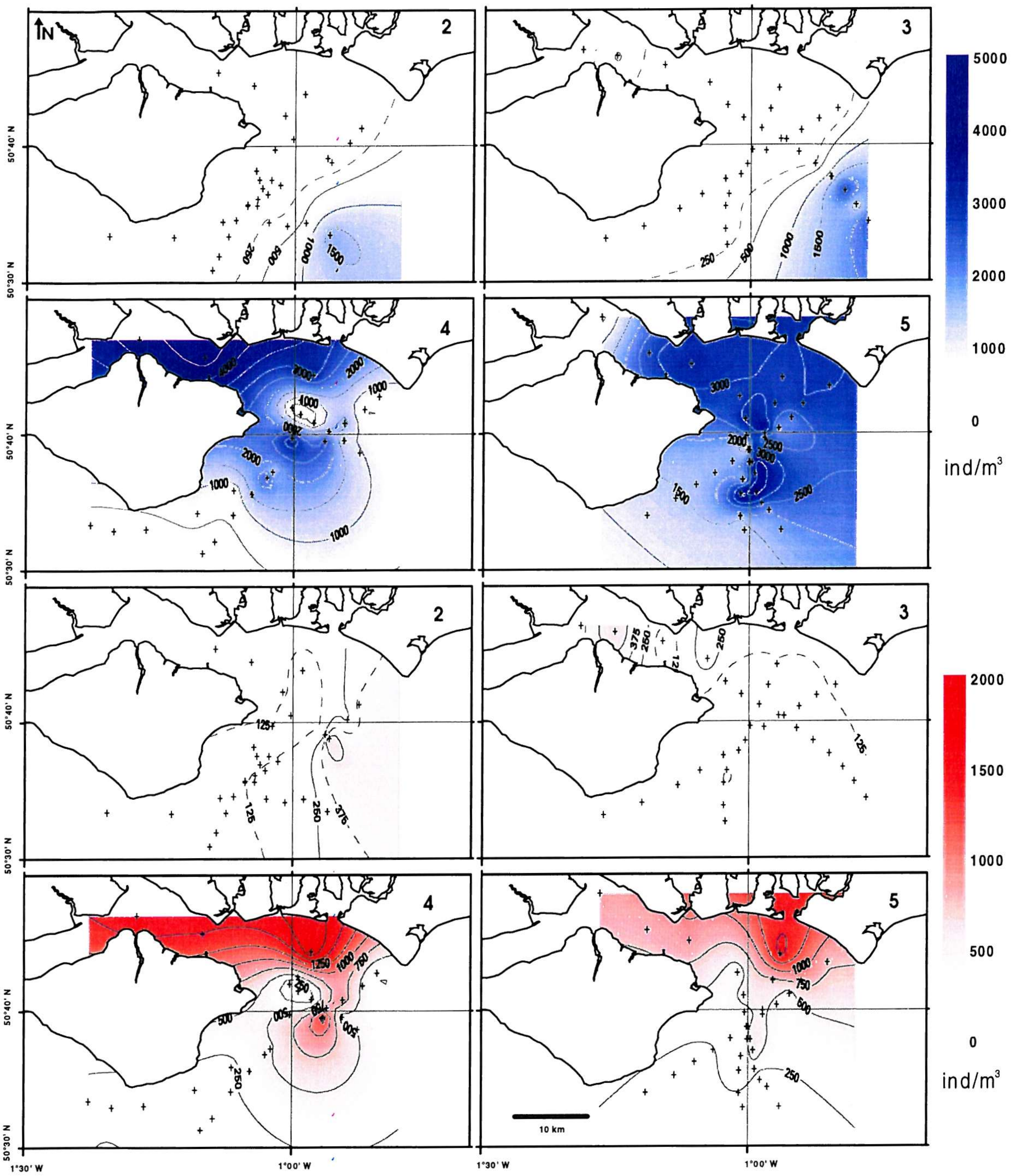


Figure 4.2: Density distribution of holoplankton (top) and meroplankton (bottom) (ind.m^{-3}).

harpacticoids), and 26 in August (*e.g. Acartia* spp., barnacle nauplii, bryozoan larvae, *C. hamatus*, *Oikopleura* sp. and others). During some cruises there are also marked increases in particular taxa: amphipods, fish larvae and *Littorina* spp. larvae for cruise 2; fish eggs for cruise 3; *T. longicornis*, *P. brevicornis*, *C. hamatus*, *Oikopleura* sp., *E. acutifrons* and *Acartia* spp. for cruise 4; and 'gastropods 3', *Sagitta* sp., *Para/Pseudocalanus* spp., *I. clavipes*, *O. nana*, bivalve larvae and *L. wollastoni* for cruise 5. At this scale of observation, there is no preponderance of the meroplankton amongst these, as could be expected from a 'pulsed' recruitment cycle.

Despite the major changes in abundance and distribution of mesozooplankton observed, the diversity of the community is stable: the number of taxa, *H'* and *J'* remain around 30, 2.0-2.2 and 1.5-1.4 respectively, throughout the season. The variance of these statistics within cruises is low, especially in cruise 5, and one-way ANOVA detects a significant decrease in *H'* (not *J'*) between cruises ($F_{3,118} = 3.18$, P<0.05). This is mainly due to the higher *H'* of cruise 2 (SNK *post-hoc* test, P<0.05). Thus the major changes in abundances are not accompanied by a corresponding shift in dominance.

Cruises 4 and 5 see an increase in diversity from coastal to Channel waters (not shown), associated with a significant negative correlation between density and *H'* (For cruise 4: *r*=-0.8; n= 25; P <0.01; cruise 5: *r*=-0.5; n=32; P< 0.01; significance values are only indicative of a trend, since abundance and *H'* are not strictly independent). No suggestion of such a pattern or significance is found for cruises 2 and 3.

4.C.2.b. *Numerical Dominance*

For all dates there is a slightly greater diversity of types in the meroplankton compared with the holoplankton (figure 4.3, by about 5%). This, together with the overall number of meroplanktonic taxa counted, remains at similar levels throughout the sampling period. The holoplankton is consistently numerically dominant, though by a small margin in June. The proportion goes up to ~73% in July, ending at over 83% of total numbers in cruise 5. For each cruise calanoid copepods represent 77, 87, 66 and 68 % of total holoplankton numbers, and thus the proportion of taxa such as *Oikopleura* sp., *Sagitta* sp., *O. nana*, fish eggs or *E. acutifrons* (and others) increase slightly in July/August.

The spatial distribution of meroplankton dominance (figure 4.4) is stable, though this is somewhat masked by the smaller proportions encountered in the later surveys. In all cruises greater proportions occur within the East Solent, across eastwards to Selsey Bill, with a decreasing seaward gradient. Already in cruise 3 the extent of the larval dominance

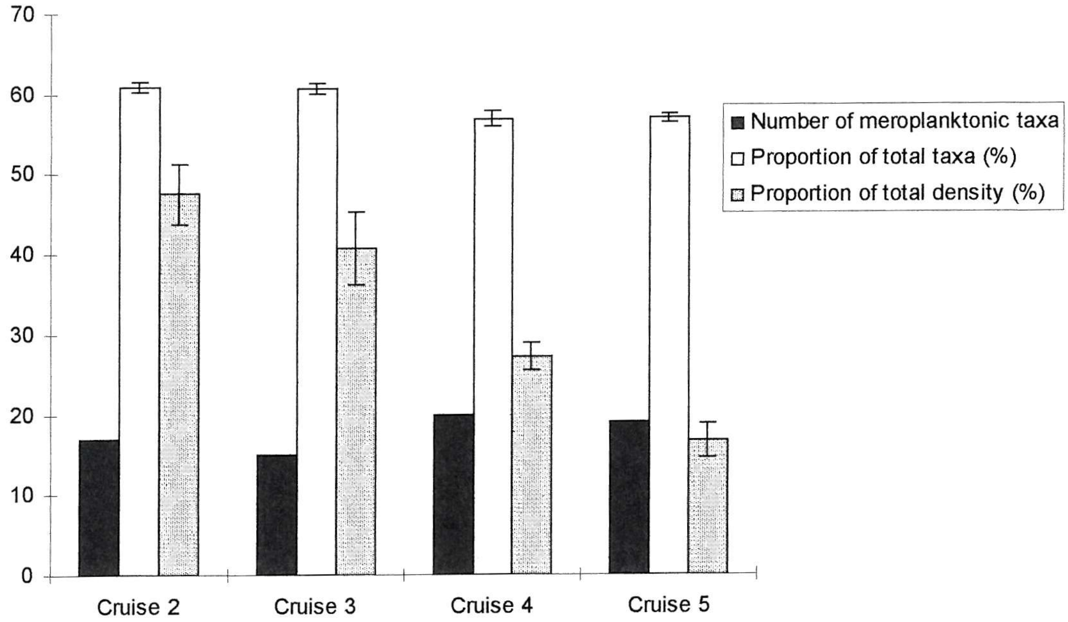


Figure 4.3: Number of meroplanktonic taxa, proportion of total taxa (%) and proportion of total abundance for cruises 2-5. Error bars are standard errors of the means.

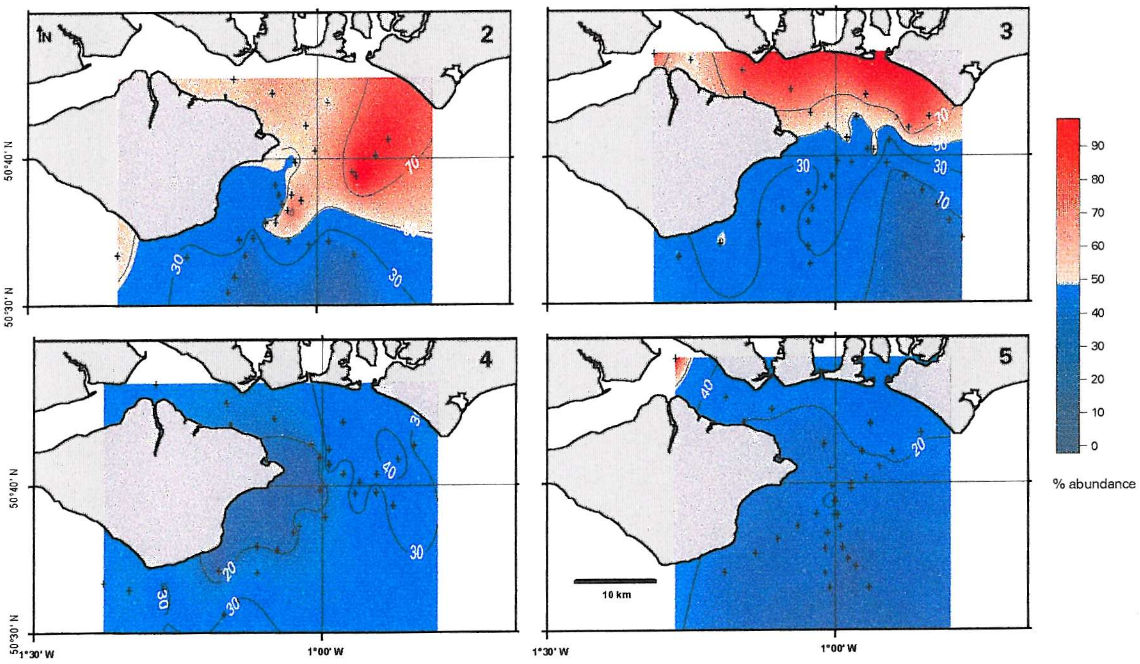


Figure 4.4: Proportion of meroplankton density to total density (%) for cruises 2-5.

patch is reduced compared with cruise 2, following the substantial increase in other taxa and the small decrease in meroplankton numbers.

The proportions of dominant species for each cruise are represented in figure 4.5. These occur in abundances greater than 1% of the total number of individuals (they all also occur incidentally in over 5% of stations). The number of taxa presented varies (in order of cruises: 14, 12, 9, 13), but the ratio to total number of taxa identified remains roughly at ~⅓. Calanoid copepod abundance represents 42, 71, 48 and 57% respectively of these subsets, while the proportions for meroplankton is 49, 22, 30 and 18%. The sum of these two figures goes down regularly from ~90% in June to ~80% in July/August, again indicating the rise of other taxa.

The pattern of dominance itself is similar across cruises and taxa can be separated into three groups: one dominant taxon (cruise 2: *Crepidula* larvae; cruise 3: *T. longicornis*; cruise 4: *Acartia* spp.; cruise 5: *Acartia* spp.) which range from 18 % (cruise 4) to 38 % (cruise 5); a group of taxa of intermediate dominance (cruise 2: decapod Larvae, *T. longicornis*, *Acartia* spp., *C. hamatus*; cruise 3: *C. hamatus*, *Acartia* spp.; cruise 4: *Oikopleura* sp., *Crepidula* larvae, *C. hamatus*, *T. longicornis*; cruise 5: *Oikopleura* sp.), and a group of 'rare' taxa.

Of these 32 taxa, seven are present throughout the season: *Acartia* spp., Barnacle nauplii, *C. hamatus*, Fish eggs, *Crepidula* larvae, *Oikopleura* sp. and *T. longicornis*. 'Gastropods 2', *O. nana* and caridean larvae can probably be added to this list though they were not counted in all cruises. None is consistently dominant, though *Acartia* spp., Barnacle nauplii, *C. hamatus* and *Crepidula* larvae are in the first two groups in all cruises. *Acartia* spp., *T. longicornis* and *C. hamatus* tend to dominate in cruises 2 and 3, but these differ in the importance of the meroplanktonic *Crepidula* larvae and Decapod Larvae (cruise 2), and Barnacle nauplii (cruise 3). Cruises 4 and 5 are consistent in having *Acartia* spp., *Oikopleura* sp., *Crepidula* larvae and *C. hamatus* in the four most dominant taxa.

The evolution in time of the abundance of dominant taxa is displayed graphically in figure 4.6. The trend is of a maximum in August for most taxa, though this is not the case for some numerically important taxa such as *T. longicornis*, harpacticoids, *Crepidula* larvae, caridean and other decapod larvae. All however see an increase when June is compared to July-August. Seven holoplanktonic taxa see a constant increase during the sampling period: *Acartia* spp., *C. hamatus*, *Isias clavipes* (in August mainly), *Oikopleura* sp., *P. brevicornis*, and *Sagitta* sp. Of the meroplankton only 'Gastropods 2' and barnacle nauplii do so. Despite the differences underlined between June and July/August, a number

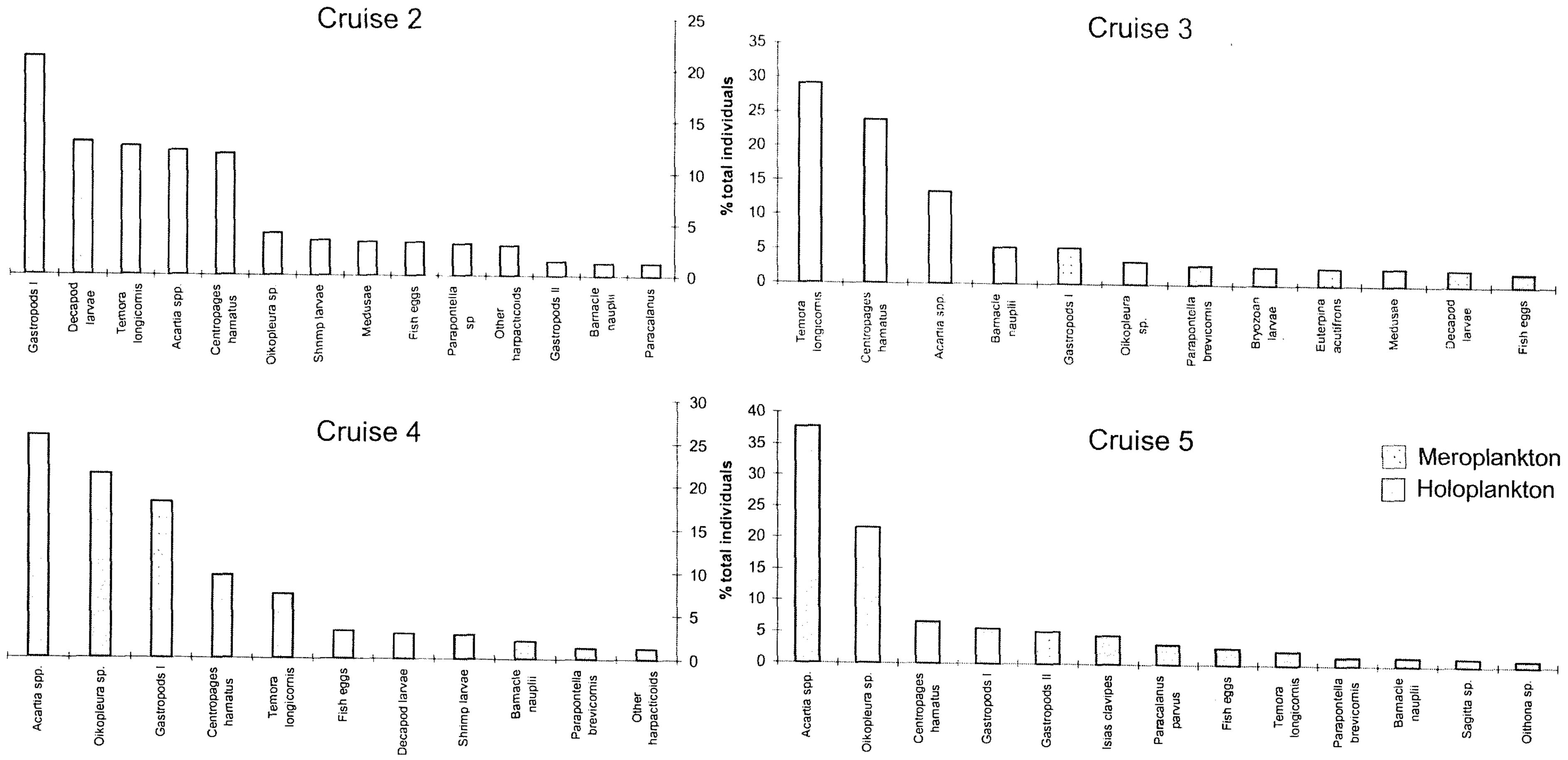


Figure 4.5: Percentage occurrence of dominant taxa (>1% of total abundance), for cruises 2-5.

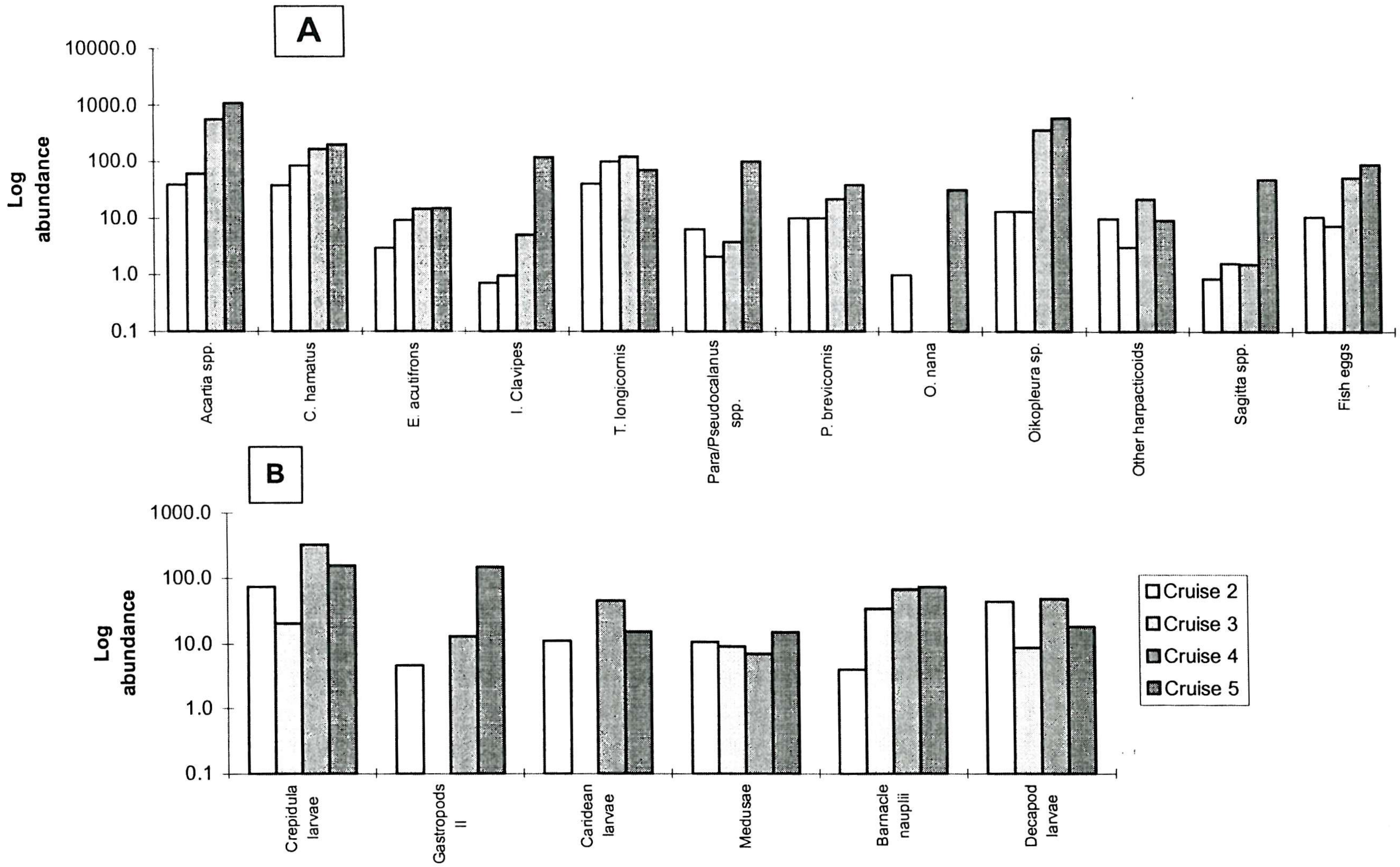


Figure 4.6: Abundance of dominant taxa (>1% overall abundance) for cruises 2-5. A: Holoplankton; B: Meroplankton.

of taxa see an important change between cruises 2 and 3, most notably echinoderm larvae, barnacle nauplii, bryozoan larvae, ascidian larvae, *E. acutifrons*, *T. longicornis* which see important increases in abundances, much larger than their intra-cruise variance (between 300% to 1800%).

4.C.3. Whole Community Analysis

4.C.3.a. *Correspondence Analysis*

A summary of the CA conditions and results for the whole community ('WC' hereafter) analysis can be found in table 4.2. The CA ordination plots are displayed in figures 4.7 to 4.10.

The spread of stations and species over the first two axes of the ordinations is relatively homogeneous for all cruises, indicating an adequate representation of the data. This is partly a consequence of removing major outliers, which otherwise would tend to create one overbearing dimension and group other points towards the centre. It explains the relatively high proportion of total inertia accounted for by the first two dimensions: between 27 % and 50 % for dimension 1, and around 20% (cruises 2, 3, 4) and 13 % (cruise 5) for dimension 2. Five dimensions are necessary to explain satisfactorily the inertia of cruise 3 (table 4.2), whose first two dimensions consequently explain less than 50% of the total. Nevertheless these are high values for CA in ecological studies (see *e.g.* Jongman *et al.*, 1995), and overall the percentage of variance explained by the dimensions extracted varies from 50% (cr. 5) to 77% (cr. 4). This indicates that the community is structured by a relatively low number of factors. The overall quality of the CAs is high with generally over half of all points over 0.5 (*i.e.* $\alpha \leq 45°$).

There is a decrease in overall variance between June and July/August (inertia values are 0.235, 0.301, 0.089 and 0.067 respectively). This is especially noticeable in dimensions 1 and 2 (in the same order: 0.086, 0.081, 0.044 and 0.026 for dim. 1), reflecting, on average, a more homogeneous distribution of abundances between stations in July and August, relatively to the absolute abundance levels. When the average station and taxa contributions to inertia are compared between cruises, a significant difference at $\alpha = 0.001$ is found between June and July/August, but not within these groups ($F_{3,80} = 34.4$ for stations, 12.0 for taxa). This can be interpreted as 1) the differences between cruises are much greater than the differences within (high F ratios), and 2) there is a greater seasonal difference in the distribution of abundances across stations, than across taxa.

Cruise	Stations × taxa	taxa / stations removed from analysis	n. of dimensions; % inertia explained by CA	Main contributors to dimension inertia (and % of inertia)				
2	31 × 24	-	3 66.0%	1 (36.7%)	2 (21.1%)	3 (8.2%)		
				11, 21, 19, 20, 10 Fie, Lit, Gal, Par	**11,** 29, 10 **Par**, Fie, Cal	**29**, 23, 7 **Dem**, Eut, Spi		
3	33 × 24	Lit	5 71.8%	1 (27.0%)	2 (17.1%)	3 (12.4%)	4 (9.6%)	5 (5.6%)
				9, Cal, 8, Stu, 11 **Ban**, Sag, Gal, Tem	**21**, 4, 9, 3 **Cal**, Med, Gal	**16**, 15, 2, 18, 14 **Fie, Oik**	**16**, 21, Stu, 20 **Oth**, Ban	**19**, ER, 22, 2 **Aca**, Fil, Ban
4	26 × 17	Ga2	3 76.7%	1 (49.5%)	2 (20.6%)	3 (6.5%)		
				28, 20, 27, 29, 5(1) **Fie, Bry,** Shr	**Cal**, 21, ER **Ban**, Del	**7**, 19, 12 **Med, Lab**		
5	32 × 23	Ban, Ga3	2 51.1%	1 (38.0%)	2 (13.1%)			
				29, 10, 11, 18, 20, 17 **Fie,** Pop, Ga2	**9**, 1, 29, 20, 21 **Lab**, Biv, Isi			

Table 4.2: Summary of the Correspondence Analyses on the station × taxa matrices for cruises 2 - 5 (**whole community**): taxa and stations excluded from the analyses, number of dimensions included in the CA (as chosen by the Scree test), and main contributors to the inertia of each dimension (>50% when summed). In bold are stations or taxa which contribute over 20% of the inertia of that dimension.

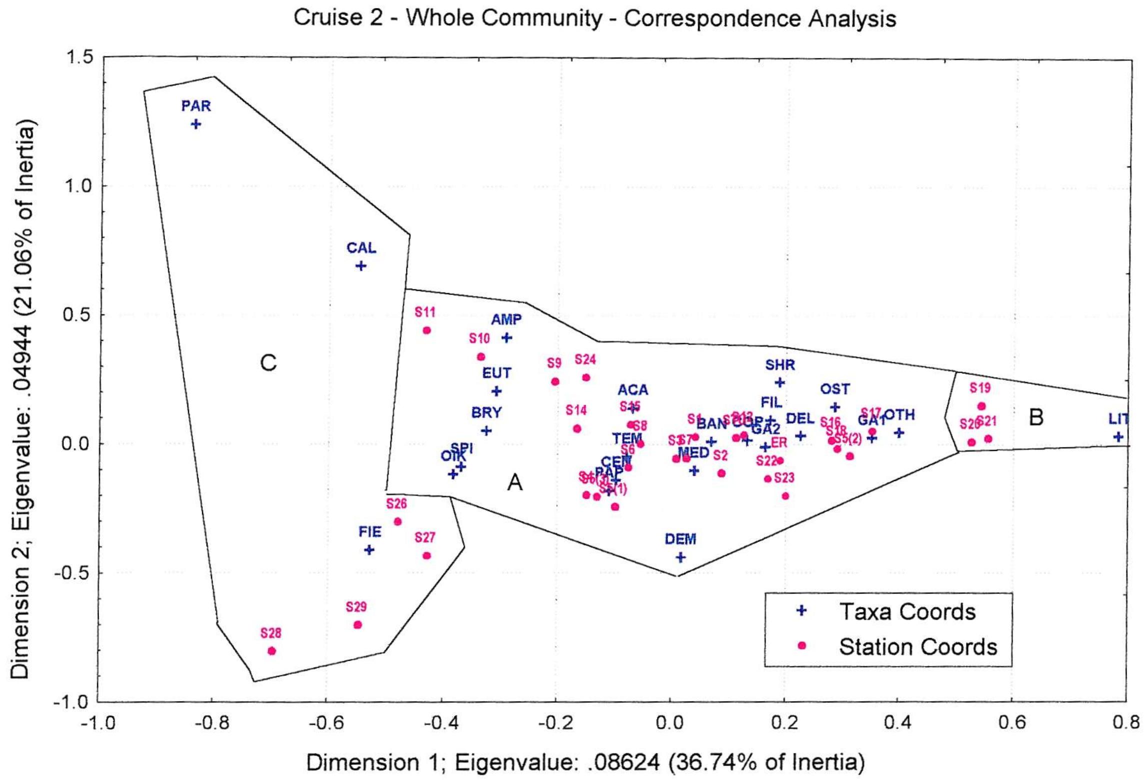


Figure 4.7: Cruise 2 correspondence analysis on whole community taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

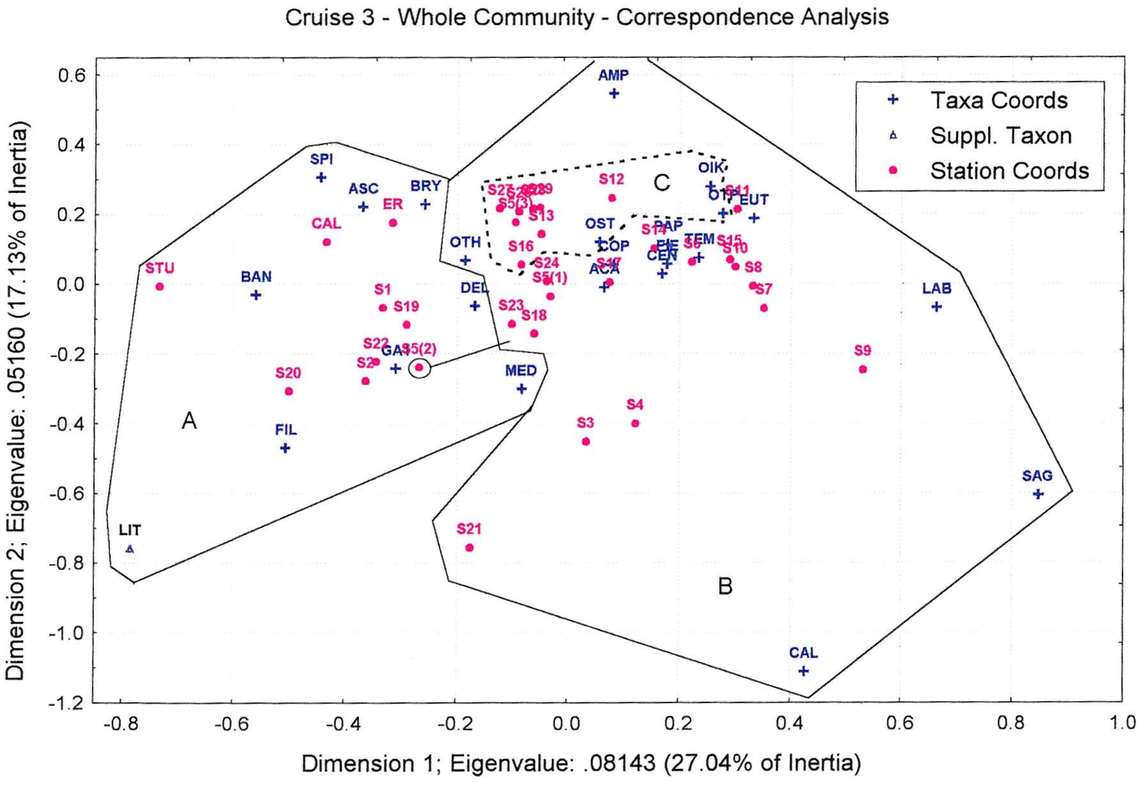


Figure 4.8: Cruise 3 correspondence analysis on whole community taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

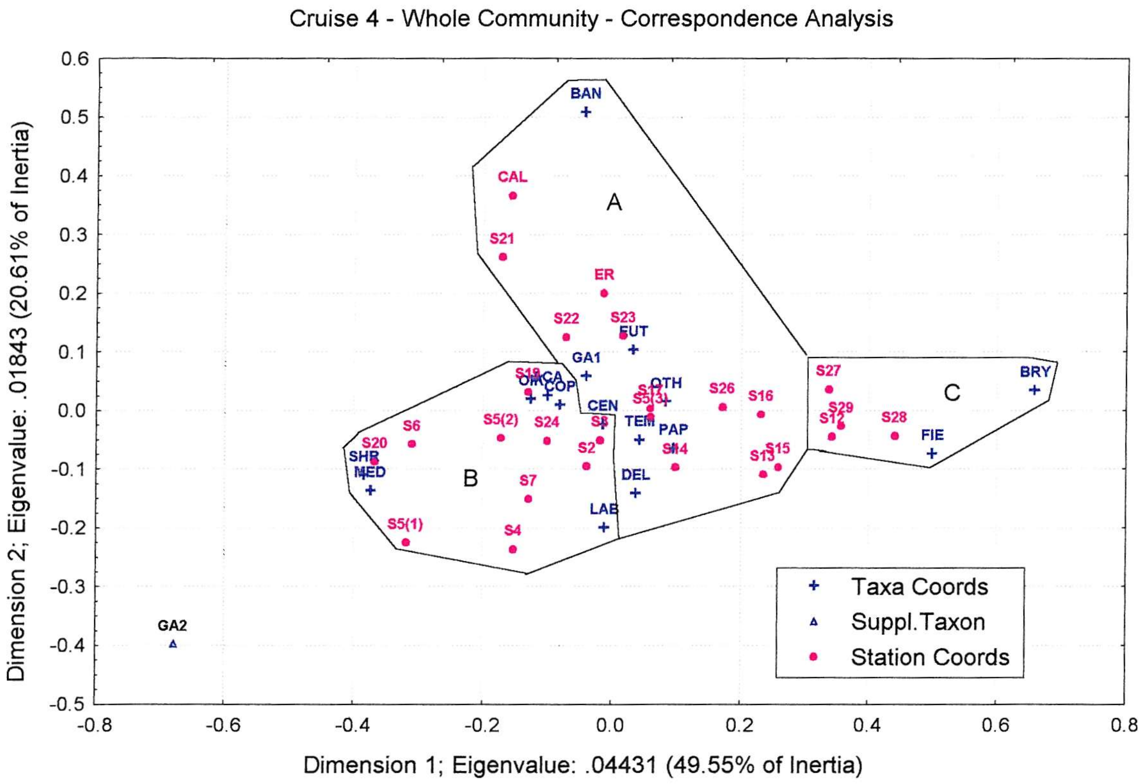


Figure 4.9: Cruise 4 correspondence analysis on whole community taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

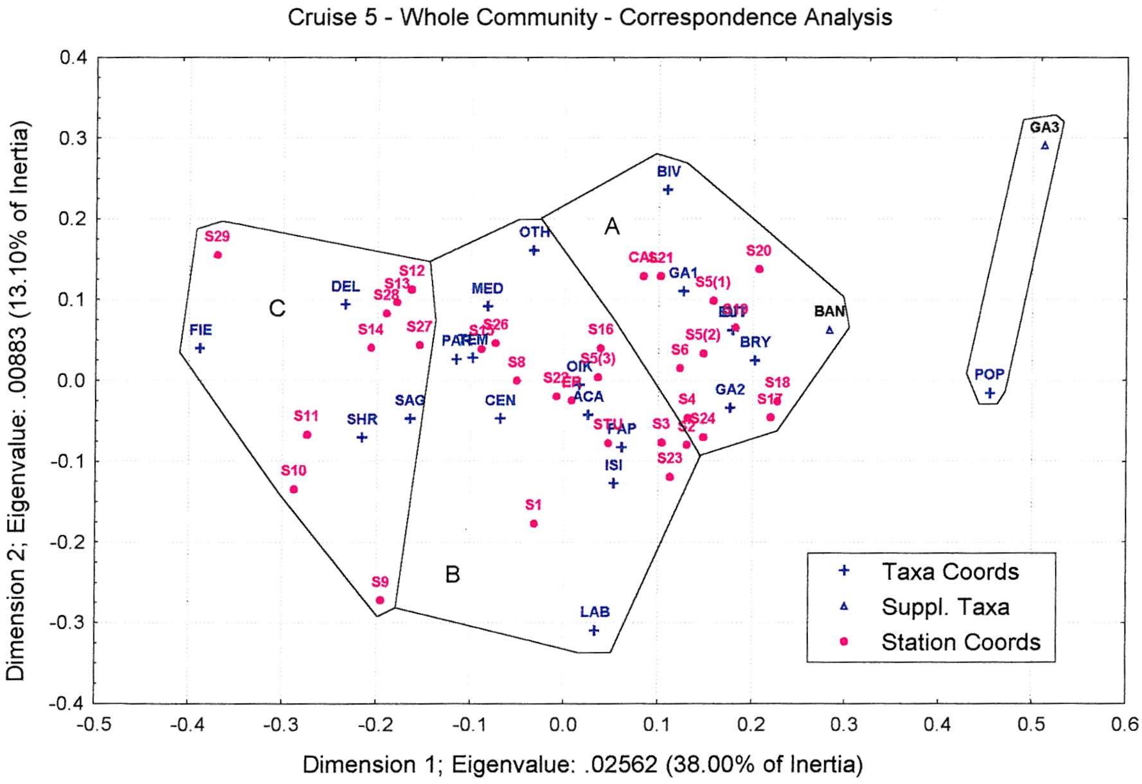


Figure 4.10: Cruise 5 correspondence analysis on whole community taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

For cruise 2 it was not necessary to remove the influence of points that contributed too greatly to the overall inertia, and thus no taxa were found to have an outlying distribution, nor did any station have a very unusual taxa composition. For other cruises, certain taxa had to be excluded, and added as supplementary points in the analysis. These are all meroplanktonic, and three out of four are gastropod taxa (*Littorina* spp. larvae, 'gastropods 2', 'gastropods 3' and barnacle nauplii). Their spatial distribution is shown in figures A.4.1 to A.4.4. They show a restricted distribution. In cruise 3, *Littorina* spp. larvae are strongly associated with central stations, and those towards the upper end of the East Solent. 'Gastropods 2' (cruise 4) are strongly clustered in central stations. For cruise 5, barnacle nauplii are associated with Solent and northeastern areas, with low numbers to the Southwest; 'Gastropods 3' are associated with eastern stations.

For those that were included, we can determine the major contributors to the inertia explained by the dimensions of the CA (summarised in table 4.2 and below). In most cases a group of points of 2-4 taxa and/or 3-6 stations dominate the contribution to inertia, from around 30% for taxa and 15-30% for stations downwards. Thus the organisation of the data sets can be explained by a relatively low number of taxa or stations, and this is especially true in July and August, which can also be linked to the low inertia of these data sets. The quality of their representation in the chosen number of dimensions is high, which can be seen on the ordination diagrams: these taxa tend to be at either end, and close to, the axes of the dimensions they contribute to the most. The spatial distribution of taxa contributing over 50% of inertia to dimensions 1 or 2 (as a group), generally well defined, is described below. It can be seen (with others) in figures A.4.1-A.4.4.

- Cruise 2 (3 dimensions extracted):
  - Dimension 1: separates southern stations (10, 11, 26-29...) from northern / Bracklesham Bay stations (19-21); Solent stations do not contribute greatly to this dimension. Fish eggs contribute 16% to the inertia and show a strong southern distribution, as do *Para/Pseudocalanus* spp. (mainly SE stations, 10% inertia), *C. helgolandicus* (4%), and spionid larvae (3%). *Littorina* spp. larvae (15%) are at the other end of the dimension and show a marked northern distribution. *Crepidula* larvae (12%) show low abundances to the SW.
  - Dimension 2 separates mainly southern stations into east and west. *Para/Pseudocalanus* spp. (39%) is strongly associated with south-eastern stations. Fish eggs (18%) contribute also to this dimension, this time with lower abundances to the SW. Northern stations are not so much separated along this axis.

- Cruise 3 (5 dimensions extracted):
  - Excluded from the CA: *Littorina* spp. larvae. Spatially these are associated with Solent and central stations, and figure at the low extreme of dimension 1 with a cosine^2 of ~0.20.
  - Dimension 1: The greatest separation is along transect 1, with Solent stations (*e.g.* Sturbridge, Calshot) at one end (low) and SE stations (7-11) at the other (Bracklesham Bay stations - 19-21 - are also at one end of this dimension but with a relatively low cosine^2). Barnacle nauplii are the greatest contributors (27%), and are very abundant in the Solent. *Sagitta* sp. (11%) is most abundant to the SE, and *Crepidula* larvae (9.5%) have high numbers in the Solent and low numbers in SW stations. These taxa are ordered accordingly along dimension 1, with *Sagitta* sp. towards the left end of the axis, fish larvae and *Crepidula* larvae and barnacle nauplii at the other. Dimension 1 separates also neatly between holoplankton and meroplankton, with few exceptions: 'other polychaete larvae' are to the right of the axis origin (meroplanktonic taxa are to the left), and 'other harpacticoids' and fish larvae are to the left.
  - Dimension 2: This is a straightforward N-S separation between central & Bracklesham Bay stations (*e.g.* 21, 3, 4, 2, 20, and 22) on the one hand and Southern stations (11, 12, 27, 28, 29) on the other, with stations 7-10 intermediate. *C. helgolandicus* is the greatest contributor (36%) and has an eastern / south-eastern distribution; its coordinates in the ordination put it closer to the 'northern' end, showing its strong association with stations 21 to the east.
  - Dimension 3 (included because of the number of dimensions extracted) is influenced mainly by Fish eggs (38%) and *Oikopleura* sp. (12%) which both have a south-eastern distribution (also southern for fish eggs). The separation of stations along this dimension, though not shown here, separates SW stations from Solent and the SE.
- Cruise 4 (3 dimensions extracted):
  - Excluded from the CA: 'gastropods 2': this taxa is concentrated in central/ Bracklesham Bay stations. It is at the (lower) extremes of both dimensions 1 and 2; with in both cases low cosine^2.
  - Dimension 1 is again a N-S separation with Solent-Bracklesham Bay opposed to southern stations. The main contributors have high cosine^2 and are distributed at the extremes: fish eggs (33%) and *M. membranicea* larvae (29%) towards southern

  stations, and caridean larvae (19%) and medusae (10%) at the 'northern' end. Other taxa, except barnacle nauplii, are close to the origin of the ordination.
  - Dimension 2 separates mainly Solent stations from central stations, with southern stations poorly represented by the axis. Barnacle nauplii contribute much more than other taxa (68%) to defining this dimension, and have marked northern distribution; the separation of other taxa is limited along this dimension.

- Cruise 5 (2 dimensions extracted)
  - Excluded from the CA: barnacle nauplii, which show high numbers in the Solent and low numbers to the SW; and 'gastropods 3', with a strong central/eastern distribution.
  - Dimension 1 is a N/S separation, with southern stations most spread out along the axis and opposed to Bracklesham Bay stations. Solent stations are towards the centre and generally show poor quality values for this dimension in particular, and in general for the CA. Fish eggs (29%) have a marked southern distribution and are placed close to the axis of dimension 1 with southern stations, together with taxa such as caridean larvae, other decapod larvae and *Sagitta* sp. Polychaete post-larvae are at the extreme of NE stations, with 'gastropods 2', *M. membranicea* larvae, *E. acutifrons*, *Crepidula* and bivalve larvae. Again we have a good holoplankton/meroplankton separation, though not as clear as in cruise 3: here most meroplanktonic taxa are beyond 0.1 on the axis, except caridean shrimp and other decapod larvae.
  - Dimension 2 has low cosine^2 values, mostly below 0.5, and there is not a clear spatial interpretation from the ordination. However *L. wollastoni* (30% contribution) shows highest abundances in the central Solent and low values at Calshot, to the SW and directly off Bracklesham Bay, which can be linked to the ordination diagram since stations to the right of the origin of dimension 2 tend to show low *L. wollastoni* abundances, as opposed to more central stations with high abundances. The pattern is similar for bivalve larvae (18%) and *I. clavipes* (11%).

These results show that there is a high variance associated with certain (littoral) meroplanktonic taxa (barnacle nauplii, *Littorina* spp. larvae 'gastropods 2 & 3'), which are predominantly at the coast, which is not seen in any of the holoplanktonic taxa. The CAs separate stations principally along a N/S axis, with some variation, such that dimension 2 can separate Solent from Bracklesham Bay stations, or the southern stations can be separated in eastern and western groups. In all cruises meroplanktonic taxa are predominantly associated with 'inshore' stations, though there are individual exceptions. Southern stations can be associated with fish eggs, *C. helgolandicus, Sagitta* spp., but also taxa such as spionid larvae, *M. membranicea* or decapod larvae.

4.C.3.b. *Clustering*

The clustering dendrograms can be seen in figure A.4.5 (A & B). Between units of the cluster analyses, cruises 2 and 3 show higher distance values than 4 and 5, indicating the wider spread / higher inertia within the dimensions of the CA. This is illustrated for dimensions 1 and 2 in figures 4.7-4.10 by a greater spread of points in the first two cruises, and a greater range in the axes. Nevertheless they can be separated into spatially well defined clusters, as illustrated in figure 4.11. These also appear in the ordination diagrams (figures 4.7-4.10) where, except in cruise 3, they are separated along the axes of dimension 1 or 1 and 2, despite the fact that 5 to 7 axes were used in the clustering. This is further indication that the first two dimensions generally represent the overall structure of the data. In cruise 3, where 5 axes were extracted, there is a higher level of dissimilarity and one sub-cluster (group C) was defined because of its spatial distinctiveness: it is part of a larger group in both cluster and ordination diagrams.

The cluster analysis confirms what seemed to be the case from the separation along the first two axes of the CA, *i.e.* two axes of separation appear to a greater-or-lesser extent, one N/S and the other E/W. They separate stations into three groups (A, B and C in figure 4.11). These groupings are also associated in the cluster diagrams with taxa, which are used to characterise them below. Because points are more spread out along dimension 1, these groupings tend also to separate along this axis. For those taxa that contribute distinctively to the dimensions of the CA (>50% as a group), their percentage contribution and dimension is given; it is in bold type for those that contribute most to a given dimension (usually >20%). Species distributions on figures A.4.1 to A.4.4 have been ordered in relation to group membership.

- Cruise 2: 3 groups. The separation in groups is unequal, with one large group, and two smaller groups at either ends of dimension 1.

- Group A: stations range from East Ryde to station 13 and include the majority of taxa, including *Crepidula* larvae which contribute 12% to dimension 1, decapod megalopa (**74%, dim. 3**), *E. acutifrons* (4.1%, dim. 3) and spionid larvae (3.8%, dim 3). These four taxa have in common relatively high abundances in central/southern stations. The

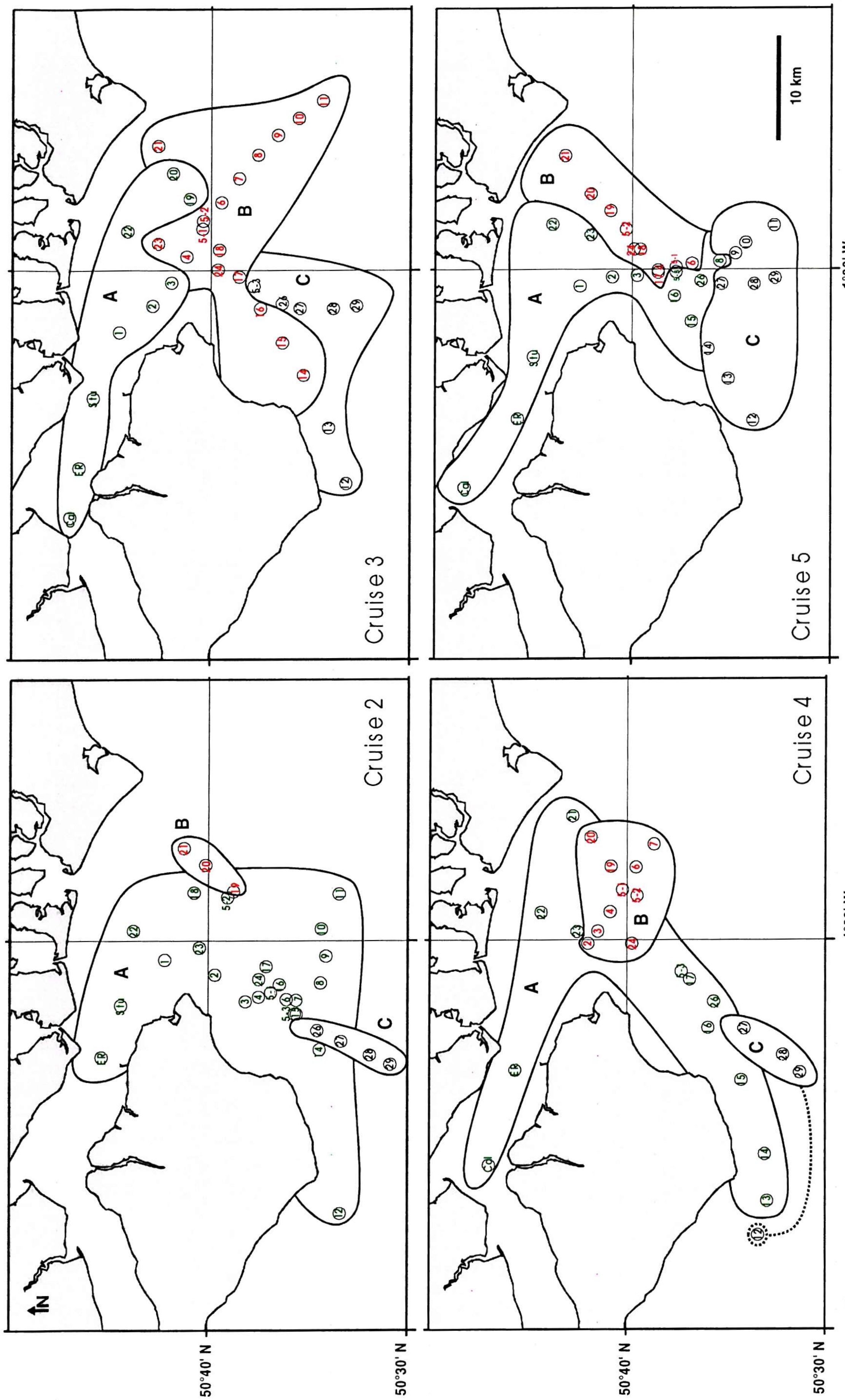


Figure 4.11: Station groups as derived from the cluster analysis of station scores on the CA dimensions (whole community), cruises 2-5.

group as a whole however covers several types of distribution (figure A.4.1): the majority are well distributed over the stations, with a tendency to higher numbers to the SE; others have a more southern distribution: caridean larvae, decapod megalopa, spionid larvae, *Oikopleura* sp., bryozoan larvae, amphipods and *E. acutifrons*. Caridean larvae excepted these also have low numbers in NE stations.

- Group B: 'Bracklesham Bay' stations (19, 20, 21): *Littorina* spp. larvae (dim. 1, 15%), with high numbers of this taxa in these three stations. This taxa is clearly associated with this group of stations.
- Group C: 'South-western' stations (26, 27, 28, 29), characterised by fish eggs (**17%, dim. 1**, 18%, dim. 2), *Para/Pseudocalanus* spp. (**39%, dim. 2**), *C. helgolandicus* (12%, dim. 2). All three have low abundances over most of the sampling area, but high numbers to the SW. The great majority of taxa, fish eggs excepted, see their minima in stations 26-29.

- Cruise 3: 3 groups.

Because of the relatively high level of dissimilarity of the cluster analysis, only two groups can be distinguished on the dendrogram. However one subgroup (group C) is represented here and in figure 4.11 because of its spatial and taxonomic distinctiveness.

- Group A: Solent stations (Calshot, East Ryde, Sturbridge, 1, 2, 19, 20, and 22). These stations are characterised by a high proportion of meroplankton, with higher numbers in the Solent. Some taxa however see also high numbers the South (figure A.4.1: decapod larvae, medusae (11%, dim. 2), *M. membranicea* larvae, ascidian larvae, spionid larvae). *Crepidula* larvae (9%, dim. 1 and 2), barnacle nauplii, *Littorina* spp. larvae (supplementary point in CA) and fish larvae have predominantly 'Solent' distributions. Barnacle nauplii are the only taxon of this group to contribute over 20% to a dimension of the CA (**27% to dim. 1**).
- Groups B and C:

- Group B: 'Central/SE' stations (3, 4, 5(1), 5(2), 6, 7, 8, 10, 11, 14, 15, 17, 18, 23, 24 – grouped with 16, 9, 21); these are grouped with what can be described as euryhaline holoplanktonic taxa: copepod nauplii, *T. longicornis* (6%, dim. 1), *C. hamatus*, *Acartia* spp. (**34%, dim.5**), *Euterpina*, fish eggs (**38%, dim 3**), *Sagitta* sp. (11%, dim 1). They all have a similar distribution, namely high numbers to the SE.

- Group C: 'Southern' stations (12, 13, 26, 27, 28, 29 and 5(3)): Mainly holoplanktonic taxa, with more stenohaline characteristics: *C. helgolandicus* (**36%, dim. 2**), *L. wollastoni*, *Oikopleura* sp. (12%, dim. 3), ostracods and amphipods, 'other polychaete larvae', harpacticoids. These taxa tend to have numbers more evenly distributed to the South.

- Cruise 4: 3 Groups.

- Group A: 'Solent' and 'South-western' stations (Calshot, East Ryde, 13, 14, 15, 16, 17, 21, 22, 23, 26, 5(3)): *E. acutifrons*, *Crepidula* larvae, barnacle nauplii (**68%, dim. 2**), decapod larvae (8%, dim. 2), *P. brevicornis*, 'Other harpacticoids' and *T. longicornis*. Taxa from this group tend to show a ubiquitous distribution, with however higher numbers towards the Solent (figure A.4.1)
- Group B: 'Bracklesham Bay' stations (2, 3, 4, 5(1), 5(2), 6, 7, 20, 24, 19): A majority of holoplanktonic taxa: medusae (**36%, dim 3**), caridean larvae (19%, dim. 1), *L. wollastoni* (22%, dim. 3), *Oikopleura* sp., copepod nauplii, *Acartia* spp., and *C. hamatus*. These taxa are strongly associated with NE stations, with low numbers to the SW.
- Group C: 'Southern' stations (27, 28, 29 and 12): fish eggs (**33%, dim. 1**), *M. membranicea* larvae (29%, dim. 1). Station 12 is the only one to be linked with a non-proximate group of stations, and like this group it has a high abundance of *M. membranicea* larvae. Both taxa show strong N/S differences in abundance.

- Cruise 5: 3 Groups.

Outliers: 'gastropods 3' and polychaete post-larvae. These taxa have very similar distributions and are associated with central/eastern stations.

- Group A: 'Solent' stations (East Ryde, Sturbridge, 1, 2, 3, 5(3), 8, 15, 16, 22, 23, 26): Mainly holoplanktonic taxa: *Oikopleura* sp., *C. hamatus*, *Para/Pseudocalanus* spp., *T. longicornis*, 'Other harpacticoids', *Acartia* spp., *P. brevicornis, I. clavipes* (11%, dim. 2), *Labidocera* sp. (**30%, dim. 2**); and medusae. These taxa have in common low numbers at Calshot, lower numbers in the SW and higher numbers towards the Solent or the NE.
- Group B: 'Bracklesham Bay' stations (4, 5(1), 5(2), 6, 17, 18, 19, 20, 21, 24): Many meroplanktonic taxa: *M. membranicea* larvae, 'gastropods 2' (7%, dim. 1), *Crepidula*

larvae, bivalve larvae (20%, dim. 2), barnacle nauplii; and *C. helgolandicus*, *O. nana*, *E. acutifrons*. Most of these taxa are more abundant in Bracklesham Bay / Solent stations.

- Group C: 'Southern' stations (9, 10, 11, 12, 13, 14, 27, 28, and 29): caridean larvae, other decapod larvae, *Sagitta* sp., and fish eggs (**29%, dim. 1**). Predominantly southern distributions, low numbers to the NE.

Generally stations and taxa can be separated into three groups, which can be described to a greater-or-lesser extent as: **Group A**, stations from the Solent and central sampling area, **Group B** stations to the East/Bracklesham Bay, and **Group C**: Southern stations. The size and extent of these groups varies very much between cruises. Solent stations can be amalgamated with stations from Sandown Bay and the South of the Isle of Wight, as in cruises 2 and 4, or with Sandown bay stations only (cruise 5); or they can be restricted to the north of Nab Tower (cruise 3). Southern stations can form a medium-sized, distinct group (cruises 3 and 5) or small clusters (cruises 2 and 4). Finally eastern stations can be grouped to a smaller or greater extent with intermediate/Bracklesham Bay stations and extend to Sandown Bay (cruise 3) and vary from 3 stations (cruise 2) to 17 (cruise 3). Despite this variability the clustering confirms somewhat the separation along the CA axes, but shows that the separation between groups is not necessarily a strong one, and that it changes between June and July. There is a N/S distinction in all four cruises, and the E/W separation, visible in the 'Bracklesham Bay stations' is most distinctive in July and August.

Because of the distribution of points along dimensions 1 and 2 of the CA, this separation tends to follow these axes, as can be seen from the ordination diagrams. In cruise 3, group C was distinguished from the rest of group B, separated along dimension 2. Within groups, there is a tendency to segregate according to contribution to dimensions. In cruise 2, group A includes decapod megalopa, *E. acutifrons* and spionid larvae, the three main contributors to the inertia of dimension 3. Group C includes *Para/Pseudocalanus* spp., *C. helgolandicus* and fish eggs, the three main contributors to dimension 2. In cruise 3 the pattern is less clear, but group A tends to contribute to dimension 1 (barnacle nauplii, *Crepidula* larvae) and group C to dimension 2 (*C. helgolandicus*). In cruise 4 the separation is group A: dimension 2 (barnacle nauplii, decapod larvae), group B: dimension 3 (medusae, *L. wollastoni*) and group C: dimension 1 (fish eggs, *M. membranicea* larvae). And in cruise 5: Group A: dimension 2 (*L. wollastoni*, *I. clavipes*), group C: dimension 1 (fish eggs). Other groups not mentioned show a mixture of contributions. This would indicate that:

(a) Quality values are high for the CAs ('heavy' points, in the sense of having greater inertia, are close together).

(b) Within station groups, taxa distributions are relatively uniform.

(c) There are few mutually exclusive distributions. This can confirmed by the spatial distribution of the taxa, which, when ordered by groups (figures A.4.1-A.4.4), show distinct similarities.

The distribution of taxa itself however is clearly not limited to the station groups. Thus station clusters can be thought of as 'zones of convergence' of community composition, rather than restricted areas of dominance. This would tend to be confirmed by the absence of strong hydrographic gradients observed in chapter 2, and would indicate a hydrodynamical constraint rather than hydrographic.

Generally, Group C is the most characteristic, and in cruises 2 and 3 is associated with a preponderance of holoplankton, especially when 'heavy' taxa (which carry a large part of the CA inertia) are considered. It is also smaller than groups A and B, except in cruise 2 where group B is composed of one taxa and 3 stations. It is associated with fish eggs in cruises 2, 4 and 5, *C. helgolandicus* in cruises 2 and 3 and generally with taxa of stenohaline-marine characteristics (*C. helgolandicus*, *Para/Pseudocalanus* spp., *Oikopleura* sp., *Sagitta* sp.) though we also see polychaete larvae in cruise 3, *M. membranicea* larvae in cruise 4 and decapod larvae in cruise 5, indicating that there is a degree of mixing between areas, and possibly a shift in the populations.

Group A is the largest group in cruise 2, 4 and 5 both in number of taxa and stations, and seems to include a number of taxa which do not show marked distribution patterns, as well as those with restricted Solent distributions. In cruises 2, 3, and 4, most of its 'heavy' taxa are meroplanktonic, notably *Crepidula* larvae (cruises 2 and 3) and barnacle nauplii (cruises 3 and 4). In cruise 3, it includes only meroplanktonic taxa, fish larvae excepted, however in cruise 5 it is mainly composed of holoplanktonic taxa, which probably indicates an evolution of the community, for example 'southern' species becoming more prominent as the season progresses, and numbers increase in the Solent. Group B can be seen as intermediate between A and C in terms of size, though in cruise 2 it is associated with *Littorina* spp. larvae only. In cruise 3 it is poorly defined, but includes holoplanktonic taxa only, both in cruise 4, and a majority of meroplanktonic taxa in cruise 5, which again shows a shift in the spatial organisation of the community, such that group B seems to be not as greatly influenced by the increase in holoplanktonic taxa. Apart from *L. wollastoni* in cruise 4, 'heavy' taxa in the last two cruises are meroplanktonic.

4.C.4. MANOVA & SNK tests

Figure 4.12 shows the correspondence between station and taxa groupings (A, B, C), and outliers for cruise 5 ('gastropods 3' and polychaete post-larvae), from table 4.3. Average abundances are back-transformed averages, *i.e.* anti-log of average $\log_{10}$ abundances, and therefore are still transformed values, and should be interpreted as such (Sokal & Rohlf, 1995, pp. 413-415; for other -cautionary- notes on data transformation, see also Downing *et al.*, 1987). The station groups are as defined in the preceding sections; taxa groups are defined in the same way, *i.e.* through the cluster analysis, and as such they have a one-to-one correspondence with the station groups; thus station group A forms a cluster with taxa from taxa group A. These results are concerned with the differences in abundances between station groups, rather than changes in community composition.

Station groups B and C ('SGB and SGC' hereafter) in Cruise 2 are small (n=3 and n=4 respectively), and thus the MANOVA results for this cruise should be treated with caution. ANOVA is generally robust to departures from normality, but can be sensitive to small or unequal sample sizes. Small sample sizes tend to reduce the power of ANOVA, increase the chance of a type II error and thus reduce the chance of detecting differences between groups when they exist. Despite this, the separation between station groups for their constituent taxa is significant for all cruises, and between all groups, at $\alpha = 0.05$, and for most at $\alpha = 0.01$, indicating clear abundance differences between station groups. The individual *F* tests (figure 4.12) show that about half the number of taxa within station groups show significant differences (~⅔ for cruise 5). There is no preponderance of meroplankton or holoplankton amongst these taxa, representing ~ 50% each, both in total and in the 'significantly different', and thus the factors inducing spatial differences in abundances act on the two sub-communities. However the distribution of significant taxa between groups can be unequal, certain groups contributing many more taxa than others relatively to their size, for example group A in cruise 3 and group B, cruise 5; or conversely few or even none as in group A, cruise 4. Thus, although for this taxa group as a whole there is a significant difference between station groups, no individual taxon has significantly different abundances between groups. It should be remembered that in this context the individual *F* tests do not represent true probabilities, but should be considered as an index of contribution to the overall statistic.

Comparing relative average abundances, (table 4.3), taxa groups do not necessarily see their maximum abundance in their related station group: TGB is the most abundant in SGC in cruise 3, TGB in SGA (cruise 4) and TGA in SGB and SGC (cruise 5).

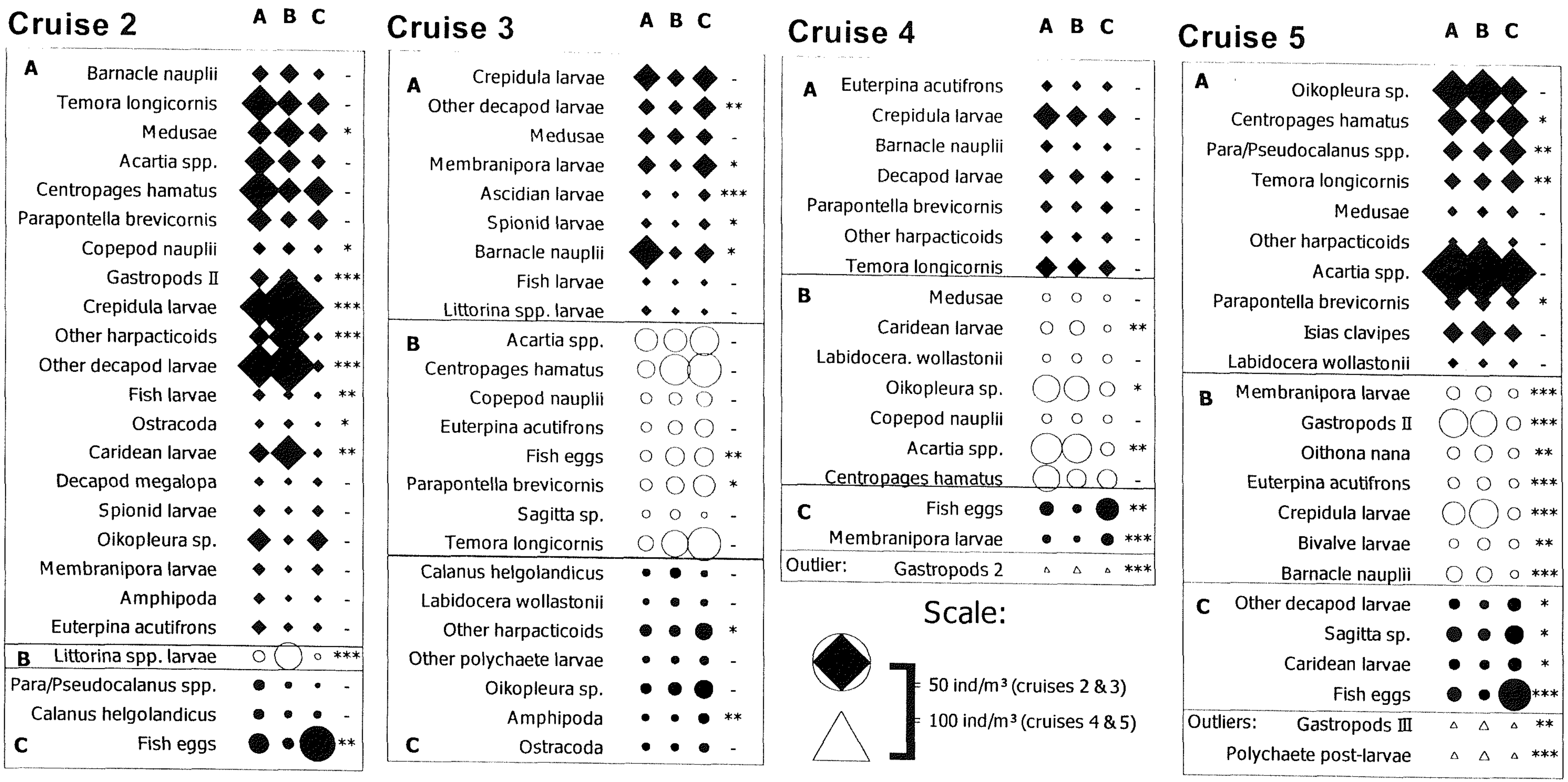


Figure 4.12: Back-transformed taxa abundances ($\log_{10}$ scale), from table 4.3, arranged by groups resulting from the cluster analysis (A, B, C). Asterisks denote the significance of the individual F tests between average $\log_{10}$ abundances of taxa between station groupings; *: $0.05>P>0.01$; **: $0.01>P>0.001$; ***: $P<0.001$. *n.b.:* Crepidula *larvae in cruise 2, group B are at a smaller scale for clarity. See table 4.4 for values.*

Cruise 2

Taxa groups:	Station groups:	A (n=24)	B (n=3)	C (n=4)	
A (P<0.001)	Barnacle nauplii	3.22	4.80	0.89	-
	Temora longicomis	23.00	9.49	7.07	-
	Medusae	8.78	14.41	4.71	*
	Acartia spp.	14.93	7.48	2.10	-
	Centropages hamatus	29.86	8.90	14.01	-
	Parapontella brevicomis	8.46	3.31	5.53	-
	Copepod nauplii	1.42	1.56	0.34	*
	Gastropods II	4.51	3.93	0.29	***
	Crepidula larvae	26.22	264.92	0.77	***
	Other harpacticoids	6.10	30.57	0.31	***
	Decapod larvae	34.65	55.68	1.29	***
	Fish larvae	1.25	0.61	0.14	**
	Ostracoda	0.48	0.65	0.02	*
	Candean larvae	5.57	21.04	0.41	**
	Decapod megalopa	0.49	0.22	0.49	-
	Spionid larvae	1.14	0.27	1.06	-
	Oikopleura sp.	7.99	0.63	6.01	-
	Membranipora larvae	1.35	0.17	0.98	-
	Amphipoda	1.02	0.12	0.14	-
	Euterpina acutifrons	2.04	0.49	0.43	-
B (P<0.001)	*Littorina* spp. larvae	0.95	11.06	0.02	***
C (P<0.05)	*Para/Pseudocalanus* spp.	0.795	0.082	0.000	-
	Calanus helgolandicus	0.709	0.175	0.167	-
	Fish eggs	5.256	0.876	21.283	**
	Averages of groups A	*9.1*	*21.46 **	*2.3*	
	B	*0.9*	*11.1*	*0.0*	
	C	*2.3*	*0.4*	*7.1*	

* 6.74 without *Crepidula* larvae

Cruise 3

Taxa groups:	Station groups:	A (n=9)	B (n=17)	C (n=7)	
A (P<0.001)	*Crepidula* larvae	17.42	5.80	15.05	-
	Decapod larvae	5.03	3.53	12.40	**
	Medusae	5.37	5.58	5.59	-
	Membranipora larvae	6.38	2.09	14.28	*
	Ascidian larvae	0.62	0.22	2.13	***
	Spionid larvae	1.23	0.35	1.73	*
	Barnacle nauplii	31.19	2.44	8.07	*
	Fish larvae	0.46	0.14	0.21	-
	Littorina spp. larvae	1.05	0.33	0.16	-
B (P<0.001)	*Acartia* spp.	10.70	10.99	19.49	-
	Centropages hamatus	5.37	22.47	28.54	-
	Copepod nauplii	1.26	2.11	3.67	-
	Euterpina acutifrons	0.93	2.82	5.89	-
	Fish eggs	1.39	6.59	6.62	**
	Parapontella brevicomis	1.70	5.34	9.55	*
	Sagitta sp.	0.27	0.79	0.03	-
	Temora longicomis	3.65	15.87	27.53	-
C (P<0.001)	*Calanus helgolandicus*	0.27	0.99	0.12	-
	Labidocera wollastonii	0.08	0.54	0.20	-
	Other harpacticoids	1.64	1.43	5.19	*
	Other polychaete larvae	0.18	0.33	0.56	-
	Oikopleura sp.	1.30	2.49	6.21	-
	Amphipoda	0.17	0.20	0.97	**
	Ostracoda	0.30	0.32	0.82	-
	Averages of groups: A	*7.6*	*2.3*	*6.6*	
	B	*3.2*	*8.4*	*12.7*	
	C	*0.6*	*0.9*	*2.0*	

Cruise 4

Taxa groups	Station groups	A (n=13)	B (n=9)	C (n=4)	
A (P<0.05)	*Euterpina acutifrons*	10.47	6.33	8.57	-
	Crepidula larvae	159.34	81.28	54.93	-
	Barnacle nauplii	19.88	3.63	5.12	-
	Decapod larvae	34.55	33.50	21.93	-
	Parapontella brevicomis	18.61	12.50	18.21	-
	Other harpacticoids	18.65	8.72	11.89	-
	Temora longicomis	86.79	57.67	44.47	-
B (P<0.01)	Medusae	3.07	5.55	0.87	*
	Candean larvae	16.47	27.35	1.33	**
	Labidocera wollastonii	3.16	5.76	4.68	-
	Oikopleura sp	147.90	120.87	28.28	*
	Copepod nauplii	6.95	7.45	3.77	-
	Acartia spp	204.66	179.54	21.92	**
	Centropages hamatus	143.82	59.39	60.63	-
C (P<0.01)	Fish eggs	24.40	4.53	93.74	**
	Membranipora larvae	4.28	0.82	15.98	***
Outlier (P<0.001)	Gastropods 2	0.26	2.47	0.00	***
	Averages of groups A	*49.8*	*29.1*	*23.6*	
	B	*75.1*	*58.0*	*17.4*	
	C	*14.3*	*2.7*	*54.9*	

Cruise 5

Taxa groups:	Station groups:	A (n=12)	B (n=11)	C (n=9)	
A (P<0.001)	*Oikopleura* sp.	392.79	458.50	178.10	-
	Centropages hamatus	189.03	121.11	233.61	*
	Para/pseudocalanus spp.	67.67	62.26	151.60	**
	Temora longicomis	44.32	53.39	102.67	**
	Medusae	8.44	12.11	14.93	-
	Other harpacticoids	5.50	6.90	6.94	-
	Acartia spp.	1031.00	1100.70	593.64	-
	Parapontella brevicomis	39.14	41.60	22.36	*
	Isias clavipes	75.74	126.41	51.10	-
	Labidocera wollastonii	9.10	6.20	5.33	-
B (P<0.001)	*Membranipora* larvae	20.78	32.55	6.02	***
	Gastropods II	174.32	140.93	24.67	***
	Oithona nana	17.72	45.04	8.95	**
	Euterpina acutifrons	13.35	20.97	5.56	***
	Crepidula larvae	97.31	174.48	16.79	***
	Bivalve larvae	6.59	16.77	6.74	**
	Barnacle nauplii	35.76	33.07	2.84	***
C (P<0.001)	Decapod larvae	12.00	5.10	21.00	*
	Sagitta sp.	33.42	16.66	54.36	*
	Candean larvae	9.60	6.74	18.96	*
	Fish eggs	27.37	11.15	232.16	***
Outliers (P<0.001)	Gastropods III	1.55	7.24	0.48	**
	Polychaete post-larvae	2.50	8.83	0.77	***
	Averages of groups: A	*186.27*	*198.92*	*136.03*	
	B	*52.26*	*66.26*	*10.22*	
	C	*20.60*	*9.91*	*81.62*	
	Outliers	*2.03*	*8.04*	*0.63*	

Table 4.3: Back-transformed average $\log_{10}(x+1)$ taxa densities: arranged in taxa groupings and averaged over station groupings (n.m^{-3}). P values are results from the multivariate analysis of variance between groups on the averaged $\log_{10}(x+1)$ taxa abundances. Asterisks denote the significance of the individual *F* tests between groups for each taxa (*: 0.05>P>0.01; **: 0.01>P>0.001; ***: P<0.001).

Conversely, within station groups, the maximum abundance is not necessarily represented by the associated taxa group; nevertheless in the majority of cases there is a trend for higher average abundances within station groups for taxa of that group, and conversely for a higher proportion of associated taxa between taxa groups.

When the results of the individual *F* and *post-hoc* SNK tests are detailed, we can distinguish which taxa show significantly different abundances between station groups (table A.4.3). If the result of the *F* test is significant for a particular taxon, table A.4.3 shows which group it defines best: A/B, B/C, or A/C, or a combination of these three possibilities. For example copepod nauplii (cruise 2) have significantly different abundances between station groups at $\alpha = 0.05$; the *F*/SNK tests shows that the difference is significant between groups SGA and SGC on one hand, and SGB and SGC on the other. Therefore we can characterise group SGC, the common factor, by low relative copepod nauplii abundances. Thus a taxa which is significantly different between A/B characterises groups A and B; one that differentiates between A/B and B/C characterises group B only, since there is no difference between A and C; and one that makes three distinctions characterises all three in terms of low, intermediate and high abundances. This is summarised for the data in table 4.4. Taxa which are important contributors to the inertia of the CA are highlighted, and we see here the influence of the CA in that for cruises 3, 4 and 5, one of the taxa which separates between all three station groups also contributes most to dimension 1 of the CA: barnacle nauplii (cruise 3), *M. membranicea* larvae (cruise 4), fish eggs (cruise 5). In cruise 2 *Crepidula* larvae also separate the three groups, but this taxon is the third contributor to dimension 1 (table 4.2).

Cruise 2

Station groups

Taxa Groups	A	B	C
A	<>*GA1* <>OTH +FIL <>SHR	+MED +*GA1* +OTH +SHR	-MED -COP -GA2 -*GA1* -OTH -DEL -OST -SHR
B		+*LIT*	
C			+*FIE*

Cruise 3

Station groups

Taxa Groups	A	B	C
A	<>ASC ***+BAN***	-ASC ***-BAN***	+DEL +BRY +ASC +SPI ***<>BAN***
B	***-FIE*** -PAP		+PAP
C			***+OTH*** +AMP

Cruise 4

B	+OIK	***+MED***	***-MED*** -SHR -OIK -ACA
C	***<>BRY***	***-BRY***	***+FIE*** ***+BRY***
Outlier:		+GA2	

Cruise 5

A		-CEN	+CEN +PAR +TEM -PAP
B	<>EUT	+OIT +EUT +*BIV*	-BRY -GA2 -EUT -GA1 -BAN
C	***<>FIE***	***-FIE***	+DEL +SAG +SHR ***+FIE***
Outliers:	<>*POL*	+GA3 +*POP*	-*POP*

Table 4.4: Summary of the individual *F* and SNK tests: characteristic taxa for each station group, arranged by taxa groups. + denotes significantly higher abundances; - lower abundances; <> intermediate abundances. In italic type are important contributors to the inertia of a CA dimension (from table 4.3); in bold are those that contribute >20% to a dimension. For taxa abbreviations see table A.4.1.

Again SGC is the most characterised group, having the most taxa in its column; *i.e.* it has the greatest differences between groups. SGA and SGB see similar levels of abundances and therefore the strongest cline of taxa abundances can be seen between groups A & B on the one hand and C on the other. SGA and SGB tend to contain more ubiquitous taxa, with less differentiation across groups. As could be guessed from table 4.3, the differences between groups A and B are thus more a result of the community composition than strong differences in abundances, whereas for the southern group of stations, both are likely to play a part.

There is a tendency for groups to be characterised positively by their corresponding taxa: for example, in cruise 2, fish and caridean shrimp larvae, from TGA, characterise SGA; *Littorina* spp. larvae (TGB), SGB; and fish eggs (TGC), SGC. The pattern is similar for other cruises. Nevertheless taxa groups can strongly characterise a non-associated station group: in cruises 2 and 4, all TGA taxa show low values in SGC; the opposite is true in cruises 3 and 5; in cruises 4 and 5, SGC has low TGB taxa. Or a taxa group can be uncharacteristic of station groups, as for SGA in cruise 4.

Specifically, the station and taxa groupings can be detailed cruise by cruise:

- Cruise 2: As noted above, the results of the MANOVA/*F*/SNK tests for this cruise should be treated with caution because of the differences in sample sizes. Nevertheless, the differences in abundances are quite marked, the MANOVA detects an effect between the three groups at $\alpha=0.05$, and the three taxa groups contribute significantly to the differences between station groups. Nevertheless, when individual taxa are looked at there is little overall differentiation. The main difference is between SGA/SGB and SGC, from of a deficit of taxa group A ('TGA') in SGC. SGA is characterised by increased abundances of fish larvae, and, not significantly ('n.s.' hereafter), by higher abundances of *T. longicornis*, *Acartia* spp., *C. hamatus* and *Oikopleura* sp. These taxa tend to have a southern distribution within SGA (figure A.4.1). SGB shows very high levels of *Crepidula*, *Littorina* spp. and caridean larvae, and harpacticoids. There are also higher numbers of other decapod larvae and medusae (n.s), and thus this group sees increased densities of meroplanktonic taxa, though these were not associated with it in the cluster analysis. The Southern group of stations is defined by the presence of fish eggs, and low numbers of a number of taxa from group A. The most variable taxa across groups are *Crepidula* and caridean larvae, and harpacticoids.

  Regarding the taxa group as a whole, TGA has the highest overall abundance (table 4.3, figure 4.12) and TGC the lowest, with TGA highest both in SGA and SGB (but not if the exceptional numbers of *Crepidula* are excluded). Decapod larvae, *C. hamatus*, *Crepidula* larvae, *T. longicornis* and *Acartia* spp. are the main factors for this high abundance in TGA, but as was seen earlier, for some of these taxa their distribution is mostly to the south of SGA. Both TGA and TGB have their lowest abundance in SGC. TGC has highest abundance in SGC, mainly due to fish eggs and lowest in SGB. *Para/Pseudocalanus* spp. and decapod megalopae, important contributors to dimensions 2 and 3 of the CA, do not show significantly different abundances across groups.

- Cruise 3: Here the separation is more equal between station groups. SGA is mainly a meroplanktonic group, with increased barnacle nauplii numbers, low numbers of fish eggs and *P. brevicornis*, but also high numbers of *Crepidula* and *Littorina* spp. larvae

(n.s.). SGB sees low numbers of barnacle nauplii and *M. membranicea* larvae, but is not otherwise different from the other two groups, and can be considered composed of a large proportion of ubiquitous taxa, with low numbers of meroplankton (TGA), intermediate numbers of euryhaline holoplankton (TGB) and stenohaline species (TGC). Group C is defined by increased abundances of a number of taxa, mainly harpacticoids, amphipods and ostracods, and a group of meroplanktonic taxa from TGA (decapod larvae, *M. membranicea*, ascidian and spionid larvae). It has also higher numbers of most taxa from TGB (n.s., *e.g. Acartia* spp., *C. hamatus*, and *T. longicornis*). Barnacle nauplii and ascidian larvae are most variable across groups.
Again the greatest difference in average abundances is between TGC and the other two groups: this time TGC has the lowest average abundance in all three, but its highest level is in TGC. TGA is most abundant in SGA, and TGB in SGC; however TGB is also dominant in SGB. This can be attributed to high numbers of barnacle nauplii and *Crepidula* larvae in TGA/SGA, high numbers of *C. hamatus, T. longicornis* and *Acartia* spp. in TGB/SGB, and conversely low numbers of these taxa in the other station groups. The high numbers of TGB in SGC are mainly due again to *C. hamatus*, *T. longicornis* and *Acartia* spp. (fig 4.12, table 4.3). Despite the important numbers of TGA and TGB, TGC is still most abundant in SGC, due to higher numbers in that group of all TGC, bar *C. helgolandicus* and *L. wolastonii.*

- Cruise 4: Meroplankton and holoplankton are found equally in all three groups. TGA can be considered as a group of ubiquitous taxa since no individual taxa are found to be significantly different across station groups. SGA is characterised by high numbers of *Oikopleura* sp., and average values of *M. membranicea* larvae. It also sees (n.s.) higher numbers of *Crepidula* larvae, *T. longicornis*, *Oikopleura* sp., *Acartia* spp. and *C. hamatus.* SGB is characterised by the presence of medusae and a lack of *M. membranicea* larvae, with also (n.s.) higher numbers of caridean larvae, *L. wolastonii* and copepod nauplii. SGC sees low numbers of most taxa, mostly from TGB (medusae, caridean larvae, *Oikopleura* sp. and *Acartia* spp.), but high numbers of fish eggs and *M. membranicea* larvae. These are most variable across groups.
  Here the most abundant taxa group is TGB, in SGA, mainly due to *Acartia* spp., *C. hamatus* and *Oikopleura* sp.; it is also the most abundant in SGB (same taxa), but TGC dominates SGC with high numbers of fish eggs and *M. membranicea* larvae. Across taxa groups, TGA is most abundant in SGA (for all taxa, esp. *Crepidula* larvae, *T. longicornis* and harpacticoids), TGB in SGA (only for the three taxa mentioned

above) and TGC in SGC (fish eggs and *M. membranicea* larvae). The outlier, 'gastropods 2' is absent in SGC, has low numbers in SGA and most of its individuals are found in SGB.

- Cruise 5 sees is a higher proportion of significantly varying taxa, however again most are characteristic of SGC, leaving SGA defined only by taxa which have significant differences across all groups (*E. acutifrons*, fish eggs and polychaete post-larvae). In fact the only taxa to see their maxima in SGA are *L. wollastoni*, 'gastropods 2' and barnacle nauplii. SGB is characterised by three taxa from TGB (*O. nana*, *E. acutifrons* and bivalve larvae), by the two outliers 'gastropods 3' and polychaete post-larvae, and by a deficit of fish eggs. Overall, it is the station group with highest abundances. SGC is defined by increased abundances of TGA (*C. hamatus*, *Para/Pseudocalanus* spp. and *T. longicornis*), indicating the high overall holoplanktonic abundances, and TGC (decapod larvae, *Sagitta* sp., caridean larvae and fish eggs), and by low abundances of polychaete post-larvae, TGB (*M. membranicea* larvae, 'gastropods 2', *E. acutifrons*, *Crepidula* larvae and barnacle nauplii), and *P. brevicornis* from TGA.

  Overall TGA clearly dominates the abundances since it is most abundant in all station groups. This is principally due to the very high numbers of *Acartia* spp., and also to *Oikopleura* sp., *C. hamatus*, *I. clavipes* and *T. longicornis*. In SGB, *P. brevicornis* is also important. Nevertheless, TGB is most abundant in SGB (for 5 out of 7 taxa: *Crepidula* larvae, *O. nana*, *E. acutifrons*, *M. membranicea* larvae, bivalve larvae) and TGC most abundant in SGC (all taxa: fish eggs, *Sagitta* sp., other decapod larvae and caridean larvae).

These results confirm that the group of southern stations is specific, in that it has overall significantly low abundances, and this for all four cruises. Fish eggs are particularly indicative of this area, but on the whole only cruises 3 and 5 see a number of other taxa increasing in SGC whilst in cruises 2 and 4 it is principally characterised by the absence of 'A' and 'B' taxa. Cruises 3 and 5 are also those where SGC is somewhat larger - presumably where it is best covered by the sampling stations, and also where the tidal coefficients are smallest. There is thus the possible effect of tidal state on the efficiency of sampling this group, which may explain the size differences between cruises of the various groups (rather than community evolution). We see again clear seasonal shifts between the three groups, such that no station group has a permanent indicative taxon; there is therefore, despite the permanence of the three station groups, a high degree of variability at the seasonal level. Groups A and B remain the most similar, with few taxa which serve to distinguish them specifically. These are fish larvae (cruise 2, group A), *Littorina* spp. larvae (cruise 2, group B); *O. nana,* bivalve larvae, and 'gastropods 3' (cruise 5, group B).

To summarise these results:

In terms of ecological separation, groups A and B are relatively homogeneous, but evolve during the season. The separation between groups is weakest in June, and strongest in July and particularly in August. This is seen both for the cluster analysis/CA and for overall average abundances. In cruise 2 the area sees little structure at the level of the community, but there is an E/W separation with high numbers of meroplankton to the East (*Crepidula, Littorina* spp., caridean and other decapod larvae, and medusae). The southern group of station is restricted, and though characterised by stenohaline taxa in the cluster analysis, their abundances are higher in station group A - which extends over a large area. In cruise 3 the main separation in the cluster analysis is between A and B/C, but in terms of the *F* tests, SGC is again the most defined. There is a N/S separation, with meroplankton close to the coast, euryhaline / holoplanktonic taxa in central stations and stenohaline taxa further out, but no clear E/W separation. In cruise 4 however, SGB can be seen as an intermediate group, with no preponderance of a particular sub-community, but a stronger separation from the cluster analysis. In cruise 5 we see both a E/W separation between groups A & B of meroplankton (E) and holoplankton/euryhaline taxa (Solent), and a southern group of stations, with clear abundance differences.

4.C.5. Community Sub-Groups

To assess the relative importance of the holo- and meroplanktonic components of the community, CA and clustering were performed, as in sections 4.C.3.a and 4.C.3.b separately on these two subsets.

4.C.5.a. *Correspondence Analysis*

Tables A.4.4 and A.4.5, summarising the CAs on the community sub-groups, can be seen in appendix A. In both cases, as with the WC analysis, species excluded because of their overbearing influence on the first dimensions have strong spatial variances. For holoplankton, *C. helgolandicus* and *Para/Pseudocalanus* spp. both have similar southern maxima in cruise 2; in cruise 3, *C. helgolandicus* was again excluded, together with *Sagitta* sp. and harpacticoids which all show eastern/south-eastern density patterns; Fish larvae

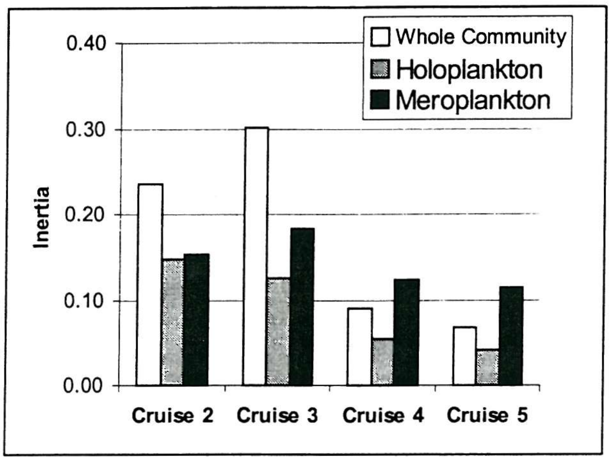


Figure 4.13: Inertia of the stations × taxa matrices as calculated by the correspondence analyses.

(also excluded) are abundant in the Solent. There are no excluded taxa in cruises 4 and 5 for holoplankton.

For meroplankton, we find the same taxa as were excluded from the WC analysis: *Littorina* larvae, 'gastropods 2', and 'gastropods 3' (respectively, cr. 3, 4 and 5), but without this time barnacle nauplii (cr.5 previously). Added to these are decapod megalopa (cr. 2) who tend to have a Solent/central distribution, with however a maximum in station 29 to the South.

The inertia of the data sets varies according to figure 4.13. For holoplankton, the trend is consistently downwards, but the inertia of the WC follows that of meroplankton in having a maximum in cruise 3. Meroplankton however does not have the proportionally large differences shown by both WC and holoplankton between cruises 2 and 3 on one hand and 4 and 5 on the other compared with holoplankton. The inertia of the meroplankton data set is greater in July and August, which consequently probably accounts for an important fraction of that variance in the first two cruises. In that respect we can characterise the June cruises as 'holoplankton influenced', and the July / August as 'meroplankton influenced', at least from the point of view of contribution to variance. It should be kept in mind however that inertia is not an absolute value, and as such comparisons between cruises should be limited to relative levels.

Specifically, the groups formed *via* cluster analysis can be compared.

4.C.5.b. *Clustering*

Similarity between units is variable across cruises (figures A.4.6 A & B, and A.4.7 A & B), again a reflection of the different overall inertia of the data sets at each date, and thus follows the same patterns as in figure 4.13 above. The CAs themselves however extract only a proportion of this overall variance (tables A.4.4 and A.4.5), between 50 and 90% (average: 71%). Despite this the groupings in the ordination diagrams show good separation along dimensions 1 and 2 (figures A.4.8 to A.4.15), indicating a good representation of the overall data sets by these two dimensions in particular, and the CAs in general. The spatial representation of these groupings (figures 4.14 & 4.15) also reveals defined clusters of stations, although this time with more 'orphaned' stations, or as in the case of meroplankton/cruise 3 (figure 4.15), a whole cluster (stations 5-1, 6, 19 and 20). However both subsets show a north/south separation, though for holoplankton/cruise 2, the southern group is restricted to a band of stations (figure 4.14). The group of NE stations is distinguished only for meroplankton, in cruises 4 and 5: thus for holoplankton only two groups are distinguished in each cruise, three for meroplankton in cruises 3, 4 and 5. Solent stations tend to be amalgamated with central stations, except for meroplankton/cruise 5, and for holoplankton/cruise 3 where Calshot and East Ryde are grouped with southern stations. Within each cruise, the WC analysis shares varying characteristics with the subsets which are compared below:

- Cruise 2: The WC groupings follow the holoplankton, in that the larger southern meroplankton group is not seen, and instead a small band of stations is distinguished, although these are extended northwards to include stations 5-1, 5-3, 4 and 24, compared with WC. They are characterised by fish eggs in both cases, and also *Oikopleura* sp. for holoplankton. Bracklesham bay stations, associated with *Littorina* spp. in WC, do not cluster in the sub-components.
- Cruise 3: Both sub-components show a larger group of southern stations extending more (holoplankton) or less (meroplankton) to transect 1, as opposed to WC, which is restricted to transects 2 (2 stations) and 3 (5 stations). WC follows meroplankton in separating Solent stations (though stations 3 and 22 are excluded in the meroplankton), and in having a group of central stations, whereas holoplankton sees Solent and central stations amalgamated.

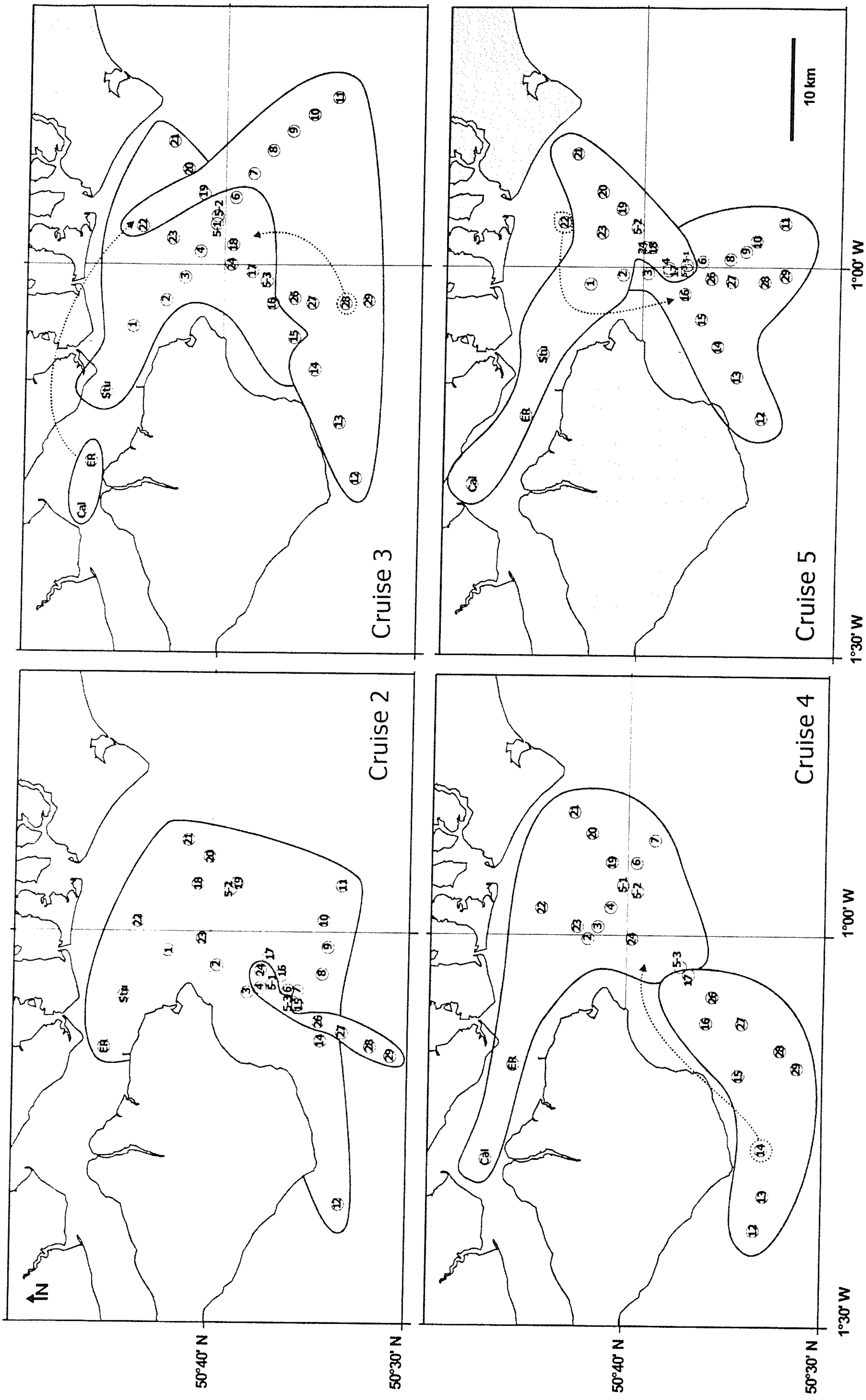


Figure 4.14: Station groups as derived from the cluster analysis of station scores on the correspondence analysis dimensions (holoplankton), cruise 2-5.

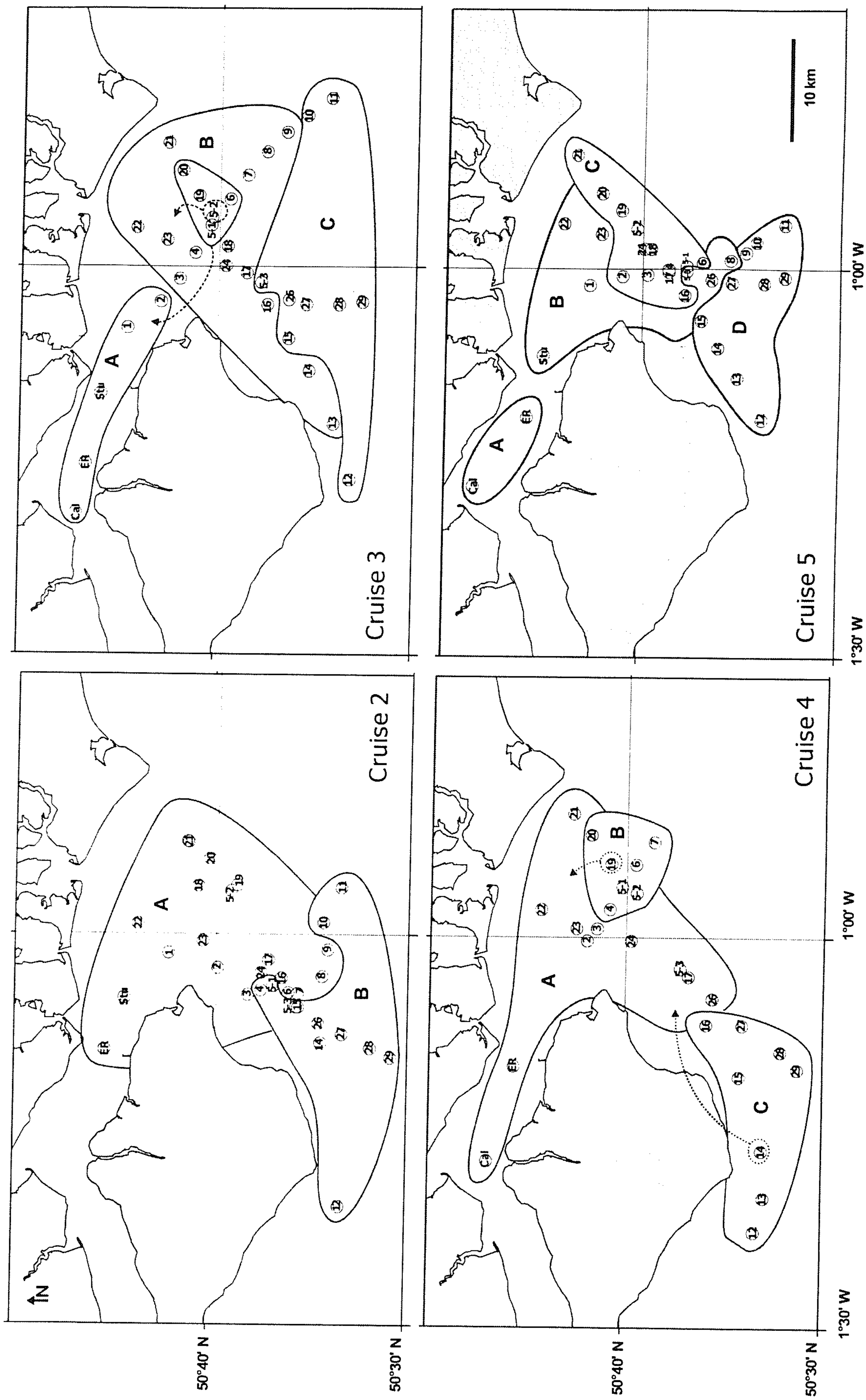


Figure 4.15: Station groups as derived from the cluster analysis of station scores on the correspondence analysis dimensions (meroplankton), cruise 2-5.

- Cruise 4: The holoplankton and meroplankton share some similarities, *i.e.* the separation of a southern group, with station 14 'orphaned' from the central/Solent group. This does not appear in the WC analysis. However holoplankton does not distinguish the group of stations off Bracklesham Bay as do WC and meroplankton.
- Cruise 5: Here the WC analysis follows closely the meroplankton pattern, indicating a strong influence of this sub-group on the distribution of inertia of the WC data set. As for cruise 4, meroplankton distinguishes a group of stations off Bracklesham Bay, whereas holoplankton does not. Furthermore, the southern group is identical in both.

These analyses see a lesser spatial coherence, compared with WC, with a number of 'orphaned' stations; however the spatial patterns remain distinctive, with some variations between the two sub-communities. The meroplankton analysis tends to show a greater amount of structure, with at least three groups distinguished in cruises 3-5, as opposed to the two that emerge from the holoplankton, reflecting a greater diversity of spatial structure in the meroplanktonic populations. The N/S separation is also clearer in the meroplankton, and the 'Bracklesham Bay' group of stations appears in cruises 3-5 (thought linked to the Solent in cruise 3), but does not appear at all in the holoplankton, which therefore sees no distinction between 'Solent' stations and 'Bracklesham Bay'.

From these results, it appears that the WC groupings reflect both the patterns seen in the subcommunities, with important differences: the Bracklesham Bay group of stations is predominantly present in the meroplankton populations, since for holoplankton it is not separated from Solent populations. It seems to be predominantly present in July and August, since in June it is poorly defined: principally by one taxa in cruise 2 (*Littorina* spp. larvae), and as a sub-group of the Solent stations in cruise 3. The southern group however is present in both subcommunities, to a similar extent in both, with a clearer pattern for the meroplankton in cruise 2. The patterns seen in the WC reflect these trends, in that Bracklesham Bay stations are poorly distinguished in cruises 2 and 3, but clearly present in cruises 4 and 5. The southern group is present in all four cruises, but to a lesser extent in cruise 4 compared with both subgroups; it seems therefore that in this case treating the two subgroups together leads to a loss of information.

4.C.6. Taxa-Environment Relationships

4.C.6.a. *General*

For each cruise, Canonical Correlation Analyses (CCA) were performed on the whole data, and the two subsets separately. So that a direct comparison could be done with the CAs, the same outlying taxa were excluded and added as supplementary points; correlations were done separately for these taxa and all are predominantly correlated with temperature: for cruise 3, *Littorina* spp. larvae is correlated with temperature ($r_s = 0.57$, n = 33, $P<0.01$) and transmission ($r_s = 0.36$, n = 33, $P<0.05$); in cruise 4, 'gastropods 2' is correlated strongest with temperature ($r_s = 0.21$, n = 26) and salinity ($r_s = 0.18$, n = 26) but these are not significant at $\alpha = 0.05$; and in cruise 5, barnacle nauplii are correlated with temperature ($r_s = 0.77$, n = 30, $P<0.01$) and transmission ($r_s = -0.52$, n = 30, $P<0.01$), and 'gastropods 3' with temperature ($r_s = 0.43$, n = 30, $P<0.05$). Again these significance values do not take autocorrelation into account so should be treated with caution.

In all cases the CCAs show high species/environment and environmental values/dimensions correlations (tables 4.5 & 4.6). The ranges of values for the species-environment correlation are for dimension 1: 0.87-0.91 (WC analysis), 0.65-0.89 (holoplankton), and 0.76-0.89 (meroplankton). The proportion of variance of the stations × taxa matrix CA explained by the CCA is 31-51% (WC), 26-46% (holoplankton) and 34-56% (meroplankton). Of this (explained) variance, the first 2 dimensions of the CCA explain between 90 and 100%; the potential energy anomaly (ϕ) was never retained by the procedure of forward selection, and therefore does not explain significantly any proportion of the variance of the data set (at $\alpha = 0.01$). Transmission was retained in cruise 3 for meroplankton and in cruise 4 (WC, holo- and meroplankton), leaving temperature, salinity, transmission and fluorescence as main factors.

Differences between the three analyses are slight: for confirmation, the same values and patterns are found in the sum of all unconstrained eigenvalues as in figure 4.13 (section 4.C.5.a). This time the trend for canonical eigenvalues follows that of the holoplankton in having a steady decrease during the season, which is not the case for meroplankton: thus the constrained ordination fits the holoplankton pattern closer than the meroplankton, indicating that the holoplankton is possibly more important in driving the variance of the whole data set, when constrained by environmental variables.

4.C.6.b. *Whole community*

The high correlations between the CCA dimensions and the environmental variables is immediately apparent when figure 4.16 is compared with figures 4.7-4.10: the constrained ordinations (CCA) are virtually identical to the unconstrained CAs, for all cruises (with reversed axes in cruises 2, 3 and 5, and a different relative spread of taxa and stations along the dimensions). Thus even when forced to be linear combinations of the environmental variables, the dimensions of the CCA turn out very close to the indirect analysis. As a consequence, and also because of the low number of variables, the environmental axes are close to that of the CCA dimensions. Thus the ordination of taxa and stations along the first 2 dimensions can in most cases be directly interpreted as environmental gradients. Because taxa/station groups from the CA/cluster analyses tend to be separated along the CA dimensions, this also means that these groups can be directly linked to environmental variables, and the reader can refer to figures 4.7-4.10 for the separation of taxa/station groups along the first two CA/CCA dimensions. Both the eigenvalues (the proportion of variance explained) and the canonical coefficients (the change in community composition along dimensions) are usually high. These are next detailed date-by-date:

- Cruise 2:

  Dimension 1 is correlated equally with salinity (+0.44), and negatively with temperature (-0.44), with similar canonical coefficients. Therefore it separates high salinity/low temperature from low salinity/high temperature stations: Bracklesham bay stations (**station group B**) at the low salinity end and **southern stations** (26-29, 10-11) at the other. Taxa group C (*Para/Pseudocalanus*, *C. helgolandicus*, fish eggs), together with amphipoda, *E. acutifrons*, *M. membranicea* larvae, *Oikopleura* sp., and spionid larvae have high scores on this axis, and *Littorina* spp. larvae (taxa group B), 'Other harpacticoids', ostracods, *Crepidula* larvae, decapod larvae, 'gastropods 2' have low scores.

  Dimension 2 is essentially a fluorescence/chlorophyll gradient (+0.31) which separates mainly stations from **group C**; at the other end we find station **group B** and **SW stations** (9-11) and station 12. Taxa are fish eggs, *P. brevicornis*, *Oikopleura* sp., *C. hamatus*, spionid larvae at low fluorescence, and *Para/Pseudocalanus* spp., amphipoda, ostracods and *C. helgolandicus* at the higher end.

Cruise 2

	Whole Community				**Holoplankton**				**Meroplankton**			
axis	1	2	3	4	1	2	3	4	1	2	3	4
eigenvalues	0.071	0.019	0.010	0.045	0.046	0.017	0.006	0.035	0.040	0.010	0.005	0.039
Spp-env. correlation	**0.91**	**0.64**	**0.89**	0.00	**0.79**	**0.73**	**0.79**	0.00	**0.76**	**0.66**	**0.53**	0.00
Cumulative percentage variance:												
- of species data:	29.6	37.5	41.6	60.5	30.4	41.9	45.9	69.1	24.6	31.1	33.8	57.6
- of species-environment relation:	71.0	90.1	100.0	0.0	66.2	91.3	100.0	0.0	72.7	91.8	100.0	0.0
Sum of all unconstrained eigenvalues	0.239				0.151				0.162			
Sum of all canonical eigenvalues	0.100				0.069				0.055			
Proportion of CA explained by CCA:	**41.8%**				**45.7%**				**34.0%**			

Cruise 3

axis	1	2	3	4	1	2	3	4	1	2	3	4
eigenvalues	0.059	0.031	0.044	0.029	0.024	0.016	0.039	0.021	0.044	0.032	0.008	0.028
Spp-env. correlation	**0.88**	**0.83**	0.00	0.00	**0.65**	**0.82**	0.00	0.00	**0.83**	**0.83**	**0.68**	0.00
Cumulative percentage variance:												
- of species data:	20.5	31.4	46.7	56.7	16.1	26.8	52.5	66.3	24.6	42.3	46.5	62.3
- of species-environment relation:	65.1	100.0	0.0	0.0	60.0	100.0	0.0	0.0	52.8	90.9	100.0	0.0
Sum of all unconstrained eigenvalues	0.287				0.151				0.18			
Sum of all canonical eigenvalues	0.090				0.040				0.084			
Proportion of CA explained by CCA:	**31.4%**				**26.5%**				**46.7%**			

Cruise 4

axis	1	2	3	4	1	2	3	4	1	2	3	4
eigenvalues	0.032	0.012	0.002	0.015	0.022	0.001	0.010	0.006	0.042	0.024	0.003	0.027
Spp-env. correlation	**0.87**	**0.81**	**0.68**	0.00	**0.87**	**0.60**	0.00	0.00	**0.81**	**0.81**	**0.55**	0.00
Cumulative percentage variance:												
- of species data:	36.3	49.5	51.5	68.5	41.8	44.2	62.6	73.3	34	53.6	55.8	77.6
- of species-environment relation:	70.4	96.3	100.0	0.0	94.5	100.0	0.0	0.0	60.9	96.2	100.0	0.0
Sum of all unconstrained eigenvalues	0.089				0.054				0.123			
Sum of all canonical eigenvalues	0.046				0.024				0.069			
Proportion of CA explained by CCA:	**51.7%**				**44.4%**				**56.1%**			

Cruise 5

axis	1	2	3	4	1	2	3	4	1	2	3	4
eigenvalues	0.021	0.005	0.010	0.009	0.017	0.003	0.010	0.008	0.034	0.012	0.020	0.014
Spp-env. correlation	**0.89**	**0.82**	0.00	0.00	**0.88**	**0.62**	0.00	0.00	**0.89**	**0.71**	0.00	0.00
Cumulative percentage variance:												
- of species data:	29.6	36	50.6	63.1	31.9	36.8	56.8	71.6	29.8	40	57.5	69.3
- of species-environment relation:	82.3	100.0	0.0	0.0	86.8	100.0	0.0	0.0	74.5	100.0	0.0	0.0
Sum of all unconstrained eigenvalues	0.071				0.052				0.115			
Sum of all canonical eigenvalues	0.026				0.019				0.046			
Proportion of CA explained by CCA:	**36.6%**				**36.5%**				**40.0%**			

Table 4.5: Summary of the Canonical Correspondence Analyses results: eigenvalues, correlations between species and environment; proportion of variance explained by the CCAs (proportion of CAs and of species-environment relationships). Sal=Salinity; Temp=Temperature; Fluo=Fluorescence; Trans=Transmission (continued in table 4.6).

		Whole Community					Holoplankton					Meroplankton			
		canonical coefficients		correlation coefficients			canonical coefficients		correlation coefficients			canonical coefficients		correlation coefficients	
	Axis variable	Axis 1	Axis 2	Axis 1	Axis 2	Axis variable	Axis 1	Axis 2	Axis 1	Axis 2	Axis variable	Axis 1	Axis 2	Axis 1	Axis 2
Cruise 2	**Sal**	0.22	-0.15	**0.44**	0.02	**Sal**	-0.29	-0.03	**-0.36**	-0.20	**Sal**	0.15	-0.23	0.35	-0.19
	Temp	-0.21	-0.20	**-0.44**	-0.17	**Temp**	0.03	0.15	0.26	0.23	**Temp**	-0.23	-0.16	**-0.40**	-0.01
	Fluo	-0.16	0.31	-0.11	**0.31**	**Fluo**	0.29	-0.27	0.24	**-0.29**	**Fluo**	-0.15	-0.20	-0.12	**-0.22**
Cruise 3	**Temp**	0.43	0.21	**0.46**	0.14	**Temp**	0.20	0.31	0.13	**0.34**	**Sal**	0.16	-0.09	-0.31	0.06
	Fluo	0.16	-0.40	0.24	**-0.37**	**Fluo**	-0.37	0.12	**-0.34**	0.18	**Temp**	0.21	0.36	**0.41**	**0.16**
											Tran	-0.21	0.29	-0.39	0.14
Cruise 4	**Sal**	-0.09	-0.22	0.07	**-0.25**	**Temp**	-0.34	-0.09	**-0.36**	-0.08	**Sal**	-0.16	-0.24	-0.02	**-0.31**
	Temp	-0.36	0.08	**-0.37**	0.15	**Tran**	-0.15	0.17	-0.19	**0.17**	**Temp**	-0.36	0.16	**-0.34**	0.25
	Tran	-0.20	-0.20	-0.23	-0.18						**Tran**	-0.26	-0.20	-0.28	-0.17
Cruise 5	**Sal**	-0.13	-0.25	-0.05	**-0.26**	**Sal**	-0.05	-0.22	0.03	**-0.22**	**Sal**	-0.12	-0.32	-0.01	**-0.33**
	Temp	-0.38	0.03	**-0.36**	0.09	**Temp**	-0.36	-0.02	**-0.36**	0.03	**Temp**	-0.43	0.01	**-0.41**	0.09

Table 4.6: (continued from table 4.5) Summary of the Canonical Correspondence Analyses (axes 1 and 2): canonical coefficients and correlation coefficients.

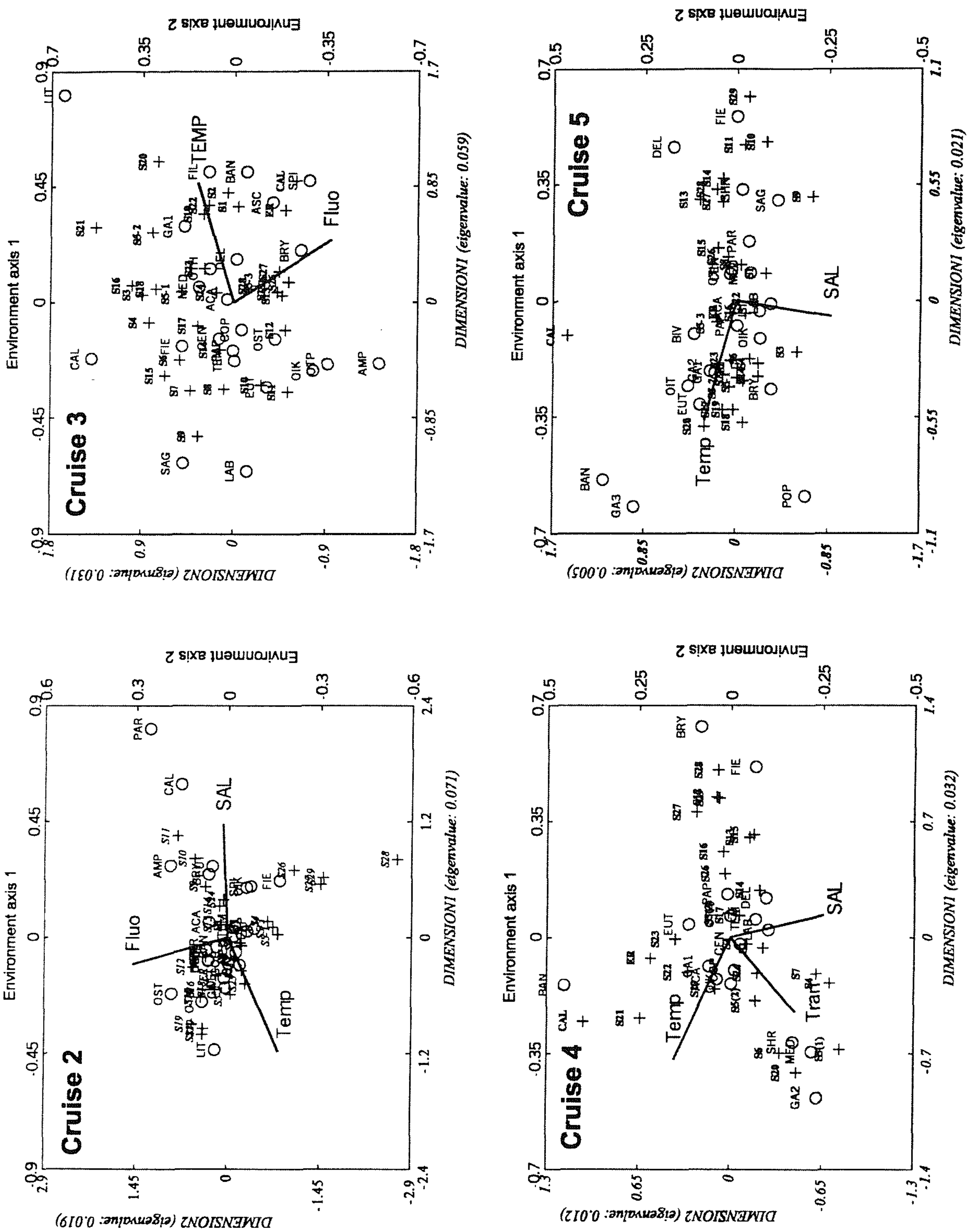


Figure 4.16: Station (+) and taxa ( ) scores on dimensions 1 and 2 of the Canonical Correspondence Analysis (CCA) on station × species and station × environment matrices (whole community). The length of the environmental arrows is proportional to their correlation with the CCA dimensions (maximum = 1).'Sal'= salinity; 'Temp'= temperature; 'Fluo'= fluorescence; 'Trans'= transmission. For taxa and station abbreviations see table A.4.1.

- Cruise 3: Two dimensions extract most of the variance explained by the CCA. Dimension 1 is a strong temperature gradient (+0.46) with a high explanatory power (canonical coefficient 0.43) separating neatly the meroplanktonic TGA, which all are to the right of the origin of this axis (also *Acartia* and 'Other harpacticoids'), from holoplankton. Most of TGC have low scores on this dimension, and most of TGB intermediate scores (except *E. acutifrons* and *Sagitta* sp.). Station groups are also distributed clearly with **SGA**: high scores; **SGB**: low scores; **SGC**: intermediate.

  Dimension 2 is again a (negative) fluorescence gradient (-0.36) with also a high negative canonical coefficient (-0.40). **SGB** is spread over the axis, but **SGA** has high scores and **SGC** low scores.
- Cruise 4:

  Dimension 1 is principally a negative temperature gradient (-0.37), with some influence of transmission (-0.20); it separates mainly **SGC** and **SGA** (high scores/ low temperature) from **SGB** (low scores/ high temperature). The pattern is identical for taxa groups, *i.e.* fish eggs and *M. membranicea* larvae (TGC) at the high salinity end and taxa such as medusae, caridean larvae, *Acartia* spp. at the other; the exception being barnacle nauplii which have a low score on this axis and are therefore with TGB at the low salinity end.

  Dimension 2 is principally a salinity gradient, with however not an overbearing influence (salinity:-0.25; temperature: 0.15; transmission: -0.18). The canonical coefficients are about the same for both salinity and transmission (-0.22 and –0.20), but low for temperature (0.08) and thus the latter has a small effect on community composition despite the correlation. This dimension is a poor separator of taxa groups A and C; all but *Acartia* spp. from TGB have low (high salinity) scores. Stations are better segregated, with, correspondingly, **SGB** at the lower end (except station 19). **SGC** is sandwiched between **SGA** stations on the higher (low salinity/transmission). **Solent stations** (Calshot, East Ryde, 22, 23) are particularly well separated and opposed to **SGB**, making this predominantly a W/E gradient with 'gastropods 2' (outlier), medusae, caridean larvae to the east and barnacle nauplii strongly associated with the Solent.

- Cruise 5:

  Dimension 1 is a clear temperature gradient (-0.36, compared with –0.05 for salinity), with a high canonical coefficient (-0.38) separating the taxa and station groups along its axis. **SGC**/TGC at the low temperature end, **SGA**/TGA in intermediate values (clustered around the origin), and **SGB**/TGB towards high temperatures. Polychaete post-larvae and 'gastropods 3', outliers, are at the extreme of the high temperature values.

  Dimension 2 is clearly a salinity gradient (-0.26), which poorly describes station groups and TGC: the spread around the origin is small (figure 4.17), except Calshot, which is at the maximum (lowest salinity). However taxa groups A and B are well represented, with TGB clustered towards the low salinities (*e.g.* barnacle nauplii, *O. nana*, bivalve larvae) – except *M. membranicea* larvae, close to the 'high salinity limit' for taxa. TGA on the other hand has intermediate/low scores. The two outliers are at opposite ends: 'gastropods 3' with TGB (low salinities) and polychaete post-larvae at the other.

4.C.6.c. *Community Subgroups*

As in the WC analysis, the CCAs on sub-communities conform closely to the CAs (figures 4.17 & 4.18, compared with figures A.4.8-A.4.15), allowing for differences in spread along the dimensions between stations and taxa. The correlation and canonical coefficients are high (tables 4.5 & 4.6 above), and there are no major differences in the selection ofenvironmental variables: they are the same for all three in cruises 2 and 5. Holoplankton and WC analyses show temperature and fluorescence as main factors in cruise 3, and salinity, temperature and transmission for meroplankton. In cruise 4 WC follows the meroplankton in having salinity, temperature and transmission as constraining variables (temperature and transmission for holoplankton). Within these distinctions the relative importance of the environmental factors in explaining the changes in community structure show some detail: temperature is systematically the most important factor in the meroplankton ordinations, with salinity relatively important in cruises 2 and 3. In cruises 4 and 5 salinity is negligible in explaining dimension 1, but transmission is relatively important in cruise 4. For holoplankton, temperature is also the main influence in cruises 4 and 5, but salinity is the main factor in cruise 2, with fluorescence also an important component (in both dimensions); the main factor in cruise 3 is fluorescence.

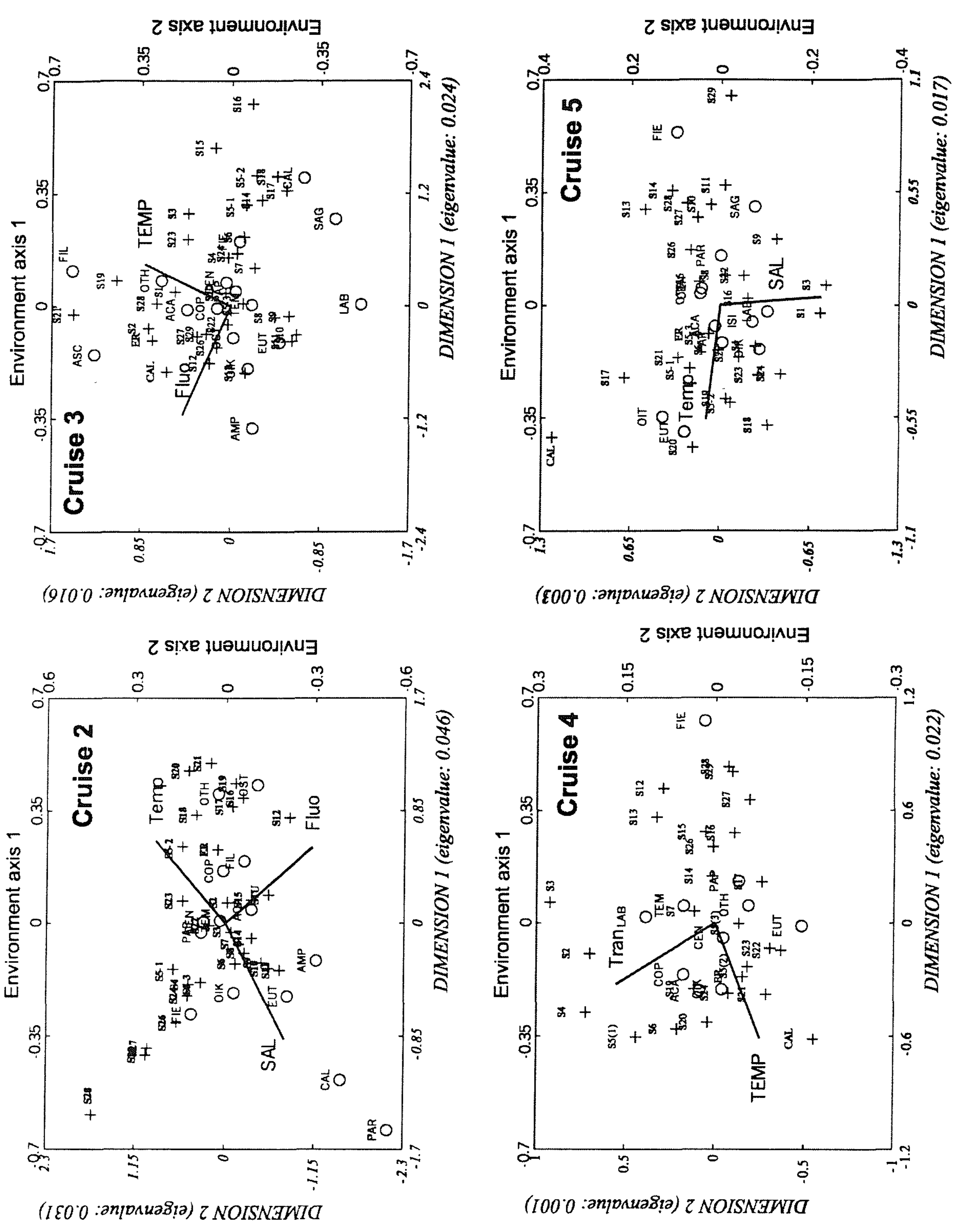


Figure 4.17: Station (+) and taxa ( ) scores on dimensions 1 and 2 of the Canonical Correspondence Analysis (CCA) on station × species and station × environment matrices (holoplankton). The length of the environmental arrows is proportional to their correlation with the CCA dimensions (maximum = 1).‘Sal=salinity; Temp= temperature; Fluo= fluorescence; Trans= transmission. For taxa and station abbreviations see table A.4.1.

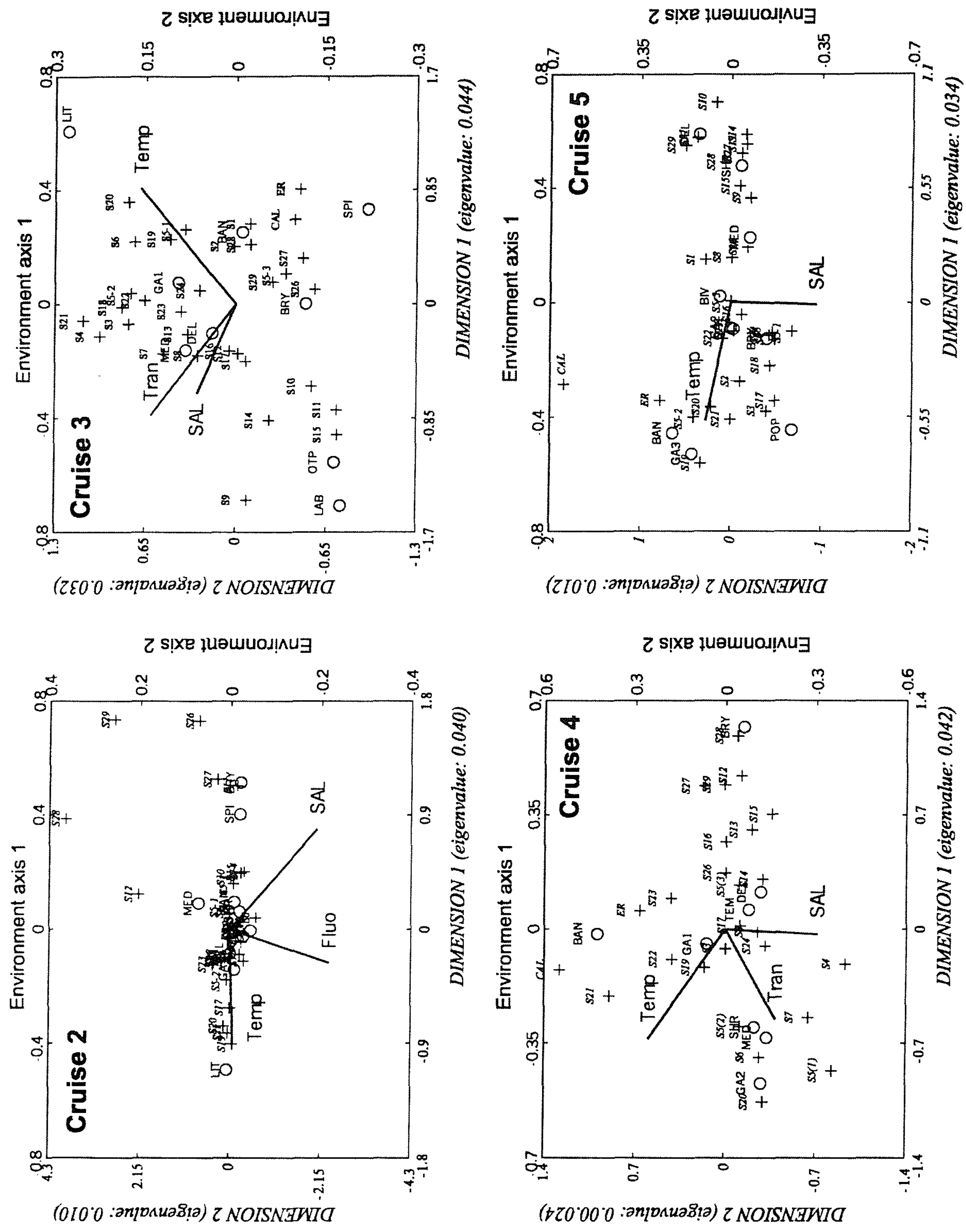


Figure 4.18: Station (+) and taxa ( ) scores on dimensions 1 and 2 of the Canonical Correspondence Analysis (CCA) on station × species and station × environment matrices (holoplankton). The length of the environmental arrows is proportional to their correlation with the CCA dimensions (maximum = 1).'Sal=salinity; Temp=temperature; Fluo=fluorescence; Trans=transmission. For taxa and station abbreviations see table A.4.1.

Linking the CCA ordinations (figures 4.17 and 4.18) to the separation of station/taxa groups along the CA axes (figures A.4.8-A.4.15) and their spatial distribution (figures 4.14 & 4.15), we can describe the separation of the station/taxa groups in terms of environmental factors. For holoplankton, the separation between groups is oriented N/S and is always along dimension 1, which is a function of salinity (also, to a lesser extent, fluorescence in cruise 2), fluorescence (cruise 3), and temperature (cruise 4 and 5). For meroplankton the separation is between three groups in cruises 3-5 and two in cruise 2. For cruises 4 and 5 the separation between the three groups is along dimension 1, with temperature as the controlling factor, as it is in cruise 2 but for 2 groups. Cruise 3 has 2 axes of separation, with temperature and transmission as main influences (*n.b.*: transmission and salinity are highly correlated for this cruise – figure 4.18 – and thought CCA chooses transmission as a better descriptor, it is likely that salinity, which here has a relatively high correlation coefficient, is also important).

These results reveal the strong constraining of the community structure by the measured environmental variables. In particular the ordination separates well the groups formed by cluster analysis, indicating that environmental variables can be linked to group separation and therefore to changes in community structure. They also show that the station groups are distinctive environmental features, which act on both subcommunities, with however some differences. The meroplankton is clearly linked to temperature across the season, however the link does not seem to increase particularly in proportion to the change in temperature seen between June and July. This is not the case for holoplankton, which seems to has a stronger link to temperature in the last two cruises. It also is linked to fluorescence in the June cruises. The analyses on the subcommunities follow the CA patterns, which were shown to be different between each other, and therefore it can be concluded that the environmental variables act differently on the two subgroups.

4.D. Discussion

4.D.1. Sampling

The strong currents found in the area have an important effect on the repositioning of stations, and therefore the mesozooplankton distribution patterns found will depend to some extent on the reliability of the method. The coherence of the hydrographic measurements for the repositioned situation has already been established in chapter 2, and shows that spatial trends of physical factors are resolved by this technique. For plankton samples, aggregative behaviours, diffusion, vertical movement or changes in depth of populations are not taken into account. The latter includes the depth distribution of certain species, or as described in section B.5.d, the change in mean depth of a population (vertical migration), either diel (DVM), or tidal (through STST or increased turbulence). Planktonic organisms may show aggregation patterns at different depths regardless of the stratification or turbulence levels (*e.g.* Lagadeuc *et al.*, 1997). For organisms which show constant, if irregular, depth profiles, the sampling will be biased. This in itself may not effect comparisons between stations, but it will change the relative importance of taxa, and will be influenced by turbulence, and therefore tidal state. Because sampling was done during the day, the same applies to DVM. Tidal effects and tidal vertical migration are therefore potentially the greatest sources of error.

Few studies deal with this explicitly in euryhaline environments, concerning themselves mainly with estuaries (but see Brylinski & Aelbrecht, 1993 for a counter-example). Even fewer are done in a Lagrangian context, *i.e.* changes in community are seldom separated from changes in water masses going past the sampling station. There are exceptions, such as Wiafe & Frid (1996), sampling a community dominated by *Oithona similaris, Pseudocalanus* spp., *Acartia clausi, A. longiremis*, and *Temora longiremis*. Following drogues, they saw evidence of changes in community structure (as measured by principal component analysis) over a tidal cycle. The community 'unit' was better described as several consecutive samples together, and the change from one unit to the other could be tied to changes in advective processes (wind and/or tide), while changes within units were attributed to biological effects (*e.g.* predator escape, vertical migration). They conclude by showing that community structure remained stable for at least 3 hours at a time. In a Eulerian (fixed point) context, Zagami *et al.* (1996) showed that tidal variation can be accompanied by biomass variation, and that community composition varied at longer term seasonal scales; Gray (1996) has similar data for larval fish assemblages. In an estuarine context, Dauvin *et al.* (1998) found that the vertical distribution of certain taxa changed with the phase of the tidal cycle and/or the time of day. For example *C. hamatus* showed significantly higher abundance at flood tide than at ebb; *E. acutifrons* and barnacle nauplii showed higher abundances at ebb; and gastropod larvae, *Oikopleura dioica*, *Pseudocalanus elongatus*, *T. longicornis*, *Acartia* spp. and ostracods did not show any significant differences. For all species bar *E. acutifrons*, *O. dioica* and larvae of the polychaete *Pectinaria koreni,* there were more-or-less pronounced differences between day and night abundance distributions; again however these are Eulerian measurements. These effects will be compounded by constant-depth sampling, though oblique tows do not in themselves solve the problem (*e.g.* Lee & McAlice, 1979). Despite these remarks, from such studies we can conclude that 1) In the Lagrangian context, successive samples are similar to each other, though they may not be 'typical', and 2) in general the effect of tidal oscillation has been shown to increase density at flood tide (even in a Lagrangian context, *e.g.* Kimmerer *et al.*, 1998). Thus the community composition will tend to change in parallel. If the community changes are great enough across the sampling area and/or differences in relative abundances are great then repositioning may be sufficient to correct the bias. For the present study, CL98 found no statistical difference between samples taken at 5 and 10m depth, despite sampling at different tidal states. It does appear however from her figures that when peak densities are reached, abundances tend to be higher at 10m compared with 5 m, for most taxa bar *T. longicornis*, *I. clavipes*, gastropod larvae and *P. brevicornis.* This difference was most noticeable in Southampton Water, and Kostopoulou (1997) has shown conclusively that vertical distributions could change markedly with tidal state and time of day for copepods of this area. This was linked to DVM and turbulence levels. The effect is likely to be lesser in non-estuarine areas, but would imply that the depth distribution of most taxa is unequal at least during part of the sampling period and that the abundances given here are somewhat underestimated. The effect will be most noticeable on ubiquitous taxa which could show artefactual periodicities, and taxa which are likely to show marked vertical distributions such as harpacticoid copepods.

4.D.2. Abundance Measures

For a station close to Sturbridge, CL98 reports abundances, at 5 m depth, of 680 ind.m^{-3} in June 1995 (2024 ind.m^{-3} at 10 m), 598 ind.m^{-3} in July and 2883 ind.m^{-3} in August. This compares with abundances found here at Sturbridge of 371 ind.m^{-3} in cruise 2 (values at Sturbridge in cruise 3 shows an untypical 40 ind.m^{-3}), 6298 ind.m^{-3} (East Ryde, cruise 4) and 4398 ind.m^{-3} in cruise 5. These discrepancies can be due to a) Differences in sampling equipment: the nets used in Castro-Longoria's (1998) study were of the same mesh size but with smaller lengths and aperture (150 × 50 cm). This implies differences in sampling efficiency and volumes sampled; b) 'natural variability', as for example described above, and c) differences in sampling position (tidal movement was not taken into account). June samples in this study see lower abundances, July / August higher, it is therefore likely that the 'natural variability' is an important factor here since the bias is not constant, though of course clogging may play a role in recording lower numbers at high abundances in July and August. Furthermore one would expect lower abundances in the smaller net because of the stronger associated bow-wave, but this is not the case in June (though volumes are smaller). Nevertheless these discrepancies limit comparisons. When specific taxa are looked at the shifts in abundances compare well between the two studies for the Solent. Absolute abundances tend not to agree however, with no apparent pattern of over- or under-estimation.

In May, CL98 found abundances of up to 14181 ind.m^{-3} in the Solent, over twice the maximum of 6298 ind.m^{-3} found at East Ryde in cruise 4, and × 7 the maximum of cruise 2 found at station 11. From the June minima, numbers then rose to ~2880 ind.m^{-3} in August. Chlorophyll *a* values were found to be ~6 μg.l^{-1} in May, down to ~1 μg.l^{-1} in June and consistently decreasing beyond this date. Thus the sampling period of the present survey starts just after the seasonal mesozooplankton / phytoplankton peak, and ends during the second zooplankton increase, which for some taxa ends in September-October. There is no corresponding chlorophyll maximum in late summer, suggesting a high level of grazing. In both surveys fluorescence values at Sturbridge consistently decrease over the season, but spatially different dynamics are seen, since this is not the case for total average values in the present survey: maximum is reached in July, which could be interpreted as a lag of the zooplankton production such has been observed elsewhere in coastal waters (Fransz & Gieskes, 1984). This would be confirmed by the zooplankton trends, since there is a general increase in both cases of similar magnitude. As seen in chapter 2, stratification is minimal in the area and the double zooplankton peak cannot be linked to the 'classic' pattern of phytoplanktonic production linked to the establishment of a thermocline (Sverdrup, 1953), as is more common in the western English Channel (*e.g.* Pingree *et al.*, 1978; Le Fèvre *et al.*, 1983), with the consequent effects on zooplankton (*e.g.* Robinson *et al.*, 1986). Other similar areas of the English Channel are characterised by several small peaks, or a continuous production (*e.g.* Hoch, 1998; Hoch & Garreau, 1998; Le Fèvre-Lehöerff, 1993) as nutrients are remineralised. Suspended particulate matter may also be a limiting factor on phytoplankton, since it was found to reach high levels, especially compared to further offshore, in May 1995 (Fluxmanche II, 1998). A factor particular to this area also the very high densities of *Crepidula,* which may compete with the zooplankton over part of the phytoplanktonic production. However low values of primary production (<150 $gC.m^{-2}.yr^{-1}$) have also been modelled by Hoch (1998) for the Solent area, whose model includes nutrient input and regeneration in the water column, and an extinction coefficient; V. Hart (Southampton Oceanography Centre) has also reported nutrient values close to the detection limit for the sampling period (pers. comm.). This pattern is consistent with other sites in the English Channel. Le Fèvre-lehöerff *et al.* (1993) report similar trends for monthly averages of zooplankton biomass over the period 1976-1991 at several sites on the French coast. Differences were found between sites, related to local hydrodynamic conditions and suspended solids concentrations, with Western Channel sites more 'inertial', less productive and with strong but limited peaks in abundance.

The sampling period does not include the main zooplanktonic bloom which occurs in April-May, but differences still occur between taxa and the distinction can be made between early/late taxa over the three months of sampling. Thus the rise in abundances seen here corresponds to a succession sequence, similar to patterns observed *e.g.* on the French coast by Le Fèvre-Lehöerff *et al.* (1983). Boreo-arctic species such as *C. helgolandicus*, *E. affinis* see successful recruitment in late spring or early summer. Atlantic-Mediterranean taxa such as *E. acutifrons*, *Sagitta* sp. in late summer. Le Fèvre-Lehöerff (1993) attributes global abundance patterns to climatic factors, and the differences between taxa (mainly calanoids) to differential success of recruitment. For example *T. longicornis, C. hamatus* and *A. clausi* are seen to have simultaneous spawning events 4 or 5 times/year, linked to phytoplanktonic blooms. Recruitment success is maximum in April/May for *T. longicornis* (2nd spawning event), in July for *C. hamatus* (3rd) and in September for *A. clausi* (4th). This concords also with recruitment patterns seen off Plymouth by Digby (1950), and the work of CL98, and others, which have also shown the important effects of salinity, and especially temperature, on the different egg production and hatching rates of *Acartia* congeners and other copepods. Here this phased recruitment pattern is also visible in the meroplankton, and in fact there is no major difference with the holoplankton at this scale of observations, both having a group of taxa dominant in all four cruises (*e.g. Acartia* spp., *C. hamatus*, *Crepidula* larvae, barnacle nauplii), and another which varies across cruises. Thus there is no evidence of more 'pulsed' cycles for the meroplankton as could be expected. This could be linked to the low proportion of *e.g.* polychaete larvae which tend to have more restricted spawning periods, but it is more likely that the sampling scale does not permit to resolve this, since the intervals between cruises 3-5 are longer than (*e.g.*) the average copepod generation time (Digby, 1950). There is a slight difference in maximum abundance between the two (July for meroplankton, August for holoplankton, not statistically significant), but this is unlike that reported by Robinson *et al.* (1986), who found the reverse pattern in the western English Channel.

The measures of diversity are essentially stable throughout the season, so that the relationship between taxa abundances remains similar despite the shift in species composition. This is also reflected in the proportion of 'dominant' taxa (>1% abundance) which remains at ~⅔. This would indicate that as a whole the community is in a growth phase, rather than one where competition is important since shifts in abundance are not accompanied by the development of a particular taxa at the expense of others.

4.D.3. 'Key Taxa'

The different analyses performed on the data are complementary in that they look at the variations of taxa across stations. From this, we can classify these into three categories:

1) 'Structuring taxa', which represent best the ecological variations across the area. These contribute most to the CA dimensions (table 4.3), but also include the taxa excluded from the analysis, *i.e. Littorina* spp. larvae in cruise 2, 'gastropods 2' in cruise 4 and in cruise 5 barnacle nauplii and 'gastropods 3'.
2) 'Characteristic taxa', which are not representative of the community as a whole but characterise station groups (table 4.5).
3) 'Key taxa', closely correlated with the CA dimensions but with marked abundance clines across station groups. These are *Crepidula* (cruise 2), barnacle nauplii and fish eggs (cruise 3), bryozoan larvae (cruise 4), fish eggs, and polychaete post-larvae (cruise 5).

These taxa either typify the variations of the community across the sampling area, or characterise specific groups of stations. They will be influenced in different ways by hydrographic and hydrodynamic factors: 'structuring' taxa will tend to follow gradients of environmental factors. 'Characteristic taxa' will be more sensitive to processes of retention or aggregation in particular areas, as they interact with generation time or larval life span, or they will show very restricted areas of occurrence along an environmental gradient. 'Key taxa' will exhibit marked variations along environmental gradients, and exhibit sub-populations within the area.

4.D.4. The Mesozooplanktonic Community

The community sampled is essentially euryhaline-marine. There is a limited presence of true-estuarine taxa, but a high proportion of taxa such as *Acartia* spp., *C. hamatus, E. acutifrons, O. nana,* and others frequently reported in zones of freshwater influence of the English Channel, and a moderate presence of more stenohaline species (*e.g. T. longicornis, C. helgolandicus, Oikopleura* sp. and *Para/Pseudocalanus* spp.). This is also evident in the lack of strong relationship of the community with salinity, usually the determining factor in more typically estuarine environments (*e.g.* Laprise & Dodson, 1994) or indeed in similar coastal environments (*e.g.* Williams, 1984). There are few holoplanktonic predators, but *Oikopleura* sp. is the second most dominant taxa after *Acartia* spp. in July and August, indicating that smaller organisms are probably an important component of the plankton. *Sagitta* sp. is in low numbers until August, where it reaches ~50 ind.m^{-3}. Tentatively, this could mean that this is in fact *S. setosa* rather than *S. elegans*. For the Bay of S^t Brieuc, Vallet & Dauvin (1999) report maximum abundances of *S. setosa* in July-August, and Vallet & Dauvin (1999) see a small maximum *S. elegans* peak in June (Ibanez & Dallot, 1969 also see a maximum *S. setosa* peak in July-August). This - together with the presence of *Calanus helgolandicus* - would fit in with the idea that the Solent fits within the 'eastern English Channel' area, as seen in the benthos, since *S. setosa* is associated with water masses of the Eastern English Channel.

Another potentially important group of zooplankton predators are fish larvae, which are most abundant in June, at less than 1.5 ind.m^{-3} (possibly undersampled by the WP-2 nets). Similarly to CL98, there were no records of the ctenophore *Pleurobrachia pileus,* and only one of the scyphomedusa *Aurelia aurita.* These are often found in estuaries (*e.g.* Wang *et al.*, 1995, Lucas, 1994), and *A. aurita* and *P. pileus* are both found in Southampton Water (Lucas, 1993; Lucas & Williams, 1994, 1995) and *P. pileus* in Portsmouth Harbour. However they are also known to occur in stenohaline environments (C. Lucas, Southampton Oceanography Centre, pers. comm.), so their absence here remains to be explained. In any case, this leaves meroplanktonic taxa such as certain decapod larvae as potentially important predators, with *Sagitta* sp. in late summer.

4.D.5. The Meroplanktonic Compartment

The proportion of meroplankton is high, with high numbers of barnacle nauplii, decapod larvae, and very high numbers of *Crepidula* larvae, which can be linked to its widespread and abundant occurrence in the Solent. This high proportion has also been noted in other bays, such as Arcachon bay (Castel & Courties, 1982; Sautour & Castel, 1993), though this not always the case (*e.g.* Archambault *et al,* 1998).Conversely, there are few polychaete, bivalve and echinoderm larvae, which may well be undersampled because of their size (especially bivalves, echinoderms or spionids); *O. edulis* larvae have for example been seen in great numbers in the water column in July close to Calshot, but at a size of ~100 µm (T. S. Morgan, Southampton Oceanography Centre, pers. comm.). For some species it is also likely that the breeding season has been missed: this is probably the case for *Lanice conchilega*, which occurs both in the subtidal and in several isolated sandy patches around the coast. Juveniles were observed to have settled in the Bembridge and Ryde populations in May 1995 (pers. obs.). Many benthic organisms are also known to match their reproduction cycle to phytoplankton production events (Thorson, 1946; Starr *et al.*, 1990), and as mentioned earlier, the main phytoplanktonic bloom occurs in May. In any case, just as certain decapod larvae are likely to compete with predators, larvae such as *Crepidula*, which feed in the water column, are likely to be important competitors of the holoplankton.

There is a clear link between meroplankton dominance and distance from shore, mainly due to the numbers of littoral taxa such as *Crepidula* and barnacle nauplii, which can be tied to the large densities of the gastropod in the East Solent, and the barnacle populations observed in the West Solent, at Bembridge (in the intertidal), and on boulders in most areas of the outer approaches. *Elminius modestus* is abundant in the area, and is often associated with oyster beds (Knight-Jones & Waugh, 1949). There are probably also important colonies associated with the harbours; at any rate these are two near-shore taxa, and this is reflected in the distribution of their larvae which contribute greatly to the distinction between station groups, both in the CA and the SNK tests. This is particularly noticeable in cruises 3-5, though the 'centre of mass' of *Crepidula* larvae is predominantly off Bracklesham Bay, whereas for barnacle nauplii it is closer to Calshot, confirming the origin of this population as probably the West Solent, and indicating that Bracklesham Bay may be a concentration zone for *Crepidula*. Zinger (1989) found higher numbers of both these larvae towards the mouth of Southampton Water, compared with inside the estuary.

Littorina spp. larvae originate probably from Bembridge, which is the only intertidal rocky shore of the immediate area and which supports a number of macrophyte species, although they may also occur in some areas south of the Isle of Wight and towards Calshot. These are practically absent from cruises 4 and 5, but in June show a marked distribution associated with central stations, and very little dispersal; These behave as passive particles in the water column, and therefore are most likely to reflect principal current patterns of the area, which seem to promote little dispersion. They also have a long pelagic life (6 weeks for *L. littorea*: Kraeuter, 1974). Based on their similar distributions, the same dependence on current patterns may apply to 'gastropods 2' in cruise 4, and 'gastropods 3', and 'polychaete post-larvae' in cruise 5, though this taxon is probably not 'passive': this taxon is thought to be composed predominantly of *Nephtys* spp. metatrochophore II or erpochaete larvae. These two stages are though by Cazaux (1981) to last up to 35 days in the plankton and 15 days close to the benthos, and this is consistent with Oyenekan's (1986) observation that *Nephtys hombergii* has a peak spawning in July in Southampton water. The very restricted distribution seen in cruise 5, compared with a distribution of adults predominantly found in the East Solent, could imply either strong retention mechanisms, or active aggregation. *N. hombergii* juveniles may settle in nursery areas, then migrate to a recruitment habitat (Olive, 1977).

Some meroplanktonic distributions seem to indicate that two populations were sampled: this is the case mainly for spionid, *M. membranicea*, and ascidian larvae, which showed a similar distribution in cruise 3. These could be associated with a Bembridge source population, and a second, unknown, originating from the south of the Isle of Wight - possibly originating from the West Solent or Southampton Water, explaining their association with the southern group of stations in cruise 4, though the intermediate salinities observed there are present in all cruises. They could also be mixed in from the East, entering through the eastwards residual flow described in Chapter 2.

4.D.6. Seasonal Evolution of the Holo/meroplanktonic Compartments

The evolution of the densities of the two sub-communities, and their spatial pattern, give us an indication of the different constraints imposed upon them. The holoplankton sees a much greater variation in absolute abundances, and an increase over the whole area, starting with relatively low numbers towards the coast (and a negative correlation with salinity), and ending with a decreasing shore to sea abundance gradient (and a positive correlation with salinity and temperature). The increase in meroplankton is more restricted both in numbers and in its geographical extent, and does not change fundamentally in its geographic distribution, however the variance across stations becomes greater than that of the holoplankton, for which the increase is more uniform across the region. June cruises are characterised by lower abundances, with close-to-equal shares of holo- and meroplankton. The inertia of the June data sets are greater, due to increased differences in abundance between taxa, but more so to differences between stations - as could be inferred from the diversity values, which stay at similar levels. Thus the June data set has lower abundances, but more spatial variation. This occurs after the main zooplankton bloom; populations may still be food limited, explaining the significant correlation between fluorescence and total abundance seen in cruises 2 and 3. This is mainly true for the holoplankton, whose highest abundances occur towards the central Channel, where SPM values are much lower (Chapter 1; *Fluxmanche II*, 1998), and therefore where production can be assumed to be less limited by low light levels. Meroplankton occur closer to shore, reflecting the distribution of adult populations and their 'de-coupling' from phytoplankton distributions, but also a mechanism that prevents the widespread dispersal of larvae across the region.

4.D.7. Evolution of Station Groups

There are important shifts in the community, most noticeably between cruises 3 and 4, but also between the two June cruises, despite their similarities and the short time between the two. Certain taxa such as barnacle nauplii, *Crepidula* larvae or *T. longicornis*, display large fluctuations, and thus this does reflect a 'true', rapid evolution; but there is also the possible effect of the tide which in cruise 2 was above average (coefficient ~ 78; table A.2.2), and in cruise 3 at Neaps (~55). This might have resulted, given the different areas surveyed because of repositioning, in more defined gradients of community structure, because, for example, of lower tidal mixing and the reinforcement of hydrographic gradients or wind effects, at the expense of tidal-hydrodynamical factors. This may effect particularly the sampling of the southern group of stations, distinguished by the SNK test mainly by the absence of species from groups A and B in cruises 2 and 4, rather than by a positive association, with characteristic species (though it is clearly visible in the meroplankton). This could be confirmed by the widening of the temperature gradient noted in chapter 2, but hydrodynamic factors may also be important in explaining the differences seen, as they vary with the tide (this will be looked at further in chapter 5).

The SNK results show that station groups A and B are similar in the distribution of abundances, and there is little evidence to think that group C becomes more prominent in the latter part of the sampling period, as average temperatures and salinities increase. Thus there is a global effect of groups, as shown by the MANOVA results, but the main community evolution occurs within groups A and B, which are presumably more or less successfully sampled at each cruise. When compared statistically, few taxa are characteristic of particular station groups, and thus these may be best described as 'zones of convergence' of taxa, rather than sub-communities or singular biotopes. Tidal state may also exerts some influence on these results. Thus in cruise 3 (Neaps) there is a poor E/W distinction but a clear N/S gradient, whilst for other cruises, with tides above average, the E/W distinction is present. The area is dynamic, and a degree of mixing between areas is likely to occur, explaining the relative homogeneity of groups A and B, and the absence of strong gradients or faunistic clines within the euryhaline zone. This could indicate a predominance of hydrographic factors in determining the N/S separation (with a distinction both in the mero-and holoplankton), and a predominance of hydrodynamic effects in distinguishing between groups A and B. The distinction between groups is reinforced with time, as group B is mainly distinguished by clustering in July and August, and this mainly in the meroplankton. Thus meroplankton can be seen as the principal driving factor in the evolution of the 'faunistic clines' revealed by the analyses, whilst the tendency for holoplankton is to homogenise groups and reduce the overall variance.

4.D.8. Links to Environmental Variables

Several authors have reported on marked separations between coastal and off-shore communities within the English Channel, particularly within its eastern part. This is linked mainly to a frontal structure which act to separate water masses as they drift eastwards (Brylinski & Lagadeuc, 1990). Here the station groupings cannot be seen as permanent features, as their constituent taxa fluctuate and there are no clear hydrographic boundaries. Nevertheless, as groups, they are strongly linked to environmental factors, as shown by the CCA, with a large proportion of the data set explained by temperature, salinity, transmission or fluorescence. This is not to say that these are direct cause and effect relationships, since CCA, although it uses regression in its algorithm, is essentially a multivariate correlation tool.

Temperature is an important constraint for both subgroups and in all cruises, but is the main factor influencing meroplankton at all dates. For holoplankton there is also a correlation with fluorescence which appears in cruises 2 and 3, which can be linked to the correlation seen between total abundance and fluorescence. Salinity is relatively important in cruise 2, especially for holoplankton, but not beyond this date. Several authors have reported decreasing abundances of euryhaline species linked to higher salinities, for example *T. longicornis* and *Acartia* spp. in the Baie de Seine (Dauvin et al., 1998), or increased abundances at intermediate salinities, such as for *C. hamatus* in the Bristol Channel (Williams, 1984). Thus the increase in copepod numbers seen during the season could be partly linked to the penetration of populations from further offshore. This is the case in several other areas of the English Channel, such as in the Normano-breton Gulf and the Mont Saint-Michel Bay (Le Fèvre-Lehoërff *et al.*, 1986) and elsewhere (Dauvin, 1997).

'Temperature' probably includes a number of factors, for example bathymetry, and therefore distance from coast. This would partly explain its link to meroplankton over the four cruises, which is in higher proportions closer to shore (and therefore closer to adult populations). The lack of link with fluorescence for this subgroup indicates a 'de-coupling' of the relationship between meroplankton and phytoplankton distributions, meroplankton thus also being under constraints such as dispersal. This is not so much the case for holoplankton, for which temperature becomes the main constraint only in July and August. The link with fluorescence may imply a stronger food limitation, but also possibly similar hydrodynamical mechanisms acting on the zoo- and phytoplankton which could result in similar distributions. In July and August, the link to temperature certainly integrates several factors, though primary production seems not to be one of them judging from the lack of correlation. This could imply that food is no longer limiting, and that holoplanktonic populations are limited by growth rates. This has been observed for example for the North Sea (Fransz & Gieskes, 1984); a large proportion of the primary production is not used by the zooplankton in coastal waters (presumably benefiting the benthos, in particular *Crepidula*), because of the comparatively low growth rates of zooplankton. Temperature has been shown to determine in part copepod growth rates and egg-hatching success (CL98), which could be the determining factor in explaining holoplanktonic distributions here. This goes against several studies, which highlight a reinforcement of the link between zooplankton and salinity, and a weakening of the effects of temperature during the summer (*e.g.* Laprise & Dodson, 1994; Williams, 1984). This effect may still occur here, though it is masked by the overriding influence of temperature on abundances: in cruise 3, at the start of the zooplanktonic increase, the Bracklesham Bay station group (B) is mainly a holoplanktonic/ euryhaline group; in cruise 4 we see groups A and B associated with both, and in August group B is mainly meroplanktonic and group A holoplanktonic. This could suggest a gradual increase of offshore taxa, as the salinity increases across the area, and a greater characterisation of group B by meroplankton as the presence of holoplankton becomes more important in the Solent. A similar pattern has been observed by Williams (1984) in the Bristol Channel. Presumably, as the season wears on, remineralisation processes allow the growth of the phyto- and holoplankton, and these will be more important close to shore where soft sediments occur. Temperature is then the major structuring agent.

4.E. Summary

- The community sampled is essentially euryhaline-marine, and sampled a few weeks after the main bloom. There is a trend of increasing overall numbers, which is already underway in June, and which is seen in the majority of taxa, but less so in the meroplankton.
- Holoplankton and meroplankton were observed to have different temporal and spatial dynamics. The increase in numbers is greater in the holoplankton, which is dominated by *Temora longicornis*, *Acartia* spp. and *Centropages hamatus* in June, and *Oikopleura* sp., *Centropages hamatus* and *Temora longicornis* in July and August. The greatest change in holoplankton density occurs towards the coast, as salinity decreases, and part of this increase may be explained by the penetration of populations from the English Channel. The meroplankton is dominated by littoral taxa, particularly *Crepidula* larvae, barnacle nauplii, but also *Membranipora membranicea*, decapod and 'gastropods 2' larvae (which may not originate from the Solent area). The increase in numbers is more restricted than the holoplankton, and high densities occur close to shore throughout the sampling period.
- Three station groups were identified, essentially corresponding to Solent, Bracklesham Bay and southern stations. The component species of these groups were seen to change to a great extent between cruises. In terms of abundances, the southern group was most distinctive; there appeared to be little differences between Solent and Bracklesham Bay groups.
- Analyses on subcommunities revealed that the meroplankton was the principal factor in determining the Bracklesham Bay group of stations, but that this distinction was weak in June. The southern group was distinguished in both, and in all cruises.
- Environmental variables were shown to be strongly correlated to changes in community structure. This was linked to the separation of station groups which were ordered along the CCA axes.
- The main structuring environmental variables for the June cruises were salinity, temperature and fluorescence for holoplankton, and temperature, salinity and transmission for meroplankton. Temperature was the most important factor in July and August for both groups, together with some effect of transmission in July. Salinity showed little correlation in these cruises with community structure.

- This was interpreted in light of the different dynamics regulating the two subcommunities. It is hypothesised that the N/S axis is mainly the result of a hydrological gradient, though inhibition of N/S cross-tidal mixing may have some effect. The Solent/Bracklesham Bay distinction is possibly linked to a combination of hydrodynamic and hydrographic factors, interacting with the seasonal evolution of component species.

Chapter 5: Zooplankton Transport and Dispersal

5.A. Introduction

5.A.1. Modelling

The history of model development in biological oceanography is relatively short, with the first models of plankton cycles appearing in mid-1930s and 1940s, and the first biological models integrating circulation fields created in the 1960s and 1970s (Hofmann, 1993). However its development and success in the last 25 years has been considerable, as can be seen from the few examples discussed in the introduction to part B, and modelling is now part of most multidisciplinary research programs. As a rule, models can be divided into 'theoretical' and 'applied' categories, the former using simplified mathematical concepts for process and parameter studies. These have been driving ecological theory since it became a quantitative science, and have by now a long history going back, at least, to the logistic equation (Verlhust, 1838). The work of Hill (1991a, 1991c) or Richards *et al.* (1995), can be cited in example, as it pertains to transport: These authors describe the effect on horizontal transport of interactions between idealised patterns of tidal oscillation, shear flow, vertical migration and mortality. Hill (1991) also describes the theoretical effects of advection and diffusion on an idealised larval patch. These results give us an insight into what it is possible to expect under realistic conditions, and despite their relative simplicity, can reveal complex patterns of behaviour. Dekshenieks *et al.* (1996) and Dekshenieks *et al.* (1997), for example, show that even small changes in behavioural patterns, mortality or vertical currents can result in very different horizontal distributions and survival (in this case, of *Crassostrea virginica* larvae). These models can be highly complex and integrate population dynamics in time and space; this approach has paralleled the development of the metapopulation concept (Ruxton, 1996; Hanski, 1998), which explicitly deals with the dispersal and exchanges of spatially distinct subpopulations.

Large interdisciplinary programs have driven the development of 'applied models', which concern specific geographic areas and show a range of complexity according to the questions being asked, and the situations they are applied to. In their simplest form they are little more than 'theoretical' models, but applied to situations where measured factors are though to be close to the idealised situation. In their most advanced form they include complex circulation models (3-dimensional quasi-geostrophic, including freshwater inputs, stratification, wind stress, and other factors), and biological models including a range of parameters such as vertical migration, life-cycle stages, predation, reproduction, several trophic levels and others.

5.A.2. Objectives

As seen in chapter 2, the 2-dimensionnal hydrodynamic model developed at IFREMER has revealed a complex pattern of circulation at the level of the English Channel, with numerous recirculating cells of lesser or greater intensity, therefore more-or-less sensitive to wind effects. This variability across the Channel will lead to a number of situations, ranging from areas of strong and permanent areas of retention, to areas of permanent export. In between will be areas which will experience varying conditions, with wind being the main driving force behind the local variability. This will affect holoplanktonic populations in maintaining or homogenising populations, and the effect on benthic populations will occur through larvae, which will experience dispersal or retention from parent populations and suitable settlement substrates. In the preceding chapter, it was seen that the mesozooplanktonic communities of the Solent area are closely linked to environmental parameters; however these may act on two levels to create such a pattern: 1) by creating hydrological gradients which segregate populations according to tolerance range; this is likely to be the case for station group C, which appears in both holo-and meroplankton subcommunities; and 2) by being tied to hydrodynamic factors, which may act to separate populations according to the different residence times of different areas, or mix together different water masses; this may be the case for the group A/ group B distinction, which is apparent principally in the meroplankton cluster analyses. In practice, the two will be linked: Boxall & Robinson (1987) hypothesise that the strong E/W tidal flows to the south of the Isle of Wight result in the inhibition of cross-tidal mixing.

In the following sections, the 2-dimensionnal hydrodynamic model of the Channel presented in chapter 2 (to which diffusion and mortality terms have been added) will be used to test the potential effects of long-term tidal currents on the mesozooplanktonic communities of the East Solent. Specifically, the following hypothesis will be tested: the residual gyre observed off Bracklesham Bay acts to retain particles in the area, but this effect is wind sensitive, and under certain conditions recirculation breaks down.

5.B. Methods

5.B.1. The model

The model design has been briefly described in chapter 2 (section 2.B.5). The adaptation of the model for Personal Computer use was done by Pascal Bailly-du-Bois of the IPSN, with further modifications, model runs and data extraction in collaboration with Ms Céline Ellien (Océanologie Biologique, Université Paris VI). It uses a supplied data base of residual currents and tidal and wind data and interpolates between 8 different fixed situations. In this section, a sequence of diffusion and mortality calculations are added, so as to solve the equation of motion in its classic form (Salomon , 1990; Salomon & Breton, 1991, 1993):

$$\frac{\partial C}{\partial t}+u\frac{\partial C}{\partial x}+v\frac{\partial C}{\partial y}-K\frac{\partial^2 C}{\partial x^2}-K\frac{\partial^2 C}{\partial y^2}-mC=0 \qquad (5.1)$$

where C is the concentration per unit volume, u, v are velocity components, K is the dispersion coefficient, x, y are horizontal coordinates, m is mortality, and t is time. The model allows for wind and tidal state to be taken into account in the calculations, but does not include behaviour and therefore particles are considered as passive in the water column.

5.B.2. Model Runs

Within the model both tide and wind can be held constant, and therefore their respective effects can be assessed separately or in conjunction. For the purposes of this study, the methodology can be separated into two sections:

1. Measuring the effects of wind and tide on the dispersal of particles within the Solent area.
2. Measuring the influence of zones outside the Solent area. Three areas were chosen: West (Poole Bay), South (South of the Isle of Wight), and East (West Sussex coast). These release positions are illustrated in figure 5.1.

For constant conditions, 3 wind speeds were chosen corresponding to low wind (3 $m.s^{-1}$), intermediate (9 $m.s^{-1}$) and strong (12 $m.s^{-1}$), in 8 wind directions (0-360° in 45° sectors), and three tidal states (Neaps, average, Springs); 'true' conditions were also calculated, using measured wind and tides. Wind data was measured at La Hague (Cotentin Peninsula) by Météo France. This wind data set was used to calibrate the model, and

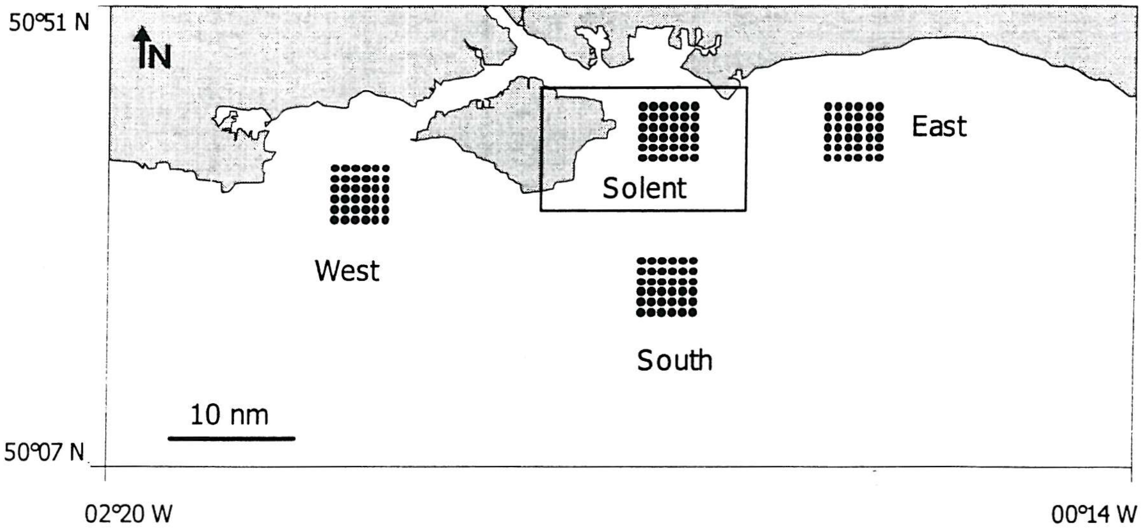


Figure 5.1: Release areas for simulation situations. The rectangle surrounding the 'Solent' area corresponds to the limits of the final percentage retention calculations.

therefore is best suited to run it in realistic situations, although it will not necessarily coincide with local conditions. Agoumi *et al.* (1983) have demonstrated that this station was the most suitable for determining wind forcing conditions over the entire Channel. From this database, it appears that winds between 3 and 9 $m.s^{-1}$ occur 75% of the time during the spring and summer months (15% for < 3 $m.s^{-1}$ and 10% for >9 $m.s^{-1}$). 12 $m.s^{-1}$ winds can be considered as exceptional.

For model runs in conditions of wind and measured tide, these were chosen so as to coincide with the cruises described in the preceding chapters. Thus the dispersal of particles was followed between cruise 2 and 3 (7 days), between cruise 3 and 4 (35 days) and between cruises 4 and 5 (25 days). Tidal state is as published by the SHOM (supplied by F. Dumas, IFREMER Brest), and is measured as tidal coefficient, which in theory varies from 20 (maximum Neaps) to 120 (maximum Springs) with 70 being an average tide. Over the sampling period (June-August 1995) it ranged from 33 to 106, and averaged 71. The variation of tidal coefficient with time can be seen in figure 5.2. The 1-week June simulation between cruises 2 and 3 occurs on a descending Spring tide (average: 72). Both July and August simulations cover, in order, a Neap and a Spring tide. They end at the start of the following Neaps, and average at 70; however the second simulation sees a slightly greater variation overall (ranges are 66 and 73, with identical maxima of 106). The wind data used to run the model can be seen in figure 5.3: it is bimodal, with 42% of winds from E to NNE and 38% from S to W. 15% occur from W to N and other sectors are approximately equal at 1% each. This bimodality occurs between July and August,

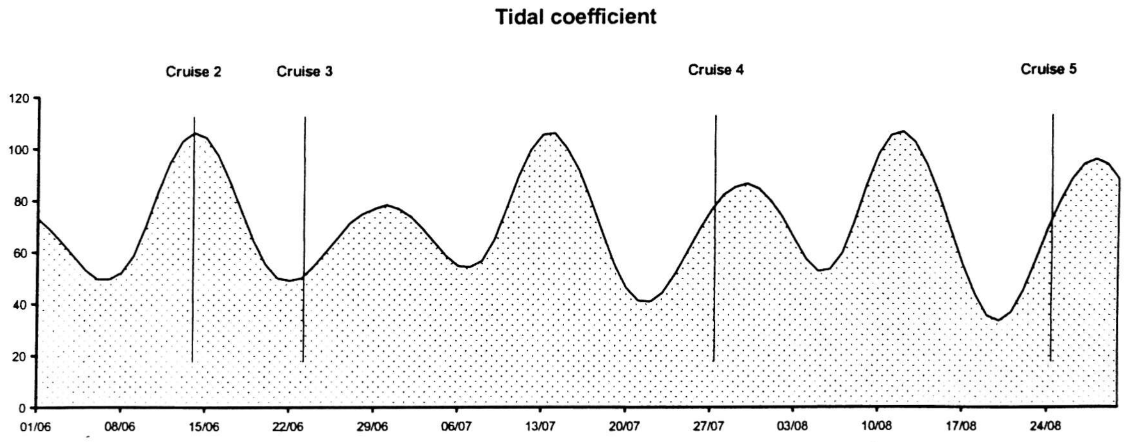


Figure 5.2: Tidal coefficients for the period 01/06/1995 to 31/08/1995 as used to run the model. From the Service Hydrologique et Océanographique de la Marine.

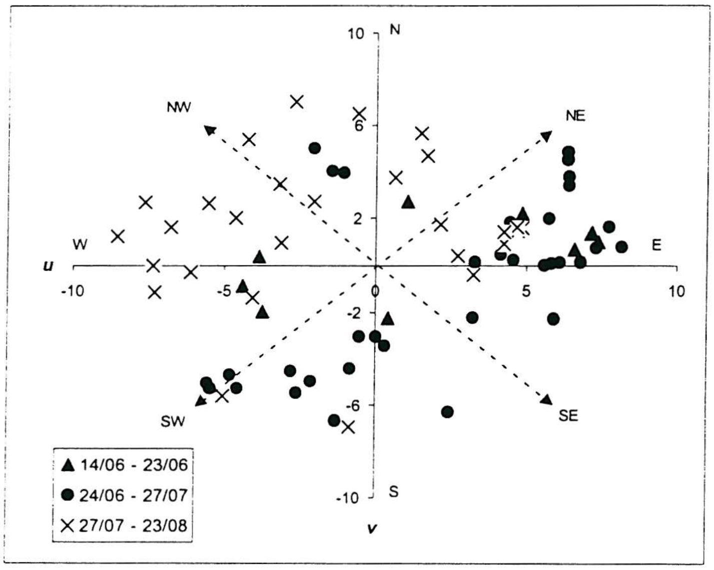


Figure 5.3: *u* and *v* components of wind data used for model runs (measured at La Hague, Cotentin Peninsula), for the period 14/06/1995 to 23/08/1995.

with the former seeing mostly SW to N winds, and the latter NE to SW. June winds are equally divided between E and W winds. Average wind speeds are 5.2, 5.7 and 5.5 $m.s^{-1}$ respectively for June, July and August model runs. The ranges are similar, at ~5 $m.s^{-1}$, as are maxima at 7-8 $m.s^{-1}$.

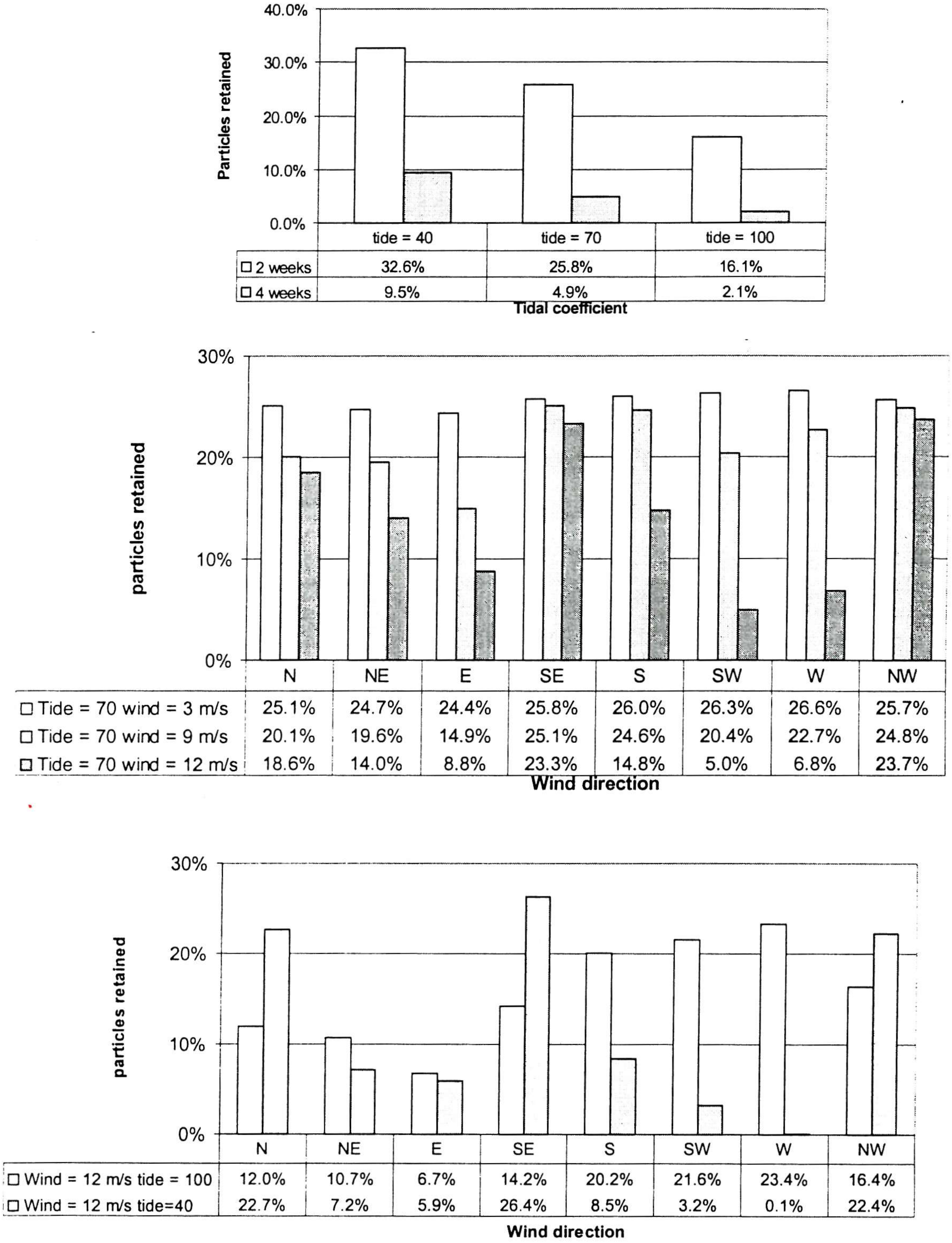
At each release area an arbitrary number of 1×10^{20} particles was released, in an area of 6 × 6 nm, and thus the results are expressed as percentages of the release either remaining, or imported into, the zone delimited in figure 5.1; this corresponds approximately to the areas sampled and described in chapters 1-4. So that the resulting percentages would remain meaningful, an instantaneous mortality rate of $6\%.day^{-1}$ was chosen (Rumrill, 1990; Morgan, 1995; C. Ellien, Université Paris VI, pers. comm.). It integrates many variables, as mortality varies with several factors, including age, sex, temperature, food availability and quality, and of course species; it is particularly difficult to obtain mortality rates *in situ*, but from the literature to date this would seem a conservative value, at least for invertebrate larvae (Morgan, 1995), so that percentages in the results section are probably 'worst-case' possibilities. For holoplanktonic species, particularly copepod nauplii, this may be an underestimation, however, as will be seen in the results section, an attempt has been made at separating the effects of advection/diffusion processes and mortality. It is calculated as $N_t = N_0 e^{-mt}$, where N_t is the population at time t, N_0 is the population at time $t = 0$, and m is the instantaneous mortality factor for $m = 0.06$. This corresponds to a mortality of 50% after ~11 days; this can be compared with *e.g.* Hatcher *et al.*, (1996), who measured *in situ* losses of scallop larvae, after a point release, of 50% in two weeks (mainly from predation). To assess the variability of the dispersal patterns, one month model simulations were run from the Solent release point for June, July and August of the years available in the tide and wind database, *i.e.* 1985-1995.

5.C. Results

The percentage of particles retained in the Solent area (as defined in figure 5.1) are summarised for the various model runs in figure 5.4, and will be commented upon in the relevant sections.

5.C.1. Tides

The effects of tidal state on the advection and dispersion of a patch of zooplankton in the Solent area, for periods of 2 and 4 weeks, can be seen in figures 5.4 (A) and 5.5. Over the two week period the situation is relatively similar at Neaps, Springs or at an average tide: the tendency is for retention in the area. Bearing in mind that by natural mortality alone the population will be reduced to ~41% after 15 days (for a mortality of $6\%.\mathrm{day}^{-1}$), the figure of 32% retention for a constant Neap tide shows the effect of the recirculation cell on the dispersal of particles. The evolution of the particle patches in time reveals the relative importance of advective and diffusive processes: at the lower tidal coefficient the pattern of extension is principally outwards from all sides, with some higher concentration in the Bracklesham Bay area; but the major extension occurs to the south and east. As the tidal coefficient is increased, advection becomes more important to the SW, and NW through the East Solent, with less expansion of the patch eastwards. Particles are also seen being entrained within the anticyclonic tidal residual gyre off Bracklesham Bay. On the Neap tide situation, highest concentrations are found within the Solent, although there is some advection to the SW, which can then be seen being advected eastwards. Despite the obvious importance of advection in determining the fate of particles, the strong tide situation also shows that there is a wider spread of particles across the area, possibly due to diffusion processes linked to increased current velocities (Salomon & Breton, 1993), and thus stronger tides both increase the role of advection but also the spread of the particles across the area. These factors result in lower absolute numbers retained in the area of interest with increasing tidal coefficient. Supplementary model runs and calculations show that, for a given tidal coefficient, the percentage of particles retained approximately follows an exponential decrease with time, but, for a tidal coefficient of 70, has a faster decrease for about 10 days, and a slower decrease after that (figure A.5.1). This was used to approximate daily loss rates and residence times, using an exponential function based on losses after 15 and 30 days. Thus figures in figure 5.4 can be



	tide = 40	tide = 70	tide = 100
☐ 2 weeks	32.6%	25.8%	16.1%
☐ 4 weeks	9.5%	4.9%	2.1%

	N	NE	E	SE	S	SW	W	NW
☐ Tide = 70 wind = 3 m/s	25.1%	24.7%	24.4%	25.8%	26.0%	26.3%	26.6%	25.7%
☐ Tide = 70 wind = 9 m/s	20.1%	19.6%	14.9%	25.1%	24.6%	20.4%	22.7%	24.8%
☐ Tide = 70 wind = 12 m/s	18.6%	14.0%	8.8%	23.3%	14.8%	5.0%	6.8%	23.7%

	N	NE	E	SE	S	SW	W	NW
☐ Wind = 12 m/s tide = 100	12.0%	10.7%	6.7%	14.2%	20.2%	21.6%	23.4%	16.4%
☐ Wind = 12 m/s tide=40	22.7%	7.2%	5.9%	26.4%	8.5%	3.2%	0.1%	22.4%

Figure 5.4: Percentage of particles retained in the 'Solent area' (see figure 5.1) relatively to the number initially released, in different conditions of tide (A, 2 and 4 weeks) and wind (B, 2 weeks), and for a wind speed of 12 m.s^{-1} at tidal coefficients 40 and 100 (C, 1 week).

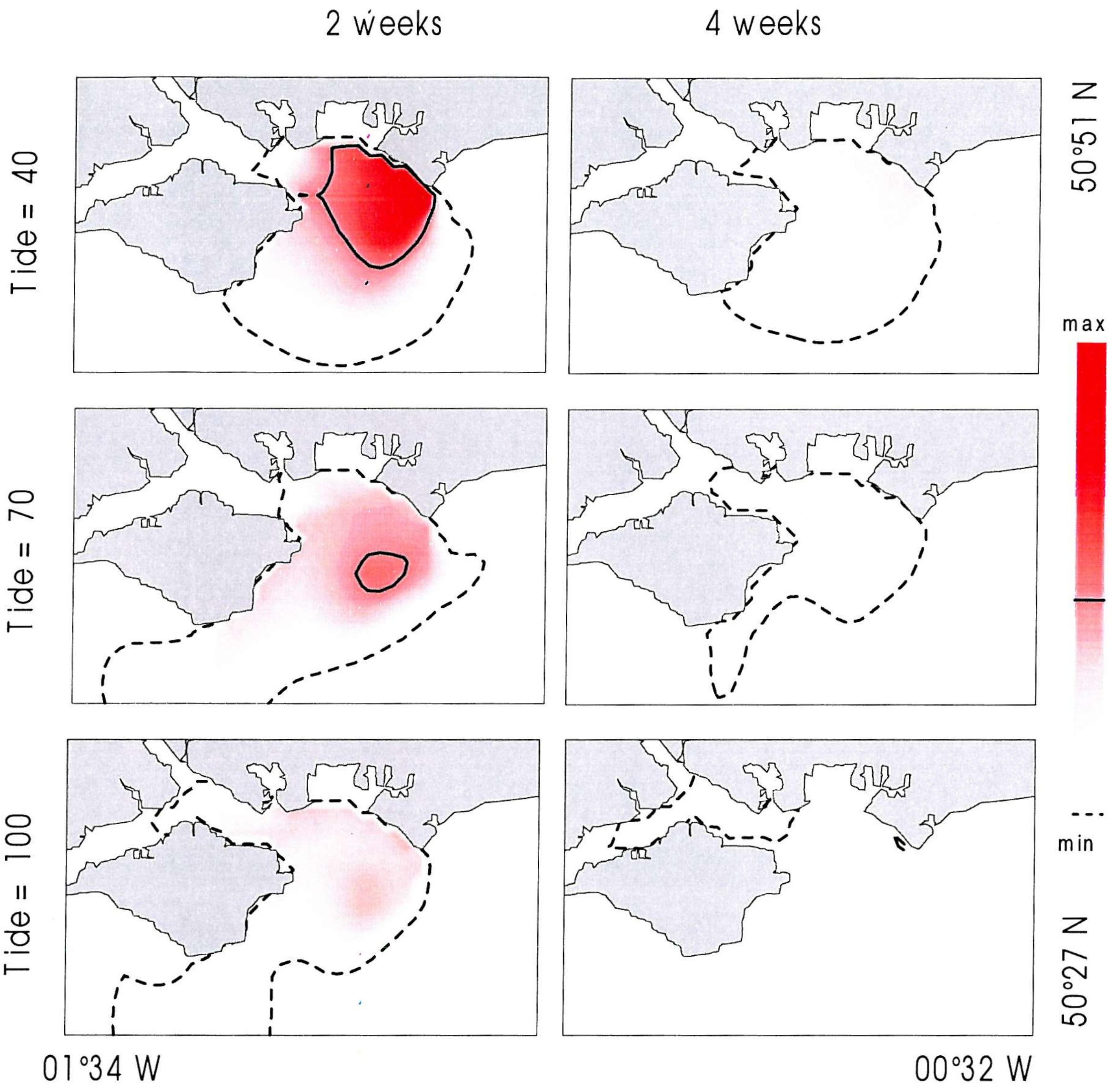


Figure 5.5: Patterns of particle dispersal under the influence of no wind and 3 tidal coefficients (Neaps = 40, average = 70 and Springs = 100) for a 2 week period. Release and final count areas correspond to that on figure 5.1. Colour scale is from maximum concentration (red) to minimum concentration (white). Isolines represent a difference of 1 order of magnitude, for comparison between maps.

	Mortality	Percentage losses due to advection/diffusion (per day)									
	6%	1%		3%		6%		9%		12%	
Time (Days)	M	M+A/D	A/D	M+A/D	A/D	M+A/D	A/D	M+A/D	A/D	M+A/D	A/D
7	65.7	61.3	93.2	53.3	81.1	43.2	65.7	35.0	53.3	28.4	43.2
14	43.2	37.5	86.9	28.4	65.7	18.6	43.2	12.2	28.4	8.0	18.6
21	28.4	23.0	81.1	15.1	53.3	8.0	28.4	4.3	15.1	2.3	8.0
28	18.6	14.1	75.6	8.0	43.2	3.5	18.6	1.5	8.0	0.6	3.5
Residence time:	11.6	69.3		23.1		11.6		7.7		5.8	

Table 5.1: Approximate relationship between time, losses due to mortality (M) and advection/ diffusion (A/D), expressed as percentage particles retained in the 'Solent area' (figure 5.1), and residence times. Column 'M' shows losses due to M alone; columns 'M+A/D' express losses due to M and A/D for a given loss factor; and columns A/D represent losses due to A/D alone for a given loss factor. Residence times are given in days and represent the time taken for 50% of the population to be lost through A/D. These figures assume a logarithmic relationship between losses due to A/D and time, which should be regarded as an approximation (see figure A.5.1).

approximated as corresponding to a loss factor equal to natural mortality for Springs (6%.day^{-1}), 3%.day^{-1} on an average tide and 1%.day^{-1} at Neaps; table 5.1 shows the relative importance of mortality and advection. Figures extrapolated below 15 days are likely to be somewhat underestimated, and those extrapolated beyond overestimated.

5.C.2. Wind

For an average tide and a wind velocity of 3 m.s^{-1}, wind direction has virtually no incidence either on the pattern of dispersal or on the quantity of particles retained, and therefore the model runs are not illustrated here; the retention values are given in figure 5.4 above, and the pattern is similar to that of *e.g.* a NE wind of 9 m.s^{-1} (figure 5.6). 15% of particles remain after two weeks, which approximate losses of 3%.day^{-1} due to transport alone. This is identical to the no-wind situation, and therefore the model detects very little effect for winds equal to or lower than 3 m.s^{-1}. For the variation that does occur, the most important losses occur for an easterly wind.

For winds of 9 m.s^{-1}, losses are still relatively low, with only easterly and north-easterly winds resulting in less than 20% retention (15% retention for E winds, *i.e.* ~7%.day^{-1} due to transport). Losses in this case occur through the East Solent and to the SW. Overall there is very little transport to the East, and this occurs mainly for W and SW winds. The proportion of losses for these situations remains small.

These trends can be reinforced by model runs of 2 weeks for winds of 12 m.s^{-1}. Although these are far from realistic, they allow a comparison to be made with previous runs, and preliminary tests have shown that the approximate pattern of exponential decrease in time

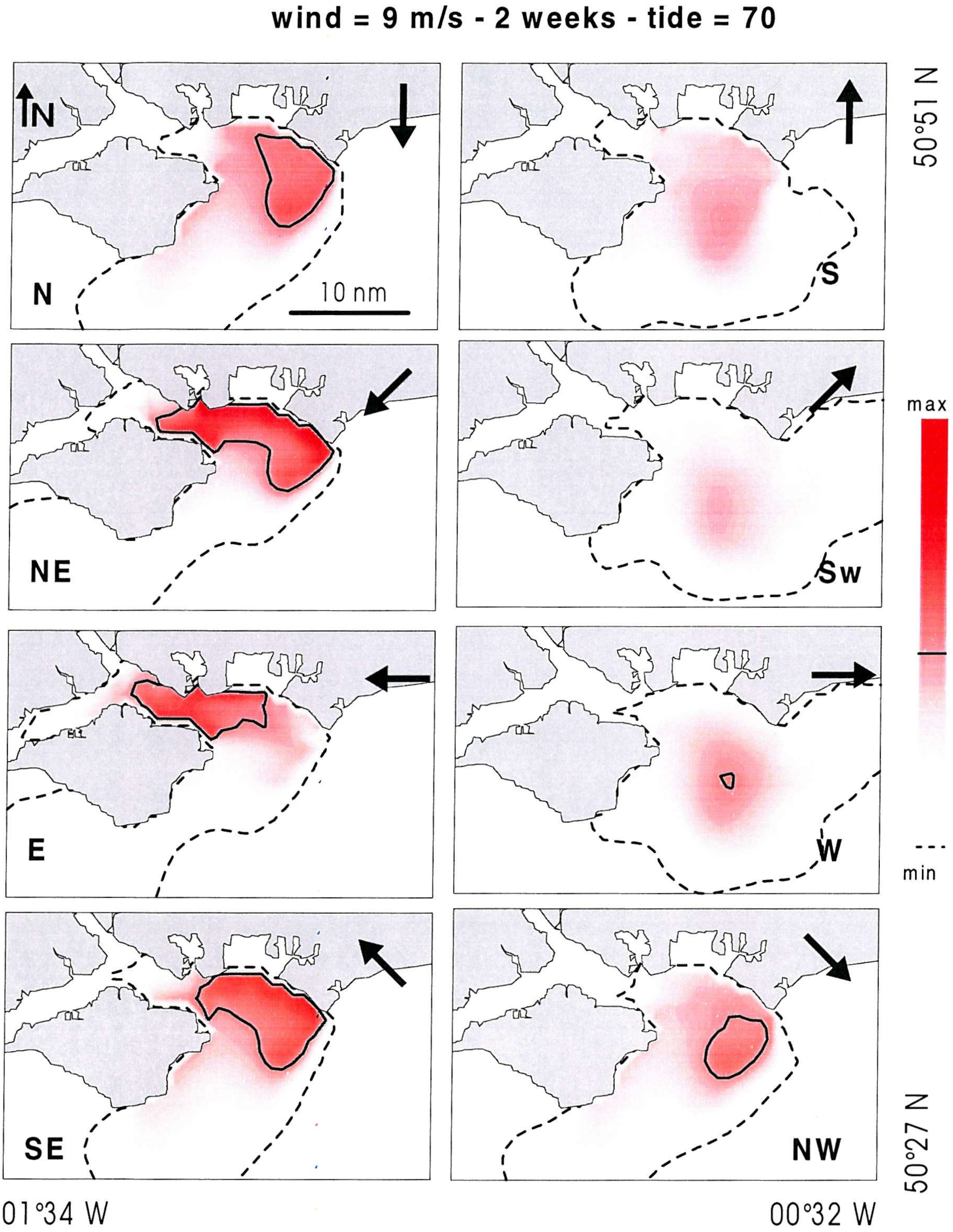


Figure 5.6: Patterns of particle dispersal under the influence of a wind of 9 ms^{-1} wind and an average tide (coefficient = 70) for a 2 week period. Release and final count areas correspond to that on figure 5.1. Colour scale is from maximum concentration (red) to minimum concentration (white). Isolines represent a difference of 1 order of magnitude, for comparison between maps.

holds when wind is included in the simulations. These results are displayed in figure 5.4 (B), and the dispersal patterns can be seen in figure 5.7. They show that for all wind directions, increased wind is always paralleled with increased losses from the area; however even for strong sustained winds, losses are small for NW and SE winds. Presumably, in the first case the land mass does not allow for enough fetch, and in the second the particles are trapped within the area; however they do not exit *via* the East Solent as they do for a E/NE wind. The greatest losses are this time from SW winds (instead of E, for $9.m.s^{-1}$), indicating that there is probably a threshold effect for SW winds, above which the anticyclonic residual circulation breaks down (as in chapter 2); in this case losses due to advection/diffusion are of ~13%.day^{-1}, *i.e.* ~ 4 times the losses due to tide alone. This threshold effect also occurs for S and W winds, which show a marked difference between 9 and 12 $m.s^{-1}$, relatively to the difference between 3 and 9 $m.s^{-1}$, above what could be expected from a log-relationship. For the worst case scenario of a SW wind of 12 $m.s^{-1}$, the figures imply losses of 14%.day^{-1}, *i.e.* over 2 weeks, at least 9 in 10 individuals are exported out of the area.

5.C.3. Wind & Tide

To look further at the interaction of wind & tide, 12 $m.s^{-1}$ winds were simulated over a 2 week period for tides of coefficient 40 and 100. In this case the deviations from an exponential decrease are great, and no logarithmic or linear relationship between wind strength and loss percentages was found; similarly for a given wind speed there seems to be no relationship between losses and tidal coefficient (unlike the 'no wind' situation), highlighting the role of threshold effects when tide and wind interact. The results are displayed in figure 5.4 (C) for retention percentages; the patterns of dispersal can be seen in figure 5.8 (only the results for Spring tides are displayed here). These can be compared with results displayed in figure 5.7 and 5.4 (B), for a tidal coefficient of 70.

Concerning the percentage of retention, and comparing tidal coefficients of 40, 70 and 100, three types of situations are observed:

1. Increasing tidal coefficient is followed by increasing losses (N, SE).
2. Increasing tidal coefficient is followed by decreasing losses (S, SW, W).
3. Minimum losses occur at average tide (NE, E, NW).

Thus, for S, SW and W winds, tidal effects counteract the easterly transport, by trapping particles in the East Solent gyre. For N and SE winds, transport through the East Solent and to the south is reinforced. For NE, E and NW winds, wind seems to switch between two patterns. For NE and E winds, the pattern of dispersal tends to be southward, whereas

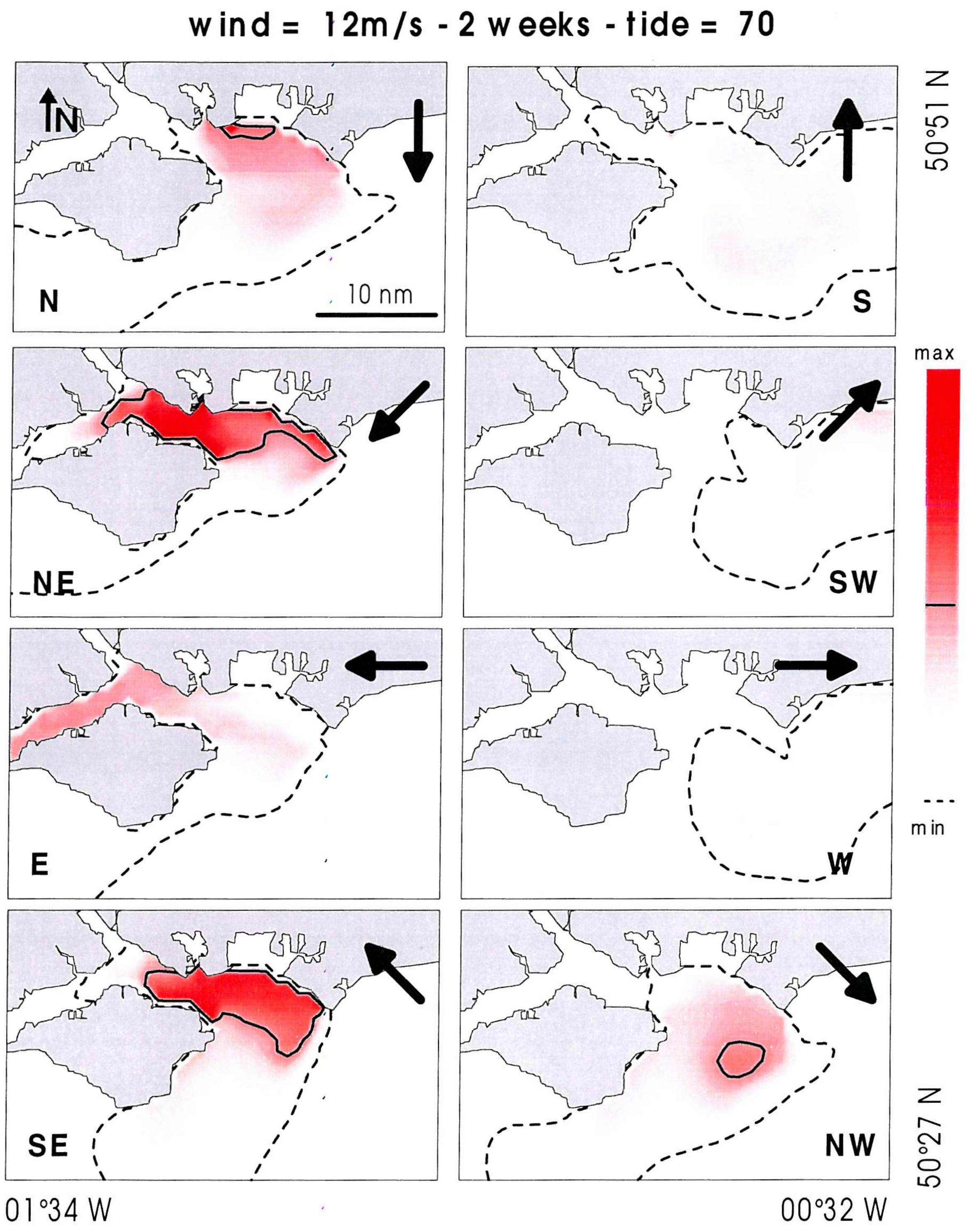


Figure 5.7: Patterns of particle dispersal under the influence of a wind of 12 ms^{-1} and an average tide (coefficient = 70) for a 2 week period. Release and final count areas correspond to that on figure 5.1. Colour scale is from maximum concentration (red) to minimum concentration (white). Isolines represent a difference of 1 order of magnitude, for comparison between maps.

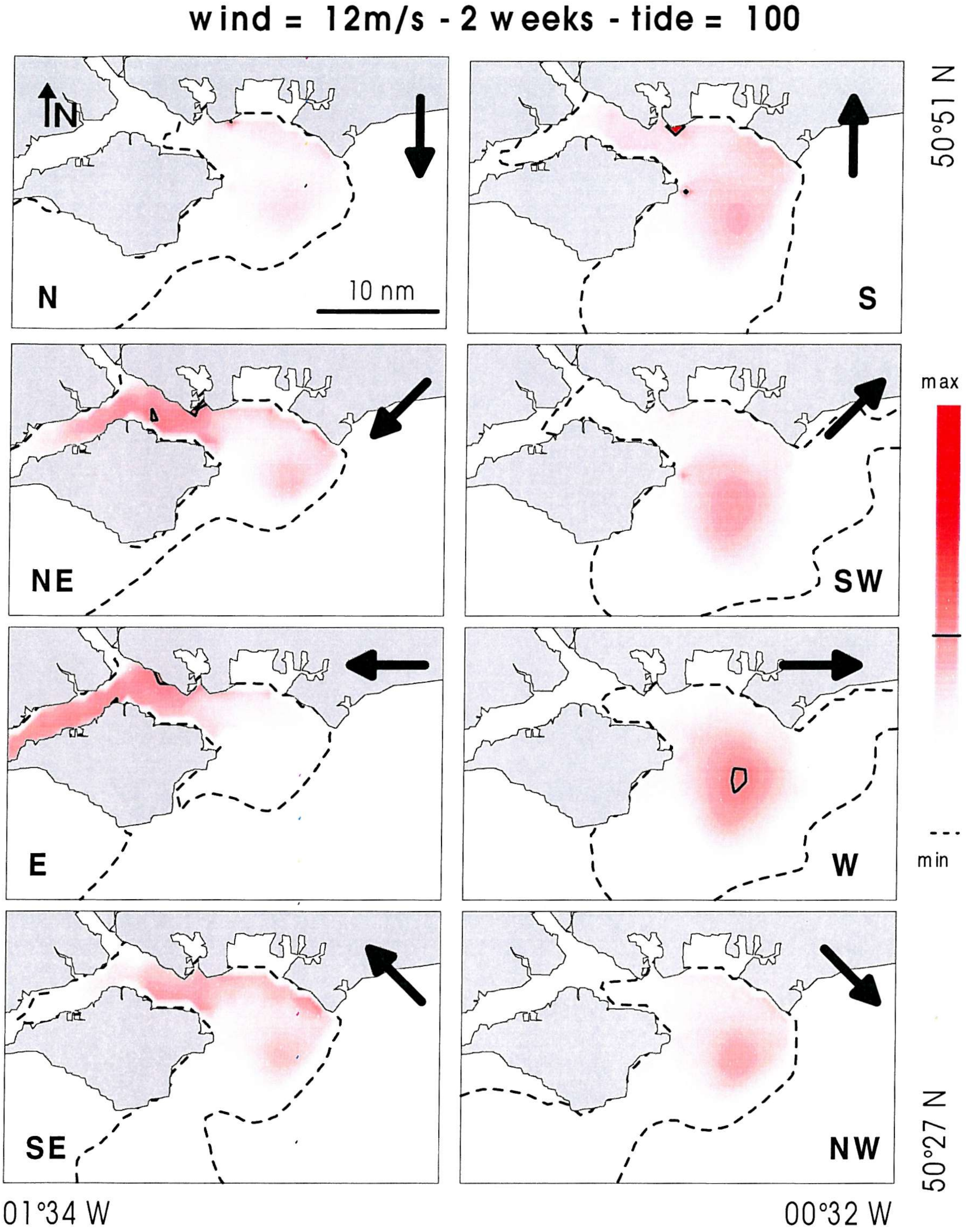


Figure 5.8: Patterns of particle dispersal under the influence of a wind of 12 ms^{-1} and a Spring tide (coefficient = 100) for a 2 week period. Release and final count areas correspond to that on figure 5.1. Colour scale is from maximum concentration (red) to minimum concentration (white). Isoline represents identical concentration for comparison between maps.

for tide only the main export is through the Solent channel. For NW winds, easterly transport is greater for a weaker tidal coefficient, and as tidal coefficient increases westerly transport increases (this was also checked by running simulations with a tidal coefficient of 40, not shown). In these last situations, the absolute differences between retention figures are not large compared with other wind directions, but relatively important since for example this can lead to twice as many particles retained over 2 weeks for a coefficient of 70 compared with 40, for a NW wind (corresponding to losses of ~11.5% and ~7.0%.day^{-1} respectively).

To summarise the interaction of wind and tide effects, these results show:

1. Increasing tide and winds separately increases the overall dispersal of particles.
2. The pattern of dispersal is dependent on wind direction.
3. The resulting effect will depend on the relative strengths of tide and wind: increasing the tidal coefficient can counterbalance wind effects, enhance them, or switch from one pattern to the other according to wind direction.

5.C.4. Measured Conditions of Wind & Tide & Influence of Surrounding Areas

For releases in surrounding areas, the quantity of particles imported into the area of interest was measured as the percentage of particles present in the 'Solent area', relatively to the number originally released (table 5.2). Although this does not measure precisely imports from surrounding areas in general, it allows comparisons between the different situations to be made. These are presented in figure 5.9.

From the results under forced wind and tides (figures 5.5-5.7), and if we assume as a rough approximation that it is the tidal coefficient averaged over time that affects transport patterns, we could expect average conditions throughout the simulation period: wind is

	Model simulations		
Release area:	June 14 to 22	June 22 to July 27	July 27 to August 24
Solent	58.6%	1.6%	6.0%
East	13.9%	1.8%	5.2%
South	1.6%	0.6%	1.0%
West	0.0%	0.0%	0.0%

Table 5.2: Percentage of released particles present in the Solent area at the end of the model simulations (see figure 5.1 for locations of start and end positions).

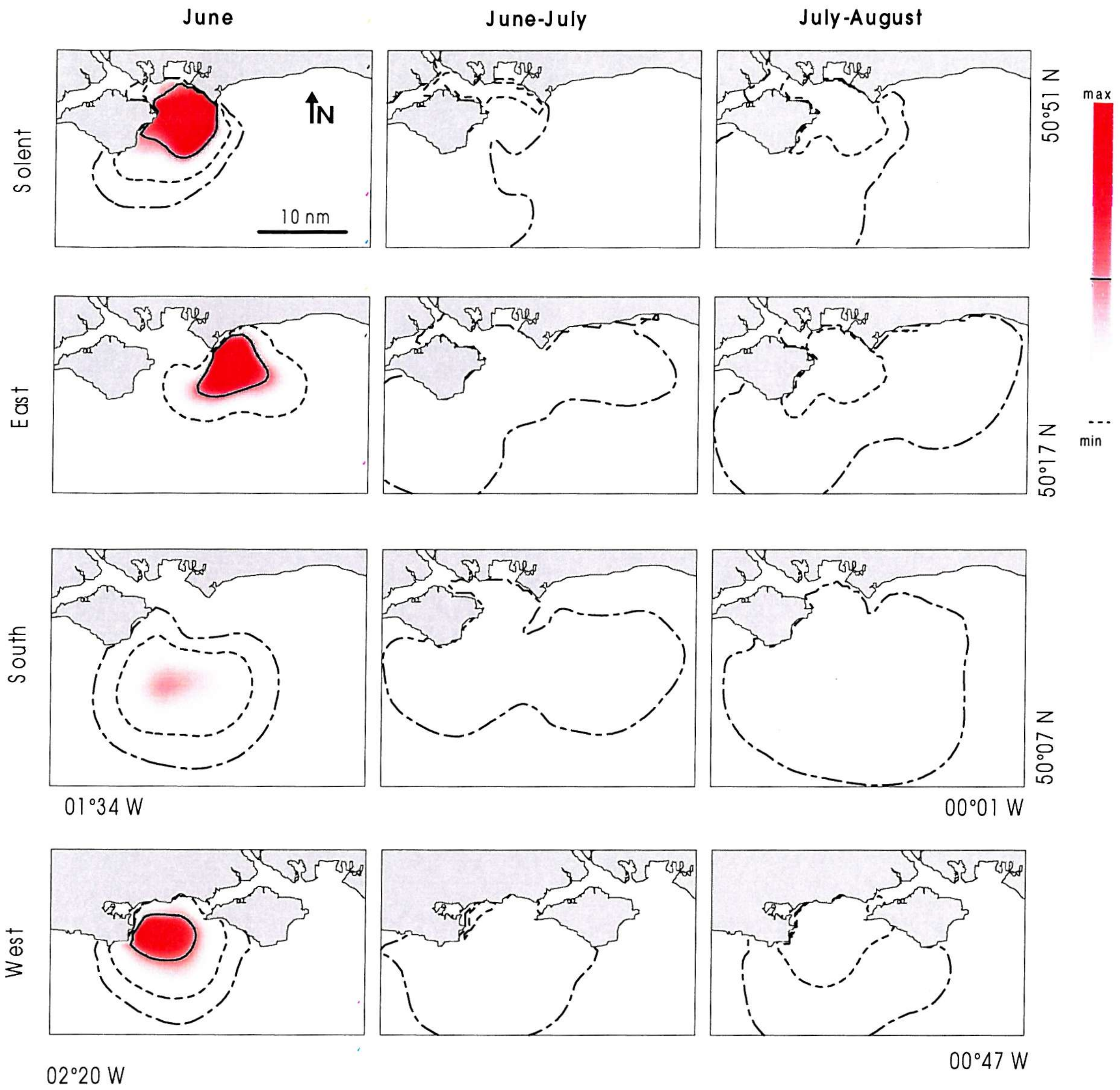


Figure 5.9: Patterns of particle dispersal under measured wind and tide conditions. Release and final count areas correspond to that on figure 5.1. Simulation periods correspond to June 15 - June 23; June 23 - July 27; July 27 - August 23 1995. Colour scale is from maximum concentration (red) to minimum concentration (white). Isolines are at × 10^{-1} intervals and are at identical concentrations between maps.

variable throughout the period, and experiences several reversals; average wind velocities are relatively weak.

In practice, for all release points, the one week simulations show little more than a general diffusion pattern, and over such a period the spread is similar across releases. For the Solent, July and August simulations vary mainly in the relative importance of the southward transport out of the area, though the general pattern is identical: the highest concentration values are to be found close to shore, and transport is mainly through the Solent, with some advection southwards. Considering that the model runs last four weeks, there is overall little displacement through the Solent, and the patch is essentially static, though it is outside of the count area defined in figure 5.1. The higher frequency of easterly winds in July and westerlies in August can be linked to the difference between months, which results in the equivalent of a 6%.day^{-1} loss in July, and 4%.day^{-1} in August. It can also be noted that Neap tides coincide with N to NE winds in July, which tend to drive transport southward (figure 5.6), and with N to W in August, which promote transport through the Solent.

The eastern release simulation sees the highest inputs into the Solent area, compared with South or West: the patch maintains to some degree its integrity and is shifted westwards rapidly, since after only a week, 14% of the original particles are in the area, and this despite losses from mortality. In July and August the proportions of 'Solent' and 'East' particles are close, and even higher for 'East' in July; in both cases maximum concentrations are close to shore and are being trapped in the recirculation cell off Bracklesham Bay. However part of the eastern patch is also entrained south of the Isle of Wight. Apart from a residual 'trail' to the east, patterns are very similar at the end of the simulations in August between the two release situations.

For the southern release, diffusion becomes very significant; in June it maintains its position, and in July and August the patch is spread and therefore diluted, mostly eastwards but also to the north. Final inputs into the Solent are however low, but again higher in August than in July. Other model runs (not shown) have also shown that over longer periods the patch is not advected much further east than is evident for July in figure 5.6.

The eastern release shows little diffusion or advection, and indeed there is very little difference between the three simulations, and there seems to be strong retention close to shore; consequently the input into the Solent area is negligible.

These results can be compared with the 'summer' situation of figure 2.2. The model confirms the patterns of near-shore westward flow, entrainment in Bracklesham Bay recirculation cell, and advection to the South and then East. We also see here the influence of a residual flow through the Solent, which may be important in retaining zooplanktonic populations for long periods of time, in what is essentially a sheltered environment. The eastern advection seen further south is also confirmed, though it is limited and does not see a rapid advection towards the Dover Straits, as was observed in the Lagrangian drifter experiments (Chapter 2).

5.C.5. Year-to-year variability

The results of monthly retention figures for the years 1985-1995 can be seen in table 5.3.

	Month		
Year	June	July	August
1985	6.9	6.6	4.1
1986	3.5	6.0	4.8
1987	4.9	5.7	4.5
1988	4.6	6.0	5.8
1989	4.9	5.1	4.1
1990	6.7	3.6	5.5
1991	5.7	4.5	3.2
1992	4.0	5.2	5.6
1993	4.8	5.1	4.2
1994	4.4	3.5	4.0
1995	1.8	2.3	5.2
average	4.8	4.9	4.6
range	5.1	4.3	2.6
coefficient of variation	30%	27%	18%

Table 5.3: Percentage retention of particles after 30 days simulations in the 'Solent area' (see figure 5.1), for years 1985-1995; average, range and coefficient of variation for each month.

The average retention values do not differ significantly between months (one-way ANOVA, α=0.05), indicating similar climatic effects over the three months, or little effect if variation there is. Within months, the range of values is however quite wide across the decade, resulting in a coefficient of variation (V^* = [standard deviation/ mean×100]×[1+(1/4n)]; Sokal & Rohlf, 1995, pp. 57-59) which decreases from 30% in June to 27% in July and 18% in August, and a range reduced by half. The maximum range, between June 1985 and June 1995, represents a factor of ~4. These figures and daily loss rates are roughly proportional, so that they will vary to a similar extent around an average of ~4%.day^{-1}; this is equivalent to 50% of the population being lost out of the system in 17 days. Maximum losses occur in June 1995 (7%.day^{-1}), which seems an exceptional year also for July. This trend can be linked to the greater occurrence of easterly winds in June (figure A.5.1). A significant correlation was found between the percentage losses in June and July and the ratio of E to W winds (figure A.5.2; $r_s = 0.7$ in both months, n=11, P<0.05), such that an increasing proportion of westerly winds is followed by increased losses: averages are 5.2, 4.9, and 5.7 m.s^{-1} for each month; June and July averages are not statistically different from each other, but they are from the August average ($F_{3,\ 1196} = 14.0$; P<<0.01; *Post-hoc* SNK test, P<<0.01); yet no significant relationship is picked up in this month, and thus it would seem that it is predominantly wind direction rather than strength which is linked to higher losses. Thus for measured conditions, three facts stand out: 1) Within months, higher losses are associated with easterly winds; 2) The variability in dispersal levels diminishes from June to August; and 3) The average retention does not vary much across the season, but the (non-significant) decrease observed can be linked to stronger westerlies.

5.D. Discussion

The model incorporates several simplifying assumptions:

1. Freshwater inputs and stratification are ignored.
2. Currents are depth-integrated.
3. Particle behaviour is not included (vertical position).
4. Currents used to model transport are time-averaged.
5. Mortality is a constant factor of time.

Concerning point 1, stratification does not occur beyond Calshot (chapter 2), and given other uncertainties, it is probably reasonable to ignore it. The effects of baroclinic currents are more difficult to assess; as noted by Prandle (1991), these may be significant in regions of freshwater influence, and this author found that this led to greater residual currents than those predicted by modelling alone. This could be the situation observed here with OSCR (chapter 2). Thus it is possible that the residuals used in the model are somewhat of an underestimation, and the extrapolation to longer time scales should be done with caution.

For point 2, model validations have shown that this is a reasonable assumptions from the physical point of view; however when combined with point 3 (particle behaviour, *i.e.* vertical migration), this of course will result in inaccuracies as discussed in the context of sampling in chapter 4. Here the consequence will be that dispersal as measured here will be an average possible displacement, since the regulation of vertical position can both promote dispersal (surface on ebb, bottom at flood) or retention (the opposite). From the literature there are few cases were enhanced dispersal is shown to occur (young crab stages in estuaries for example), and in most cases retention is promoted; thus the patterns modelled here are likely to lie between 'close to reality' and 'maximum possible displacement'; where the actual distribution lies in between these two points will depend on the average behaviour of individual species.

The effect of the time-averaging of currents (point 4) is difficult to assess since it concerns the resolution of the physical model, and how well the residual currents represent advective patterns once tidal oscillation has been removed. Here we have to rely on the extensive calibration and verification undertaken within *Fluxmanche* (chapter 2, section 2.B.5.b), and the comparisons made with OSCR data in chapter 2; at any rate, extrapolating patterns at time scales shorter than a week is inappropriate, and thus short-term variability cannot be assessed from these results. There may be local effects which go undetected, such as small gyres that have been reported in the Solent at certain stages of the tidal cycle (Clark & Gurnell, 1987).

As for point 5 (mortality), retention figures and patterns of dispersal should be taken as relative to this mortality figure, but more realistic than if it had not been included. An attempt was made to calculate the percentage losses due to advection and diffusion alone, and these can be used to assess their effects independently of mortality.

From the results, both tide and wind appear to play an important role in determining the pattern of transport. Tide alone explains losses of at least 6%.day^{-1} at Springs (probably more for short time scales), which is equivalent to the chosen mortality factor, down to ~1.5%.day^{-1} at Neaps; however the crucial factor seems to be the interaction between tide and wind, with effects dictated by wind direction and the relative strengths of tidal currents and wind velocity. The recirculation cell off Bracklesham Bay is a determining feature, which allows under most circumstances a strong retention of particles in the area, whether or not combined with wind, and, for winds <9m.s^{-1}, only easterly winds result in over 5% losses per day. When winds of 12 m.s^{-1} are included, only two situations, from N and SE, result in a systematic increase in losses with increased tidal coefficient and wind speed. The potential effects of strong winds can however be marked, especially for SW and W winds, where losses may reach 17%.day^{-1} and 40%.day^{-1} at Neaps; yet at Springs the retention values for these situations is close to the no-wind situation, highlighting the importance of threshold effects. Only NW, NE and E winds seem relatively unaffected by tide (in that tidal state does not cause variation); of these, the last two cause losses of up to 13%.day^{-1}, mainly through the East Solent.

Applied to real conditions of wind and tide, the dispersal pattern varies little across the season, and the pattern is similar in that most of the dispersal is through the Solent and somewhat to the South. For 1995, losses are relatively important in June and July compared with August; this seems linked to Easterly winds which occur in at a greater frequency during this period. This is confirmed by the significant relationship between the occurrence of easterly winds and losses at the decadal scale, at least for June and July when winds are more variable (no differences in average speed was detected). Thus it seems that the area is most sensitive to winds from this direction, and that they are the most important factor in determining the year-to-year and probably month-to month variability. This would indicate that for other wind situations, particularly W and SW, tidal effects are on average sufficient to counterbalance their effects, and that threshold wind speeds are reached only exceptionally during this season. The difference between maximum and minimum retention is of a factor of ~4. For species with dense planktonic populations, such as *Crepidula*, this is unlikely to cause local extinction or recruitment failure; however for species with low numbers, or which show a strong year-to-year variability, this may prove critical.

Nevertheless, the idea that the Solent area is, on average, a zone of retention is also confirmed by the dispersal patterns for June-August 1985-1996 (not shown), which show little dispersal overall, and differ mainly by the southward extent of the patch. For June, only 1985 sees a small displacement eastwards, and this year has also the highest retention value encountered.

The tendency of the tidal residual circulation, as it interacts with winds, is thus to constrain quite markedly the advective patterns of the area in June-August, under most naturally-occurring circumstances, though exceptional winds may have strong, if short-term effects which may not be picked up by the present simulations. Strong SW winds could result in the flushing out of local populations to the east, such as can be seen in other shallow, wind-influenced areas (*e.g.* Geyer, 1997); these effects will, in all likelihood, be transitory and the rapid influx of eastern populations into the outer approaches may - at least for holoplanktonic species - soon compensate for this phenomenon. NE winds are potentially a greater loss factor, since under this regime the particles are essentially lost from the system. However the most common case seems to be retention, most of which occurs through a residual movement through the East Solent; this process is slow, and the main patch does not transit sufficiently quickly to find its way completely through the West Solent over the maximum simulation period of 1 month. However the resolution of the model in such shallow channels may not be sufficient to represent true residual flow, which in reality will be influenced, for example, by non-linear tidal dynamics caused by friction. Small, local eddies, and occasional estuarine flows at the mouths of Southampton Water or the Medina River may act to modify this pattern, as will wind stress combined with atmospheric pressure. The quantification of such effects entails further field measurements, but we can at least rely on the data by Dyer & King (1975) who found that the residual flow in the West Solent was small, variable, dependent on meteorological effects and principally westwards.

Despite this pattern of retention, the area is not isolated, as the Bracklesham Bay recirculation cell rapidly incorporates particles from the east (under average conditions); the pattern is of a southern entrance of the eastern flow into the Solent area, first around, then into the anticyclonic recirculation cell; part of the eastern flow is then advected southward, but the majority is trapped close to shore and is rapidly mixed with local populations. Particles are then subject to the same regime as that observed for Solent waters. There is little input from the South, and this area is principally a zone of export for Solent populations, and seems to be itself part of a larger recirculation pattern. There is little interaction with waters West of the Isle of Wight which themselves are strongly contained close to shore.

The impact of these patterns on zooplanktonic populations will depend on several biological factors: vertical positioning, as mentioned previously, which may counter or reinforce the existing average circulation pattern, but also generation time and population dynamics (for holoplankton: Ketchum, 1954; Davis, 1984; Lynch *et al.*, 1998) or larval life span (for meroplankton: Scheltema, 1986; Okubo, 1994; chapter 12 in Brown & Rothery, 1993). Crawford *et al.* (1990), for example, discuss the influence of a recirculating eddy, which was found to increase the residence time in Hecate Strait (British Columbia): it allowed recruitment of certain fish species to take place where otherwise wind-driven advection would cause a residence time shorter than the larval life duration. If we accept an average loss rate of ~4%.day^{-1} due to physical processes, this will be close to what can be expected from mortality, and therefore potentially double the overall loss rate; yet this still represents a residence time of 17 days. This can be compared with the generation time of several copepod species, and the larval life time of invertebrate larvae. Archambault *et al.* (1998) have calculated generation times for *Eurytemora* sp. of ~19 days, and of ~24 days for *Acartia longiremis*. These authors do not give temperature values for these calculations but mention elsewhere (Archambault & Bourget, 1999) temperatures of 8-11°C in the same area and during the same period, and thus generation times in the present case are likely to be shorter. This month-to-month variability could also influence the relative success of cohorts, for those species with several recruitment events, either by retention or dispersal in itself, or by retaining eggs in the Bracklesham Bay area. The warmer waters found there could potentially influence the egg hatching success and subsequent development of copepods in periods of retention.

Larval life duration is variable across species, but for the dominant species (*Crepidula fornicata*), is of the same order (2-3 weeks), which is also a typical time for a number of invertebrate larvae (Thorson, 1957). Whether these patterns will have any effect will of course depend on the minimum density or flux required for successful recruitment or population growth, itself tied to the relationship between residence time, production rates and mortality/larval life time. In extreme situations, such as seems to be the case in June 1995, the combined losses reach over 13%.day^{-1}, (*i.e.* a residence time of 9 days). For populations that cannot compensate for these losses, this may lead to recruitment failure.

The fact that a principal export route may be through the Solent may however greatly mitigate the impact of these losses, since here residence times seem to be long and therefore provide a 'reservoir' for local populations; this would provide a mechanism by which the increased meroplankton densities seen close to shore in the field (chapter 4) could maintain themselves without being advected out of the system, independently of behavioural adaptations.

Chapter 6: General Discussion and Conclusions

6.A. General

At the seasonal scale, zooplankton abundance variations are highly correlated with phytoplankton availability (Dickey-Collas, 1996), salinity (Williams, 1981), and temperature (Le Fèvre-Lehöerff *et al.*, 1993). This 'regional stochasticity' (Hanski, 1998) hides important local fluctuations, such that local communities exhibit a wide variety of patterns, reflecting the prevailing local hydrographic, hydrodynamic, geomorphological, and biological conditions (Le Fèvre-Lehöerff *et al.*, 1983). This is true both for the seasonal evolution of communities, and the spatial organisation of populations. Brylinski *et al.* (1988), for example, have shown that for *Temora longicornis*, separate populations could be distinguished on either side of an 'ecological discontinuity' induced by a frontal structure in the eastern English Channel. The two populations, characterised by their size structure, were thought to have diverged several weeks earlier, further west, and then drifted separately towards the Dover Straits.

Despite a general W-E long term circulation pattern, the English Channel also displays a number of recirculation cells close to its coasts, which vary in strength (Chapter 1; figure 1.1; Salomon & Breton, 1991, 1993). The potential for such patterns of circulation, along with hydrodynamic factors in general, to drive population processes is important, and gyres may act at several levels (introduction to part B). For holoplankton, they may determine the local composition of planktonic communities by limiting exchanges between water masses, or serve to concentrate organisms in a particular locality; for meroplankton gyres may act to limit dispersal and keep cohorts in restricted areas; and they can contribute to environmental fluctuation when sensitive to wind effects. The hypothesis that a tidal-residual gyre was present to the east of the Isle of Wight formed part of the basis for the present work, which was aimed at determining:

1) Whether the temporal and spatial dynamics of mesozooplanktonic populations of the East Solent and Outer Approaches can be understood in terms of physical factors.

2) If the different constraints acting upon the holo- and mero-planktonic compartments of the mesozooplankton are seen in their relative distributions.

These hypotheses were tested in the context of the characteristics of the physical oceanography of the area, particularly in relation to the Bracklesham Bay gyre, and the 'biological environment' represented by benthic populations. The following sections will discuss the results obtained in light of these questions.

6.B. Limitations

Synoptic surveys are relatively rare in coastal oceanography, particularly those concerned with planktonic studies, and especially with respect to zooplankton. There are several reasons for this, but the development of automated methods of sampling and counting organisms, concurrent with physical data, may solve part of the problem (*e.g.* Currie *et al.*, 1998). However, there remains an inherent difficulty in studying what is in effect an 'open environment', where the frame of reference oscillates at 12 h intervals, with displacements of several hundred metres, and where advective effects mean that local processes of growth, reproduction and recruitment may appear to be disconnected from each other (Hughes, 1990). This problem cannot be solved easily, as it involves adapting our scales of observation to two systems: the physical environment, and the biological processes of interest. Studies such as the present one must find a scale at which both can be resolved. Two complementary attempts were made at solving these apparent conflicts: the use of *pseudo*-Lagrangian repositioning, to explicitly transform the Eulerian sampling design into a Lagrangian frame of reference; and the use of modelling, to resolve spatial and temporal gaps in the data. Specific problems with these techniques have been dealt with in the relevant sections, however there is a more general point to be made about their use.

Within the context of repositioning, it can be seen that the maps produced from the cruise data are effectively 'snapshots' of the physical and biological parameters of interest, and that the 'true' picture of the measured parameters is one of constant flux and spatial rearrangement. Thus the OSCR data of surface residual currents, averaged over one month in 1995 and 1996, remove the short-term variance. This is necessary within the context of long-term transport, but also may potentially hide important processes, as is shown for example by the *pseudo*-Lagrangian particle tracking (chapter 2), which showed important differences between trajectories starting at Springs or at Neaps. This is not taken into account in the calculation of 'long-term' residual circulation, and obviously the same applies to the tidal-residual currents calculated by modelling. For a larva that must settle within one or two weeks, currents averaged over one month may not be meaningful. Biological phenomena such as fertilisation, spawning, settlement, or even predation and competition, may operate during small 'windows of opportunity', which will not be resolved by the scale of the present survey, nor by the modelling discussed in chapter 5. This may be of particular importance, for example, for the effects of local hydrodynamic processes, which may act to create environmental heterogeneity at small scales. The Bracklesham Bay gyre is an example of a process that can be resolved, but the Vectis site is a case in point of a small scale structure which has a very localised but strong effect on the local characteristics, in this case on benthic populations. Such 'islands' are potentially of great importance for the dynamics of local populations, and the pelagic environment may be no exception. Cassie's (1968) remark that "perhaps planktologists are the only group of ecologists who still express some mild surprise that their biota are not randomly distributed in space [...]" is probably no longer true; nevertheless, there is still a growing realisation that understanding small-scale spatial and temporal patterns may be a precondition for understanding the functioning of the coastal ecosystem as a whole (Seuront & Lagadeuc, 1998).

6.C. The Physical Environment of the Solent Area

The physical oceanography data did not reveal strong gradients of salinity and temperature, which, given the tidal currents encountered, may not be entirely surprising. Taking into consideration the limitations discussed above, and those dealt with within individual chapters, this should not be taken as a sign that the environment is not highly structured: the fluorescence and potential energy anomaly data are probable indicators of short-term (ϕ) or small-scale (fluorescence) lower level processes which were not resolved. Vertically however, the area is homogeneous and stratification is limited. Three distinguishing features of the area are: 1) A general Solent-S increasing salinity gradient, with most of the change occurring in the upper Solent; 2) Waters of intermediate salinities S of the Isle of Wight; and 3) Higher salinities to the SE of the sampling area. The SPM distributions follow a clear Southampton Water - SE diminishing gradient. The seasonal evolution of this pattern yields a narrowing of the temperature and salinity gradients, such that the gradient that remains is principally one of temperature alone, from the Solent and Bracklesham Bay to the S and SE.

The existence of a tidal residual recirculation cell is confirmed by the results given in chapter 1, namely the harmonic analysis performed on the time-series of instantaneous surface currents measured by OSCR. This confirms several other studies which have found a good concordance between modelling and OSCR measurements, including regions of shallow and complex bathymetry (Prandle, 1991), together with other comparisons between the model used in the present study and OSCR during the *Fluxmanche I* program. In this case, this may be a sign of the accuracy of the two techniques, but could also stem from the fact that the tidal dynamics are predominantly driven by the M_2 constituent, which can often be well resolved even with coarse-resolution models. The greatest uncertainty that remains concerning these results is the actual magnitude of the residual currents. Since there are inaccuracies involved in both methods, they do not measure or model precisely the same phenomena, and the differences between the two data sets are ~30% for average velocities. Acoustic Doppler Current Profiler (ADCP) data was obtained during the survey, although it could not be analysed in time for this study, and this could possibly help to solve this question. For the time being, it can be noted that the model situation that conforms best to the OSCR data does not include wind. This can be seen in the context of the modelling results of chapter 5, showing that for measured conditions of wind and tide, the modelled recirculation pattern was present throughout the season and seemed little influenced by climatic conditions occurring at the time. There is further confirmation of this when comparing the 1995 and 1996 deployments of OSCR, which despite the different positions and ranges, concur well. There are areas of discrepancies, particularly in zones of weak residuals, but the overall agreement is encouraging. These results also confirm the original ideas discussed by Boxall & Robinson (1987), and schematised in figure 2.2, *i.e.* a general westward flow, with a recirculation cell off Bracklesham Bay, along with southern, then eastward advection. The modelling also suggests a long residence time in the East Solent, and this area may be an important retention zone in itself; here, confirmation from field measurements or modelling at greater resolution is needed, since the model is not designed for such conditions. The residual current through the West Solent is, however, known to be small.

Both the particle tracking simulations and the repositioning of stations show that the actual trajectories of particles will be complex and variable across the area, and will change according to the Spring/Neap cycle. Unfortunately, few dates were available for particle release, which did not allow a more in-depth analysis of the effects of tide as measured by OSCR, or a statistical treatment on a number of release points, as is usual for other particle-based models (*e.g.* for *Calanus*: Hannah *et al.*, 1997). Had such analysis been possible it would have permitted a comparison with the model. The range of OSCR is a limiting factor, being of the order of ~20 km, which corresponds to no more than a few days transit time for an average residual current.

Overall, the physical oceanography undergoes a relatively classic evolution over the summer, and a fairly homogeneous pattern across the area, which is not marked by strong hydrographic boundaries. The hydrodynamic data, on the other hand, did show a great degree of structure, with relatively stable patterns at the scale of observation.

6.D. The Mesozooplanktonic Community of the Solent Area

Although there is no scarcity of studies concerned with the spatial distribution of mesozooplankton (*e.g.* coastal zooplankton: Gaard, 1999; ichthyoplankton: Grioche *et al.*, 1999; community structure: Mackas, 1984), or the seasonal changes in spatial patterns (*e.g.* fish eggs: Laprise & Pepin, 1995), surprisingly few were found which specifically distinguish between mero- and holoplankton as distinct subcommunities. At a certain level, the distinction is a spurious one, since larvae, once in the water column, may be just as intricate a part of the community as holoplanktonic species, as they may interact through competition for resources or predation. It is thought that the evolutionary pressure responsible for planktotrophic larvae may be, in most cases, the need to shift into a different trophic environment, rather than dispersal *per se*, possibly to avoid taxing adult resources (Giangrande *et al.*, 1994). The variability of food availability is though to be an important factor in determining the evolution of the length of larval life (a consequence of the "settlement-timing hypothesis"; Todd & Doyle, 1981; Grant & Williamson, 1985), at least for certain groups (Strathmann, 1986). Indeed, this may well also be the case for holoplankton, for which the link to primary production is crucial, and which may have several more-or-less successful recruitment events per year. Certain holoplanktonic species, particularly cnidarians, have a benthic stage, and numerous species of copepods have resting eggs which lie dormant in the benthos (Grice & Marcus, 1981). Both may therefore share some of their constraints. However, in general the constraints imposed upon the two are different, particularly in the case of littoral or near-shore benthic species which must rejoin an area of limited geographical extent from within "a highly diffusive and dispersive environment" (Jumars, 1993). Thus the life-cycle strategies of the two groups are often fundamentally different, as they result from adaptations to different factors such as benthic and planktonic mortality rates, in relation to predation, reproductive cost, food availability and dispersal needs (Giangrande *et al.*, 1994).

Archambault *et al.* (1998) have used this distinction to compare different sizes of bays, and relate this to the ratio of holoplankton (H) and meroplankton (M) abundances. Their hypotheses were that 1) Physical processes of retention would mean that there would be increased zooplankton abundances within embayments (Okubo, 1973); 2) If the M/H ratio was greater inside than outside embayments, this was due to increased meroplankton production from within the bay (by benthic adults); 3) if M/H was smaller inside embayments then elevated holoplanktonic production was greater inside embayments; and 4) if M/H was equal within and outside of embayments, then physical retention alone was responsible for the elevated abundances. Comparing 4 embayments and an area close to a straight coast, they found increased abundances of zooplankton within bays, but no significant differences between H and M abundances. They concluded that physical factors, particularly the presence of eddies within the bays, rather than differential production rates, acted to explain the increased zooplankton numbers. In the rare cases where they found lower numbers within the bays, this was associated with particular wind patterns that acted to flush out the embayments. H/M ratios were not tested statistically in the present study, but it seems clear that the two subgroups follow different dynamics. This is most visible in the overall shifts in abundances and their spatial distributions. Differences were also found in the organisation of the community structure, and its temporal evolution during the observation period. This is most notable in the differences seen in the correlations with environmental variables, such as the relationship between holoplankton and fluorescence, and the constant link of meroplankton with temperature. However, the link to hydrodynamic factors, and the recirculation cell in particular, can only be inferred from the different strands of evidence gathered here. These include the observations of Boxall & Robinson (1987), the modelling results of tidal residual currents and of transport and dispersal patterns, OSCR measurements, and the presence of a more-or-less discrete mesozooplanktonic group sampled in the zone of the gyre. To this can possibly be added the link hypothesised by Paphitis (1997) between the gyre and an area of sand deposition, over the same area, observed by this author and Hydraulics Research (1993) (figures 3.1 and 3.10).

Concerning the group of stations and its faunistic (mesozooplanktonic) distinctiveness, there do not seem to be important abundance differences between this group (Bracklesham Bay) and the Solent community, and therefore the distinction is principally one of community composition. It is seen in all four cruises, most notably in the meroplanktonic station groupings, and is strongest in July and August in both subcommunities, when temperature is strongly correlated with community changes. In the whole community analysis, this group is systematically found at an extreme of the CA/CCA dimension 1, therefore implying that it is strongly correlated with one of the environmental variables, principally temperature. Thus, within the context of the original hypotheses, it is likely that the effect of the gyre on the mesozooplanktonic community occurs at several levels:

1) Through retention, or indeed exclusion, which could explain its association in cruises 3 and 5 solely with (respectively) holoplanktonic and meroplanktonic taxa.

2) Through its link to bathymetry, resulting in its association with relatively warm and lower salinity waters (hence for some species: increased growth, egg-hatching success, or its association with euryhaline taxa in cruise 3)
3) Through mixing with near-shore populations from the east (as shown by modelling).

The changes in community structure between the June cruises is also paralleled by a significant increase in temperature, though the absolute difference may not be great, indicating that the differentiation of the subcommunities may occur rapidly and establish itself soon after the general rise in abundance. The modelling results however may indicate that, rather than a closed system, the East Solent and the Bracklesham Bay areas communicate to a large extent, if only through diffusion linked to tidal oscillation. It is likely that under variable wind conditions and/or at Neaps, there may be a temporary breakdown or relaxing of the residual circulation, and a higher degree of mixing between the two areas, framed within the context on an area of overall retention. The losses that do occur from the system are most probably to the south, and the sampling in that area of ascidian or *Membranipora membranicea* larvae (in cruise 4) may be linked to such advection patterns. Group C on the other hand could be linked to a hydrographic gradient which does not appear in the physical data of chapter 1; or it could result from the inhibition of cross-tidal mixing, as observed by Boxall & Robinson (1987), which would be in agreement with a general southward residual circulation in that area. In this case, the increase in copepod populations seen in July and August would result from local production, concurring with Archambault's *et al.* (1998) idea, and explaining the low numbers that remain to the South. The low cross-mixing would add a further mechanism by which retention may operate, and its effect on nutrient transfers and the subsequent role on phytoplankton production could be of particular interest.

6.E. Relationships Between Benthic and Pelagic Compartments

The links between the benthic and pelagic compartments of marine ecosystems take on many forms, and in coastal waters are important at all trophic levels in one form or another. Most ecological models of production therefore now include biogeochemical cycling (*e.g.* Chardy, 1987). However the view that the benthos is principally a sink or source of nutrients is changing, and the role of meroplanktonic larva as important vectors of benthic-pelagic exchange is being recognised (*e.g.* Marcus & Boero, 1998). In the present case, this idea is exemplified in June, where the meroplankton is predominant numerically over the holoplankton in near-shore stations (figure 4.4), and although this was not measured, it could also be reflected in the overall biomass or carbon flux, if the benthos is productive. The principal taxa are *Crepidula fornicata* larvae, barnacle nauplii and decapod larvae. In July and August, when average numbers have risen to over 1800 and 2800 ind.m^{-3}, *Crepidula* larvae are still in the four most common taxa. The impact of this species on the tropho-dynamics of the pelagic community are potentially important, through competition for food, or as prey for carnivores. This has yet to be studied for this species.

Crepidula fornicata is also the dominant species amongst the benthos, where as discussed in chapter 3 it is probably of major importance in shaping the sedimentary and biotic compartments of the benthic ecosystem. The population of the Solent has been established for several decades ("[*Crepidula*] has long been established in the Solent"; Holme, 1961). Recent data on its distribution on this side of the Channel is scarce; Holme (1961) described its range in the English Channel as restricted to the Portland and Wight shipping channels. Barnes *et al.* (1973) describe it as having extended its range beyond Lyme Bay, with "dense" settlements in Poole Bay, its "Channel headquarters" in the Solent, and its most important densities in Essex estuaries. Thus the closest *Crepidula* populations of consequence are likely to be in the Essex estuaries to the East, and Poole Bay to the West. The modelling results of chapter 5, and the distance from the eastern populations, would point to a small likelihood of significant and regular recruitment from other populations to the Solent, which would make it essentially dependent on self recruitment (and on replenishment by imported oyster stocks or ballast water...). Given the numbers encountered on the benthos and in the water column, and the sexual behaviour of this species, it is unlikely that fertilisation or fecundity are important limiting factors, leaving larval mortality (including advection/diffusion) and pre- and post-settlement processes as the main limiting factors of recruitment (Ólafson *et al.*, 1994). Interestingly, the model results for the 'Western' releases (figure 5.9) show the occurrence of another retention cell off Poole Bay. Barnes *et al.* (1973) report *Crepidula* as having disappeared from the Liverpool area (where it was introduced in 1872); it would be interesting to compare the areas of mass occurrence of *Crepidula* with areas of retention. At any rate, as discussed in chapter 3, the stable presence of this species, and therefore the stability of the community as a whole, may be partly dependent on the pattern of recruitment of *Crepidula*, which was clearly associated with Solent or Bracklesham Bay stations.

For other meroplanktonic taxa, the consequences of the hydrographic and hydrodynamic processes of the Solent area will depend to a large extent on the length of the larval phase, on larval behaviour, and on the time of release. This is somewhat shown by the OSCR particle tracking simulations, and by the modelling results which show the effects of the

Spring/Neap cycle and winds on the outcome of dispersal. For example, as seen in chapter 4, *Littorina* spp. larvae were restricted to central stations, despite their long larval life of 4 to 5 weeks (Kraeuter, 1974), and therefore their potential for dispersal. *Littorina littorea* has been shown to increase spawning output on Spring tides (Grahame, 1975), seen by Grahame and Branch (1985) as a dispersal-enhancing strategy. In cases such as the Solent, this may well lead to the opposite pattern. Species with a lunar-tidal spawning rhythm may in fact maximise the potential for retention, being able to counter the environmental variability induced by wind effects, and the consequences of a long pelagic life in terms of dispersal. Many taxa, particularly decapods, are known to have tide-synchronised (and/or diurnal) reproductive or hatching rhythms (*e.g.* Gomez-Gutiérrez & Sànchez-Ortiz, 1997; Morgan, 1996). If retention areas are common enough, this could represent an adaptation favouring the recruitment close to parent populations, or alternatively, it could also reinforce the idea hinted at in the introduction to part B, that the range of a species is defined by its 'compatibility' with local conditions. For local *Littorina* spp., the areas of possible recruitment occur mainly to the West of the Isle of Wight, and are restricted to a few sites in the Solent. As Günther (1992) and others have argued, dispersal strategies may be an adaptation to the inherent instability of the marine environment, leading to a certain "elasticity" (resilience) of marine ecosystems, but with little local adaptation (however see Morgan, 1996).

6.F. Long-Term Trends

Marine ecosystems typically show large inter-annual variations (*e.g.* Gaard, 1999; Davoult *et al.*, 1998), and thus the problem of recruitment and population variability has preoccupied biological oceanographers since the early days of marine ecology (Jumars, 1993). Early work focused on stock-recruitment of fisheries (Grosberg & Levitan, 1992), and since Thorson (1946, 1950, 1966) first hypothesised that processes occurring in the plankton may affect the variability of benthic populations, research in this field has continued to develop (Young, 1990). Thiébaut (1994) and Thiébaut *et al.* (1997) have shown the relative stability of an *Abra alba* - *Pectinaria koreni* muddy fine sand community over 6 years in the Baie de Seine. Sufficient recruitment is a prerequisite of population maintenance, and therefore at least part of this persistence could be explained on the one hand by the hydrodynamics of the area (estuarine stratification and circulation, a frontal structure associated with the estuarine plume, and gyres) and the biological processes on the other. In tidally-controlled environments such as the English Channel, wind is potentially the greatest source of short-term stochasticity. A great many studies have shown its effect on larval dispersal (*e.g.* Thiébaut *et al.*, 1994; Blanton et al, 1995, Clancy & Cobb, 1995; Stoner & Smith, 1998), or it has been directly linked to recruitment variability (*e.g.* Bertness *et al.*, 1996), and to the distribution of holoplanktonic populations (*e.g.* Archambault *et al.*, 1999; Hannah *et al.*, 1998; Rand & Hinch, 1998). The interaction of wind and tidal currents has great potential for generating short-term effects such as 'flushing out' events (Geyer, 1997; Archambault *et al.*, 1998). In the Solent area, as elsewhere in the English Channel (C. Ellien, Université Paris 6, pers. comm.), the modelling results show that the short-term variability of the advective and dispersive environment may be dependent on wind effects. The major feature at the decadal scale is that average retention and monthly variability are linked, such that in early summer, average retention is maximum whilst variability is greatest, whereas in August average retention and variability are lower. The differences between average retention values were slight, however this has potentially important implications both for holo- and meroplanktonic population dynamics. 'Early' species will on average experience a greater retention, but may be subject to greater population fluctuations, whilst 'late' species will suffer (or benefit) from more losses from the area, but will see less variance in their population dynamics (if they recruit locally). To schematise, this could favour *r*-selected species in early summer, or *K*-selected species in late summer according to the prevailing conditions in any particular year, and partly explain yearly differences in species abundance - and possibly drive evolutionary processes. Be that as it may, species such as *Crepidula fornicata*, which reproduce throughout the season, may be relatively unaffected by such patterns, and 'inherent' biological variability notwithstanding, contribute to stabilising the community.

6.G. Conclusions

The waters of the Solent share many characteristics with other areas of the English Channel: *i.e.* they are dominated by strong, mainly semidiurnal tidal flows, and are subject to occasional strong winds and important daily and seasonal heat fluxes. Despite this dynamic nature, the physical environment and the mesozooplanktonic communities are related in showing a degree of structure at the regional scale. This structure varies in strength, detail and extent, and is influenced by the interaction of hydrographic and hydrodynamic factors. These act to create areas of particular physico-chemical and biological characteristics, as has been noted elsewhere in the Channel, particularly in relation to the *Fleuve Côtier* (Brylinski *et al.*, 1988; Brylinski & Lagadeuc, 1990; Brylinski & Aelbrecht, 1993). The present study goes some way to confirm the original hypothesis that hydrodynamic features in particular, such as recirculation cells, may counteract the homogenising action of tidal oscillation, and demonstrates the potential importance of these factors at smaller spatial and temporal scales. In the Solent, the interaction of mesozooplanktonic communities with hydrological gradients and the residual circulation, notably a tidal residual gyre off Bracklesham Bay, can explain an important proportion of the spatial organisation of the mesozooplankton. The distinction between holo- and meroplankton has also clearly shown that the different ways in which they interact with environmental variables can be used to assess the relative importance of these factors. The generalisation to the rest of the English Channel is yet to be addressed, but it is likely that our understanding of the processes governing the stability and fate of benthic and pelagic ecosystems will necessarily encompass such small to medium scale biological-physical interactions.

6.H. Proposals for Future Research

This study has characterised for the first time the physical oceanography and the temporal and spatial variability of mesozooplankton communities of the East Solent and approaches, and has described for the first time since Barnes *et al.* (1973) the benthic communities of the East Solent. As such it has put in place a background against which more detailed process studies can be carried out. The spatial and temporal scales can now be reduced and focused on a number of points or areas of interest.

1) 3-D hydrodynamic models of complex coastal areas are now relatively commonplace. A proper understanding of the evolution of the system cannot be reached without resolving small scale and short term phenomena, such as small gyres or local estuarine flows, particularly in the East Solent. OSCR is particularly well suited for validating such models and for measuring residual currents, and further deployments are recommended, particularly at the entrance to the East and West Solent, to the South of the Isle of Wight, and off Selsey Bill (to the South). An assessment of the relative magnitudes of tidal, wind and baroclinic residual currents should be carried out as a matter of routine, together with calibration using ADCPs or moored current meters. ADCPs could also be used to assess the spatial resolution of tidal ellipses by OSCR, and as a comparison with models. The mechanisms responsible for the N/S separation in community structure and abundance, whether or not hydrological, are of particular interest.
2) A series of short term time series (1 or more tidal cycles) could be put in place to assess both the vertical distribution of mesozooplankton species, and their interaction

with factors such as current shear, tidal or day/night cycles. Recommended areas are at the mouth of the East Solent, Calshot, in the centre and periphery of the gyre, and to the south of the Isle of Wight, so that this could be combined with an examination of the local effects of tidal or other circulation patterns.

3) Less intensive transect-type surveys could be carried out to characterise the variations in physical and biological factors on shorter time scales, particularly at times of high increase or decrease of zooplankton population and/or phytoplankton growth. The short term evolution of the Bracklesham Bay/East Solent distinction could also be assessed, for example by several transects on consecutive days.
4) There is a need for basic background biological information: population dynamics and recruitment variability of main species, year-to-year variability in the plankton, simple models of pelagic trophic interactions, and an assessment of the competition processes occurring at the benthos and in the pelagos. The dynamics of copepod resting stages, their temporal occurrence in the benthos and water column, and their role in regulating recruitment of copepods is of particular interest.
5) Species such as *Ostrea edulis, Mytilus edulis,* or *Lanice conchilega*, which are known to occur in distinct patches, or which are characterised by specific recruitment problems may prove to be interesting biological models, and their larvae need to be sampled adequately.
6) The infaunal populations of Langstone or Chichester harbours are also potentially interesting, as these are practically emptied at low tide and there are only two entrances for seawater to come into. These could provide a closed 'box' where larval supply could be monitored.
7) Molecular tools are now available to assess the level of genetic exchange between populations; at the level of the English Channel, this provides an opportunity to test models of dispersal and recruitment of benthic or pelagic species, and particularly of the relative importance of processes acting at the larval, juvenile or adult stages.

Literature Cited

Agoumi, A., M.-J. Enderlé and R. A. Gras (1983) Modélisation du régime thermique de la Manche. *Oceanologica Acta* **6**: 393-406.

Akima, H. (1978) A method of bivariate interpolation and smooth surface fitting for irregularly distributed data points. *ACM Transactions on Mathematical Software* **4**: 148-159.

Aldridge, J. N. (1997) Hydrodynamic model predictions of tidal asymmetry and observed sediment transport paths in Morecambe Bay. *Estuarine, Coastal and Shelf Science* **44**: 39-56.

Algan, O., T. Clayton, M. Tranter and M. B. Collins (1994) Estuarine mixing of clay minerals in the Solent region, southern England. *Sedimentary Geology* **92**: 241-255.

Alongi, D. M. (1998) *Coastal Ecosystem Processes.* CRC Press. 419 pp.

Anger, K., E. Spivak, C. Bas, D. Ismael and T. Luppi (1994) Hatching rhythms and dispersal in a brackish coastal lagoon in Argentina. *Helgoländer Meeresuntersuchungen* **48**: 445-466.

Antai, E. E. (1989) *Seasonal Trophodynamics of Bacterioplankton and Heterotrophic Microflagellates in Southampton Water.* PhD dissertation, University of Southampton.

Apel, J. R. (1987) *Principles of Ocean Physics.* International Geophysics Series vol. 38. Academic Press. 634 pp.

Archambault, P. and E. Bourget (1999) Influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment and diversity of benthic subtidal communities. *Journal of Experimental Marine Biology and Ecology* **241**: 309-333.

Archambault, P., J. C. Roff, E. Bourget, B. Bang and G. R. Ingram (1998) Nearshore abundance of zooplankton in relation to shoreline configuration and mechanisms involved. *Journal of Plankton Research* **20**: 671-690.

Axelsson, M. (1996) *A Preliminary Survey of the Benhic Macrofauna in the East Solent and its Approaches.* B.Sc. dissertation, University of Southampton.

Bachelet, G. and J.-C. Dauvin (1993) Distribution quantitative de la macrofaune benthique des sables intertidaux du bassin d' Arcachon. *Oceanologica Acta* **16**: 93-97.

Baretta-Bekker, J. G., E. K. Duursma and B. R. Kuipers (Eds.) (1992) *Encyclopedia of Marine Sciences.* Springer-Verlag. 311 pp.

Barnes, R. S. K., J. Coughlan and N. J. Holme (1973) A preliminary survey of the macroscopic bottom fauna of the Solent, with particular reference to *Crepidula fornicata* and *Ostrea edulis. Proceedings of The Malacological Society of London* **40**: 253-275.

Benzecri, P. J. (ed.) (1973) *L'Analyse des Correspondances.* L'Analyse des Données vol. 2. Paris: Dunod.

Bertness, M. D., S. D. Gaines and R. A. Wahle (1996) Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides. Marine Ecology - Progress Series* **137**: 103-110.

Bhaud, M. and A. J. Grehan (1990) Co-ordination of the pelagic and benthic life history phases in marine benthic invertebrates: Two examples from the Polychaeta. *La Mer* **28**: 266-272.

Black, K. P., P. J. Moran and L. S. Hammond (1991) Numerical models show coral reefs can be self-seeding. *Marine Ecology - Progress Series* **74**: 1-11.

Blain, W. R. (1980) *Tidal Hydraulics of the Western Solent.* PhD dissertation, University of Southampton.

Blanchard, M. (1997) Spread of the slipper limpet *Crepidula fornicata* (L. 1758) in Europe. Current state and consequences. *Scientia Marina* **61**(Sup. 2): 109-118.

Blanton, J., E. Wenner, F. Werner and D. Knott (1995) Effects of wind-generated coastal currents on the transport of blue crab megalopae on a shallow continental shelf. *Bulletin of Marine Science* **57**: 739-752.

Boicourt, W. C. (1988) Recruitment dependence on planktonic transport in coastal waters. *In* Rotschild, B. J. (Ed.): *Toward a Theory on Biological-Physical Interactions in the world Ocean.* NATO ASI Series vol. 239. Kluwer Academic Publishers. pp. 183-202.

Boucher, J. (1988) Space-time aspects in the dynamics of planktonic stages. *In* Rotschild, B. J. (Ed.): *Toward a Theory on Biological-Physical Interactions in the World Ocean.* NATO ASI Series vol. 239. Kluwer Academic Press Publishers. pp. 203-214.

Boxall, S. R. and I. S. Robinson (1987) Shallow sea dynamics from CZCS imagery. *Advances in Space Research* **7**: 237-246.

Broche, P., J.-C. Salomon, D. J. S and J. L. Devenon (1986) Tidal currents in the Baie de Seine: comparison of numerical modelling and High-Frequency Radar measurements. *Estuarine, Coastal and Shelf Science* **23**: 465-476.

Brockmann, C. W. and J. W. Dippner (1987) Tidal correction of oceanographic measurements. *Deutsche hydrographische Zeitung* **40**(241-260):

Brown, D. and P. Rothery (1993) *Models in Biology: Mathematics, Statistics and Computing.* John Wiley and Sons.

Bryan, P. J., J. L. Kreider and P. Y. Qian (1998) Settlement of the serpulid polychaete *Hydroides elegans* (Haswell) on the arborescent bryozoan *Bugula neritina* (L.): evidence of a chemically mediated relationship. *Journal of Experimental Marine Biology and Ecology* **220**: 171-190.

Bryant, A. D., D. Hainbucher and M. Heath (1998) Basin-scale advection and population persistence of *Calanus finmarchicus. Fisheries Oceanography* **7**: 235-244.

Brylinski, J. M. and D. Aelbrecht (1993) Plankton Transfers and Coastal Front in the Dover Strait. *Oceanologica Acta* **16**: 671-676.

Brylinski, J. M. and Y. Lagadeuc (1990) L'interface eaux côtières-eaux du large dans le Pas-de-Calais (côtes françaises): une zone frontale. *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Vie/Life sciences* **311**: 535-540.

Brylinski, J. M., D. Bentley and C. Quisthoudt (1988) Ecological discontinuity and zooplankton (copepods) in the western English-Channel. *Journal of Plankton Research* **10**: 503-513.

Burkart, C. A., G. S. Kleppel, K. Brander, D. V. Holliday and R. E. Pieper (1995) Copepod and barnacle nauplius distributions in the Irish Sea: relation to springtime hydrographic variability. *Journal of Plankton Research* **17**: 1177-1188.

Butman, C. A. (1987) Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging rôle of hydrodynamical processes. *Oceanography and Marine Biology Annual Review* **25**: 113-165.

Butman, C. A. (1986) Larval settlement of soft-sediment invertebrates: some predictions based on an analysis of near-bottom profiles. *In* Nihoul, J. C. J. (Ed.): *Marine Interface Ecohydrodynamics.* Elsevier Oceanographic Series vol. 42. New York: Elsevier Science Publishing Company. pp. 487-513.

Cabioch, L., F. Gentil, R. Glaçon and C. Retière (1977) Le macrobenthos des fonds meubles de la Manche: distribution générale et écologie. *In* Keegan, B. F., P. O. Céidigh and P. J. S. Boade (Eds.): *Biology of Benthic Organisms: Proceedings of the 11th European Marine Biology Symposium, Galway, Ire.* Pergamon Press. pp. 115-128.

Caron, A., L. Boucher, G. Desrosiers and C. Retière (1995) Population dynamics of the polychaete *Nephtys caeca* in an intertidal estuarine environment (Québec, Canada). *Journal of the Marine Biological Association of the United Kingdom* **75**: 871-884.

Cassie, R. M. (1968) Sample design. *In: Zooplankton Sampling.* UNESCO Monographs on Oceanographic Methodology vol. 2. p. 105-121.

Castel, J. and J. Veiga (1990) Distribution and retention of the copepod *Eurytemora affinis hirundoides* in a turbid estuary. *Marine Biology* **107**: 119-128.

Castel, J. and C. Courties (1982) Composition and differential distribution of zooplankton in Arcachon bay. *Journal of Plankton Research* **4**: 417-433.

Castro-Longoria, E. (1998) *Seasonal and Spatial Distribution Patterns of the Congeneric* Acartia *in the Solent - Southampton Water Estuarine System, with Special Reference to Aspects of their Fecundity.* PhD. dissertation, University of Southampton.

Castro-Longoria, E. and J. A. Williams (1996) First report of the presence of *Acartia margalefi* (Copepoda: Calanoida) in Southampton Water and Horsea Lake, UK. *Journal of Plankton Research* **18**: 567-575.

Catell, R. B. (1966) The Scree test for the number of factors. *Multivariate Behavioral Research* **1**: 245-276.

Cazaux, C. (1981) Evolution et adaptation larvaires chez les polychètes. *Océanis* **7**: 43-77.

Chapman, R. D. and H. C. Graber (1997) Validation of HF Radar measurements. *Oceanography* **10**: 76-79.

Chardy, P. (1987) Simulation Analysis of the Benthic System in the Coarse Sediment of the Golfe Normand-Breton (English-Channel). *Oceanologica Acta* **10**: 421-434.

Chia, F.-S. and J. Bucklands-Nicks (1984) Locomotion of marine invertebrate larvae: a review. *Canadian Journal of Zoology* **62**: 1205-1222.

Clancy, M. and J. S. Cobb (1997) Effect of wind and tidal advection on distribution patterns of the rock crab *Cancer irroratus* megalopae in Block Island Sound, Rhode Island. *Marine Ecology - Progress Series* **152**: 217-225.

Clark, M. J. and A. Gurnell (1987) *The Solent Estuary: Environmental background.* GEODATA Unit, University of Southampton.

Colebrook, J. M. and G. A. Robinson (1965) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north east Atlantic and the North Sea. *Bulletin of Marine Ecology* **6**: 123-129.

Collins, K. J., R. J. H. Herbert and J. J. Mallinson (1989) The marine fauna and flora of Bembridge and St Helens, Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archeology Society* **9**: 41-85.

Collins, K. J. and J. J. Mallinson (1983) *Sublittoral Survey from Selsey Bill to the East Solent.* Report to the Nature Conservancy Council.

Collins, N. R. and R. Williams (1981) Zooplankton of the Bristol Channel and Severn Estuary. The distribution of four copepods in relation to salinity. *Marine Biology* **64**: 273-283.

Commito, J. A., S. F. Thrush, R. D. Pridmore, J. E. Hewitt and V. J. Cummings (1995) Dispersal dynamics in a wind-driven benthic system. *Limnology and Oceanography* **40**: 1513-1518.

Conover, R. J. (1957) Notes on the seasonal distribution of zooplankton in Southampton Water with special reference to the genus *Acartia. Ann. Mag. Nat. Hist. Ser.* **12**: 63-67.

Crawford, D. W., A. P. M. Lockwood and D. A. Purdie (1985) *The Environmental Requirements and consequences of* Mesodinium *blooms.* NERC interim report.

Crawford, W. R., A. V. Tyler and R. E. Thomson (1990) A possible eddy retention mechanism for ichthyoplankton in Hecate Strait. *Canadian Journal of Fisheries and Aquatic Science* **47**: 1356-1363.

Criales, M. M. and M. F. McGowan (1994) Horizontal and vertical distribution of penaidean and caridean larvae and micronektonic shrimps in the Florida keys. *Bulletin of Marine Science* **54**: 843-856.

Crisp, D. J. and A. J. Southward (1958) The distribution of intertidal organisms along the coasts of the English Channel. *Journal of the Marine Biological Association of the United Kingdom* **37**: 157-208.

Crombie, D. D. (1955) Doppler spectrum of sea echo at 13.50 Mc/s. *Nature* **175**: 681-682.

Currie, W. J. S., M. R. Claereboudt and J. C. Roff (1998) Gaps and patches in the ocean: a one-dimensional analysis of planktonic distributions. *Marine Ecology-Progress Series* **171**: 15-21.

Dauvin, J. C. (ed.) (1997) *Les Biocénoses Marines et Littorales Française des Côtes Atlantique, Manche et Mer du Nord, Synthèse, Menaces et Perspéctives.* Paris: Muséum National d'Histoire Naturelle. 376 pp.

Dauvin, J. C., M. Kendall, G. Paterson, F. Gentil, I. Jirkov and M. Sheader (1994) An initial assessment of polychaete diversity in the Northeastern Atlantic Ocean. *Biodiversity Letters* **2**: 171-181.

Dauvin, J. C., E. Thiébaut and Z. X. Wang (1998) Short-term changes in the mesozooplanktonic community in the Seine ROFI (Region of Freshwater Influence) (eastern English Channel). *Journal of Plankton Research* **20**: 1145-1167.

Dauvin, J. C. and S. Zouhiri (1996) Suprabenthic crustacean fauna of a dense *Ampelisca* community from the English Channel. *Journal of the Marine Biological Association of the United Kingdom* **76**: 909-929.

Davis, C. S. (1984) Interaction of a copepod population with the mean circulation on Georges Bank. *Journal of Marine Research* **45**: 573-590.

Davoult, D., J. M. Dewarumez and A. Migné (1998) Long-term changes (1979-1994) in two coastal benthic communities (English Channel): analysis of structural developments. *Oceanologica Acta* **21**: 609-617.

Defant, A. (1950) Reality and illusion in oceanographic surveys. *Journal of Marine Research* **9**: 120-138.

Dekshenieks, M. M., E. E. Hofmann, J. M. Klinck and E. N. Powell (1996) Modelling the vertical distribution of oyster larvae in response to environmental conditions. *Marine Ecology - Progress Series* **136**: 97-110.

Dekshenieks, M. M., E. E. Hofmann, J. M. Klinck and E. N. Powell (1997) A modelling study of the effects of size- and depth-dependent predation on larval survival. *Journal of Plankton Research* **19**: 1583-1598.

Denman, K. L. and T. M. Powell (1984) Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanography and Marine Biology Annual Review* **22**: 125-168.

De Souza-Lima, H. and P. J. Le B. Williams (1978) Oxygen consumption by the planktonic population of an estuary - Southampton Water. *Estuarine, Coastal and Shelf Science* **6**: 515-521.

Dickey-Collas, M., R. J. Gowen and C. J. Fox (1996) Distribution of larval and juvenile fish in the Western Irish Sea: relationship to phytoplankton, zooplankton biomass and recurrent physical features. *Marine and Freshwater Research* **47**: 169-181.

Digby, P. S. B. (1950) The biology of small planktonic copepods of Plymouth. *Journal of the Marine Biological Association of the United Kingdom* **29**: 393-416:

Dippner, J. W. (1993) Larvae survival due to eddy activity and related phenomena in the German Bight. *Journal of Marine Systems* **4**: 303-313.

Dixon, I. and J. Moore (1987) *Survey of Harbours, Rias and Estuaries in Southern Britain.* vol. 1: The Solent System.

Downing, J. A., M. Péruse and Y. Frenette (1987) Effect of interreplicate variance on zooplankton sampling design and data analysis. *Limnology and Oceanography* **32**: 673-680.

Dunn, A. J. (1987) *The Vertical and Temporal Distribution of Phytoplankton in Southampton Water.* BSc. dissertation, University of Southampton

Dupouy, H. and D. Latrouite (1979) Le développement de la crépidule sur le gisement de coquilles Saint-Jacques de la baie de Saint-Brieuc. *Science et Pêche, Bulletin de l'Institut des Pêches Maritimes* **292**: 13-19.

Dyer, K. R. (1980) Sedimentation and sediment transport. *In The Solent Estuarine System.* NERC Publications, series C, vol. 22. pp. 20-24.

Dyer, K. R. and H. L. King (1975) The residual water flow through the Solent, South England. *Geophysical Journal of the Royal astronomical Society* **42**: 97-106.

Eggleston, D. B., L. L. Etherington and W. E. Elis (1998) Organism response to habitat patchiness: species and habitat- dependent recruitment of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* **223**: 111-132.

Eleftheriou, A. and M. D. Nicholson (1975) The effects of exposure on beach fauna. *Cahiers de Biologie Marine* **16**: 695-710.

Epifanio, C. E. (1995) Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. *Bulletin of Marine Science* **57**: 713-725.

Epifanio, C. E. (1988) Transport of crab larvae between estuaries and the continental shelf. *In* Jansson, B.-O. (Ed.): *Coastal-Offshore Ecosystem Interactions.* Lecture Notes on Coastal and Estuarine Studies vol. 22. Springer-Verlag. pp. 291-305.

Falkenhaug, T., E. Nordby, H. Svendsen and K. Tande (1995) Impact of advective processes on displacement of zooplankton biomass in a North Norwegian fjord system: a comparison between spring and autumn. *In* Skjoldal, H. R., C. Hopkins, K. E. Erikstad and H. P. Leinaas (Eds.): *Ecology of Fjords and Coastal Waters.* Elsevier Science. pp. 195-861.

Fasham, M. J. R., M. V. Angel and H. S. J. Roe (1974) An investigation of the spatial pattern of zooplankton using the Longhurst-Hardy plankton recorder. *Journal of Experimental Marine Biology and Ecology* **16**: 93-112.

Field, J. G., K. R. Clarke and R. M. Warwick (1982) A practical strategy for analysing multispecies distribution patterns. *Marine Ecology - Progress Series* **8**: 37-52.

Fisher, R. A. (1940) The precision of discriminant functions. *Annals of Eugenics* **10**: 422-429.

Fluxmanche II (1998) *Hydrodynamics and Biogeochemical Processes and Fluxes in the Channel.* Report MAST II MAS2CT940089. 216 pp.

Folk, R. L. (1980) *Petrology of Sedimentary Rocks.* Austin, Texas: Hemphill Publishing. 182 pp.

Fransz, H. G. and W. W. C. Gieskes (1984) The unbalance of phytoplankton and copepods in the North Sea. *Rapport des Procès-verbaux des Réunions du Conseil international pour l'Exploration de la Mer* **183**: 218-225.

Fréchette, M. and C. A. Butman (1989) The importance of boundary-layer flow in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L. *Limnology and Oceanography* **34**: 19-36.

Frederiksen, S., K. Sjøtun, T. E. Lein and J. Rueness (1995) Spore dispersal in *Laminaria hyperborea* (Laminariales, Phaeophyceae). *Sarsia* **80**: 47-54.

Fromentin, J. M., F. Ibanez, J. C. Dauvin, J. M. Dewarumez and B. Elkaim (1997) Long-term changes of four macrobenthic assemblages from 1978 to 1992. *Journal of the Marine Biological Association of the United Kingdom* **77**: 287-310.

Fromentin, J. M. and F. Ibanez (1994) Year-to-year changes in meteorological features of the French coast area during the last half-century - examples of 2 biological responses. *Oceanologica Acta* **17**: 285-296.

Gaard, E. (1999) The zooplankton community structure in relation to its biological and physical environment on the Faroe shelf, 1989-1997. *Journal of Plankton Research* **21**: 1133-1152.

García-Moliner, G., D. M. Mason, C. H. Greene, A. Lobo, B. Li, J. Wu and G. A. Bradshaw (1993) Description and analysis of spatial patterns. *In* Levin, S. A., T. M. Powell and J. H. Steel (Eds.): *Patch Dynamics.* Lecture Notes in Biomathematics vol. 96. Springer-Verlag. pp. 70-89.

Garrison, L. P. and J. A. Morgan (1999) Abundance and vertical distribution of drifting, post-larval *Macoma* spp. (Bivalvia: Tellinidae) in the York River, Virginia, USA. *Marine Ecology-Progress Series* **182**: 175-185.

Garvine, R. W., C. E. Epifanio, C. C. Epifanio and K.-C. Wong (1997) Transport and recruitment of blue crab larvae: a model with advection and mortality. *Estuarine, Coastal and Shelf Science* **45**: 99-111.

Gauch, H. G. j. (1982) *Multivariate analysis in community ecology.* Cambridge: Cambridge University Press.

George, J. D. and G. Hartmann-Schröeder (1985) *Polychaetes: British Amphinonids, Spintheria and Eunicida.* Synopses of the British Fauna (New Series) vol. 32. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Giangrande, A., S. Geraci and G. Belmonte (1994) Life-cycle and life-history diversity in marine invertebrates and the implications in community dynamics. *Oceanography and Marine Biology Annual Review* **32**: 305-333.

Geyer, W. R. (1997) Influence of wind on dynamics and flushing of shallow estuaries. *Estuarine, Coastal and Shelf Science* **44**: 713-722.

Gomez-Gutiérrez, J. and C. A. Sànchez-Ortiz (1997) Larval drift and population structure of the pelagic phase of *Pleuroncodes planipes* (Stimpson) (Crustacea: Galatheidae) off the southwest coast of Baja California, Mexico. *Bulletin of Marine Science* **61**: 305-325.

Gower, J. C. (1987) Introduction to ordination techniques. *In* Legendre, P. and L. Legendre (Eds.): *Developments in Numerical Ecology.* NATO ASI Series vol. G 14. Springer-Verlag.

Graham, A. (1971) *British Prosobranchs.* Synopses of the British Fauna (New Series) vol. 2. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Grahame, J. (1975) Spawning in *Littorina littorea* (L.) (Gastropoda: Prosobranchiata). *Journal of Experimental Marine Biology and Ecology* **18**: 185-196.

Grahame, J. and G. M. Branch (1985) Reproductive patterns of marine invertebrates. *Oceanography and Marine Biology Annual Review* **23**: 373-398.

Grant, A. and P. Williamson (1985) Settlement timing hypothesis: a critique. *Marine Ecology - Progress Series* **23**: 193-196.

Gray, C. A. (1996) Small-scale temporal variability in assemblages of larval fishes: implications for sampling. *Journal of Plankton Research* **18**: 1643-1657.

Green, R. H., J. M. Boyd and J. S. Macdonald (1993) Relating sets of variables in environmental studies: the Sediment Quality Triad as a Paradigm. *Environmetrics* **4**: 439-457.

Green, R. H. and G. L. Vascotto (1978) A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. *Water Research* **12**: 583-590.

Grice, G. and N. H. Marcus (1981) Dormant eggs of marine copepods. *Oceanography and Marine Biology Annual Review* **19**: 125-140.

Grioche, A., P. Koubbi and X. Harlay (1999) Spatial patterns of ichthyoplankton assemblages along the eastern English Channel French coast during spring 1995. *Estuarine Coastal and Shelf Science* **49**: 141-152.

Grosberg, R. K. and D. R. Levitan (1992) For adults only? Supply-side ecology and the history of larval biology. *Trends in Ecology and Evolution* **7**: 130-133.

Guéguéniat, P., J.-C. Salomon, M. Wartel, L. Cabioch and A. Fraizier (1993) Transfer pathways and transit times of dissolved matter in the Eastern English Channel indicated by space-time radiotracer and hydrodynamic measurement and hydrodynamic modelling. *Estuarine, Coastal and Shelf Science* **36**: 477-494.

Günther, C.-P. (1992) Dispersal of intertidal invertebrates: a strategy to react to disturbance at different scales? *Netherlands Journal of Sea Research* **30**: 45-56.

Hamon, D. and M. Blanchard (1994) *Etat de la prolifération de la crépidule (*Crepidula fornicata*) en baie de Seine.* IFREMER report.

Hannah, C. G., C. E. Naimie, J. W. Loder and F. E. Werner (1997) Upper-ocean transport mechanisms from the Gulf of Maine to Georges Bank, with implications for *Calanus* supply. *Continental Shelf Research* **17**: 1887-1911.

Hanski, I. (1998) Metapopulation dynamics. *Nature* **396**: 41-49.

Hayward, P. J. and J. S. Ryland (1990) *The Marine Fauna of the British Isles and North-West Europe.* vol. 1. Oxford Science Publications. 627 pp.

Hayward, P. J. and J. S. Ryland (1990) *The Marine Fauna of the British Isles and North-West Europe.* vol. 2. Oxford Science Publications. 996 pp.

Hayward, P. J. and J. S. Ryland (1995) *Handbook of the Marine Fauna of North-West Europe.* Oxford University Press. 800 pp.

Hill, A. E. (1993) Seasonal gyres in shelf seas. *Annales Geophysicae* **11**: 1130-1137.

Hill, A. E. (1991) Advection-diffusion-mortality solutions for investigating pelagic larval dispersal. *Marine Ecology - Progress Series* **70**: 117-128.

Hill, A. E. (1991) A mechanism for horizontal zooplankton transport by vertical migration in tidal currents. *Marine Biology* **111**: 485-492.

Hill, A. E. (1991) Vertical migration in tidal currents. *Marine Ecology - Progress Series* **75**: 39-54.

Hill, A. E. (1994) Horizontal zooplankton dispersal by diel vertical migration in S2 tidal currents on the northwest European continental shelf. *Continental Shelf Research* **14**: 491-506.

Hill, A. E., J. Brown and L. Fernand (1996) The Western Irish Sea gyre: a retention system for Norway lobster (*Nephrops norvegicus*)? *Oceanologica Acta* **19**: 357-368.

Hill, A. E., J. Brown and L. Fernand (1997) The summer gyre in the western Irish Sea: shelf sea paradigms and management implications. *Estuarine, Coastal and Shelf Science* **44**(Supplement A): 83-95.

Hill, A. E., R. Durazo and D. A. Smeed (1994) Observations of a cyclonic gyre in the western Irish Sea. *Continental Shelf Research* **14**: 479-490.

Hirschfeld, H. O. (1935) A connection between correlation and contingency. *Proceedings of the Cambridge Philosophical Society* **31**: 520-524.

Hirst, A. G. (1996) *Zooplankton Production and Energy Flow - Towards a Biological Model of Southampton Water*. PhD. dissertation, University of Southampton.

Hirst, A. G. and E. Castro-Longoria (1998) *Acartia bifilosa* (Copepoda: Calanoida): a clarification of the species and its varieties *inermis* and *intermedia*. *Journal of Plankton Research* **20**: 1119-1130.

Hiscock, K. (1998) Introduction and Atlantic-European perspective. *In* Hiscock, K. (Ed.): *Marine Nature Conservation Review. Benthic marine ecosystems of Great Britain and the north-east Atlantic.* Coasts and Seas of the United Kingdom. MNCR series Peterborough: Joint Nature Conservation Committee. pp. 3-70.

Hoch, T. (1998) Modelling pelagic food web and primary production in the English Channel. *Oceanologica Acta* **21**: 871-885.

Hoch, T. and P. Garreau (1998) Phytoplankton dynamics in the English Channel: a simplified three-dimensional approach. *Journal of Marine Systems* **16**: 133-150.

Hoffman, D. L. and G. R. Franke (1986) Correspondence analysis: graphical representation of categorical data in marketing research. *Journal of Marketing Research* **13**: 213-227.

Hofmann, E. E. (1993) Coupling of circulation and marine ecosystem models. *In* Levin, S. A., T. M. Powell and J. H. Steele (Eds.): *Patch Dynamics.* Lecture Notes in Biomathematics vol. 96. Springer-Verlag. pp. 136-161.

Holme, N. A. (1961) The bottom fauna of the English Channel. Part I. *Journal of the Marine Biological Association of the United Kingdom* **41**: 397-461.

Holme, N. A. (1966) The bottom fauna of the English Channel. Part II. *Journal of the Marine Biological Association of the United Kingdom* **46**: 401-493.

Holme, N. A. (1967) Changes in the bottom fauna of Weymouth Bay and Poole Bay following the severe winter of 1962-63. *Journal of the Marine Biological Association of the United Kingdom***47**: 397-405.

Holme, N. A. (1983) Fluctuations in the benthos of the western English Channel. *Oceanologica Acta* **Proceedings of the 17th European Marine Biology Symposium**: 121-124.

Hughes, T. P. (1990) Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology* **71**: 12-20.

Hurlbert, S. H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**: 187-211.

Hydraulics Research (1993) *South Coast Mobility Study.* HR Wallinford. Report EX 2827.

Ibanez, F. and S. Dallot (1969) Etude du cycle annuel des chaetognathes planctoniques de la rade de Villefranche par la méthode d'analyses des composantes principales. *Marine Biology* **3**: 11-17.

Ingle, R. W. (1983) *Shallow Water Crabs.* Synopses of the British Fauna (New Series) vol. 25. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Iriarte, A. (1991) *Picophytoplankton: Ecological and Physiological Studies in Culture and in Natural Coastal and Estuarine Waters*. PhD. dissertation, University of Southampton.

Iriarte, A. and D. A. Purdie (1994) Size distribution of chlorophyll *a* biomass and primary production in a temperate estuary (Southampton Water): the contribution of photosynthetic picoplankton. *Marine Ecology - Progress Series* **115**: 283-297.

Johnson, D. F. and K. W. Hess (1990) Numerical simulations of blue crab larval dispersal and recruitment. *Bulletin of Marine Science* **46**: 195-213.

Jones, A. M. and J. m. Baxter (1987) *Molluscs: Candofoveata, Solenogastres, Polyplacophora, and Scaphopoda.* Synopses of the British Fauna (New Series) vol. 37. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Jones, N. S. (1976) *British Cumaceans.* Synopses of the British Fauna (New Series) vol. 7. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Jongman, R. H. G., C. F. J. Ter Braak and O. F. R. Van Tongeren (Eds.) (1995) *Data Analysis in Community and Landscape Ecology*. Cambridge University Press.
Joyce, T. M. and P. H. Wiebe (Eds.) (1992) Warm-Core Rings. *Deep-Sea Research* **39**.

Jumars, P. A. (1993) *Concepts in Biological Oceanography - An Interdisciplinary Primer.* Oxford University Press. 348 pp.

Ketchum, B. H. (1954) Relation between circulation and planktonic populations in estuaries. *Ecology* **35**: 191-200.

Kifle, D. (1992) *Seasonal and Spatial Variations in Species Composition, Abundance, Biomass and Primary Production of Phytoplankton in Southampton Water.* PhD. dissertation, University of Southampton.

Kifle, D. and D. A. Purdie (1993) The seasonal abundance of the phototrophic ciliate *Mesodinium rubrum* in Southampton Water. *Journal of Plankton Research* **15**: 823-833.

Kimmerer, W. J., J. R. Burau and W. A. Bennett (1998) Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnology and Oceanography* **43**: 1697-1709.

King, P. E. (1974) *British Sea Spiders.* Synopses of the British Fauna (New Series) vol. 5. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Knight-Jones, E. W. and G. D. Waugh (1949) On the larval development of *Elminius modestus* Darwin. *Journal of the Marine Biological Association of the United Kingdom* **28**: 413-428.

Kostopoulou, V. (1997) *Temporal and Spatial variations in copepod distributions in Southampton Water over tidal cycles*. M.Sc. dissertation, University of Southampton.

Kraeuter, J. N. (1974) Offshore currents, larval transport and establishment of southern populations of *Littorina littorea* Linné along the U. S. Atlantic coast. *Thalassa Jugoslavica* **10**: 159-170.

Kruskal, J. B. (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrics* **29**: 1-27.

Kruskal, J. B. (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrics* **29**: 115-129.

Kruskal, J. B. and M. Wish (1978) *Multidimensional Scaling.* Beverly Hills: Sage Publications.

Lagadeuc, Y., M. Boulé and J. J. Dodson (1997) Effect of vertical mixing on the vertical distribution of copepods in coastal waters. *Journal of Plankton Research* **19**: 1183-1204.

Laprise, R. and J. J. Dodson (1994) Environmental variability as a factor controlling spatial patterns in distribution and species diversity of zooplankton in the St. Lawrence Estuary. *Marine Ecology - Progress Series* **107**: 67-81.

Laprise, R. and P. Pepin (1995) Factors influencing the spatio-temporal occurrence of fish eggs and larvae in a northern, physically dynamic coastal environment. *Marine Ecology - Progress Series* **122**: 73-92.

Larsonneur, C., P. Bouysse and J.-P. Auffret (1982) The superficial sediments of the English Channel and its Western Approaches. *Sedimentology* **29**: 851-864.

Lee, T. N., M. E. Clarke, E. Williams, A. F. Szmant and T. Berger (1994) Evolution of the Tortugas gyre and its influence on recruitment in the Florida keys. *Bulletin of Marine Science* **54**: 621-646.

Lee, T. N., C. Rooth, E. Williams, M. McGowan, A. F. Szmant and M. E. Clarke (1992) Influence of Florida Current, gyres and wind-driven circulation on transport of larvae in the Florida Keys coral reefs. *Bulletin of Marine Science* **42**: 971-1002.

Lee, W. Y. and B. J. McAlice (1979) Sampling variability of marine zooplankton in a tidal estuary. *Estuarine, Coastal and Shelf Science* **8**(565-582):

Le Fèvre, J., P. Le Corre, P. Morin and J.-L. Birroen (1983) The pelagic ecosystem in frontal stones and other environments off the West coast of Brittany. *Oceanologica Acta:* **Proceedings of the 17th European Marine Biology Symposium**: 125-129.

Le Fèvre-Lehoërff, G., H. Grossel and A. Derrien (1983) Evolution des populations planctoniques animales en Manche et au sud de la Mer du Nord *Oceanologica Acta:* Proceedings of the 17th European Marine Biology Symposium: 131-135.

Le Fèvre-Lehoërff, G., F. Quiniou and J. Y. Quintin (1986) Le zooplankton dans le golfe normano-breton. *In* Golfe normano-breton - Etude intégrée. vol. 2: Milieu Pélagique. Rapport CEE/ DERO/86.27/EL, 6 volumes.

Le Fèvre-Lehöerff, G., E. Erard-Le Denn and G. Arzul (1993) Planktonic Ecosystems in the Channel - Trophic Relations. *Oceanologica Acta* **16**: 661-670.

Legendre, L. and S. Demers (1984) Towards Dynamic Biological Oceanography and Limnology. *Canadian Journal of Fisheries and Aquatic Sciences* **41**: 2-19.

Legendre, L. and P. Legendre (1998) *Numerical Ecology.* 2nd. English edition. Amsterdam: Elsevier Science. 853 pp.

Lincoln, R. J. (1979) *British Marine Amphipoda: Gammaridae.* British Museum (Natural History). 658 pp.

Lobel, P. S. and A. R. Robinson (1986) Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. *Deep-Sea Research* **33**: 483-500.

Lockwood, A. P. M. (1986) Southampton Water and the Solent: biological effects of the multi-use of an estuarine system. *In La baie de Seine (GRECO-MANCHE).* vol. 4. Université de Caen: IFREMER. pp. 421-430.

Loder, J. W. (1980) Topographic rectification of tidal currents on the sides of Georges Bank. *Journal of Physical Oceanography* **10**: 1399-1416.

Lucas, C. and J. A. Williams (1994) Population dynamics of the scyphomedusa *Aurelia aurita* in Southampton Water. *Journal of Plankton Research* **16**: 879-895.

Lucas, C. H. (1993) *The Biology of Gelatinous Predators and their Impact on the Mesozooplankton Community of Southampton Water.* PhD. dissertation, University of Southampton.

Lucas, C. H. and J. A. Williams (1995) Gelatinous predators and their potential impact on the mesozooplankton community of Southampton Water. *In* Eleftheriou, A., A. D. Ansell and C. J. Smith (Eds.): *Proceedings of the 28th European Marine Biology Symposium, Crete, Greece, 1993.* Fredensborg: Olsen & Olsen. pp. 73-78.

Lynch, D. R., W. C. Gentleman, D. J. McGillicuddy and C. S. Davis (1998) Biological/physical simulations of *Calanus finmarchicus* population dynamics in the Gulf of Maine. *Marine Ecology-Progress Series* **169**: 189-210.

Mackas, D. L. (1984) Spatial autocorrelation of plankton community composition in a continental shelf ecosystem. *Limnology and Oceanography* **29**: 451-471.

Manly, B. F. J. (1994) *Multivariate Statistical Methods - A Primer.* Chapman and Hall. 215 pp.

Mann, K. H. and J. R. N. Lazier (1991) *Dynamics of Marine Ecosystems.* Blackwell Scientific. 466 pp.

Marcus, N. H. and F. Boero (1998) Minireview: the importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnology and Oceanography* **43**: 763-768.

Margalef, R. (1997) Turbulence and marine life. *Scientia Marina* **61**(Supl. 1): 109-123.

Marteil, L. (1963) La crépidule en France. *Science et Pêche, Bulletin de l'Institut des Pêches Maritimes,* n.121.

Mathivat-Lallier, M. H. and C. Cazaux (1990) Larval exchange and dispersion of polychaetes between a bay and the ocean. *Journal of Plankton Research* **12**: 1163-1172.

McArdle, B. H., J. E. Hewitt and S. F. Thrush (1997) Pattern from process: it is not as easy as it looks. *Journal of Experimental Marine Biology and Ecology* **216**: 229-242.

McConaugha, J. R. (1992) Decapod larvae: Dispersal, mortality, and ecology. a working hypothesis. *American Zoologist* **32**: 512-523.

Morgan, S. G. (1995) Life and death in the plankton: larval mortality and adaptation. *In* McEdward, L. (Ed.): *The Ecology of Marine Invertebrate Larvae.* CRC Press. pp. 279-321.

Morgan, S. G. (1996) Plasticity in reproductive timing by crabs in adjacent tidal regimes. *Marine Ecology - Progress Series* **139**: 105-118.

Morgan, T. S. (1997) *The Formation and Dynamics of* Pygospio elegans *tube beds in the Somme Estuary, France.* Ph.D. dissertation, University of Southampton.

Murdoch, R. C. (1989) The effects of a headland eddy on surface macro-zooplankton assemblages north of Otago Peninsula. *Estuarine, Coastal and Shelf Science* **29**: 361-363.

Naylor, E. (1972) *British Marine Isopods.* Synopses of the British Fauna (New Series) vol. 3. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Nichols, J. H., B. M. Thomson and M. Cryer (1982) Production, drift and mortality of the planktonic larvae of the edible crab (*Cancer pagurus*) off the north-east coast of England. *Netherlands Journal of Sea Research* **16**: 173-184.

Okubo, A. (1973) Effects of shoreline irregularities in streamwise dispersion in estuaries and other embayments. *Netherlands Journal of Sea Research* **6**: 213-224.

Okubo, A. (1994) The role of diffusion and related physical processes in dispersal and recruitment of marine populations. *In* Sammarco, P. W. and M. L. Heron (Eds.): *The Bio-Physics of Marine Larval Dispersal.* Coastal and Estuarine Studies vol. 45. Washington, D C: American Geophysical Union. pp.

Ólafson, E. B., C. H. Peterson and W. G. J. Ambrose (1994) Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology Annual Review* **32**: 65-109.

Olive, P. J. (1977) The life-history and population structure of the polychaetes *Nephtys caeca* and *Nephtys hombergii* with special reference to the growth rings in the teeth. *Journal of the Marine Biological Association of the United Kingdom* **57**: 133-150.

Olmi III, E. J. and R. J. Orth (1995) Introduction to the proceedings of the blue crab recruitment symposium. *Bulletin of Marine Science* **57**: 707-712.

Orbi, A. and J. C. Salomon (1988) Dynamique de marée dans le golfe Normand-Breton. *Oceanologica Acta* **11**: 55-64.

Paduan, J. D. and H. C. Graber (1997) Introduction to high-frequency Radar: reality and myth. *Oceanography* **10**: 36-39.

Paphitis, D. (1997) *Residual Circulation and Associated Sediment Dynamics: Eastern Approaches to the Solent.* M.Sc. dissertation, University of Southampton.

Pechenik, J. A. (1984) The relationship between temperature, growth rate, and duration of larval life of the gastropod *Crepidula fornicata* (L.). *Journal of Experimental Marine Biology and Ecology* **74**: 241-257.

Pechenik, J. A. and G. M. Lima (1984) Relationship between growth, differentiation, and length of larval life for individually reared larvae of the marine gastropod, *Crepidula fornicata. Biological Bulletin* **166**: 537-549.

Petersen, J. E., L. P. Sanford and W. M. Kemp (1998) Coastal plankton responses to turbulent mixing in experimental ecosystems. *Marine Ecology-Progress Series* **171**: 23-41.

Phillips, A. J. (1980) Distribution of chemical species. *In The Solent Estuarine System.* NERC Publications series C, vol. 22. pp. 44-51.

Pinca, S. and S. Dallot (1995) Meso- and macrozooplankton composition patterns related to hydrodynamic structures in the Ligurian Sea (Trophos-2 experiment, April-June 1986). *Marine Ecology - Progress Series* **126**: 49-65.

Pineda, J. (1999) Circulation and larval distribution in internal tidal bore warm fronts. *Limnology and Oceanography* **44**: 1400-1414.

Pingree, R. D. (1975) The advance and retreat of the thermocline in the continental shelf. *Journal of the Marine Biological Association of the United Kingdom* **55**: 965-974.

Pingree, R. D., P. M. Holligan, G. T. Mardell and R. N. Head (1978) The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. *Journal of the Marine Biological Association of the United Kingdom* **56**: 845-873.

Pingree, R. D. and L. Maddock (1985) Rotary currents and residual circulation around banks and islands. *Deep Sea Research* **32**: 929-947.

Pingree, R. D., G. T. Mardell and L. Maddock (1985) Tidal mixing in the Channel Isles region derived from the results of remote sensing and measurements at sea. *Estuarine, Coastal and Shelf Science* **20**: 1-18.

Pinot, J.-M., J. Tintore, J. L. Lopez-Jurado, M. L. Fernandez-de-Puelles and J. Jansa (1995) Three-dimensional circulation of a mesoscale eddy/front system and its biological implications. *Oceanologica Acta* **18**: 389-400.

Pleijel, F. and R. P. Dales (1991) *Polychaetes: British Phyllodocoideans, Typhloscolecoideans and Tomopteroideans.* Synopses of the British Fauna (New Series) vol. 45. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Prandle, D. (1991) A new view of near-shore dynamics based on observations from HF Radar. *Progress in Oceanography* **27**: 403-438.

Prandle, D. (1997) Tidal and wind-driven currents from OSCR. *Oceanography* **20**: 57-59.

Raby, D., Y. Lagadeuc, J. J. Dodson and M. Mingelbier (1994) Relationship between feeding and vertical distribution of bivalve larvae in stratified and mixed waters. *Marine Ecology - Progress Series* **103**: 275-284.

Rand, P. S. and S. G. Hinch (1998) Spatial patterns of zooplankton biomass in the northeast Pacific Ocean. *Marine Ecology-Progress Series* **171**: 181-186.

Raymont, J. E. G. and B. G. A. Carrie (1964) The production of zooplankton in Southampton Water. *Int. Rev. Ges. Hydrobiol. Hydrogr.* **49**: 185-232.

Rees, H. L., M. A. Pendle, R. Waldcock, D. S. Limpenny and S. E. Boyd (1999) A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. *ICES Journal of Marine Science* **56**: 228-246.

Richards, S. A., H. P. Possingham and B. J. Noye (1995) Larval dispersion along a straight coast with tidal currents: complex distribution patterns from a simple model. *Marine Ecology - Progress Series* **122**: 59-71.

Robinson, A. R. (1983) *Eddies in Marine Science.* Springer-Verlag. 609 pp.

Robinson, I. S. (1983) Tidally induced residual flows. In Johns, B. (Ed.): *Physical Oceanography of Coastal and Shelf Seas.* Elsevier. pp. 321-356.

Robinson, I. S. (1981) Tidal vorticity and residual circulation. *Deep-Sea Research A* **28**: 195-212.

Robinson, G. A., J. Aiken and H. G. Hunt (1986) Synoptic surveys of the western English Channel. The relationship between plankton and hydrography. *Journal of the Marine Biological Association of the United Kingdom* **66**: 201-218.

Robinson, G. A. and H. G. Hunt (1986) Continuous plankton records: annual fluctuations of the plankton in the western English Channel. *Journal of the Marine Biological Association of the United Kingdom* **66**: 791-802.

Rowe, P. M. and C. E. Epifanio (1994) Tidal stream transport of weakfish larvae in Delaware Bay, USA. *Marine Ecology - Progress Series* **110**: 105-114.

Rumrill, S. S. (1990) Natural mortality of marine invertebrate larvae. Ophelia **32**: 163-198.

Ruxton, G. D. (1996) Dispersal and chaos in spatially structured models: an individual-level approach. *Journal of Animal Ecology* **65**: 161-169.

Salas-de-Leon, D. A., M. A. Monreal-Gomez, L. Sanvicente-Anorve and C. Flores-Coto (1998) Long-term influence of currents on zooplanktonic organism distribution in the Bay of Campeche, Mexico. *Oceanologica Acta* **21**: 87-93.

Salomon, J.-C. (1990) Role of instantaneous and long-term water movements on the recruitment of benthic fauna in the English Channel. *La Mer* **28**: 211-217.

Salomon, J.-C. and M. Breton (1991) Courants résiduels de marée dans la Manche. *Oceanologica Acta* **11**: 47-53.

Salomon, J.-C. and M. Breton (1993) An atlas of long-term currents in the Channel. *Oceanologica Acta* **16**: 439-448.

Salomon, J.-C., M. Breton and P. Guéguéniat (1993) Computed residual flow through the Straights of Dover. *Oceanologica Acta* **16**: 449-455.

Salomon, J.-C., P. Guéguéniat, A. Orbi and Y. Baron (1988) A Lagrangian model for long term tidally induced transport and mixing. Verification by artificial radionuclide concentrations. *In Radionuclides: a Tool for Oceanography*. Elsevier Press. pp. 384-394.

Savage, **P. D. V.** (1965) Preliminary observations on the phytoplankton of Southampton Water. *Br. Phycol. Bull.* **2**: 515-516.

Sautour, B. and J. Castel (1993) Distribution of zooplanktonic populations in Marennes -Oléron bay (France), structure and grazing impact of copepod communities. *Oceanologica Acta* **16**: 279-290.

Seuront, L. and Y. Lagadeuc (1998) Spatio-temporal structure of tidally mixed coastal waters: variability and heterogeneity. *Journal of Plankton Research* **20**: 1387-1401.

Scheltema, R. S. (1986) On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bulletin of Marine Science* **39**: 290-322.

Schwiderski, E. W. (1983) Atlas of ocean tidal charts and maps, part 1: the semidiurnal principal lunar tide M_2. *Marine Geodesy* **6**: 219-265.

Sewell, M. A. and J. C. Watson (1993) A "Source" for asteroid larvae?: recruitment of *Pisaster ochraceus, Pycnogopodia heliantoides* and *Dermasterias imbricata* in Nootka Sound, British Columbia. *Marine Biology* **117**: 387-398.

Shanks, A. L. (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. *In* McEdward, L. (Ed.): *The Ecology of Marine Invertebrate Larvae.* CRC Press. pp. 323-367.

Simpson, J. H. and J. R. Hunter (1974) Fronts in the Irish Sea. *Nature* **250**: 404-406.

Simpson, J. H., J. Sharples and T. P. Rippeth (1991) A prescriptive model of stratification induced by fresh-water runoff. *Estuarine Coastal and Shelf Science* **33**: 23-35.

Smaldon, G. (1979) *British Coastal Shrimps and Prawns.* Synopses of the British Fauna (New Series) vol. 15. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Smith, N. P. and A. W. Stoner (1993) Computer simulation of larval transport through tidal channels: role of vertical migration. *Estuarine, Coastal and Shelf Science* **37**: 43-58.

Sneath, P. H. A. and R. R. Sokal (1973) *Numerical Taxonomy.* San Francisco: W H Freeman and Co. 573 pp.

Sokal, R. R. and F. J. Rohlf (1995) *Biometry.* New York: W. H. Freeman and Company. 887 pp.

Southward, A. J. (1983) Fluctuations in the ecosystem of the Western Channel: a summary of studies in progress. *Oceanologica Acta* **Proceedings of the 17th European Marine Biology Symposium**: 187-189.

Stancyk, S. E. and R. J. Feller (1986) Transport of non-decapod invertebrate larvae in estuaries: an overview. *Bulletin of Marine Science* **39**: 257-268.

Starr, M., J. H. Himmelman and J. C. Thierriault (1990) Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science* **247**: 1071-1074.

Stevens, L. (1997) *An Intercomparison of Methods of Spatially Detailed Surface Current Determination.* Undergraduate research project dissertation, University of Southampton.

Stoner, A. W. and N. P. Smith (1998) Across-shelf transport of gastropod larvae in the central Bahamas: rapid responses to local wind conditions. *Journal of Plankton Research* **20**: 1-16.

Strathmann, R. R. (1986) What controls the type of larval development? Summary statement for the evolution session. *Bulletin of Marine Science* **39**: 616-622.

Sundby, S. (1997) Turbulence and ichthyoplankton: Influence on vertical distributions and encounter rates. *Scientia Marina* **61** (Supl. 1): 159-176.

Svendsen, H. (1997) Physical oceanography and marine ecosystems: Some illustrative examples. *Scientia Marina* **61** (Supl. 1): 93-108.

Sverdrup, H. U. (1953) On conditions for the vernal blooming of phytoplankton. *Journal du Conseil permanent international pour l'Exploration de la Mer* **18**: 287-295.

Ter Braak, C. J. F. (1986) Canonical Correspondence-Analysis - a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167-1179.

Ter Braak, C. J. F. (1988) *CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended][canonical] correspondence analysis (version 2.1).* Agricultural Mathematics Group. Report LWA-88-02.

Thiébaut, E. (1994) *Dynamique du recrutement et dispersion larvaire de deux annélides polychètes* Owenia fusiformis *et* Pectinaria koreni *en régime mégatidal (Baie de Seine orientale, Manche).* PhD dissertation, Université Paris 6.

Thiébaut, E., L. Cabioch, J.-C. Dauvin, C. Retière and F. Gentil (1997) Spatio-temporal persistence of the *Abra alba - Pectinaria Koreni* muddy-fine sand community of the eastern bay of Seine. *Journal of the Marine Biological Association of the United Kingdom* **77**: 1165-1185.

Thiébaut, E., J.-C. Dauvin and Y. Lagadeuc (1992) Transport of *Owenia fusiformis larvae* (Annelida: Polychaeta) in the Bay of Seine. I. Vertical distribution in relation to water column stratification and ontogenetic vertical migration. *Marine Ecology - Progress Series* **80**: 29-39.

Thompson, T. E. (1988) *Molluscs: Benthic Opistobranchs.* Synopses of the British Fauna (New Series) vol. 8 (2nd edition). (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Thompson, T. E. and G. H. Brown (1976) *Molluscs: British Opistobranchs Molluscs.* Synopses of the British Fauna (New Series) vol. 8. (Kerack, D. M. and R. S. K. Barnes, eds.). Brill and Backhuys.

Thorp, C. H. (1980) The benthos of the Solent. *In The Solent Estuarine System.* NERC Publications, series C, vol. 22. pp. 76-85.

Thorson, G. (1946) Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Kommessionen fra Danemark fiskeri-og Havundersogelser Serie Plankton* **4**: 1-523.

Thorson, G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* **25**: 1-45.

Thorson, G. (1957) Bottom communities. *Journal of the Geological Society of America* **61**: 461-534.

Thorson, G. (1966) Some factors influencing the recruitment and establishment of marine benthic communities. *Netherlands Journal of Sea Research* **3**: 267-283.

Todd, C. D. and R. W. Doyle (1981) Reproductive strategies of marine benthic invertebrates: a settlement-timing hypothesis. *Marine Ecology - Progress Series* **4**: 75-83.

Torgerson, W. S. (1952) Multidimensional scaling. I. Theory and method. *Psychometrics* **17**: 401-419.

Tremblay, M. J., J. W. Loder, F. E. Werner, C. E. Naimie, F. H. Page and M. M. Sinclair (1994) Drift of sea scallop larvae *Placopecten magellanicus* on Georges Bank: a model of the roles of mean advection, larval behavior and larval origin. *Deep-Sea Research II* **41**: 7-49.

Turner, E. J., R. K. Zimmer-Faust, M. A. Palmer, M. Luckembach and N. D. Pentcheff (1994) Settlement of oyster (*Crassostrea virginica*) larvae: effects of water flow and a water-soluble chemical cue. *Limnology and Oceanography* **39**: 1579-1593.

Tyler, P. A. (1976) Sub-littoral community structure of Oxwich Bay, South Wales in relation to sedimentological, physical oceanographic and biological parameters. *In* Keegan, B. F., P. O. Céidigh and P. J. S. Boaden (Eds.): *Biology of Benthic Organisms: Proceedings of the 11th European Marine Biology Symposium, Galway, Ire.* Pergamon Press. pp. 559-566.

Tyler, P. A. and F. T. Banner (1977) The effect of coastal hydrodynamics on the echinoderm distribution in the sublittoral of Oxwich Bay, Bristol Channel. *Estuarine, Coastal and Shelf Science* **5**: 293-308.

UNESCO (1968) *Zooplankton sampling.* 174 pp.

UNESCO (1981) Tenth Report of the Joint Panel on Oceanographic Tables and Standards. 144 pp.

Vallet, C. and J. C. Dauvin (1999) Seasonal changes of macrozooplankton and Benthic Boundary layer macrofauna from the Bay of Saint-Brieuc (western English Channel). *Journal of Plankton Research* **21**: 35-49.

Van Der Spoel, S. (1994) The basis for boundaries in pelagic biogeography. *Progress in Oceanography* **34**: 121-133.

Van Guelpen, L., D. F. Markle and D. J. Duggan (1982) An evaluation of accuracy, precision and speed of several zooplankton subsampling techniques. *Journal du Conseil international pour l'Exploration de la Mer* **40**: 226-236.

Velegrakis, A. F., S. Gao, R. Lafite, J. P. Dupont, M. F. Huault, L. A. Nash and M. B. Collins (1997) Resuspension and advection processes affecting suspended particulate matter concentrations in the central English Channel. *Journal of Sea Research* **38**: 17-34.

Verlhust, P. F. (1838) Notice sur la loi que la population suit dans son accroissement. *Correpondances Mathématiques et Physiques* **10**: 113-121.

Visser, A. W., M. J. Bowman and W. R. Crawford (1990) Dynamics of tidally forced basin-wide coastal eddies. *In* Cheng, R. T. (Ed.): *Residual Currents and Long Term Transport.* Coastal and Estuarine Studies vol. 38. Springer Verlag. pp. 64-78.

Wang, Z., E. Thiébaut and J.-C. Dauvin (1995) Spring abundance and distribution of the ctenophore *Pleurobrachia pileus* in the Seine estuary: advective transport and diel vertical migration. *Marine Biology* **124**: 313-324.

Webber, N. B. (1980) Hydrography and water circulation in he Solent. *In The Solent Estuarine System.* NERC Publications, Series C, vol 22. pp. 25-35.

Whittaker, R. H. (1967) Gradient Analysis of vegetation. *Biological Reviews* **49**: 207-264.

Wiafe, G. and C. L. J. Frid (1996) Short-term temporal variation in coastal zooplankton communities: the relative importance of physical and biological mechanisms. *Journal of Plankton Research* **18**: 1485-1501.

Williams, P. J. Le B. (1980) Phytoplankton in Southampton Water. *In The Solent Estuarine System.* NERC Publications, Series C, vol 22. pp. 73-75.

Williams, R. (1984) Zooplankton of the Bristol Channel and Severn Estuary. *Marine Pollution Bulletin* **15**: 66-70.

Withers, R. G. and C. H. Thorp (1978) The macrobenthos inhabiting sandbanks in Langstone Harbour, Hampshire. *Journal of Natural History* **12**: 445-455.

Wolanski, E., T. Asaeda, A. Tanaka and E. Deleersnijder (1996) Three-dimensional island wakes in the field, laboratory experiments and numerical models. *Continental Shelf Research* **16**: 1437-1452.

Wolanski, E. and W. H. Hamner (1988) Topographically controlled fronts in the ocean and their biological significance. *Science* **241**: 177-181.

Young, C. M. (1990) Larval ecology of marine invertebrates: a sesquicentennial history. *Ophelia* **32**: 1-48.

Young, C. M. (1995) Behavior and locomotion during the dispersal phase of larval life. *In* McEdward, L. (Ed.): *The Ecology of Marine Invertebrate Larvae.* CRC Press. pp. 249-277.

Zagami, G., F. Badalamenti, L. Gugliemo and A. Manganaro (1996) Short-term variations of the zooplankton community near the straits of Messina (north-eastern Sicily): relationships with the hydrodynamic regime. *Estuarine, Coastal and Shelf Science* **42**: 667-681.

Zeng, C. and E. Naylor (1996) Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus maenas*: implications for ebb tide offshore dispersal. *Marine Ecology - Progress Series* **132**: 71-82.

Zimmerman, J. T. F. (1981) Dynamics, diffusion and geomorphological significance of tidal residual eddies. *Nature* **290**: 549-555.

Zinger, I. (1989) *Zooplankton community Structure in Southampton Water and its potential Response to Chronic Pollution.* PhD. dissertation, University of Southampton.

Zouhiri, S. and J. C. Dauvin (1996) Diel changes of the Benthic Boundary Layer macrofauna over coarse sand sediment in the western English Channel. *Oceanologica Acta* **19**: 141-153.

Appendix A: Supplementary Figures and Tables

Chapter II supplementary figures & tables:

Cruise	Tidal Coefficient	Time of High Water (Portsmouth)	Transect 1	Transect 2	Transect 3
1	**49/52**	06:00/07:00	7/06 09:30 (1)	8/06 11:35 (12)	7/06 16:30 (29)
2	**106/104**	13:00/14:00	15/06 11:00 (11)	14/06 14:45 (12)	14/06 10:45 (22)
3	**50/49**	07:00/08:00	22/06 11:40 (11)	21/06 10:58 (21)	21/06 16:02 (29)
4	**75/81**	12:00/13:00	27/07 12:50 (Calshot)	28/07 09:07 (22)	28/07 13:06 (12)
5	**56/68**	11:00/12:00	24/08 10:46 (11)	23/08 14:15 (12)	23/08 10:12 (22)

Table A.2.1: Tidal coefficients (from SHOM), time of high water (GMT + 1, Portsmouth, from Admiralty tide tables), date (1995), time (GMT+1), and starting station for transects 1, 2 and 3 for all cruises. In cruise 1, stations Calshot, East Ryde and Sturbridge were sampled on 09/06/1995

Cruise	Station	Data Collected	
		CTD	Plankton
2	1	**No**	**Yes**
	S. Sturbridge	**Yes**	**No**
	N. Sturbridge	**Yes**	**No**
	N. E Lepe	**Yes**	**No**
	E. Lepe	**Yes**	**No**
	S. E. Lepe	**Yes**	**No**
	W. Lepe	**Yes**	**No**
3	S. Sturbridge	**Yes**	**No**
	N. Sturbridge	**Yes**	**No**
5	12	**No**	**Yes**
	E. Ryde	**No**	**Yes**

Table A.2.2: Stations where partial sampling occurred (CTD data *or* plankton samples were not taken); cruise 4 not affected.

		Temperature	Transmission	Fluorometry	Phi	log(zooplankton abundance)
Cruise 1 n=31	Salinity	**-0.61**	**0.82**	-0.10	0.14	
	Temperature		**-0.72**	**-0.38**	-0.15	
	Transmission			-0.08	0.26	
	Fluorometry				-0.12	
Cruise 2 n=30	Salinity	-0.34	0.12	0.11	-0.22	**0.48**
	Temperature		**-0.50**	-0.04	0.11	-0.19
	Transmission			-0.32	**0.44**	-0.19
	Fluorometry				**-0.51**	**0.46**
	Phi					-0.28
Cruise 3 n=33	Salinity	**-0.62**	**0.89**	**-0.58**	**-0.45**	-0.06
	Temperature		**-0.64**	0.08	**0.38**	**-0.38**
	Transmission			**-0.64**	-0.28	-0.11
	Fluorometry				0.06	**0.39**
	Phi					0.06
Cruise 4 n=26	Salinity	-0.27	-0.04	0.18	-0.19	-0.17
	Temperature		0.14	-0.03	0.34	**0.53**
	Transmission			-0.10	0.23	-0.04
	Fluorometry				0.37	-0.33
	Phi					-0.02
Cruise 5 n=29	Salinity	0.26	-0.34	-0.16	**-0.61**	**0.41**
	Temperature		-0.35	0.07	**-0.48**	**0.50**
	Transmission			-0.13	**0.43**	-0.32
	Fluorometry				-0.14	-0.27
	Phi					-0.33

Table A.2.3: Correlation (Pearson's r) between temperature, salinity, fluorometry, transmission, potential energy anomaly (ϕ) and log (total zooplankton abundance). In bold type are correlations significant at the $\alpha = 0.05$ level. Autocorrelation is not taken into account in the significance testing.

Table A.2.4: First 15 tidal constituents, as measured by OSCR, in order of amplitude averaged over the OSCR measurement field for 1995 and 1996.

1995			1996		
constituent	period (days)	amplitude (cm.s^{-1})	constituent	period (days)	amplitude (cm.s^{-1})
M2	28.98	**59.3**	**M2**	28.98	**67.3**
S2	30.00	**18.0**	**S2**	30.00	**18.6**
N2	28.44	**10.7**	**N2**	28.44	**12.9**
M4	57.97	**10.2**	**MS4**	58.98	**8.1**
M6	86.95	**7.0**	**M4**	57.97	**7.8**
L2	29.53	**6.3**	**Z0**	00.00	**6.6**
MSF	01.02	**5.0**	**O1**	13.94	**6.2**
K2	30.08	**4.9**	**OO1**	16.14	**6.0**
MS4	58.98	**4.9**	**M6**	86.95	**5.8**
2MS6	87.97	**4.6**	**K2**	30.08	**5.1**
2MN6	86.41	**4.6**	**K1**	15.04	**5.0**
Z0	00.00	**4.5**	**J1**	15.59	**4.6**
O1	13.94	**4.4**	**2MS6**	87.97	**4.3**
MN4	57.42	**4.2**	**2MN6**	86.41	**4.0**
MU2	27.97	**3.4**	**MU2**	27.97	**4.0**

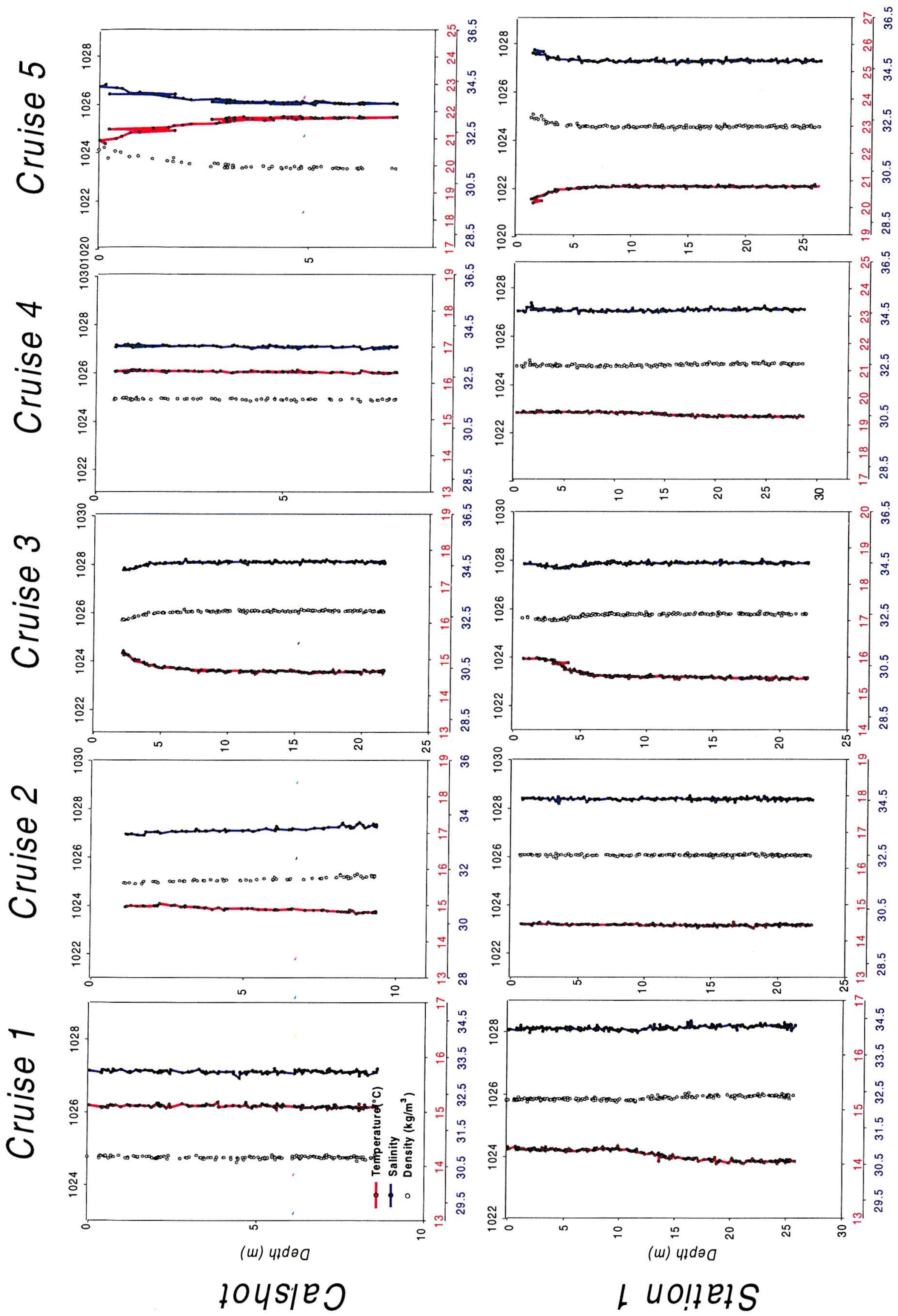


Figure A.2.1: Examples of CTD casts: vertical profiles of temperature (°C), salinity and density (kg.m^{-3}) for stations 'Calshot' and 1 (cruises 1-5).

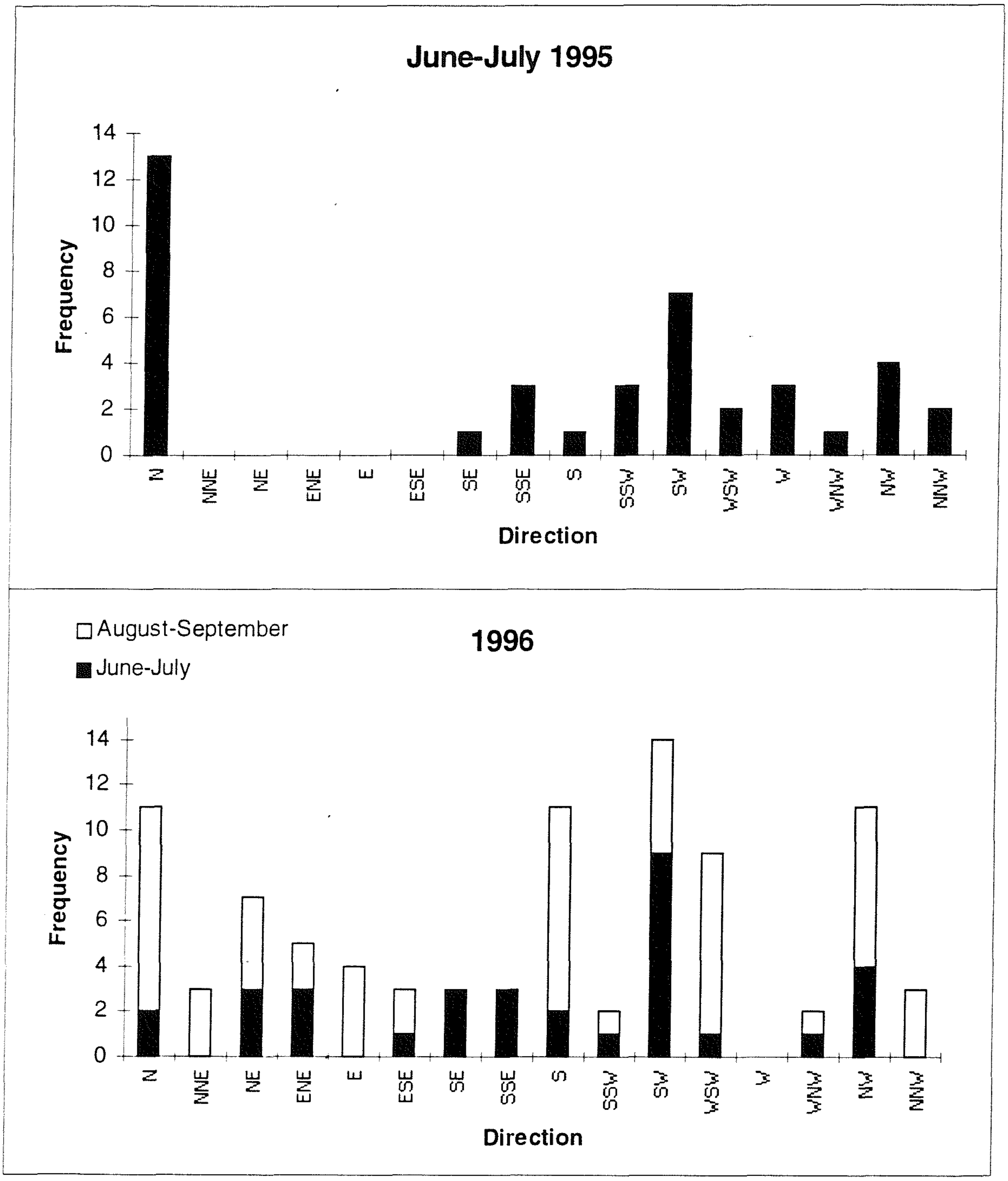


Figure A.2.2: Wind direction for June-July 1995 (top) and June-September 1996 (bottom), from Havant Borough Council, measure daily at 10:00 BST on Hayling Island.

Chapter III supplementary figures & tables:

Table A.3.1: Benthic survey log.

Date	Time	Station number	Depth (m)	Location	Notes
28/02/95	09:45	Vectis	15.0	50°42.79' N 01°03.45' W	Wind force 6; fine sand with some mud; 5 minute trawl; *Nephtys* sp. *Ampelisca* sp.; 1 bucket; 1 sediment sample
28/02/95	11:25	St. 7	7.4	50°46.93' N 01°12.86 'W	Force 6; mud with empty shells from *Crepidula* and small shell fragments; 10 minute trawl; *Crepidula* community; 2 buckets.
28/02/95	12:25	St. 5	15.6	50°46.16 'N 01°14.18' W	Force 6; oyster beds with numerous empty shells; 10 minutes trawl; important presence of mobile and sessile epifauna; 2 buckets (dredge 2/3 full); Sabellaridae present on the empty oyster shells
10/03/95	10:05	St. 4	4.6	50°48.07' N 01°16.03' W	Muddy sediments with living *Crepidula*; 10 minute trawl; 1 bucket; sediment sample
10/03/95	10:25	St. 2	3.8	50°48.07' N 01°14.07' W	Muddy sediments; *Crepidula* and *Nucula*; 10 minute trawl; 1 bucket; sediment sample
10/03/95	10:55	St. 3	19.5	50°47.02' N 01°16.03' W	Numerous empty *Crepidula* shells; 10 minute trawl; very little sediment; sessile and mobile epifauna abundant; 2 buckets
10/03/95	11:25	St. 1	9.1	50°49.47' N 01°18.08' W	Empty Crepidula shells and cobbles (Ø~1-10 cm); 10 minute trawl; very little fine sediment; (*n.b.*. only 1/4 of the *Crepidula* caught was kept - the whole catch was washed in the 1 mm sieve and in- and epifauna kept but cobbles and *Crepidula* was thrown back.
11/03/95	08:15	St. 10	7.6	50°46.02' N 01°06.48' W	Muddy-sandy sediment with empty shells of *Crepidula*; 10 minute trawl; 2 buckets (*n.b.* only 2/3 of the living *Crepidula* kept)
11/03/95	09:00	St. 8	23.8	50°46.16' N 01°10.16' W	Sandy sediment; 10 minute trawl; *Crepidula* in small numbers and *Ampelisca*; 1 bucket
11/03/95	09:42	St. 6	17.1	50°47.05' N 01°12.20' W	Fine sand; 10 minute trawl; *Crepidula* in reasonable numbers; sediment sample; 1 bucket
11/03/95	10:35	St. 9	7.4	50°45.05' N 01°08.01' W	Oyster bed; large number of empty oyster shells; 10 minute trawl; all the mobile in- and epifauna kept together with some shells for the sessile epifauna
11/03/95	11:25	St. 11	8.0	50°43.13' N 01°05.05' W	Gravel; 10 minute trawl; high abundance of various Decapoda and *Buccinum*; 3 buckets

Date	Time	Station number	Depth (m)	Location	Notes
11/03/95	12:25	St. 12	5.4	50°45.06' N 01°02.02' W	Gravel; 10 minute trawl; *Idotea, Crangon* and *Flustra*; 1 bucket
34768	13:00	St. 13	3.6	50°46.08' N 01°02.02' W	Coarse sand; 10 minute trawl; *Idotea* and some *Crepidula*; sediment sample; 2 buckets
11/03/95	13:45	St. 17	7.9	50°45.04' N 00°59.84' W	Pebbles; 10 minute trawl; *Crepidula*; 1 bucket
11/03/95	14:45	St. 22	11.9	50°44.00' N 00°58.00' W	Pebbles and gravel; 10 minute trawl; *Crepidula*; 2 buckets
11/03/95	15:25	St. 18	5.0	50°46.05' N 00°58.02' W	Pebbles; 10 minute trawl; *Crepidula*; 1 bucket
11/03/95	15:50	St. 14	4.2	50°46.38' N 00°59.78' W	Sandy sediment; two similar trawls for 10 minute put together, very little catch (sediment washed out during trawl or problem with trawl); 1 bucket
12/03/95	08:35	St. 15	10.7	50°43.06' N 01°04.05' W	Heterogenous sediment, predominantly mud; 10 minute trawl; sediment sample; 1 bucket
12/03/95	09:40	St.20	16.5	50°43.07' N 01°02.30' W	Heterogenous sediment, predominantly mud; 10 minute trawl; *Crepidula* abundant, 2 buckets
12/03/95	10:15	St. 21	11.6	50°42.01' N 01°01.98' W	Gravel sediment and empty *Crepidula* shell sediment; *Crepidula* abundant, *Corallina* on empty shells; 2 buckets
12/03/95	11:05	St. 30	13.3	50°39.63' N 01°02.22' W	Rocky substrate; sampled slightly to the south of the station to avoid the rocky outcrop; 5 minute trawl (to protect dredge); very little in sample, Porcellanidae, Amphipoda and sessile epifauna; 1 bucket
12/03/95	11:25	St. 29	15.0	50°39.08' N 01°02.22' W	Boulder and pebble sediment; 10 minute trawl; high abundance of *Flustra*; 1 bucket
12/03/95	11:50	St. 28	18.7	50°38.03' N 01°06.16' W	Pebble and coarse sand; 10 minute trawl; *Flustra* present; 1 bucket
12/03/95	12:20	St. 27	11.7	50°39.05' N 01°07.98' W	Cobbles and small amount of sand; 10 minute trawl; 1 bucket
12/03/95	12:50	St. 26	14.8	50°37.06' N 01°07.85' W	Cobbles and gravelly sand; reef of *Sabellaria*; 10 minute trawl; 2 buckets
12/03/95	13:20	St. 25	28.9	50°36.10' N 01°09.73' W	Cobbles and gravelly sand; 10 minute trawl; 1 bucket
12/03/95	14:05	St. 34	35.1	50°36.01' N 01°06.02' W	Cobbles and gravelly sand; 10 minute trawl; 1 bucket
12/03/95	14:45	St. 39	21.0	50°34.02' N 01°03.79' W	Hard substrate; 10 minute trawl; small volume of sample only; *Flustra* present; 1 bucket

Date	Time	Station number	Depth (m)	Location	Notes
12/03/95	15:35	St. 35	18.7	50°38.16' N 01°01.95' W	Gravel sediment; 10 minute trawl; some *Crepidula*; 1 bucket
12/03/95	16:25	St. 19	10.6	50°42.10' N 00°59.94' W	Pebbles and gravel sediment; 10 minute trawl; small volume in sample only; little fauna caught; 1 bucket
12/03/95	16:55	St. 16	8.4	50°44.03' N 01°01.96' W	Fine sand with some mud; two trawls of 10 minute put in the same bucket; little fauna present (*Crangon* and *Pagurus*); 1 bucket
13/03/95	09:25	St. 23	4.6	50°44.95' N 00°56.08' W	Fine sand, clean and well-sorted (washed in the dredge); 10 minute trawl; very little fauna present (*Crangon* and *Pagurus*); 1 bucket; used pipe dredge to confirm samples
13/03/95	10:10	St. 32	13.8	50°44.30' N 00°53.91' W	Heterogenous sediment, predominantly mud; 10 minute trawl; *Crepidula* and *Ampelisca* present; 2 buckets
13/03/95	10:40	St. 24	7.1	50°45.29' N 00°53.82' W	Fine sand, clean (no mud); 10 minute trawl; little fauna present; 1 bucket
13/03/95	11:05	St. 33	6.5	50°44.96' N 00°51.74' W	Fine sand; 10 minute trawl; little fauna present, some *Corystes*; 1 bucket
13/03/95	11:40	St.38	12.8	50°43.30' N 00°49.98' W	Fine sand; 10 minute trawl; Some *Corystes*, numerous *Nucula* present; 1 bucket
13/03/95	12:05	St. 42	12.3	50°42.15' N 00°50.00' W	Little sediment caught, trawled slightly to the north of the site due to presence of lobster buckets; 10 minute trawl; *Crepidula* abundant; 2 buckets
13/03/95	12:55	St. 44	24.1	50°40.02' N 00°50.09' W	Gravel sediment; numerous Amphipoda, one *Cancer pagurus*; 2 buckets
13/03/95	13:25	St. 41	22.1	50°40.02' N 00°54.19' W	Fine to medium sand; 10 minute trawl; 1 bucket (*n.b.* the dredge passed over a depression with high catch of Hydroids-possibly trapped there
13/03/95	14:05	St. 37	13.2	50°42.09' N 00°54.05' W	Coarse sand and pebble sediment; 10 minute trawl; *Crepidula* and *Flustra* present; 1 bucket
13/03/95	14:40	St. 31	13.5	50°42.04' N 00°58.17' W	Gravelly sand, gravel and empty *Crepidula* shells; 10 minute trawl; 1 bucket
14/03/95	10:15	St. 47	19.5	50°38.04' N 00°49.93' W	Boulder and gravel sediment; 10 minute trawl; 1 bucket
14/03/95	10:50	St. 48	23.2	50°36.01' N 00°50.00' W	Boulder and gravel sediment; 10 minute trawl; 1 bucket
14/03/95	11:20	St. 46	29.8	50°36.05' N 00°54.07' W	Gravel sediment; 10 minute trawl; *Crepidula* present; 1 bucket

Date	Time	Station number	Depth (m)	Location	Notes
14/03/95	11:55	St. 45	29.2	50°33.98' N 00°56.17' W	Gravel sediment; 10 minute trawl; little fauna present and poor diversity; 1 bucket
14/03/95	12:30	St. 43	33.7	50°36.35' N 00°58.06' W	Gravel sediment with blocks of clay (believed to derive from the dumping site of sludge spoil from Portsmouth, which was close by); 10 minute trawl; 1 bucket
14/03/95	13:30	St. 40	24.2	50°37.96' N 00°58.38' W	Mixture of pebbles, gravel and sand; 10 minute trawl; 1 bucket
14/03/95	14:05	St. 36	14.8	50°40.02' N 00°58.04' W	Gravel sediment; 10 minute trawl; 1 bucket

Table A.3.2: Species list for the East Solent benthic survey

Annelida; Polychaeta

Ampharetidae	*Ampharete acutifrons*	Grube
Ampharetidae	*Melinna palmata*	Grube
Aphroditidae	*Aphrodita aculeata*	(L.)
Aphroditidae	*Gattyana cirrosa*	(Pallas)
Aphroditidae	*Lepidonotus squamatus*	(L.)
Aphroditidae	*Lepidonotus clava*	(Montagu)
Aphroditidae	*Lepidasthenia argus*	Hodgson
Aphroditidae	*Sthenelais boa*	(Johnston)
Aphroditidae	*Sthenelais limicola*	(Ehlers)
Aphroditidae	*Pholoe minuta*	Petersen
Aphroditidae	sp. indet.	
Cirratulidae	*Caulleriella bioculata*	(Keferstein)
Eunicidae	*Eumida sanguinea*	(Oersted)
Eunicidae	*Lysidice ninetta*	Audouin and Milne-Edwards
Glyceridae	*Glycinde nordmanni*	(Malgrem)
Maldanidea	*Euclymene oerstedii*	(Claparède)
Nymphonidae	*Nymphon brevirostre*	Hodge
Nephtyidae	*Nephtys cirrosa*	Ehlers
Nephtyidae	*Nephtys hombergi*	Savigny
Nereidae	*Platynereis dumerilii*	Audouin and Milne-Edwards
Nereidae	*Perinereis cultrifera*	(Grube)
Orbiniidae	*Scoloplos armiger*	(Müller)
Pectinariidae	*Pectinaria koreni*	(Malgrem)
Phyllodocidae	*Eulalia viridis*	(L.)
Phyllodocidae	*Eteone longa*	(Fabricius)
Phyllodocidae	*Eteone picta*	(Quatrefages)
Phyllodocidae	*Phyllodoce mucosa*	Oersted
Sabellariidae	*Sabellaria spinulosa*	Leuckart
Sabellidae	*Sabella pavonina*	Savigny
Serpulidae	*Pomatoceros triqueter*	(L.)
Spionidae	*Spio armata*	Thulin
Spionidae	*Polydora sp.*	
Syllidae	*Autolytus (Procerea) sp.*	
Syllidae	*Streptosyllis websteri*	Southern
Syllidae	*Syllis armillaris*	(Malgrem)
Terebellidae	*Eupolymnia nebulosa*	(Montagu)
Terebellidae	*Lanice conchilega*	(Pallas)
Terebellidae	*Polycirrus sp*	
Terebellidae	sp. indet.	

Crustacea; Copepoda

(parasite on *Atylus vedlomenis*)	*Sphaeronella* sp.	

Crustacea; Malacostraca; Cumacea

Bodotriidae	*Iphinoe trispinosa*	(Goodsir)
Bodotriidae	*Vaunthompsonia cristata*	Bate
Diastylidae	*Diastylis bradyi*	Norman
Diastylidae	*Diastylis rathkei*	(Krøyer)
Diastylidae	*Diastylis rugosa*	(Sars)
Nannastacidae	*Nannastacus unguiculatus*	(Bate)
Pseudocumatidae	*Pseudocuma longicornis*	(Bate)

Malacostraca; Mysidacea

Mysidae	*Leptomysis gracilis*	(G. O. Sars)
Mysidae	*Leptomysis lingvura*	(G. O. Sars)
Mysidae	*Leptomysis mediterranea*	G. O. Sars
Mysidae	*Mysidopsis angusta*	G. O. Sars
Mysidae	*Siriella armata*	(Milne-Edwards)
Mysidae	*Siriella clausii*	G. O. Sars
Mysidae	*Schistomysis kervillei*	(G. O. Sars)
Mysidae	*Schistomysis spiritus*	(Norman)
Mysidae	*Schistomysis ornata*	(G. O. Sars)
Mysidae	*Paramysis arenosa*	(G. O. Sars)
Mysidae	*Praunus neglectus*	(G. O. Sars)
Mysidae	*Gastrosaccus spinifer*	(Goës)

Malacostraca; Isopoda

Gnathiidae	*Gnathia oxyuraea*	(Lilljeborg)
Idoteidae	*Idotea linearis*	(L.)
Idoteidae	*Idotea baltica*	(Pallas)

Malacostraca; Amphipoda

Acanthonotozomatidae	*Iphimedia eblanae*	Bate
Ampeliscidae	*Ampelisca aequicornis (?)*	Bruzelius
Ampeliscidae	*Ampelisca brevicornis*	(da Costa)
Ampeliscidae	*Ampelisca diadema*	(Costa)
Ampeliscidae	*Ampelisca macrocephala (?)*	Lilljeborg
Ampeliscidae	*Ampelisca tenuicornis*	Lilljeborg
Ampeliscidae	*Ampelisca typica*	(Bate)
Ampithoidae	*Ampithoe rubricata*	(Montagu)
Atylidae	*Atylus guttatus*	(Costa)
Atylidae	*Atylus vedlomensis*	(Bate & Westwood)
Atylidae	*Atylus svammerdami*	(Milne-Edwards)
Calliopiidae	*Apherusa ovalipes*	Norman & Scott
Calliopiidae	*Gammarellus angulosus*	(Rathke)
Corophiidae	*Siphonoecetes striatus*	Myers & McGrath
Corophiidae	*Corophium sextonae*	Crawford
Haustoriidae	*Urothoe brevicornis*	Bate
Isaeidae	*Sp. indet.*	
Pontoporeiidae	*Bathyporeia elegans*	Watkins
Pontoporeiidae	*Bathyporeia guilliamsoniana*	(Bate)
Pontoporeiidae	*Bathyporeia pelagica*	(Bate)
Dexaminidae	*Dexamine spinosa*	(Montagu)
Gammaridae	*Gammarus locusta*	(L.)
Gammaridae	*Echinogammarus marinus*	(Leach)
Leucothoidae	*Leucothoe incisa*	Robertson
Lysianassidae	*Lysianassa ceratina*	(Walker)
Melitidae	*Maera othonis*	(Milne-Edwards)
Melitidae	*Melita palmata*	(Montagu)
Melitidae	*Melita obtusata*	(Montagu)
Oedicerotidae	*Pontocrates arenarius*	(Bate)
Oedicerotidae	*Pontocrates altamarinus*	(Bate & Westwood)
Oedicerotidae	*Monoculodes carinatus*	(Bate)
Oedicerotidae	*Perioculodes longmanus*	(Bate & Westwood)
Phoxocephalidae	*Harpinia pectinata*	Sars

Malacostraca; Decapoda (Caridea)

Crangonidae	*Crangon crangon*	(L.)
Crangonidae	*Crangon allmani*	Kinahan
Crangonidae	*Pontophilus bispinosus*	Hailstone
Crangonidae	*Pontophilus trispinosus*	Hailstone
Crangonidae	*Pontophilus fasciatus*	(Risso)
Hippolytidae	*Eualus occultus*	(Lebour)
Hippolytidae	*Thoralus cranchii*	(Leach)
Hippolytidae	*Hippolyte varians*	Leach
Pandalidae	*Pandalina brevirostris*	(Rathke)
Processidae	*Processa nouveli holthuisi*	Al-Adhub & Williamson
Alpheidae	*Athanas nitescens*	(Leach)
Alpheidae	*Alpheus glaber*	(Olivi)

Malacostraca; Decapoda (Anomoura)

Paguridae	*Pagurus bernhardus*	(L.)
Paguridae	*Pagurus cuanensis*	Thomson
Paguridae	*Anapagarus chiroacanthus*	(Lilljeborg)
Paguridae	*Anapagarus hyndmanni*	Thompson
Paguridae	*Diogenes pugilator*	(Roux)
Galatheidae	*Galathea squamifera*	Leach
Galatheidae	*Galathea intermedia*	Lilljeborg
Porcellanidae	*Pisidia longicornis*	(L.)

Malacostraca;Decapoda (Brachiura)

Leucosiidae	*Ebalia tumefacta*	(Montagu)
Majidae	*Macropodia rostrata*	(L.)
Majidae	*Macropodia deflexa*	Forest
Majidae	*Macropodia linaresi*	Forest and Zariquiey
Majidae	*Inachus leptochirus*	Leach
Majidae	*Inachus phalangium*	(Fabricius)
Majidae	*Maja squinado*	(Herbst)
Corystidae	*Corystes cassivelaunus*	(Pennant)
Portunidae	*Liocarcinus arcuatus*	(Leach)
Portunidae	*Liocarcinus depurator*	(L.)
Portunidae	*Liocarcinus holsatus*	(Fabricius)
Portunidae	*Liocarcinus puber*	(L.)
Portunidae	*Liocarcinus pusillus*	(Leach)
Portunidae	*Liocarcinus species indet*	
Portunidae	*Portumnus latipes*	(Pennant)
Cancridae	*Cancer pagurus*	L.
Xanthidae	*Pilumnus hirtellus*	(L.)
Pinnotheridae	*Pinnotheres pisum*	(L.)
Grapsidae	*Brachynotus sexdentatus*	(Risso)

Polyplacophora

Acanthochitonidae	*Acanthochitona crinitus*	(Pennant)
Ischnochitonidae	*Lepidochitona cinereus*	(L.)
Lepidopleuridae	*Leptochiton asellus*	(Gmellin)

Gastropoda (Prosobranchia); Archeogastropoda

Fissurellidae	*Diodora graeca*	(L.)
Phasianellidae	*Tricolia pullus*	(L.)
Trochiidae	*Calliostoma zizyphinum*	(L.)
Trochiidae	*Gibbula umbilicalis*	(da Costa)

Gastropoda (Prosobranchia); Mesogastropoda

Calyptraeidae	*Crepidula fornicata*	(L.)
Eratoidae	*Trivia monacha*	(da Costa)
Lacunidae	*Lacuna vincta*	(Montagu)

Gastropoda (Prosobranchia); Neogastropoda

Buccinidae	*Buccinum undatum*	(L.)
Muricidae	*Ocenebra erinacea*	(L.)
Nassariidae	*Hinia incrassata*	(Ström)
Nassaridae	*Hinia reticulata*	(L.)

Gastropoda (Opistobranchia): Nudibranchia

Onchidorididae	*Onchidoris bilamellata*	(L.)
Onchidorididae	*Acanthodoris pilosa*	(Abildgaard)
Goniodorididae	*Goniodoris castanea*	Alder and Hancock

Pelecypoda

Myoida	Corbulidae	*Corbula gibba*	(Olivi)
Mytiloida	Mytidae	*Mytilus edulis*	L.
Nuculoida	Nuculidae	*Nucula nucleus*	(L.)
Nuculoida	Nuculidae	*Nucula nitidosa*	Winckworth
Pterioida	Ostreidae	*Ostrea edulis*	L.
Pterioida	Pectinidae	*Aequipecten opercularis*	(L.)
Pterioida	Pectinidae	*Chlamys varia*	(L.)
Veneroida	Cardiidae	*Parvicardium ovale*	(Sowerby)
Veneroida	Cardiidae	*Cerastoderma edule*	(L.)
Veneroida	Lutraridae	*Lutraria angustior*	(Philippi)
Veneroida	Lutraridae	*Lutraria lutraria*	(L.)
Veneroida	Mactridae	*Spisula elliptica*	(Brown)

Pycnogonida

Ammotheidae	*Achelia echinata*	Hodge
Nymphonidae	*Nymphon brevirostre*	Hodge
Nymphonidae	*Nymphon gracile*	Leach

Ophiuroidea

Amphiuridae	*Amphipholis squamata*	(Delle Chiaje)
Ophiotrichidae	*Ophiotrix fragilis*	(Abildgaard)

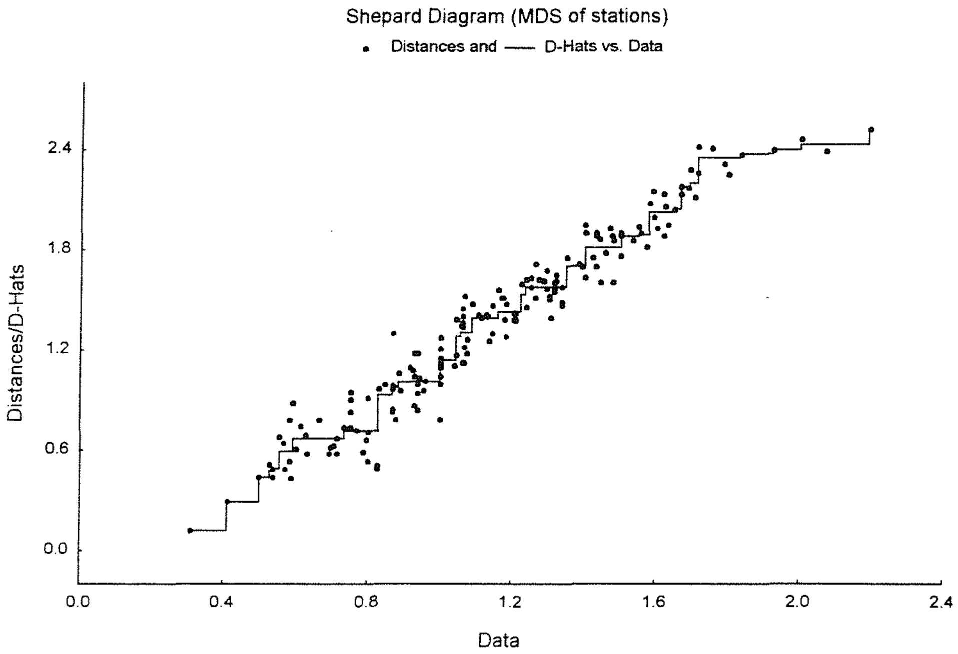


Figure A.3.1: Shepard diagram for the Multi-Dimensional Scaling analysis on the station (Bray-Curtis) distance matrix.

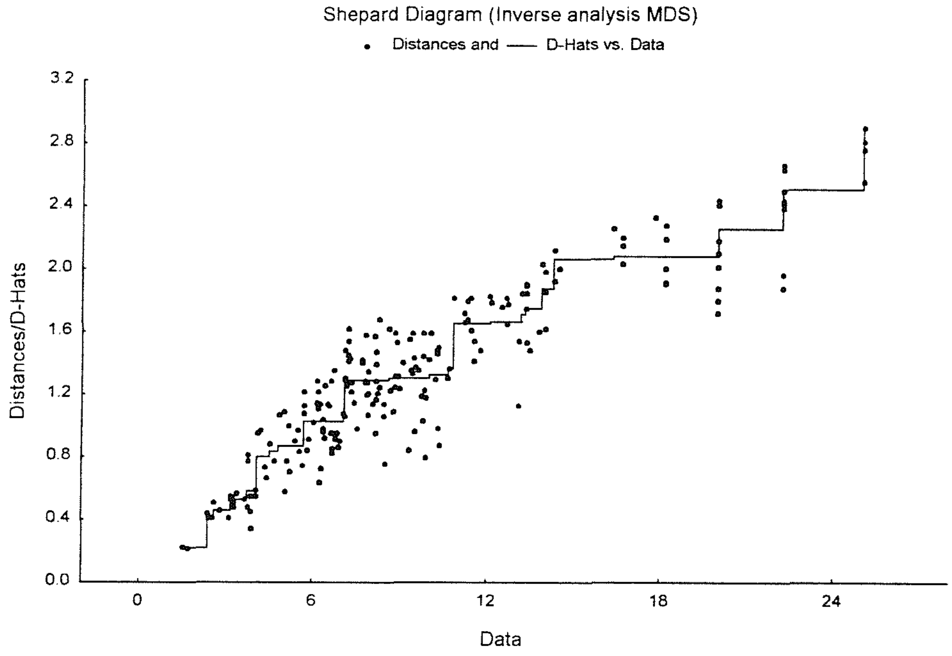


Figure A.3.2: Shepard diagram for the inverse Multi-Dimensional Scaling analysis on the species (Bray-Curtis) distance matrix.

Chapter IV supplementary figures & tables:

Taxa	Code	>1%	Taxa	Code	>1%
Acartia spp.	*ACA*	*2,3,4,5*	*Labidocera wollastonii* Lubbock	*LAB*	*3,4,5*
Amphipoda	*AMP*	*2,3*	*Lanice conchilega* larvae	*LAN*	
Ascidian larvae	*ASC*	*3*	*Littorina* spp. Larvae	*LIT*	*2,3*
Barnacle cyprids	*BAC*		*Macropodia* megalopa	*MAC*	
Barnacle nauplii	*BAN*	*2,3,4,5*	Medusae	*MED*	*2,3,4,5*
Bivalve larvae	*BIV*	*5*	Monstrilloidea	*MON*	
Membranipora membranacea (L.) larvae	*BRY*	*2,3,4,5*	Mysidaceae	*MYS*	
Calanus helgolandicus Claus	*CAL*	*2,3*	*Nephtys* spp. eggs	*NEP*	
Centropages hamatus (Lilljeborg)	*CEN*	*2,3,4,5*	*Oikopleura* sp.	*OIK*	*2,3,4,5*
Copepod nauplii	*COP*	*2,3,4*	*Oithona nana* Giesbrecht	*OIT*	*5*
Cumacea	*CUM*		Ostracoda	*OST*	*2,3*
Decapod larvae	*DEL*	*2,3,4,5*	Other harpacticoids	*OTH*	*2,3,4,5*
Decapod megalopa	*DEM*		Other polychaete larvae	*OPL*	*3*
Echinoderm larvae	*ECH*		*Para/Pseudocalanus* spp.	*PAR*	*2,5*
Eurytemora affinis (Pope)	*EUR*		*Parapontella brevicornis* Lubbock	*PAP*	*2,3,4,5*
Euterpina acutifrons (Dana)	*EUT*	*2,3,4,5*	Polychaete post-larvae	*POP*	*5*
Fish eggs	*FIE*	*2,3,4,5*	Pycnogonida	*PYC*	
Fish larvae	*FIL*	*2,3*	*Sagitta* sp.	*SAG*	*3,5*
Crepidula larvae	*GA1*	*2,3,4,5*	Caridean larvae	*SHR*	*4,5*
Gastropods II	*GA2*	*2,5*	Spionid larvae	*SPI*	*2,3*
Gastropods III	*GA3*	*5*	Syllidae	*SYL*	
Insecta	*INS*		*Temora longicornis* Müller	*TEM*	*2,3,4,5*
Isias clavipes	*ISI*	*5*	Unidentified copepods	*UNI*	
Isopoda	*ISO*				

Stations	
Calshot	*Cal*
East Ryde	*ER*
Sturbridge	*Stu*

Table A.4.1: Taxa identified and taxa and station codes used for multivariate analyses; cruises in which taxa occurred as over 1% abundance at any station.

Cruise 2 n=14	% total individuals
Crepidula larvae	21.1
Decapod larvae	12.9
Temora longicornis	12.5
Acartia spp.	12.1
Centropages hamatus	11.8
Oikopleura sp.	4.1
Caridean larvae	3.4
Medusae	3.2
Fish eggs	3.2
Parapontella brevicornis	3.1
Other harpacticoids	2.9
Gastropods II	1.4
Barnacle nauplii	1.3
Para/Pseudocalanus spp.	1.2
total=	94.3

Cruise 3 n=12	% total individuals
Temora longicornis	29.1
Centropages hamatus	23.8
Acartia spp.	13.4
Barnacle nauplii	5.3
Crepidula larvae	5.2
Oikopleura sp.	3.3
Parapontella brevicornis	2.8
Membranipora larvae	2.6
Medusae	2.5
Euterpina acutifrons	2.5
Other decapod larvae	2.4
Fish eggs	2.0
total=	95.1

Cruise 4 n=11	% total individuals
Acartia spp.	25.7
Oikopleura sp.	21.3
Crepidula larvae	18.0
Centropages hamatus	9.6
Temora longicornis	7.4
Fish eggs	3.2
Other decapod larvae	2.9
Sagitta spp.	2.8
Barnacle nauplii	2.0
Para/Pseudocalanus spp.	1.3
Ostracoda	1.3
total=	95.6

n.b.: All occur in >5% of stations

Cruise 5 n=13	% total individuals
Acartia spp.	37.8
Oikopleura sp.	21.6
Centropages hamatus	6.6
Crepidula larvae	5.6
Gastropods II	5.1
Isias clavipes	4.5
Para/Pseudocalanus spp.	3.1
Fish eggs	2.7
Temora longicornis	2.2
Parapontella brevicornis	1.4
Barnacle nauplii	1.3
Sagitta spp.	1.3
Oithona nana	1.0
total=	94.3

Table A.4.2: Percentage overall abundance for dominant taxa (>1% total abundance) for cruises 2-5.

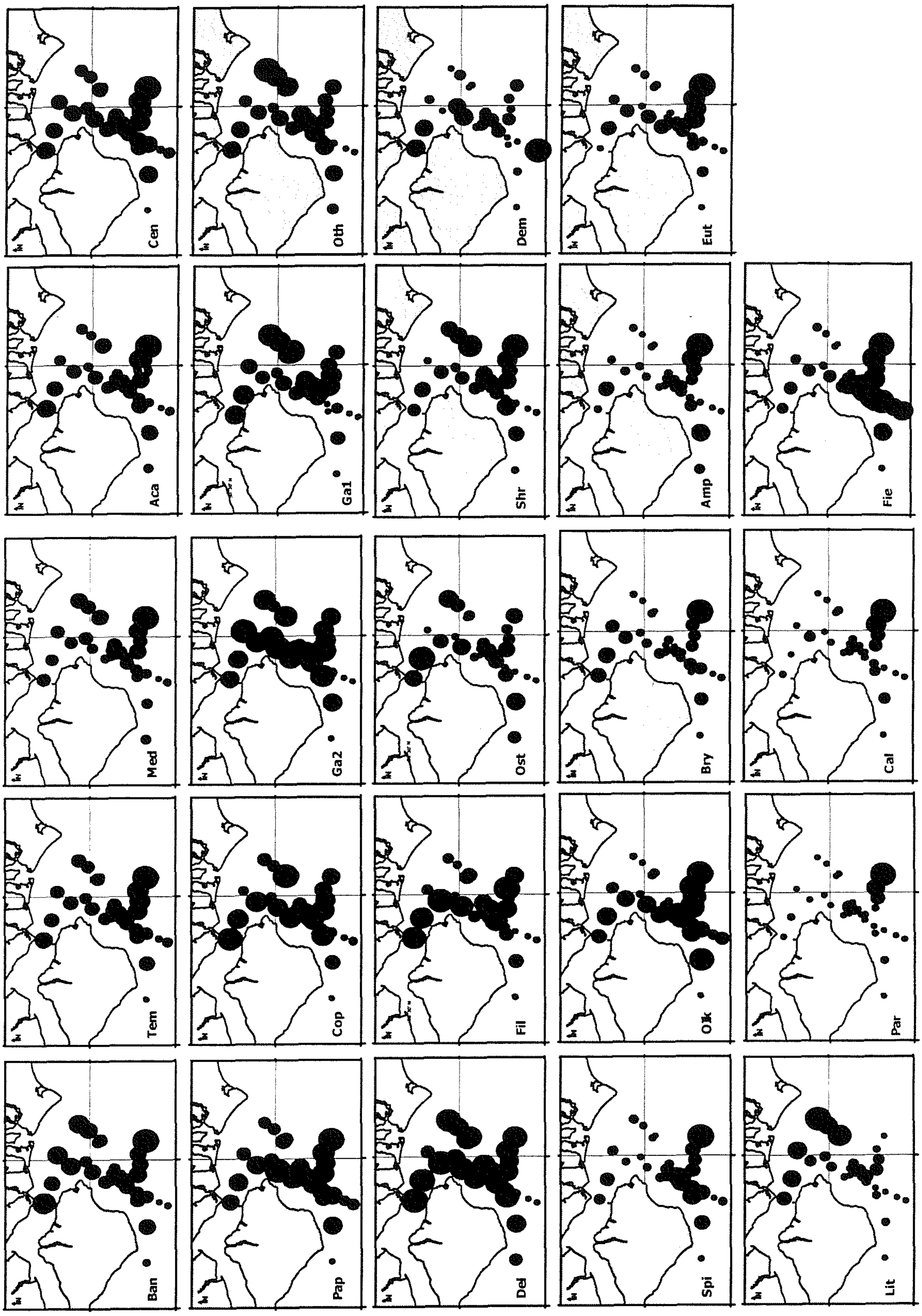


Figure A.4.1:Cruise 2: Relative abundances of taxa included in statistical analyses (log scales, from minimum to maximum abundance for each taxa), arranged in group membership from the cluster analysis on CA dimension coordinates. For taxa abbreviations see table A.4.1. Ban-Eut: group A; Litt: group B; Par-Fie: group C.

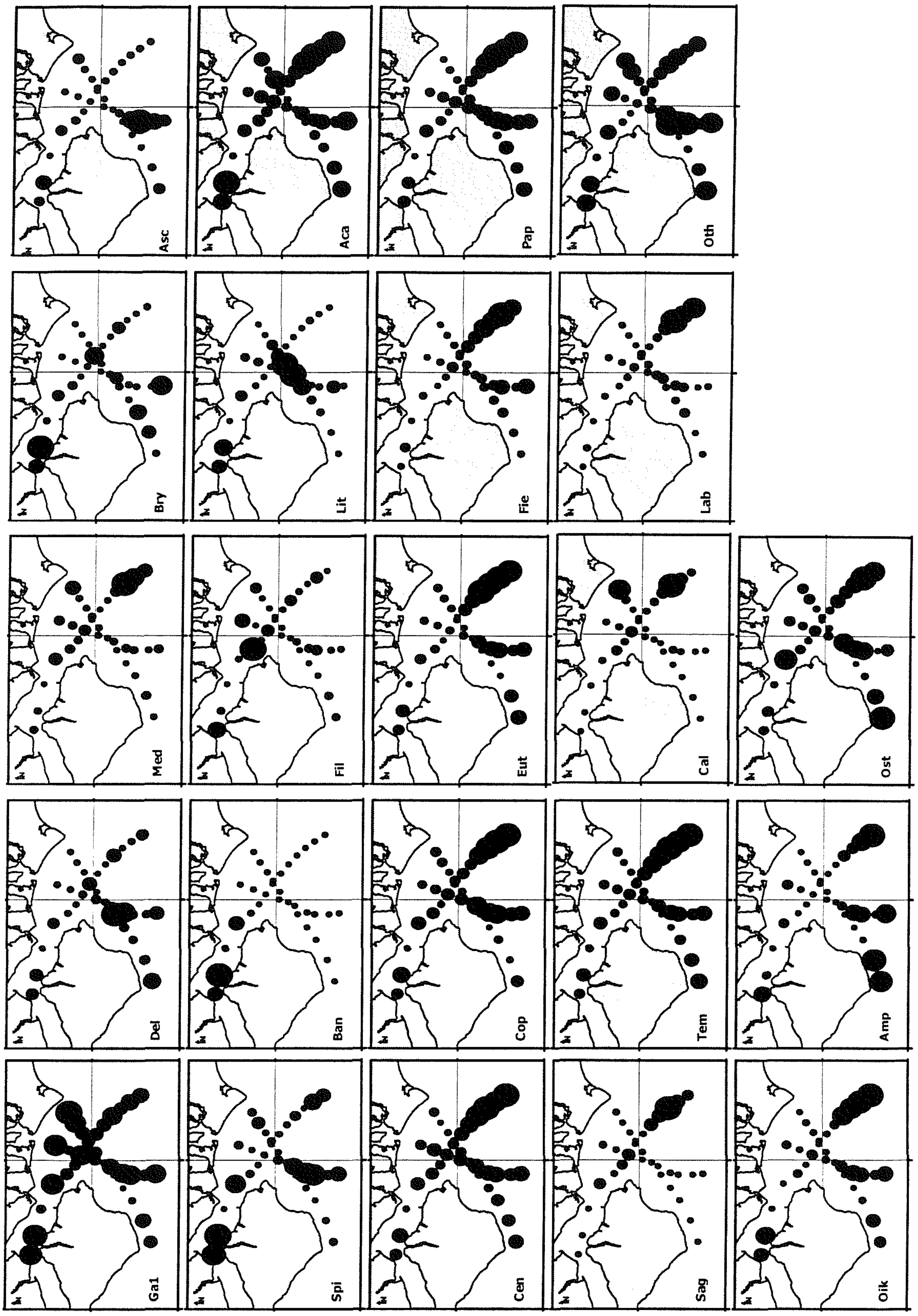


Figure A.4.2: Cruise 3: Relative abundances of taxa included in statistical analyses (log scales, from minimum to maximum abundance for each taxa), arranged in group membership from the cluster analysis on CA dimension coordinates. For taxa abbreviations see table A.4.1. Gal-Lit: group A; Aca-Tem: group B; Cal-Ost: group C.

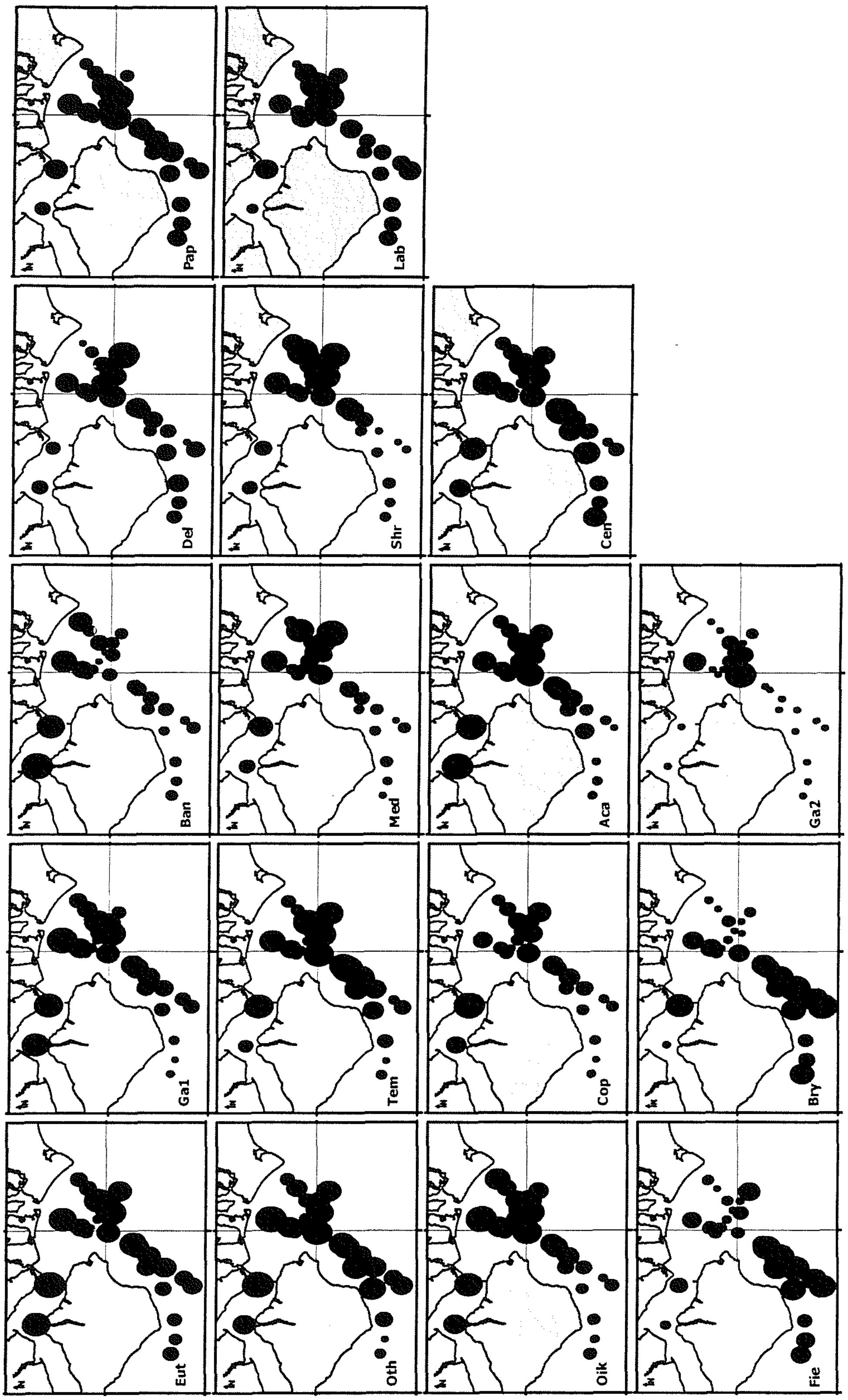


Figure A.4.3: Cruise 4: Relative abundances of taxa included in statistical analyses (log scales, from minimum to maximum abundance for each taxa), arranged in group membership from the cluster analysis on CA dimension coordinates. For taxa abbreviations see table A.4.1. Eut-Tem: group A; Med-Cen: group B; Fie & Bry: group C. Ga2 was excluded from the CA.

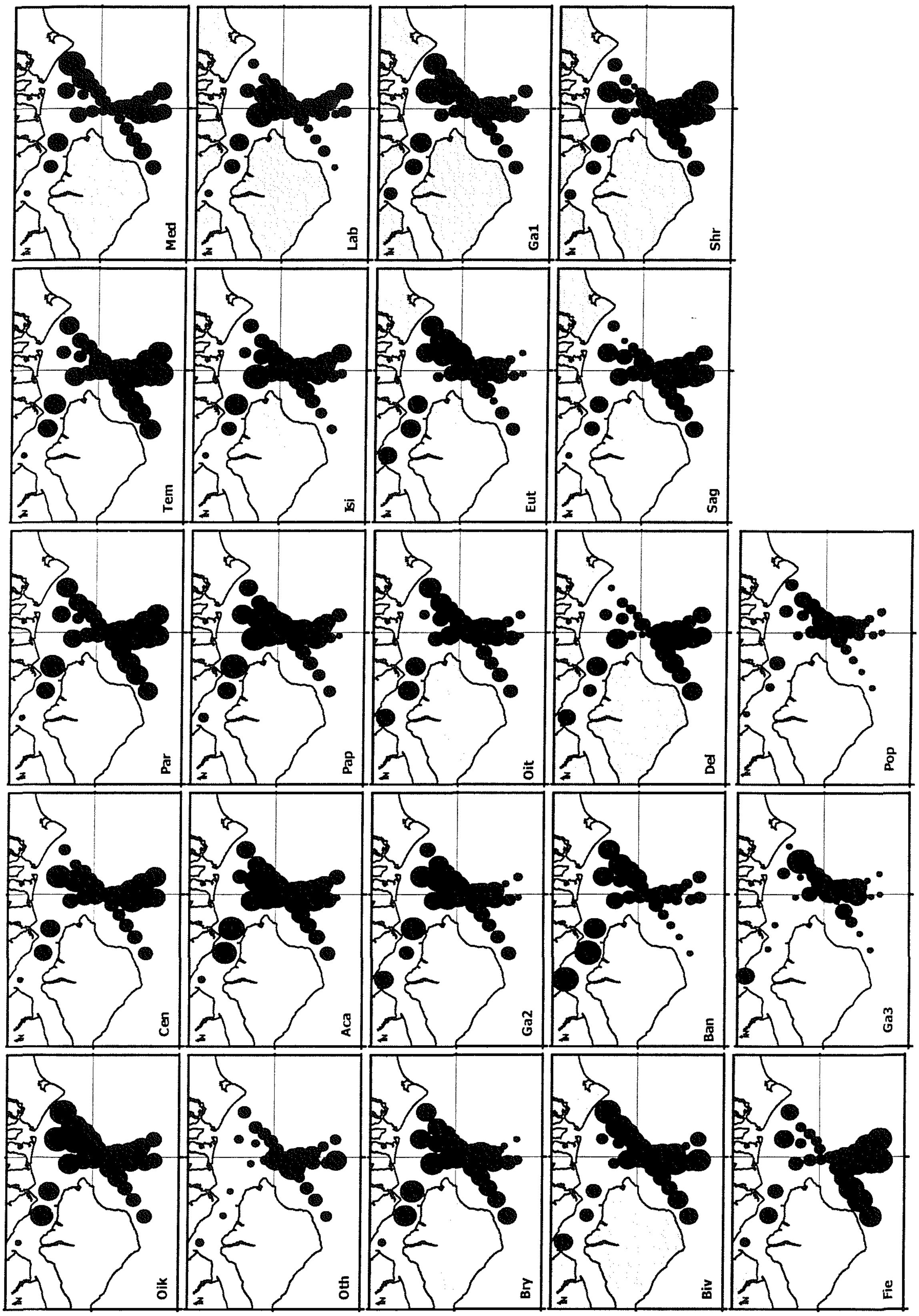


Figure A.4.4: Cruise 5: Relative abundances of taxa included in statistical analyses (log scales, from minimum to maximum abundance for each taxa), arranged in group membership from the cluster analysis on CA dimension coordinates. For taxa abbreviations see table A.4.1. Oik-Lab: group A; Bry-Bant: group B; Del-Fie: group C; Ga3 & Pop: outliers

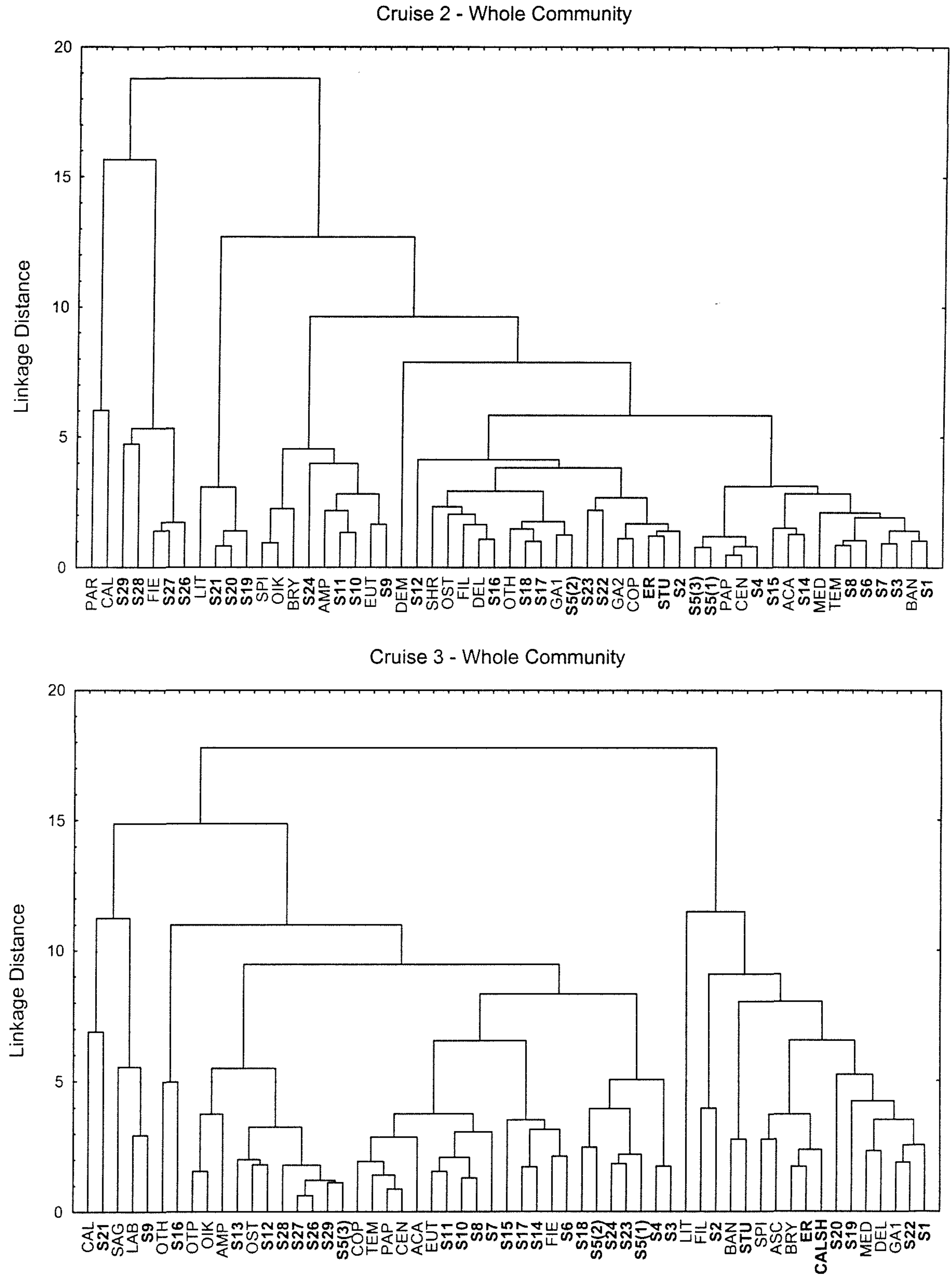


Figure A.4.5 (A): Whole Community: Cluster Analyses of stations (in **Bold**) and taxa on the coordinates in the dimensions of the Correspondence Analyses (Euclidian distance, complete linkage); Cruises 2 & 3.For abbreviations see table A.4.1.

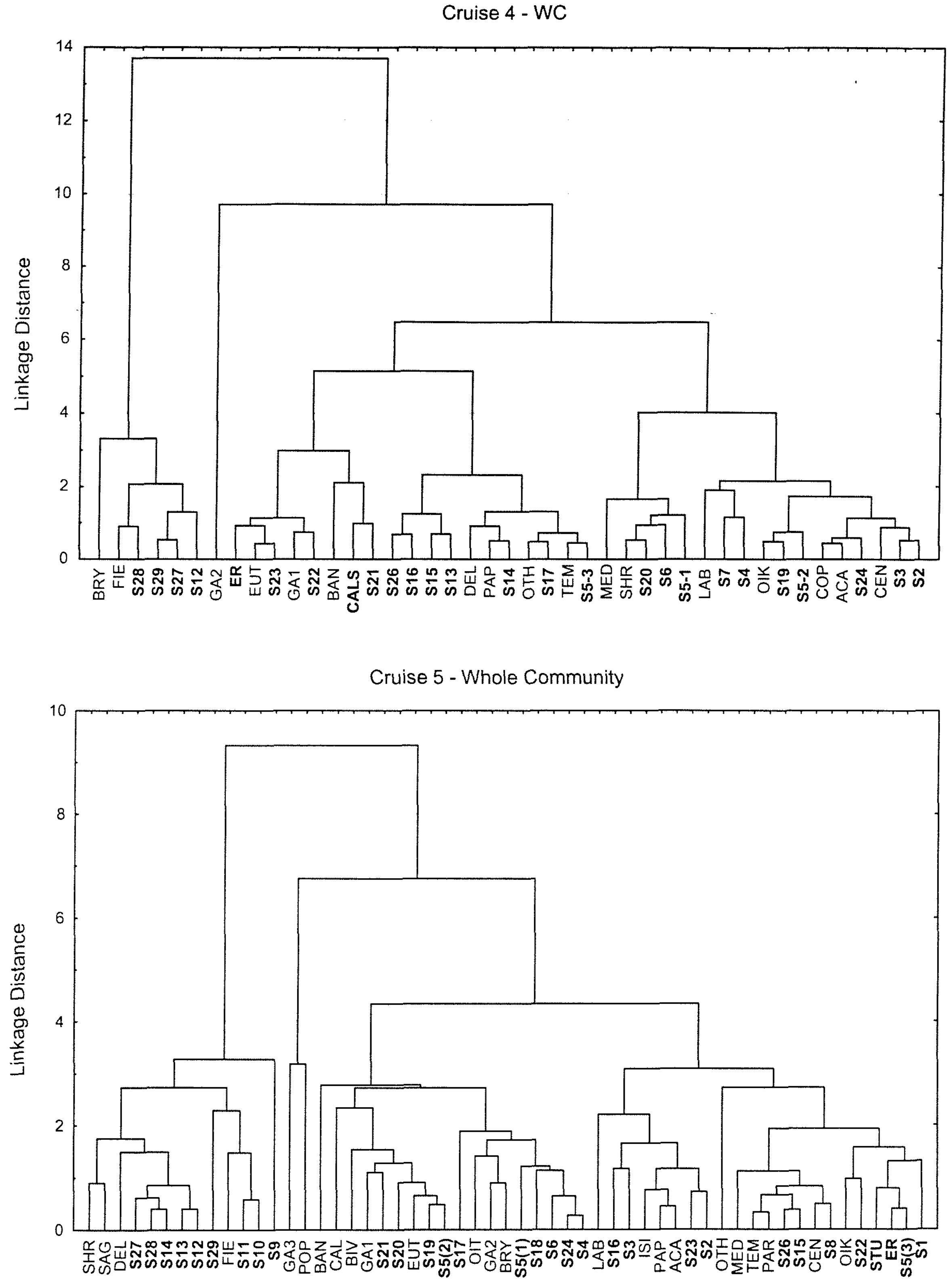


Figure A.4.5 (B): Whole Community: Cluster Analyses of stations (in **Bold**) and taxa on the coordinates in the dimensions of the Correspondence Analyses (Euclidian distance, complete linkage); Cruises 4 & 5.For abbreviations see table A.4.1.

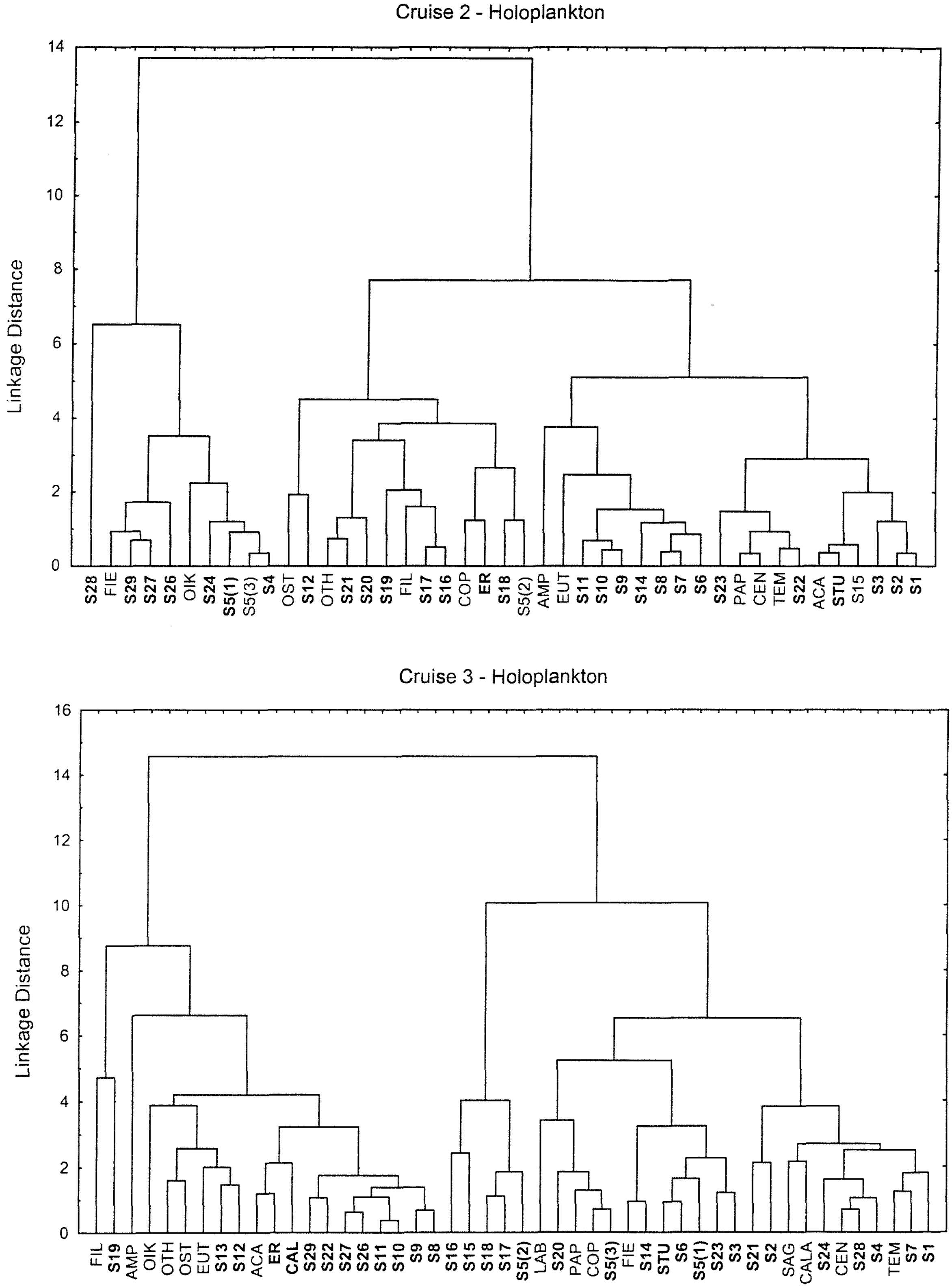
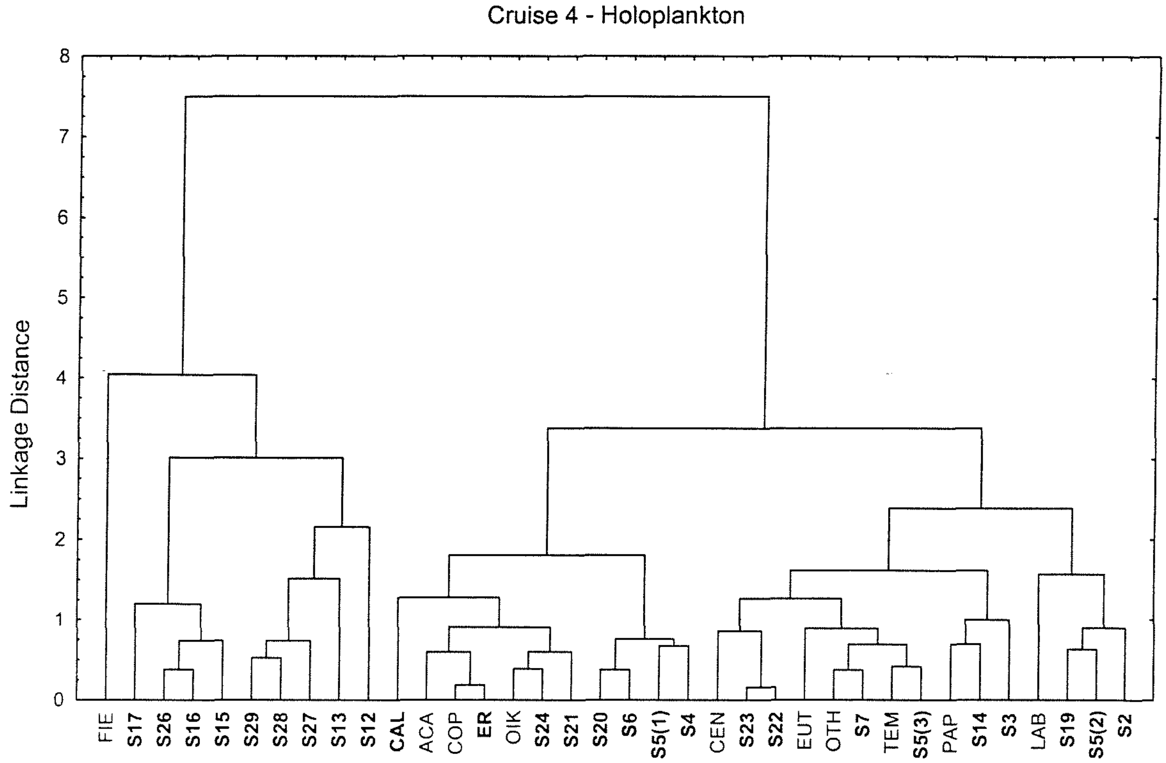


Figure A.4.6 (A): Holoplankton: Cluster Analyses of stations (in **Bold**) and taxa on the coordinates in the dimensions of the Correspondence Analyses (Euclidian distance, complete linkage); Cruises 2 & 3. For abbreviations see table A.4.1.


Cruise 4 - Holoplankton

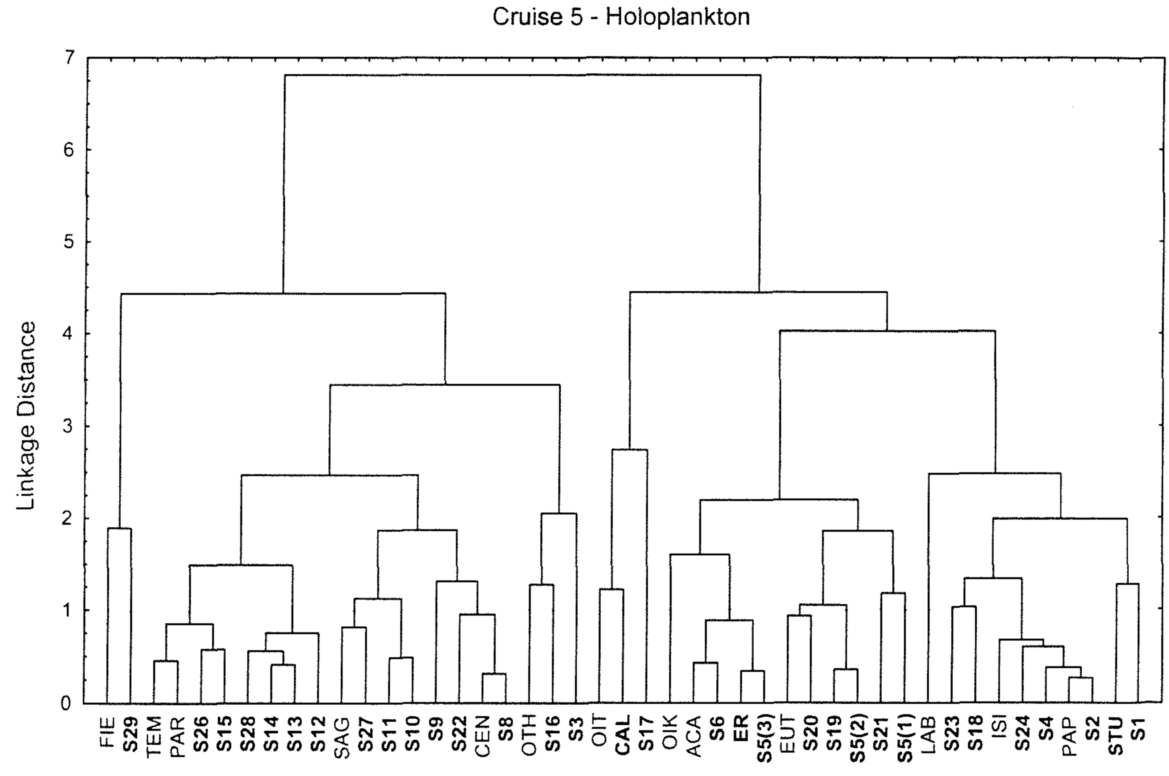

Cruise 5 - Holoplankton

Figure A.4.6 (B): Holoplankton: Cluster Analyses of stations (in **Bold**) and taxa on the coordinates in the dimensions of the Correspondence Analyses (Euclidian distance, complete linkage); Cruises 4 & 5. For abbreviations see table A.4.1.

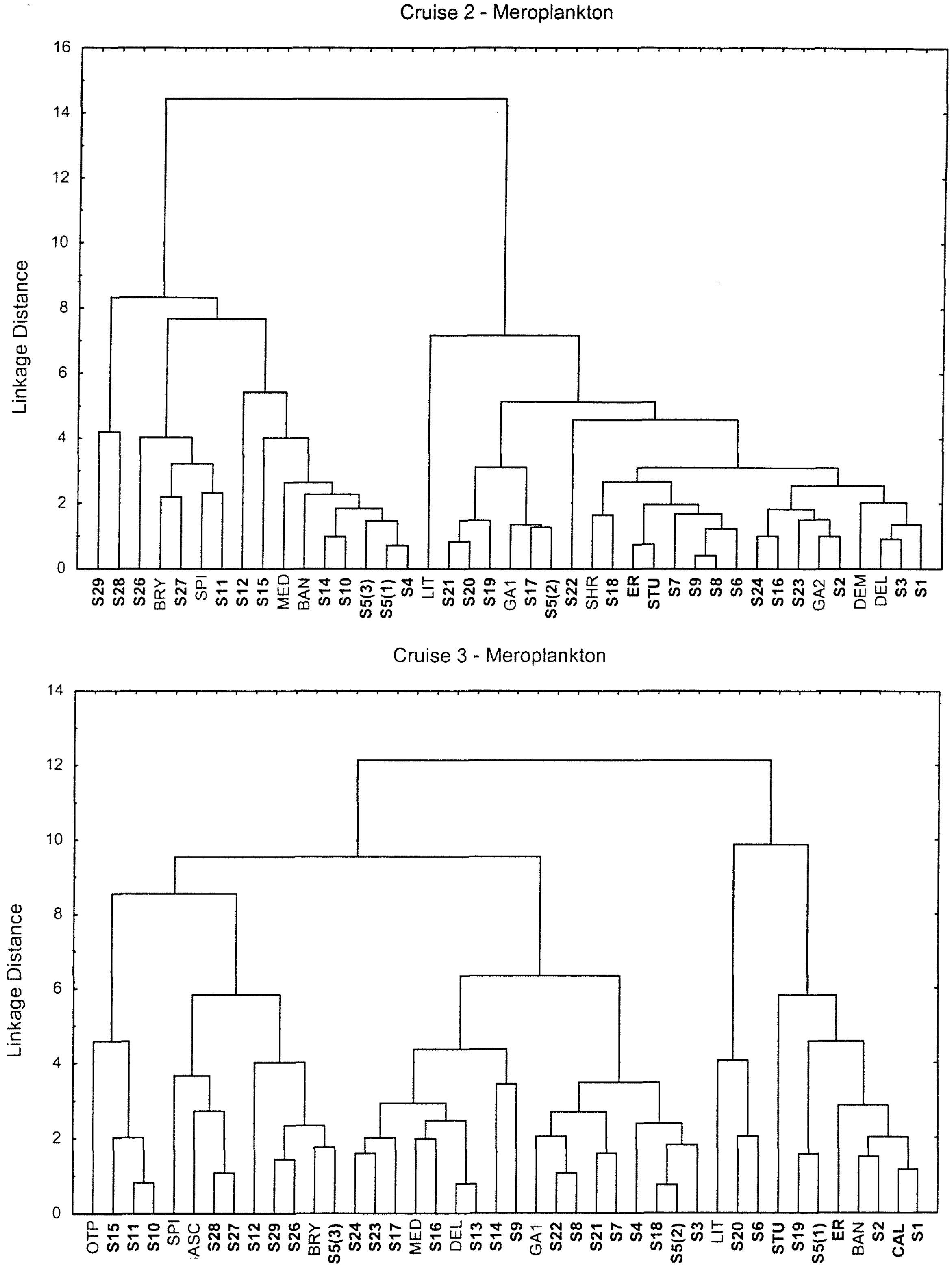
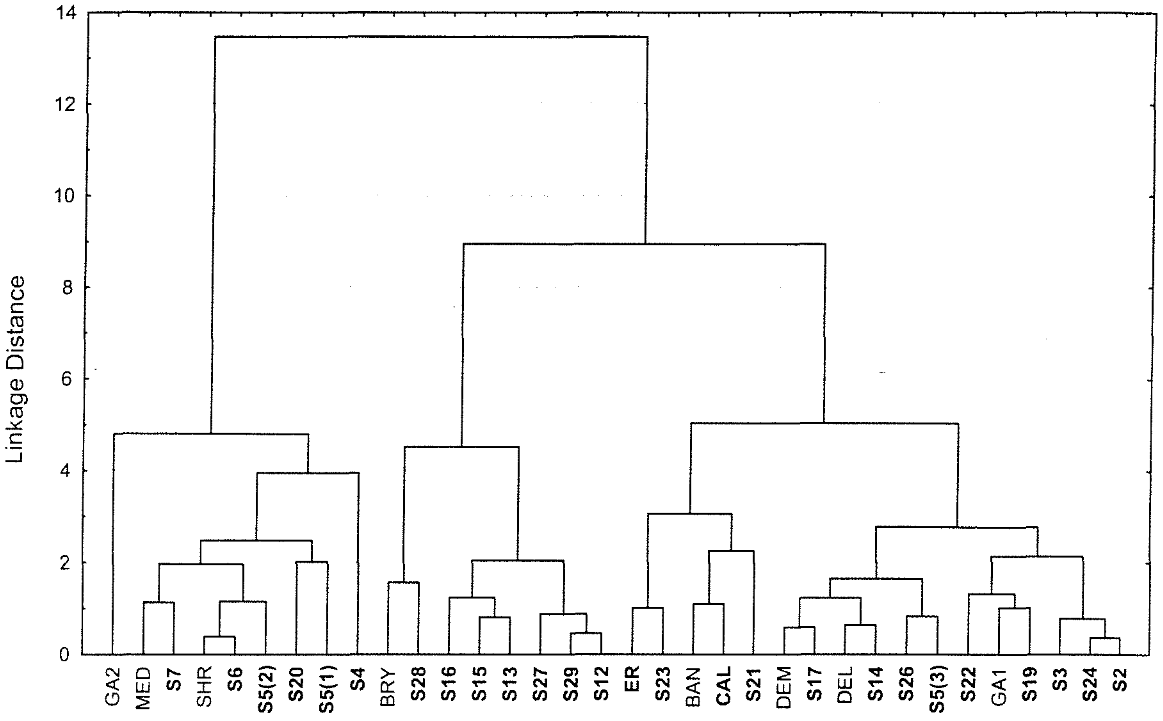
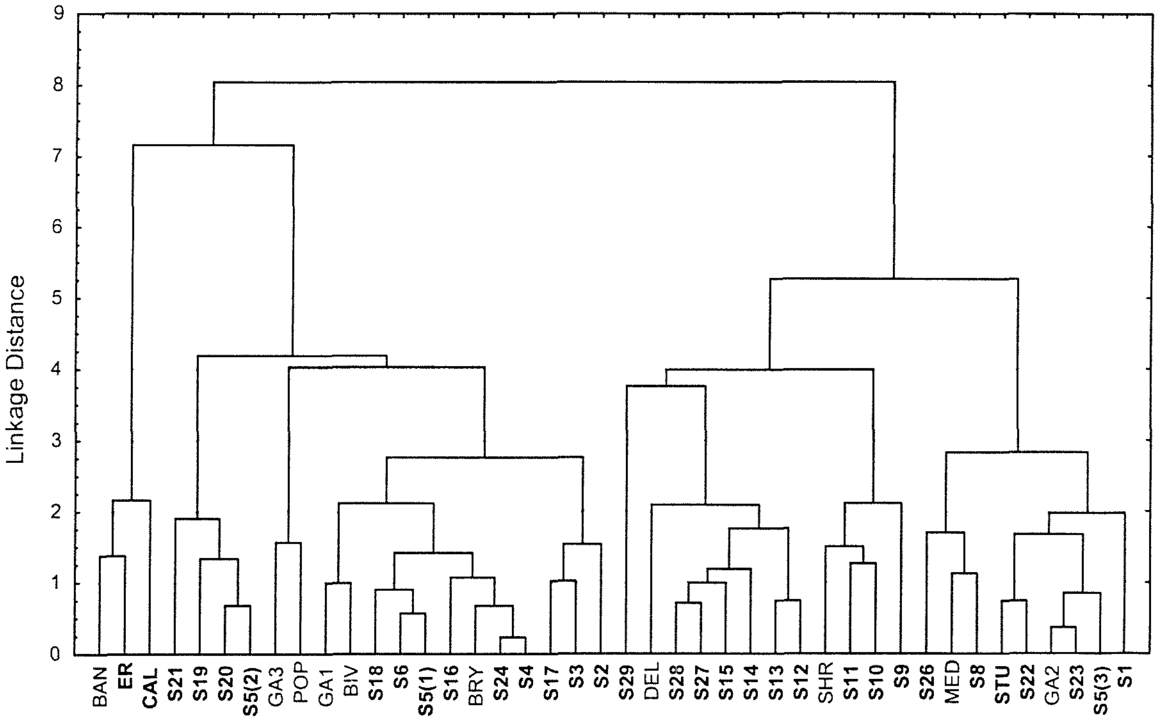


Figure A.4.7 (A): Meroplankton: Cluster Analyses of stations (in **Bold**) and taxa on the coordinates in the dimensions of the Correspondence Analyses (Euclidian distance, complete linkage); Cruises 2 & 3.For abbreviations see table A.4.1.



Cruise 4 - Meroplankton



Cruise 5 - Meroplankton

Figure A.4.7 (B): Whole Community: Cluster Analyses of stations (in **Bold**) and taxa on the coordinates in the dimensions of the Correspondence Analyses (Euclidian distance, complete linkage); Cruises 4 & 5.For abbreviations see table A.4.1.

Cruise 2

		A																				B	C		
	Between Groups:	BAN	TEM	MED	ACA	CEN	PAP	COP	GA2	GA1	OTH	DEL	FIL	OST	SHR	DEM	SPI	OIK	BRY	AMP	EUT	LIT	PAR	CAL	FIE
Station group A (n=24):	**A/B**	-	-	-	-	-	-	-	-	**	**	-	***	-	*	-	-	-	-	-	-	***	-	-	-
Station group B (n=3):	**A/C**	-	-	-	-	-	-	*	***	**	***	***	*	*	*	-	-	-	-	-	-	-	-	-	*
Station group C (n=4):	**B/C**	-	-	*	-	-	-	*	***	***	***	***	-	*	***	-	-	-	-	-	-	***	-	-	**

Cruise 3

		A									B								C						
	Between Groups:	GA1	DEL	MED	BRY	ASC	SPI	BAN	FIL	LIT	ACA	CEN	COP	EUT	FIE	PAP	SAG	TEM	CAL	LAB	OTH	OTP	OIK	AMP	OST
Station group A (n=9):	**A/B**	-	-	-	-	***	-	***	-	-	-	-	-	-	**	-	-	-	-	-	-	-	-	-	-
Station group B (n=17):	**A/C**	-	***	-	*	***	*	*	-	-	-	-	-	-	**	*	-	-	-	-	*	-	-	**	-
Station group C (n=7):	**B/C**	-	*	-	***	***	***	***	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	**	-

Cruise 4

		A							B							C	
	Between Groups:	EUT	GA1	BAN	DEL	PAP	OTH	TEM	MED	SHR	LAB	OIK	COP	ACA	CEN	FIE	BRY
Station group A (n=13):	**A/B**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*
Station group B (n=9):	**A/C**	-	-	-	-	-	-	-	-	**	-	-	-	**	-	-	*
Station group C (n=4):	**B/C**	-	-	-	-	-	-	-	*	**	-	-	-	**	-	**	***

Cruise 5

		A										B							C					
	Between Groups:	OIK	CEN	PAR	TEM	MED	OTH	ACA	PAP	ISI	LAB	BRY	GA2	OIT	EUT	GA1	BIV	BAN	DEL	SAG	SHR	FIE	GA3	POL
Station group A (n=12):	**A/B**	-	-	-	-	-	-	-	-	-	-	-		*	*	-	*	-	-	-	-	*	*	**
Station group B (n=11):	**A/C**	-	-	**	**	-	-	-	*	-	-	**	***	-	***	**	-	**	-	-	-	***	-	*
Station group C (n=9):	**B/C**	-	*	*	*	-	-	-	*	-	-	***	***	**	***	***	**	***	*	*	*	***	**	***

Table A.4.3: Summary of the SNK tests following individual *F* tests on average taxa abundances between station groupings: -: not significant; *: 0.05>P>0.01; **: 0.01>P>0.001; **: 0.001>P; for taxa abbreviations see table A.4.1.

Cruise	Stations × taxa	taxa / stations removed from analysis	n. of dimensions; % inertia explained by CA	Main contributors to dimension inertia (and % of inertia)				
2	31 × 14	Cal, Par	3 78.4%	1 (50.1%)	2 (20.0%)	3 (8.2%)		
				28, 27, 21, 19, 29, 16 **Oth, Fie,** Oik	11, 10, 28, 20, 5(2), 27 **Amp, Eut**, Aca	**12**, 21, 3, 19 **Amp, Cop**		
3	21 × 15	Cal, Fil, Oth, Sag 9,16,19,21	3 70.2%	1 (42.0%)	2 (16.5%)	3 (11.7%)		
				18, 15, 14, 17, 5(2), 13 **Fie, Oik** ,Amp, Eut	ER, 10, 23, 5(2), 13 **Aca,** Lab	1, ER, 12 **Oik, Ost**, Tem		
4	26 × 10	-	2 70.1%	1 (55.4%)	2 (14.7%)			
				29,28,27,5(1), Cal, 6 **Fie,** Oik ,Aca	**12**, 17, Cal **Lab**, Pap			
5	32 × 12	-	5 88.7%	1 (32.8%)	2 (20.9%)	3 (17.1%)	4 (12.2%)	5 (5.8%)
				29, Cal, 3 **Oit, Sag,** Eut	1, 5(1), 9, 17,20, 21 **Lab** ,Oth, Isi	**17**, 3, 20, 28, 19 **Oik**, Oit	**17**, 3, 16 **Oth, Oik**	5(1), 20, 11, 24, 29, 6 **Sag, Par**

Table A.4.4: Summary of the Correspondence Analyses on the station × taxa matrices for cruises 2 - 5 (**holoplankton**): taxa and stations excluded from the analyses, number of dimensions included in the CA (as chosen by the Scree test), and main contributors to the inertia of each dimension (>50% when summed). In bold are stations or taxa which contribute over 20% of the inertia of that dimension. For abbreviations see table A.4.1.

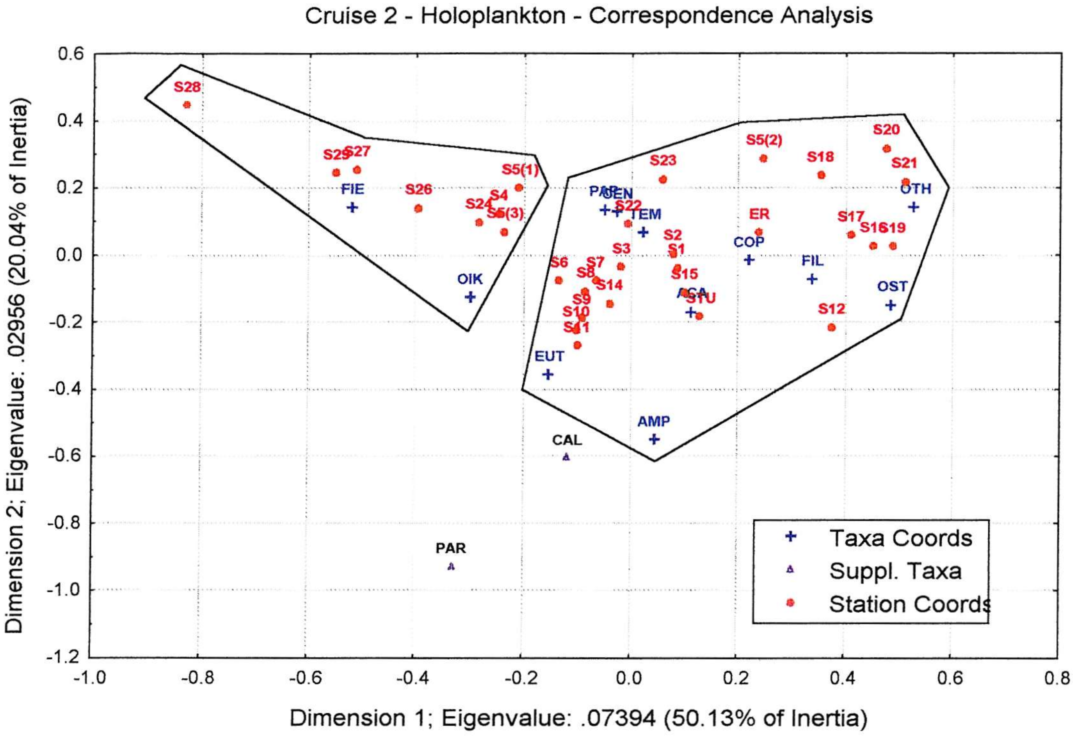


Figure A.4.8: Cruise 2 correspondence analysis on holoplankton taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

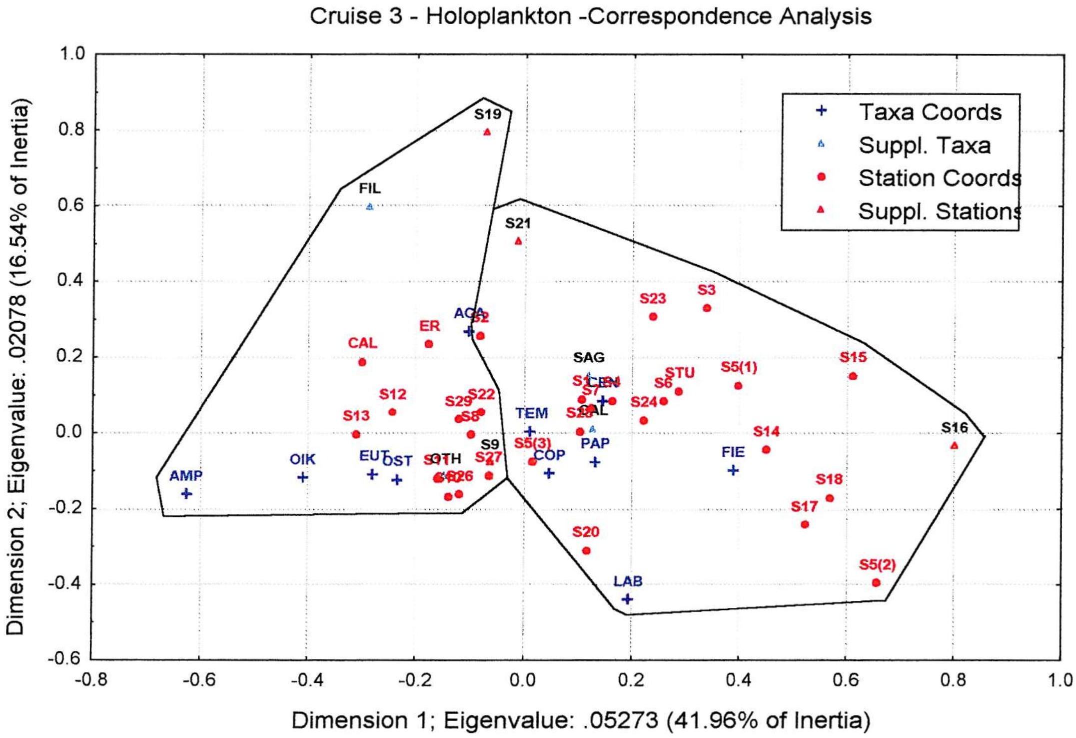


Figure A.4.9: Cruise 3 correspondence analysis on holoplankton taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

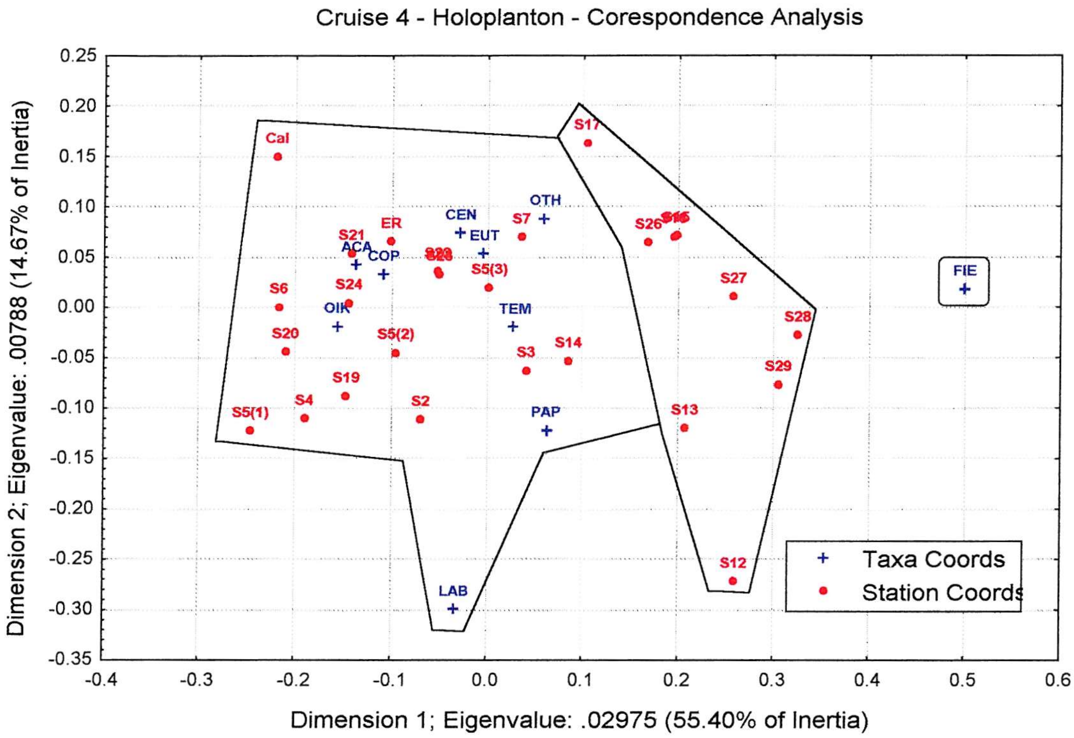


Figure A.4.10: Cruise 4 correspondence analysis on holoplankton taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

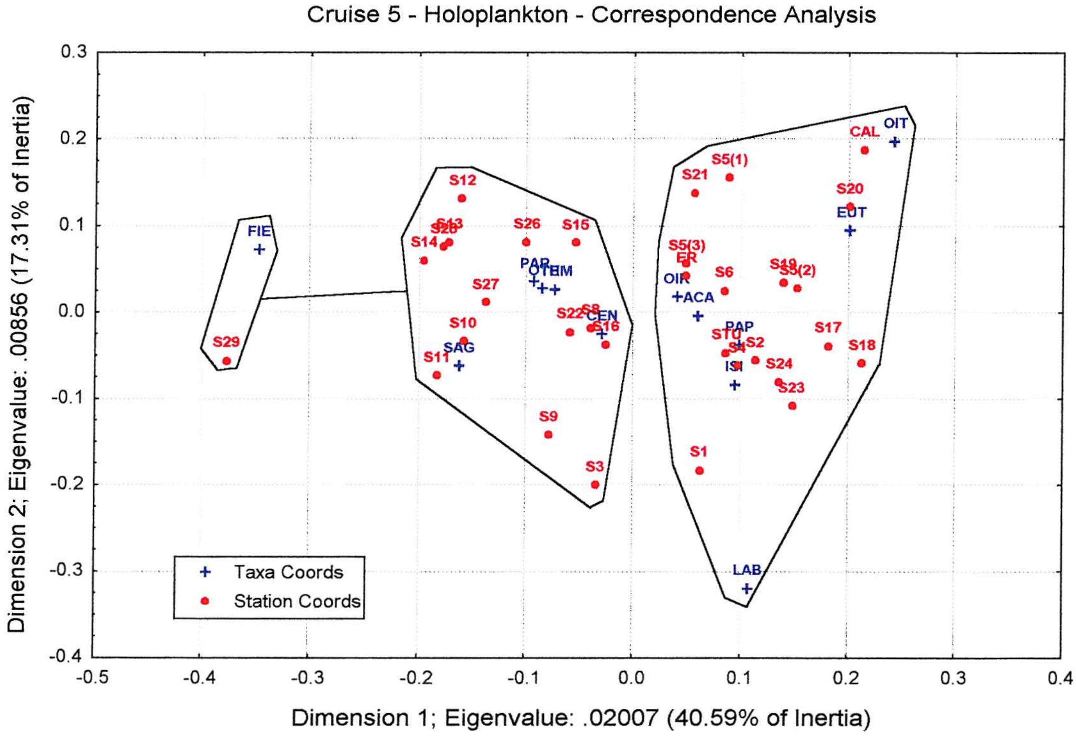


Figure A.4.11: Cruise 5 correspondence analysis on holoplankton taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

Cruise	**Stations × taxa**	**taxa / stations removed from analysis**	**n. of dimension; %inertia explained by CA**	**Main contributors to dimension inertia (and % of inertia)**			
2	31 × 10	Dem, 29	2 58.1%	1 (41.6%)		2 (16.5%)	
				26, 11, 19 **Lit, Spi, Bry,** Gal		22, 15, 12, 16 **Bry,** Del, Lit, Ban	
3	33 × 9	Lit, 20	4 81.8%	1 (34.0%)	2 (21.7%)	3 (16.5%)	4 (9.6%)
				ER, 9, 4 **Med**, Ban, Spi	STU, 26, 11 **Ban, Otp**	21, STU, 6 **Gal, Asc**	14, 11, 5(3) **Del, Otp**
4	26 × 8	GA2	3 90.3%	1 (53.1%)	2 (29.1%)	3 (8.1%)	
				20, 5(1), 28 **Bry, Shr,** Med	**CAL**, 21, ER **Ban,** Del	7, 19, 5(3) **Med, Gal**	
5	32 × 10	GA3	3 73.7%	1 (39.2%)	2 (23.4%)	3 (11.1%)	
				19, 27, 12 **Ban, Del, Shr**	**CAL**, ER, 5(1) **Ban, Pop,** Bry	**29**, 21, CAL **Ga2**, Pop, Med	

Table A.4.5: Summary of the Correspondence Analyses on the station × taxa matrices for cruises 2 - 5 (**meroplankton**): taxa and stations excluded from the analyses, number of dimensions included in the CA (as chosen by the Scree test), and main contributors to the inertia of each factor. In bold are stations or taxa which contribute over 20% of the inertia of that factor. For abbreviations see table A.4.1.

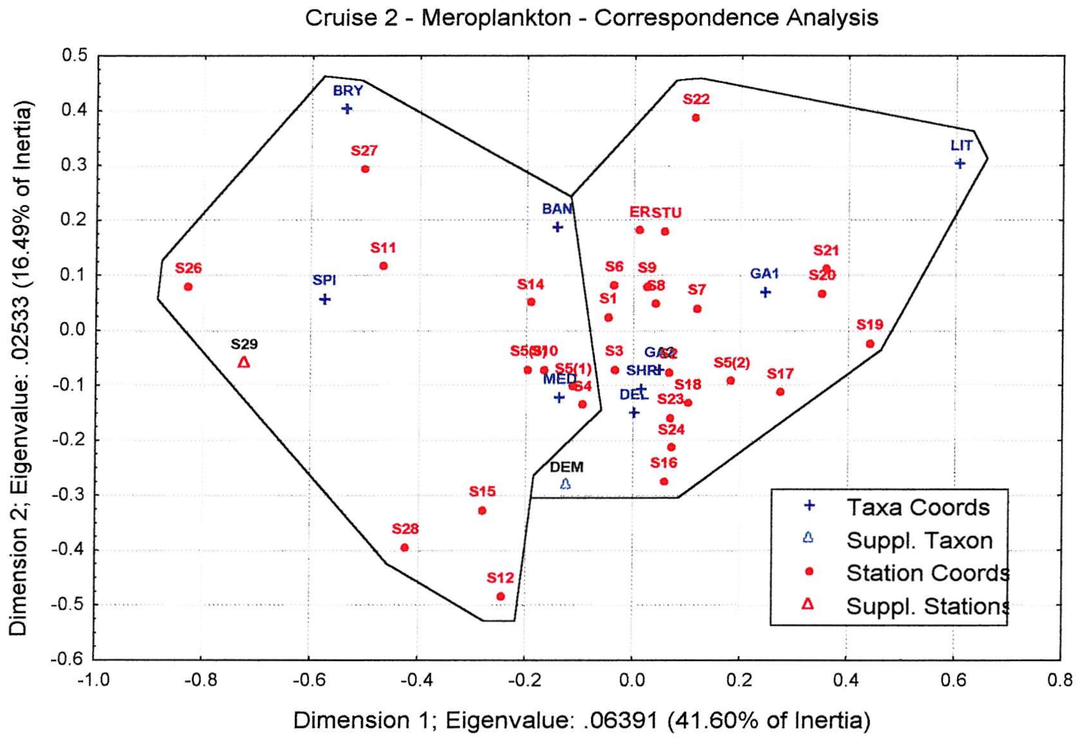


Figure A.4.12: Cruise 2 correspondence analysis on meroplankton taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

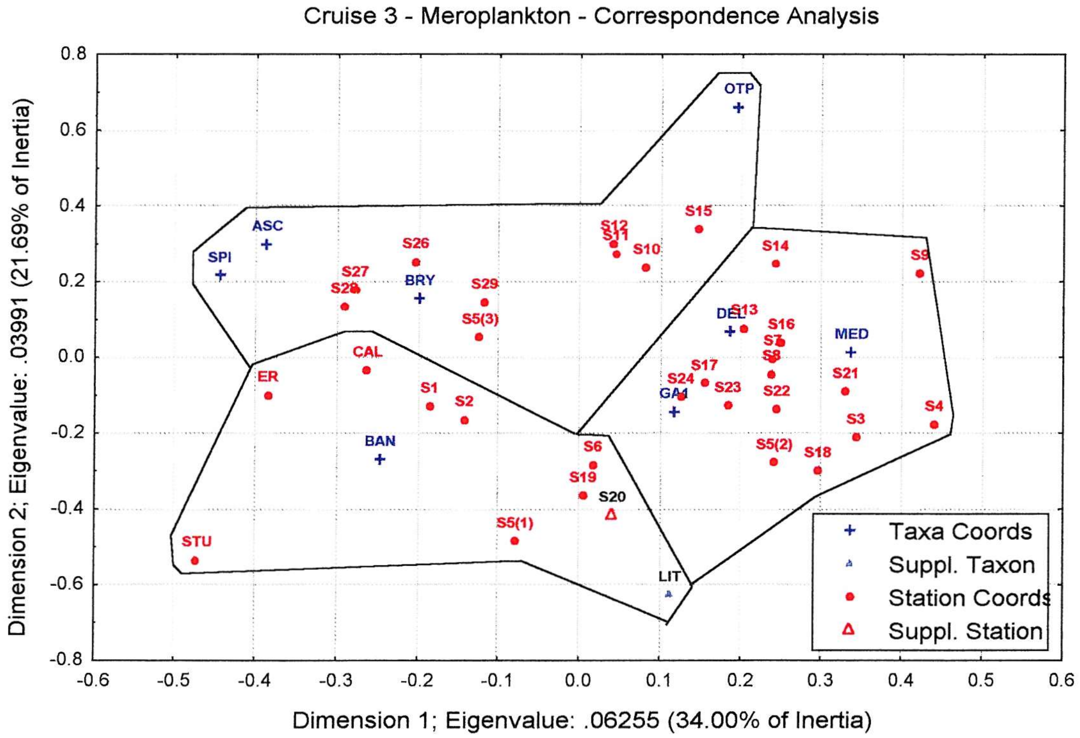


Figure A.4.13: Cruise 3 correspondence analysis on meroplankton taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

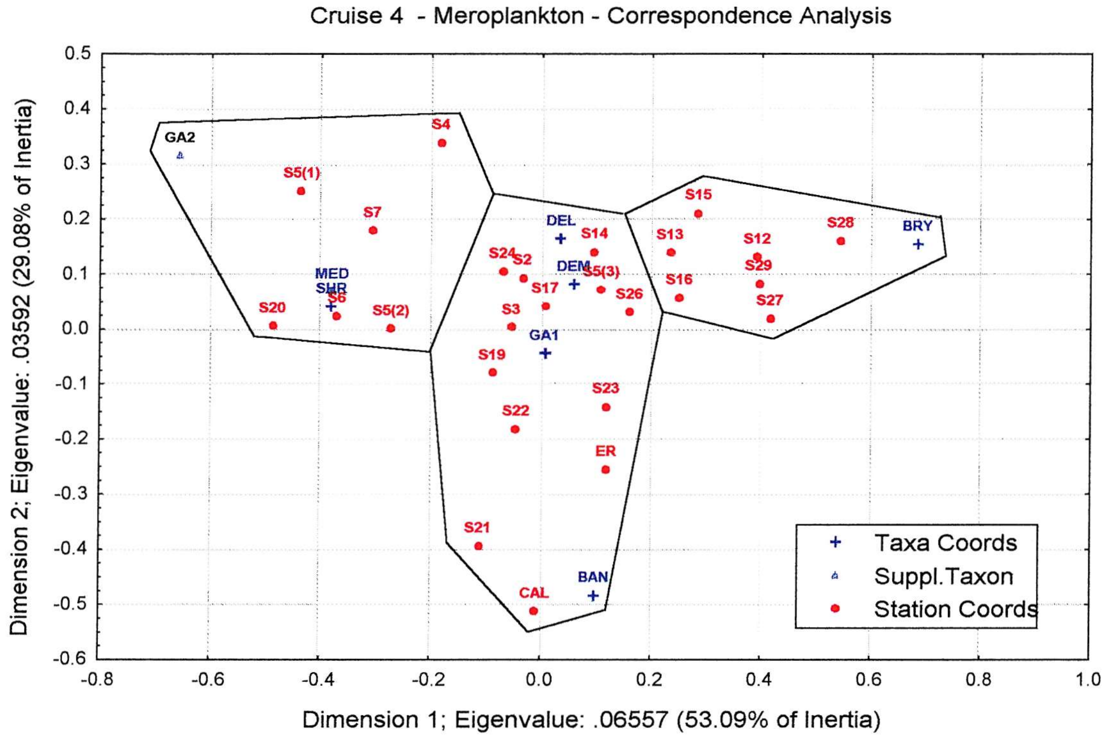


Figure A.4.14: Cruise 4 correspondence analysis on meroplankton taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

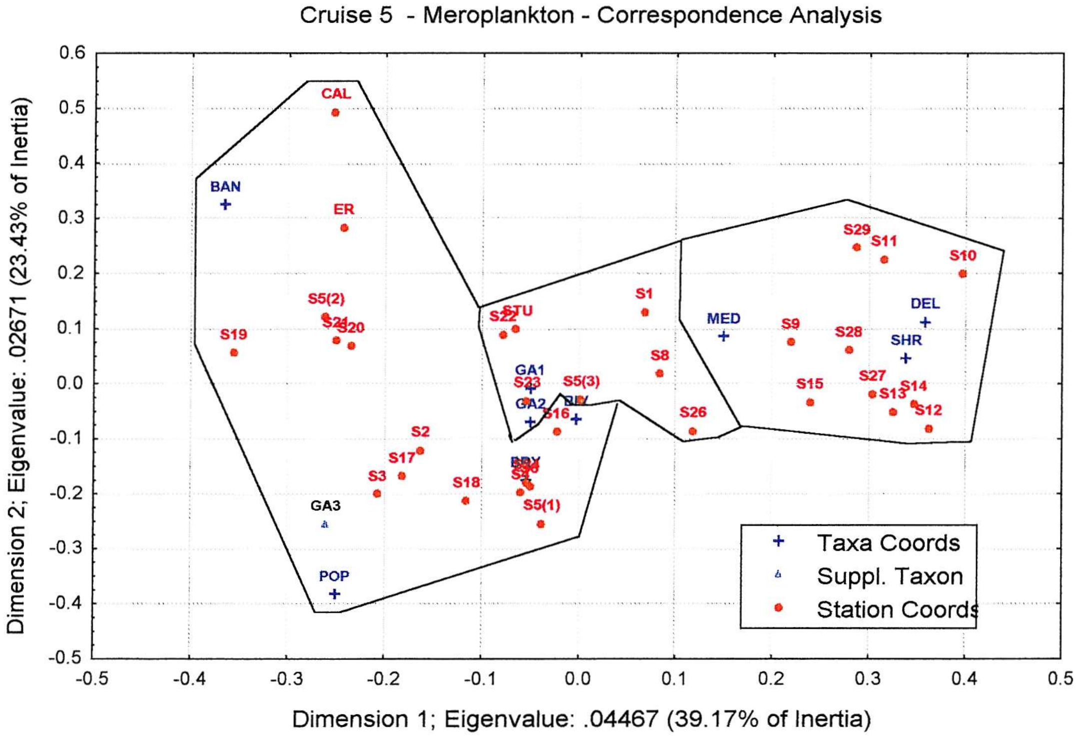


Figure A.4.15: Cruise 5 correspondence analysis on meroplankton taxa × stations matrix: ordination on dimensions 1 and 2. Groupings are according to the cluster analysis on point coordinates in the CA dimensions. For abbreviations see table A.4.1.

Chapter 5 supplementary figures:

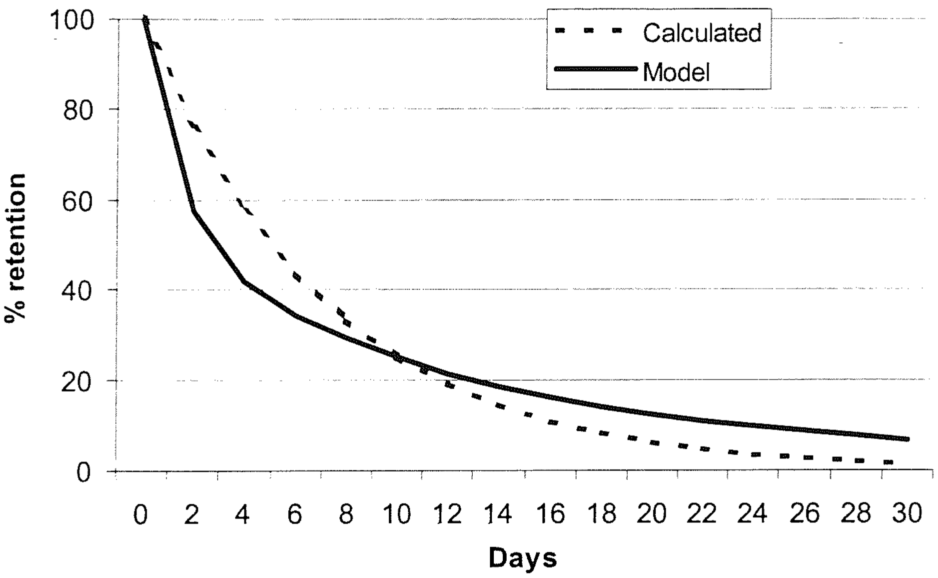


Figure A.5.1: Percentage retention *vs.*time. Solid line: as modelled within the release area (figure 5.1) for a tidal coefficient of 70 and no wind; dashed lined: as calculated using $N_t=N_0e^{-0.14t}$.

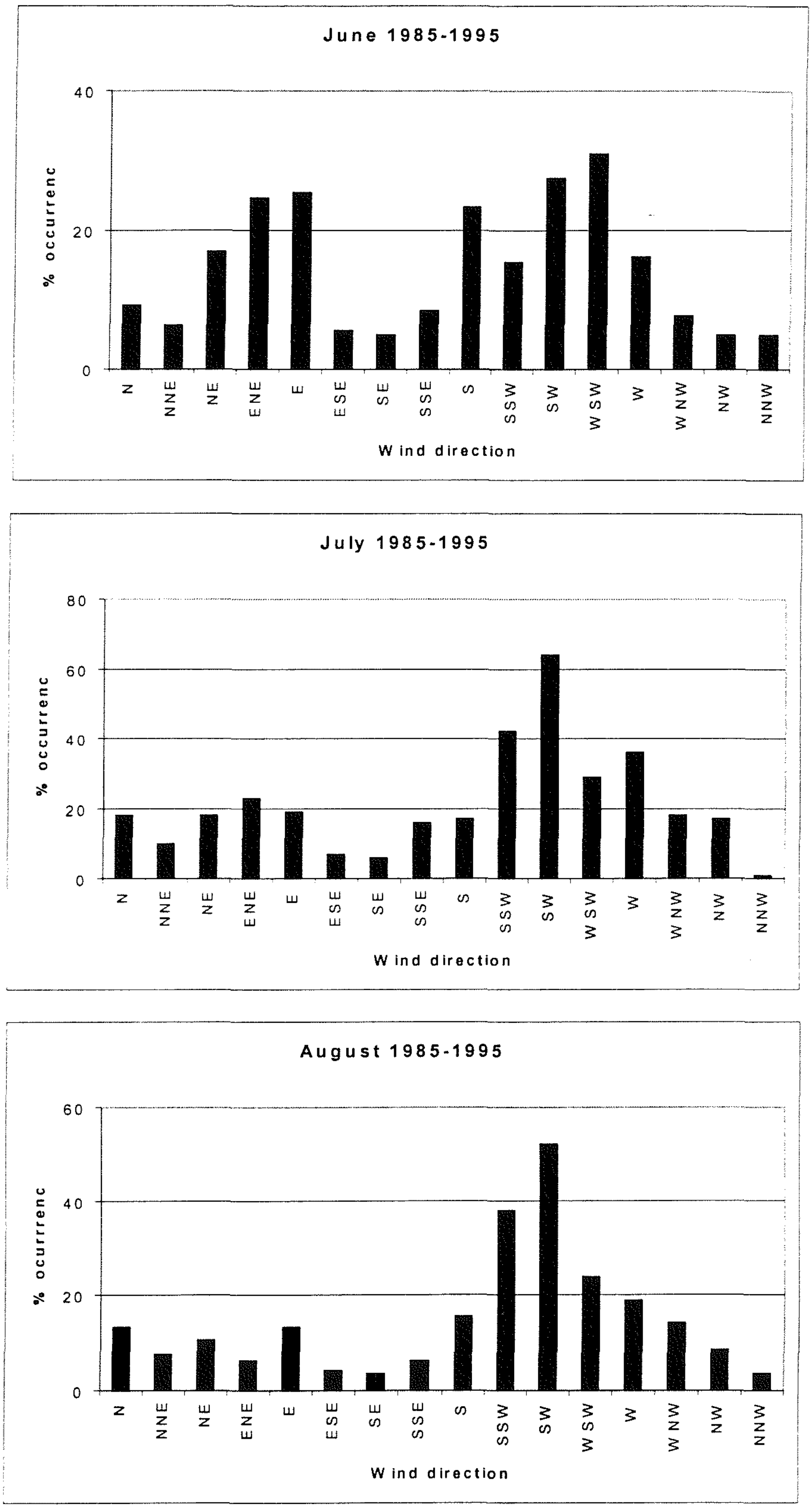
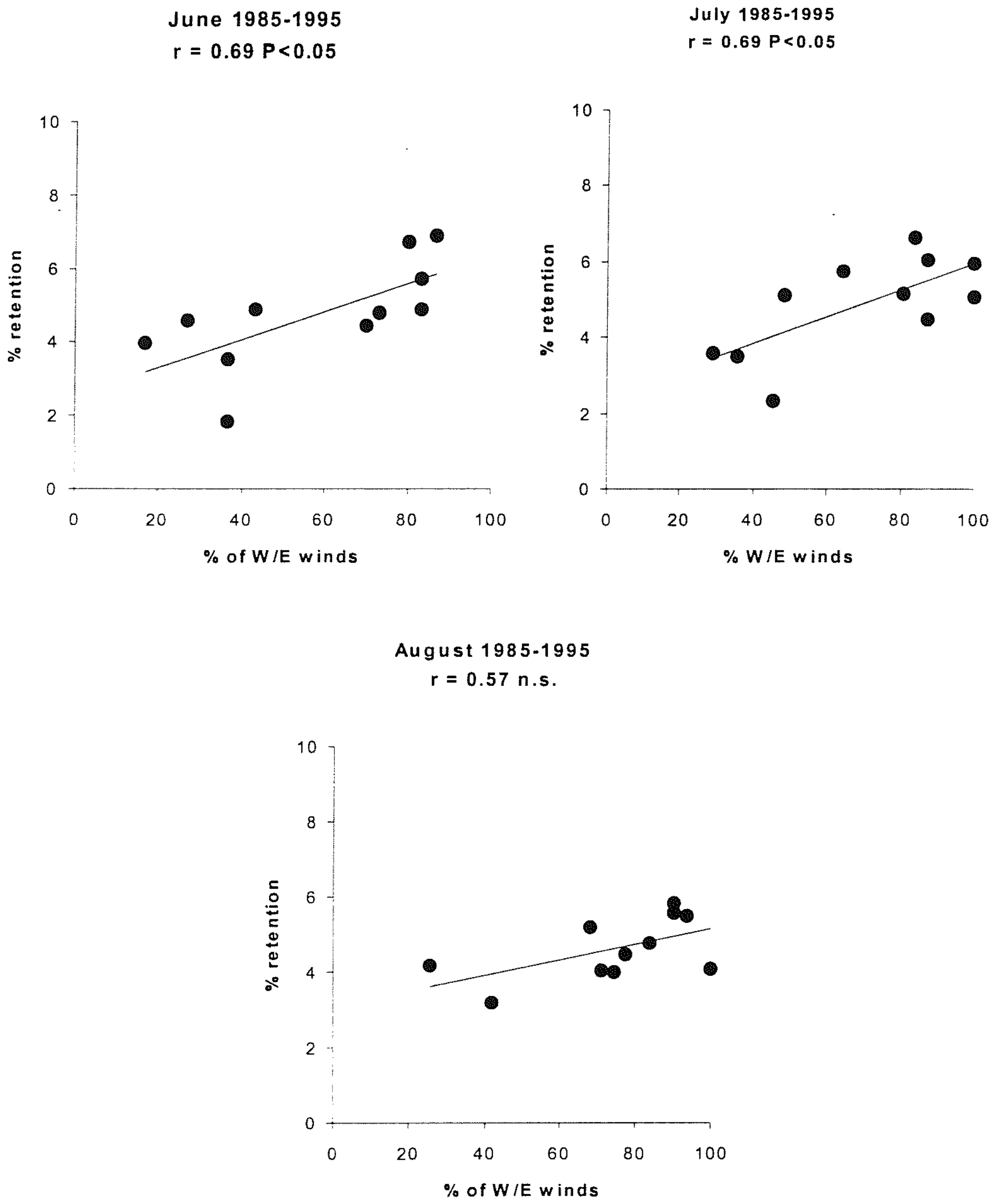


Figure A.5.2: Frequency of wind directions for June, July and August 1985-1995, measured at La Hague.



June 1985-1995
r = 0.69 P<0.05

July 1985-1995
r = 0.69 P<0.05

August 1985-1995
r = 0.57 n.s.

Figure A.5.3: Percentage of particle retention in the 'Solent area' (see figure 5.1) after 1 month model runs in conditions of measured wind and tides *vs.* the proportion of westerly (180°>α≥0°) to easterly (0°>α≥180°) winds.