Population Dynamics and Biomass of

Limapontia depressa at North Bull Island, Dublin Bay.

Population dynamics and biology of *Limnoperna depressa*
... Sound, Dublin Bay.

Mary Mackiernan B. Sc.

Thesis submitted in fulfilment of the requirements for the degree of
Master of Science in Botany
...

Population Dynamics and Biomass of *Limapontia depressa* at North Bull Island, Dublin Bay.

Mary Niamh Forrest B.Sc.Ed.

Thesis submitted in fulfilment of the requirements for the degree of

Master of Science by Research

to Trinity College, University of Dublin.

March 2001.
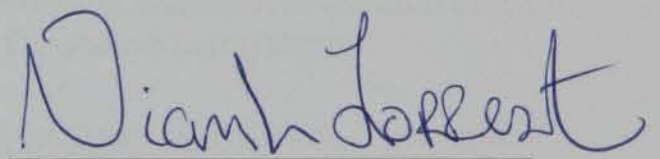
Declaration

I hereby declare that this thesis is my own work,
except where otherwise stated, and it has not been
previously submitted to this or any other university.

Permission to Copy

Reproduction in whole, or in part of the contents of
this thesis is authorised, provided the source is acknowledged,
at the discretion of the library of Trinity College, Dublin.

Mary Niamh Forrest

Acknowledgements

Summary

Over three sampling seasons between 1997 and 1999, *Limapontia depressa* was studied at North Bull Island, Dublin Bay. A detailed population study of this organism was carried out in relation to various environmental parameters such as water temperature, salinity, moisture content, sediment organic matter and sediment chlorophyll a.

Limapontia depressa displayed a sporadic life history. Animal numbers decreased significantly during the summer months, with an absence of animals at the all sites from June to September. Animal density was at its highest in January when there was a maximum of 45 animals per core (2.3 individuals cm^{-2}). An obvious growth pattern is evident from the data with the average length class increasing from a minimum of 1.1mm, which is just larger than the size of the egg capsule in November to a maximum of 5.3mm in April.

The disappearance of *Limapontia depressa* over the summer months meant that there was a strong negative relationship of population density with temperature. A negative correlation was observed between animal density and salinity, moisture content and organic matter.

Biomass estimations revealed a distinct increase in standing crop over the sampling right up to their disappearance in the summer.
Respiration measurements indicated that respiration was higher at $10^{o}C$ than at $20^{o}C$. However, this could also be interpreted as a stress indicator.

It remains unclear as to whether *Limapontia depressa* actually controls the prevalence of algal mats, but it is likely that its distribution is influenced by algal presence and *vice versa*.

Table of Contents

List of Figures

List of Tables

List of Plates

Chapter 1

General Introduction

The estuary is a transition zone where the constantly changing mixture of freshwater and seawater results in an environment that is more extreme and variable than open ocean and freshwater systems (Kennish, 1986). Physical factors, such as the intensity of tidal action, distribution of tidal currents and elevations, and compositions of sediments contribute to the overall complexity of these coastal environments. In turn, this affects species composition and distribution of flora and fauna.

The estuarine environment of Dublin Bay has undergone many changes since the late eighteenth century, not least the growth of North Bull Island. This island originally appeared as a sand-bar and its growth was expedited when the Great South Wall (1790) and the Bull Wall (1825) were built in an effort to develop Dublin Port. The island is now connected to the mainland by the Bull Bridge and a causeway which were constructed in 1819 and 1964 respectively. The construction of the causeway ensured that there was no tidal flow around the island and the area between the coast and the island was divided in two, consequently, the north and south lagoons came to exist.

The environments that were thus created are constantly under pressure from industrial, domestic and recreational attentions, which affect the natural development of the ecosystem. However, these ecosystems continue to have a vast diversity of both flora and fauna. The organisms that exist in an ecosystem have adapted and developed within the limits of their environment in such a manner that we may not always understand their role in ecosystem growth, *Limapontia depressa* being one such animal.

Chapter 2

North Bull Island Ecosystem

2.1 Dublin Bay

The crescent-shaped coastline of Dublin Bay sweeps westward and south from Howth Head to Dalkey (Fig. 2.1). The Liffey estuary divides the bay almost equally, the two arms being sandy beach tapering to rocky outcrops at Howth and Dalkey (Brunton, 1987). Therefore, the bay is almost completely enclosed to the north, west and south, measuring 10km from north to south and 10km from east to west at its widest points.

The bay is shallow, the inner third being approximately 5m deep and the 10m contour running from the southern tip of Howth to Dun Laoighaire. The depth then increases rapidly as the 15m and 20m contours mark the outer edges of the bay. A summary of the tidal levels for Dublin Bay is provided in Table 2.1. At low tide, extensive sand flats occupy the inner third of Dublin Bay. These form the North and South Bulls, better known as Sandymount and Dollymount respectively (Harris, 1977). They are separated by the Liffey and Tolka estuaries, which are the only major freshwater inputs, the River Liffey having the stronger influence. The supra-tidal part of the island is made up of the dune ridges, which is landward bordered by a salt marsh. This saltmarsh encroaches upon a lagoon drained at low tide to expose vast intertidal flats.

Table 2.1 A summary of tidal levels (m O.D.) in Dublin Bay

Mean tidal range	2.75
Neap tidal range	1.9
Spring tidal range	3.6
Highest astronomical tide	+ 4.9
Lowest astronomical tide	+ 0.2

As the population of the city of Dublin continues to grow well over the one million mark, the demands on the city and its conurbation have grown accordingly. The result is that the entire 30km perimeter is urbanised. The unavoidable industrial developments of the Dublin port area have encroached upon areas formerly used for recreation. However, the

overall recreational picture of the bay is one of an extraordinarily valuable amenity, capable of sustaining a wide variety of recreational activities (O'Sullivan, 1987).
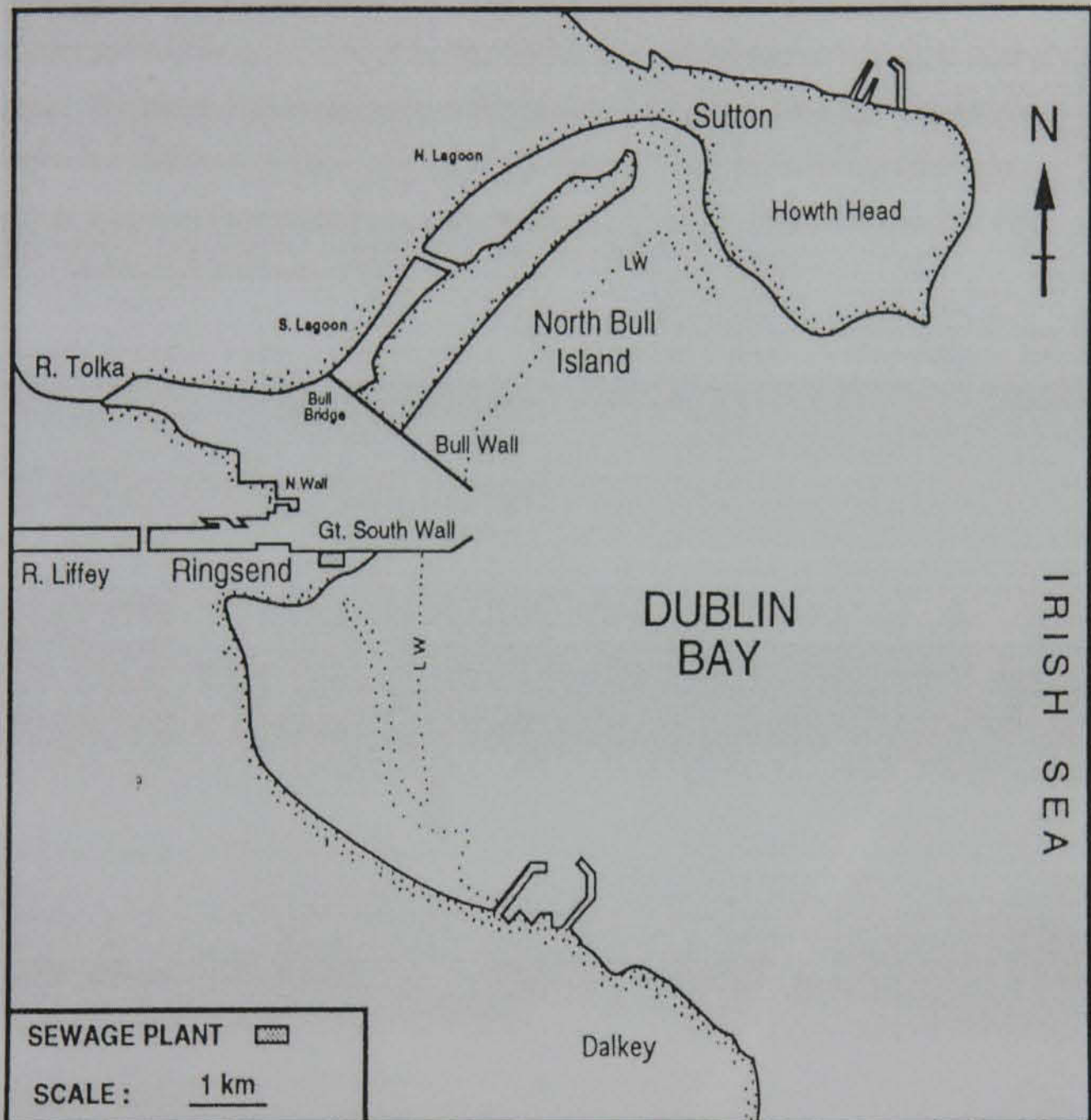
Figure 2.1 Map of Dublin Bay (after Jennings, 1996).

2.2 North Bull Island

North Bull Island (Plate 2.1) is a low-lying, dune-covered sand spit. It is 4.85km long and runs parallel to the coast in a north easterly direction between Clontarf and Sutton in the northern half of Dublin Bay (Harris, 1977). The north lagoon was chosen as the study area and therefore will be described in detail in this section.

This area is of exceptional scientific interest because of bird life, other animal and plant communities, and its changing form (An Foras Forbatha, 1977; Jeffrey *et al.*, 1977). The Nature Reserve (North Bull Island) Establishment Order, 1988 (S.I. No. 231 of 1988) covers 1,318ha of intertidal mud flats, which are important for bird populations but excludes areas such as the coastal marsh, sand dunes and the area to the south west of the lagoon. The North Bull Island area, which has been declared a UNESCO Biosphere reserve, is a registered Ramsar site under the Ramsar Convention. It has also been declared a Special Protection Area under section 4 of the EC Bird Directive 79 / 409 / EEC, (McHugh & Partners, 1991).

Plate 2.1 Aerial photograph North Bull Island.

2.2.1 Climate

The location of Ireland as an island to the east of the Atlantic Ocean in mid latitudes explains its west maritime climate of mild moist winters and cool cloudy summers (Collins & Cummins, 1996; Finch & Gardiner, 1993). For most of the year, maritime air related to the Gulf Stream helps to regulate the climate. Dublin Bay is reasonably sheltered, particularly so by the Wicklow Mountains to the south. The various climatic parameters used to describe an area are presented in Table 2.2 for North Bull Island.

Table 2.2 Summary of climatic variables applicable to North Bull Island (Data courtesy of Met Éireann).

Date	Mean Daily Air Temp. (°C)	Mean Daily Rainfall (mm)	Mean Wind Speed (knots)	Mean 10cm Soil Temp. at 0900 GMT (°C)	Mean Daily Global Solar Radiation (Joules per sq. cm.)
Jan '97	4.2	0.4			
Feb '97	6.2	2.2	16.4	5.1	508.6
Mar '97	7.7	0.5	11.4	6.7	883.0
April '97	8.8	1.6	8.2	9.3	1225.4
May '97	9.9	2.0	8.2	11.5	1813.6
June '97	12.3	4.2	9.9	13.8	1475.3
July '97	15.0	1.7	8.4	15.9	1636.4
Aug '97	16.0	2.6	8.6	16.3	1296.3
Sep '97	13.0	0.6	9.5	13.3	1041.6
Oct '97	10.5	2.2	8.8	10.3	540.9
Nov '97	8.3	2.9	9.3	7.9	246.9
Dec '97	6.4	2.9	12.6	5.4	156.4
Jan' 98	5.6	2.6	11.3	4.6	186.0
Feb '98	7.9	0.5	13.1	6.2	433.7
Mar '98	7.8	2.1	9.8	7.1	713.1
April '98	6.8	3.9	10.0	7.2	1169.0
May '98	11.3	0.9	8.5	12.1	1644.9
June '98	13.0	3.7	9.2	14.3	1619.9
July '98	14.4	1.7	10.3	15.4	1433.2
Aug '98	14.9	1.5	10.1	15.5	1448.7
Sep '98	13.3	3.2	9.5	13.5	970.8
Oct '98	10.1	2.4	12.6	9.7	613.8
Nov '98	6.9	2.6	11.5	5.9	329.0
Dec ,98	6.0	2.3	11.4	4.8	174.2
Jan '99	5.4	2.3	12.6	3.7	248.1
Feb '99	5.6	1.3	12.9	4.6	469.1
Mar '99	7.2	1.0	11.0	5.9	842.2
April '99	8.8	2.5	11.8	8.5	1372.4
May '99	11.6	1.3	9.6	12.3	1509.6
June '99	12.1	1.9	7.7	14.2	1703.2

2.2.2 Hydrography

Gross tidal movement in Dublin Bay is clockwise (Harris, 1977). In the south lagoon the flood tide enters beneath the Bull Bridge, whilst in the north lagoon the flood tide enters by Sutton Creek. Two permanent channels exist in the lagoon: one carrying the Naniken stream southwest under the Bull Bridge and the other carrying the Santry river north-east to Sutton Creek. The salt marsh encroaches upon the lagoon and drains into it at low tide exposing the sand and mudflats.

There are three types of regular rhythm, which can be used to describe the tides in Dublin Bay (Jeffrey, 1977). The first type describes daily tidal movements (Fig. 2.2a). Parts of the intertidal flats are flooded with seawater twice in twenty-four hours, and then drained, which exposes the surface to air and possibly to non-saline water in the form of rain or drainage water. The curves of daily tidal cover are asymmetrical in the Bay. The time for the tide to flow from low to high water is approximately 6 hours 40 minutes, whilst the ebb takes 5 hours 40 minutes.

The second type is an oscillation in tidal range, which occurs twice a lunar month (Fig. 2.2b). In this cycle, a period of high tidal range (spring tide) occurs at full and new moon, the difference between high and low tide then being about 3.6m in Dublin Bay (Jeffrey, 1977). This is followed by a period of low tidal range of approximately two metres. The spring tides, usually reach the 4m O.D. (Ordinance Datum) mark and retreat to about 0.4m O.D. Ordinary spring tides cover most of the salt marsh, leaving large areas of mud flat exposed when retreating. The low range neap tides cover the salt marsh only to about 3.5m O.D., and expose the flats down to about 1.5m O.D.

The third regular rhythm is one of spring tide ranges that vary through the seasons of the year. The highest spring tides are expected at the equinoxes, in March and September. These are the highest tides and are important as they impose a certain degree of salinity to the 4.7m mark on the salt marsh (Jeffrey, 1977).
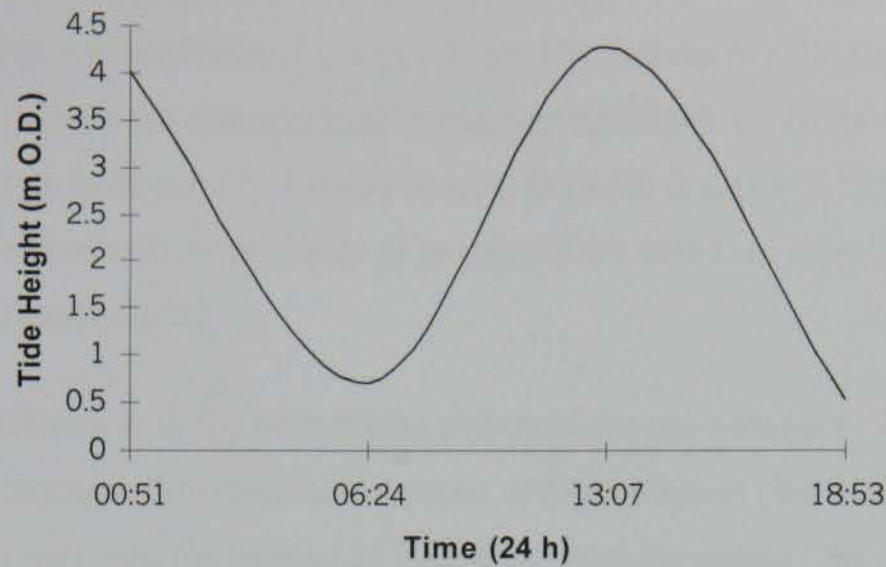
Figure 2.2a: An example of the daily tidal cycle occurring in the north lagoon for the 1st January 1998 (O.D. data, North Wall, Dublin Bay, courtesy of Proudman Oceanographic Laboratory).
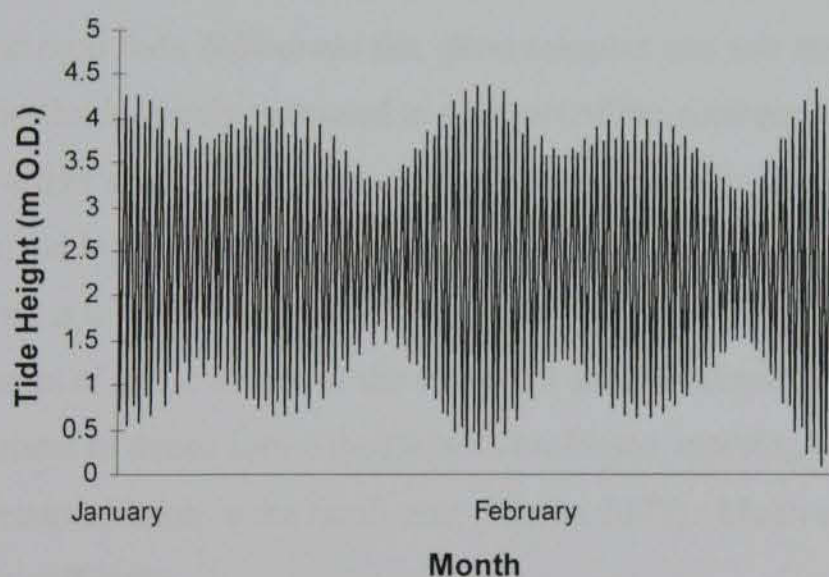
Figure 2.2b: The spring/neap tidal rhythm for the north lagoon using January and February 1998 as an example (O.D. data, North Wall, Dublin Bay, courtesy of the Proudman Oceanographic Laboratory).

The vertical range of the tide, the difference in height between consecutive high and low waters, determines the extent of seawater inundation of tidal flats and marshes, which is a major factor regulating the distribution of intertidal organisms (Kennish, 1986).

The ecological effects of tidal inundation are more variable in the estuary than in the oceanic realm, changing daily, seasonally, and through a tidal cycle. Sea water is roughly

a thousand times more concentrated than river water and consequently the majority of animals on the flats are euryhaline, i.e. can tolerate fluctuations in salinity. Whereas marine and fresh waters are characterised by constant salinities, estuarine water is particularly variable in its salinity, usually ranging between 0.5ppt and 35ppt. The horizontal and vertical salinity gradients of an estuary are determined by land runoff, precipitation and evaporation.

There are also differences in the proportions of ions in the two solutions. The contrasts in salinity and ion concentration indicate the extent of physiological change that is imposed on plants and animals with the passing of tidal cycles and the stresses they incur (Jeffrey, 1977).

2.2.3 Geomorphology

The north lagoon consists of 310ha and encompasses a variety of sub-environments, lagoonal sand and mud flats, *Salicornia* flat, dune complex and salt marsh.

The lagoonal mud flat is largely restricted to that part of the northern lagoon adjacent to the causeway. Farther away from the causeway, they become firmer muddy sand and finally grade into the lagoonal sand flat.

The *Salicornia* flat is a spreading sub-environment characterised by the presence in summer and autumn of dense stands of the succulent annual halophyte *Salicornia*.

The sub-environment of dunes forms the island's backbone, tapering off from the Bull Wall to form a recurved hook in the north-east (Harris, 1977). Much of the dune area has been modified by golf-links.

The salt marsh environment occurs between the dunes and the lagoon (Plate 2.2). On the lagoonal side there is a distinct boundary in the form of a step, up to 40cm high, which coincides with the normal high-water limit, and only the spring high tide rises above this level thus flooding the marsh. The margin with the dunes is marked by invasion of highest spring tides and by a distinct vegetational variation.

However, a saltmarsh represents a wider range of ecological conditions than either beaches or intertidal flats. Marine, freshwater and terrestrial environments and numerous intermediate conditions exist side by side to produce a complicated pattern of environments. Spatial and temporal changes such as substrate, salinity, tidal cycle, rainfall and temperature restrict the range of ecological niches available to saltmarsh organisms.

In turn, the organisms present must be adaptable structurally, physiologically and behaviourally.

2.2.4 Sedimentology

Changes in particle size composition of sediments in estuaries may cause changes in other chemical and physical properties of the sediment, which will in turn influence the animals and plants living there. Sediments with a higher water retention capability will tend to be well-sorted fine-grained sediments. Temperature and salinity change much more slowly within a sediment than the surrounding air and water. Fine-grained sediments are associated with higher organic contents and lower oxygen contents. A sedimentology profile of Bull Island is presented in Figure 2.3.
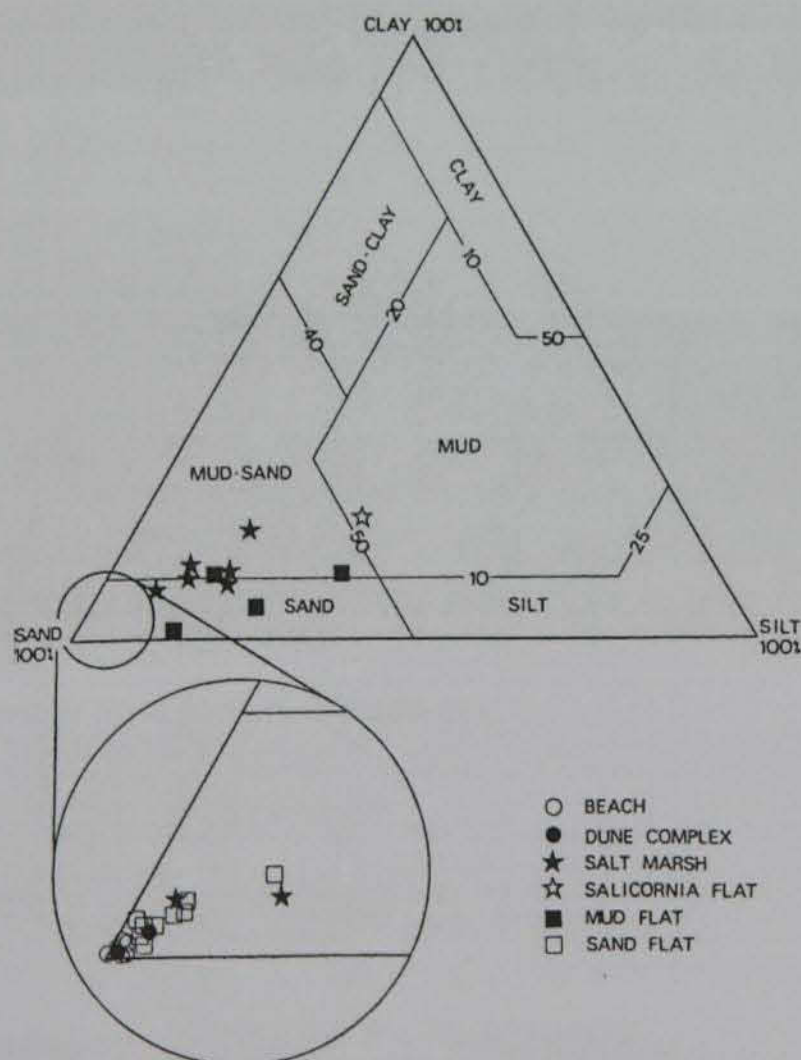
Figure 2.3 Sedimentology profile of North Bull Island (after Jeffrey *et al.*, 1977).

Plate 2.2 The saltmarsh at North Bull Island, Dublin Bay.

2.2.5 Algae

Algae present in the north lagoon include Chlorophyta, Chrysophyta, Phaeophyta and Rhodophyta, however the Chlorophyta and Chrysophyta constitute the majority of the algae found (Maguire, 1990; Jeffrey et al., 1992; Khan, 1998).

Chlorophyta or green algae comprise one of the major groups of algae (Bold & Wynne, 1985).

Members of the Ulvales include Enteromorpha, Ulva and Percursaria.

Enteromorpha is widely distributed in marine habitats, often in the intertidal zone where it is periodically exposed to air. The thallus is described as a hollow tube bounded by a single layer of cells, which may sometimes be constricted in places (Bold & Wynne, 1985). The cell walls of Enteromorpha are composed mainly of polysaccharides and there are some lipids. The two layers of cells separate along their contiguous walls to give rise to a tubular type of organisation in mature plants (Plate 2.3a).

Ulva or "sea lettuce" consists of a flat thallus with two layers of cells (Burrows, 1991) appears a pale watery-green colour when the plant is young. The colour becomes brighter and harder as the plant grows older until it appears a very dark green.

Percursaria has a thallus of unbranched filaments and possesses a yellow-green tinge often occurring entwined with other filamentous algae. The cells are thick walled and contain a large chloroplast and pyrenoids.

The Cladophorales (which includes Rhizoclonium and Cladophora) are coenocytic. Cladophora is commonly found as dark green dense tufts in brackish or marine waters (Plate 2.3b). The chloroplast is reticulate but is not completely continuous and contains many pyrenoids (Bold & Wynne, 1985).

Rhizoclonium looks like a tangle of threads but is more likely to be a yellowish colour (Barrett & Yonge, 1958). This algae is widely distributed across the salinity range from marine waters to fresh water. The cells are not as long as they are broad and contain a reticulate chloroplast with pyrenoids.

The only member of the Chrysophyta to occur is Vaucheria, which does so abundantly in the north lagoon (Jeffrey et al., 1992). This branching filamentous algae is both tubular and coenocytic and is widespread in freshwater, brackish and marine habitats. Vaucheria is amphibious, living on mud that is periodically exposed to water and air. Low light

11

intensity causes the chloroplasts to move into position to receive maximum illumination, whilst high light intensity encourages them to orientate such that they receive minimal illumination (Bold & Wynne, 1985 after Nultsch, 1974).

(a)

(b)

Figure 2.3 Algae which occur at the north lagoon, Dublin Bay; a) *Enteromorpha compressa*, b) *Cladophora rupestris* (courtesy of Professor Michael Guiry, University College Galway.).

The biomass of the green algae in the North Bull Lagoon (Figure 2.4) comprises 31% of the total algal biomass for Dublin Bay. Distribution of algae in the North Bull Lagoon is irregular owing to different substrate and algae types. Figure 2.5a and 2.5b show the spatial and temporal distribution of the algae in the north lagoon (Maguire, 1990).
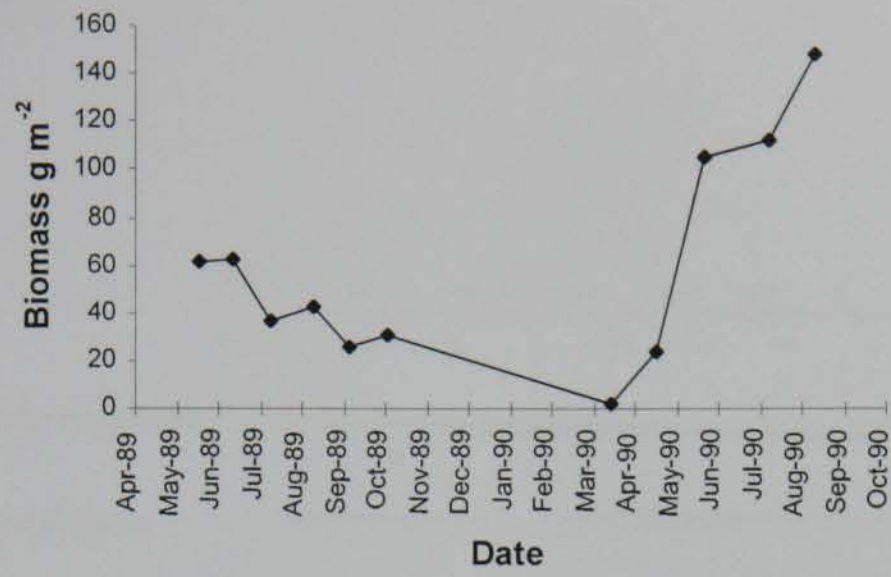
Figure 2.4 Algal biomass in the north lagoon, June 1989 to September 1990 (Jeffrey *et al.*, 1992).
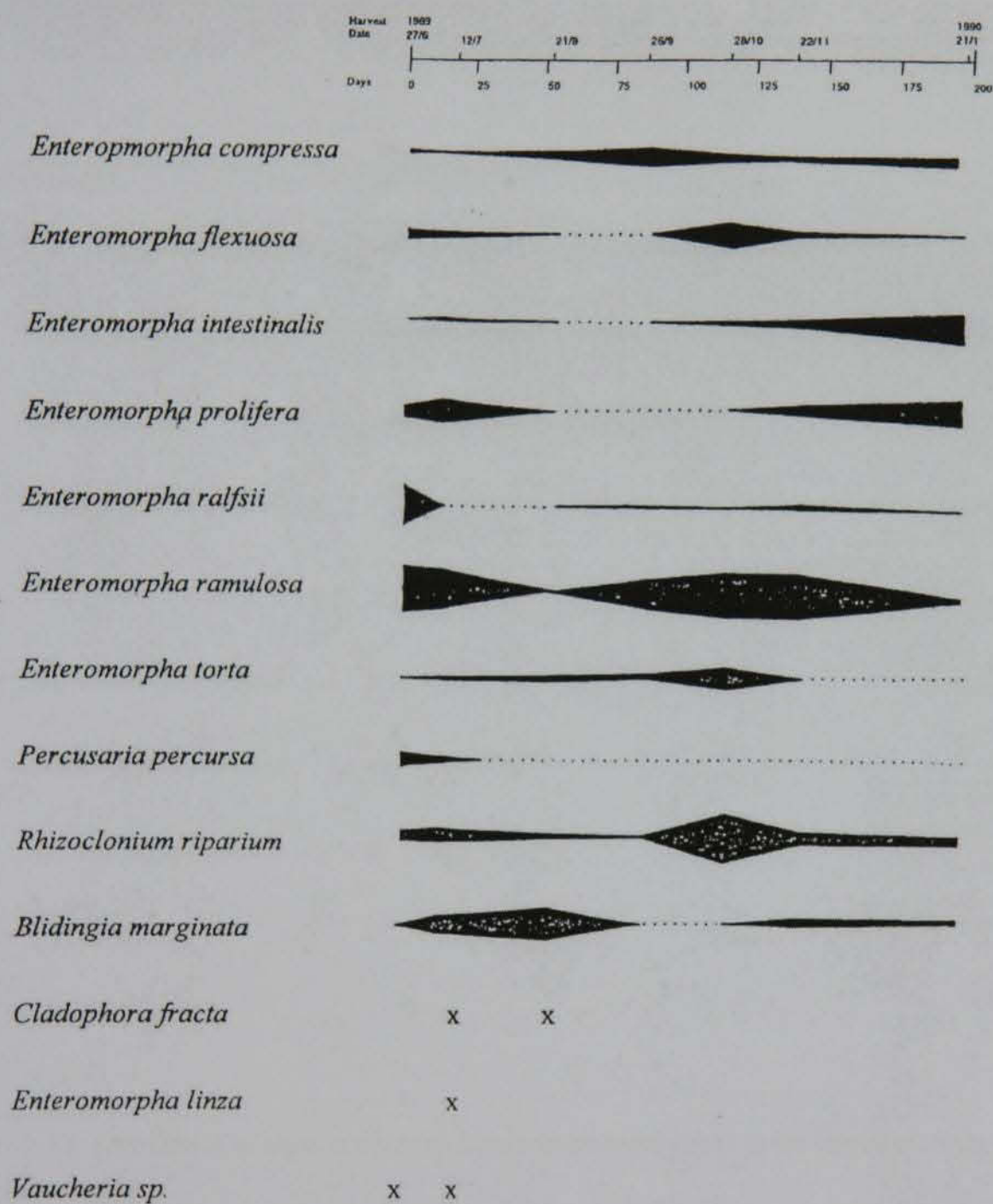
Figure 2.5a Distribution of algae adjacent to the causeway in the north lagoon (after Maguire, 1990).
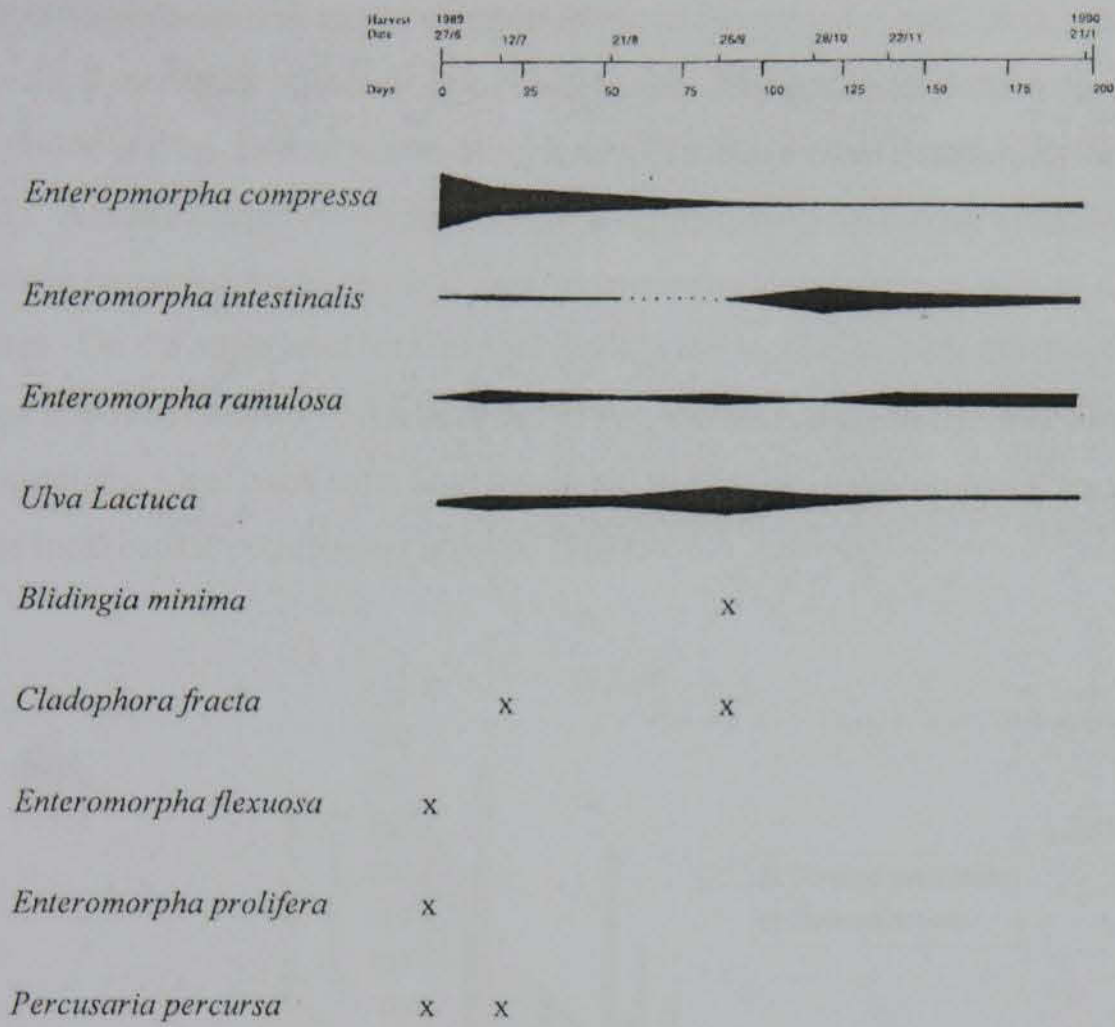
Figure 2.5 b Distribution of algae in the north lagoon in close proximity to the lagoon entrance (after Maguire, 1990).

Macroalgal blooms in the lagoons of Dublin Bay are not a recent phenomenon, but the latest work seems to indicate the intensity and the coverage of the mats are increasing, for example the establishment of the previously unrecorded *Vaucheria* mat off Kilbarrack (Jeffrey *et al.*, 1992; Brennan *et al.*, 1994). It has been postulated that inputs of nitrogen from sewage discharges are partly responsible (Jeffrey *et al.*, 1992, 1993, 1995). While these algal mats have mainly nuisance value, they do significantly affect the macrofaunal communities (Fig. 2.6) on which the majority of wading birds depend (Jeffrey *et al.*, 1992). A study carried out by the Marine Institute (1999) found that moderate algal coverage increased the biomass of various invertebrate populations such as *Corophium* species. On the other hand, as the algal mass in the lagoon exceeds the threshold for faunal impoverishment (Raffaelli *et al.*, 1989), a deterioration in the intertidal benthos is to be expected. Algal mats have been suggested as a major contributing factor in the decline of the local cockle population (Wilson, 1983).
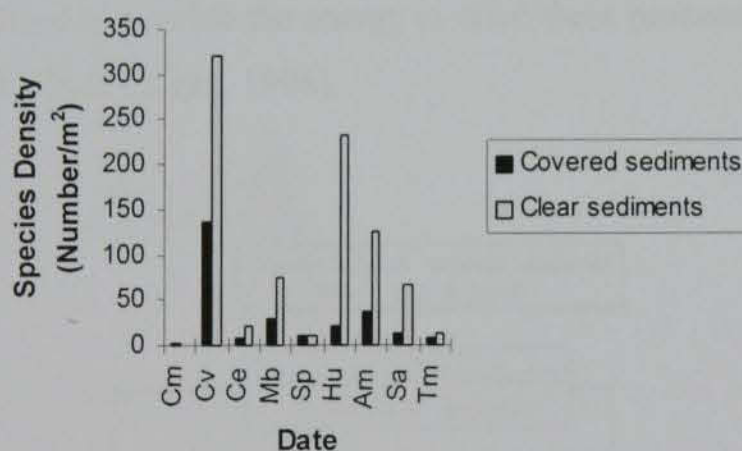
Figure .6 Mean faunal density in clear and algal covered sediments, Cm, *Carcinus maenas*; Cv, *Corophium volutator*; Ce, *Cerastoderma edule*; Mb, *Malcoma bathica*; Sc, *Scrobicularia plana*; Hu, *Hydrobia ulvae*; Am, *Arenicola marina*; Sa, *Scoloplos armiger*; Tm, *Tetrastemma melanocephalum*. (Jeffrey *et al.*, 1992).

There are few biological controls on the macroalgae, but one natural grazer is the small sacoglossan *Limapontia depressa*. It was thought at one time that *Limapontia depressa* was restricted to *Vaucheria* as a food source, however it is now known to feed on other algae such as *Cladophora*, *Chaetomorpha*, and *Rhizoclonium*. Its small size has led to it being overlooked and it has been comparatively little worked on in comparison with other estuarine invertebrates.

2.3 Estuarine Ecosystems

An ecosystem may be defined as a more or less self-contained biological system in which energy for biological processes is transmitted from one class of organism to another and within which various substances are circulated (Jeffrey, 1977). This concept may be effectively applied to intricate ecological situations.

2.3.1 Food Webs

The estuarine food web is dependent on the input of energy from sunlight and the transportation of organic matter throughout the estuary (Fig. 2.7). Within the estuary, the primary producers convert these inputs into living biological material. As the plants grow they are consumed by the herbivores (primary consumers), which are in turn utilised by the carnivores (secondary consumers) (McLusky, 1989). Some of this food will be utilised to build new tissue in growth or for reproductive products, some may be stored, and some will be oxidised to provide the energy to drive these processes, for locomotion or for maintenance (Wells & Clarke, 1996).
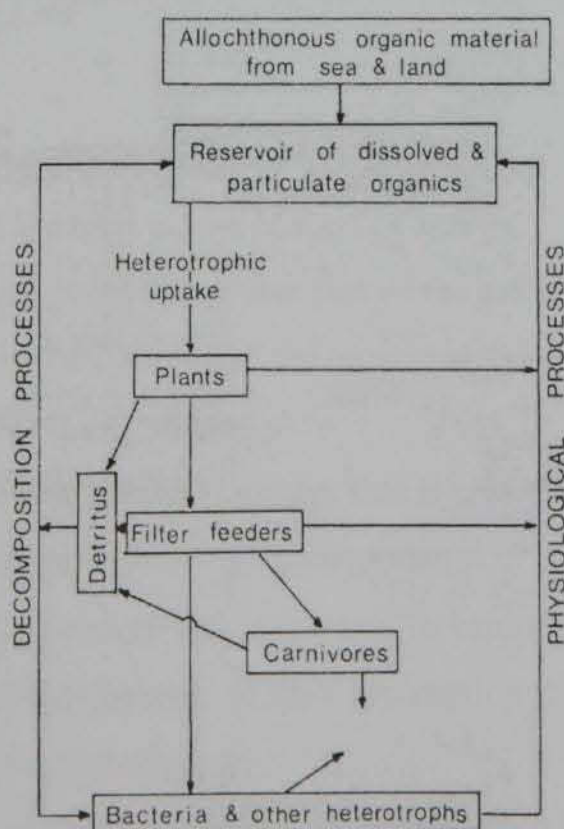
Figure 2.7 An example of an estuarine food web (after McLusky, 1989). The arrows indicate the feeding relationships of a typical northern hemisphere estuary.

2.3.2 Energetics

There are two primary aspects to the manner in which an organism takes its place within the estuarine ecosystem. The first is how the organism balances the competing demands on food intake from the various physiological processes requiring energy or raw materials - its energy budget. The second is the overall impact a species or population makes on the world around it, that is, its ecological impact (Wells & Clarke, 1996).

2.3.2.1 Energy Budgets

Energy budgets may describe energy partitioning within a single organism (individual energy budgets), energy flow through a population of a single species (population energy budgets), or energy transfer between trophic levels (community/ecosystem energy budgets), (Phillipson, 1975). An energy budget helps us to define the position of an organism in the system as well as the importance of that role and may be determined using the following:

$C = P + R + G + U + F$ (Crisp, 1984)

where   C = consumption,

        P = production,

        R = respiration,

        G = gonad output,

        U = excreta,

        F = faeces.

Consumption is defined as the total intake of food or energy.

Production or growth can be described as that part of the assimilated food or energy that is retained and incorporated in the biomass of the organism, but excluding the reproductive bodies that are released from the organism.

Respiration is that part of the assimilated energy that is converted into heat, either directly or through mechanical work performed by the organism.

Gonad output, that part of the energy that is released as reproductive bodies.

Excreta can be described as that fraction of the consumption that is absorbed and later passed out of the body as secreted material.

Faeces is that part of the consumption that is not absorbed but is voided as faeces.

However, a basic measurement necessary to utilise the above equation has not yet been mentioned. Biomass gives information on the amount of biological life and may be

defined as the amount of living substance of the organism (McLusky, 1989). The measurements of the energy budget equation may then be related to the 'standing crop' or biomass to better understand the conversion of material as it passes through the trophic level of the organism and the food web as a whole.

The mass specific production rate of production (P) over annual mean biomass (B), referred to as P/B, has been used to estimate production from biomass when other parameters such as growth and mortality are not known. Banse & Mosher (1980) found that a relationship existed between P/B and species mass at maturity over a very broad range of animal sizes. However, a scatter existed in the relation that may be influenced by ecological and life-history characteristics of populations. A relationship between P:B and body size at maturity was investigated by Heip *et al.* (1984) and was found to exist in laboratory and natural meiofaunal populations.

However, if production estimates are deduced for size classes of organisms and not solely for specific species then a modification of the Banse & Mosher (1980) relation may be used. In this case, the body size parameter that is used is the mean size of an individual in a population (time- and biomass-weighted) whose production is measured. Therefore, if this approach were to be used, production could be estimated for populations at various stages of maturity. Consequently, as production and respiration are logarithmically related, Schwinghammer *et al.* (1986) investigated the possibility of measuring both community production and respiration in this manner. They concluded that while it would be premature to promote this method as the sole means of investigating production and respiration, it would also be unwise not to suggest that it may be utilised cautiously. This word of caution has proved to be the advice of many ecologists as the resulting energy budgets are used to make inferences about the physiology and ecology of an organism or population rather than being described as a 'snapshot' of energy flow (Davies & Hatcher, 1998). There may be cases where a term of the energy budget is underestimated or where stresses involved in the measurement may have unknown effects. On the other hand, the investigation of a parameter may lead to the better understanding of a process or the development of a method which in themselves are valuable exercises.

2.3.2.2 Population Dynamics

Population dynamics, that is, changes in population size in space and time of even simple communities, have the potential to be, and indeed often are, very complex and pose a wealth of ecological questions.

If we are to understand such patterns and be able ultimately to predict changes in them, then our initial focus must be on the individual species themselves and the manner in which populations respond to internal and external ecological factors (Begon, 1996).

The above statement from Begon highlights the need to understand the actual presence of the species within the ecosystem and the pattern of its occurrence. Without knowledge of the population structure and movement, the contributions or pressures that an organism inflicts on the ecosystem are not clearly comprehended.

Chapter 3

Limapontia depressa

3.1 Natural History

Fossil shells of bivalved gastropods have been found in the Eocene-Oligocene Beds of the Paris Basin and elsewhere, and there are good reasons for assuming that sacoglossans evolved from small monotocardians during the Eocene period. They developed a new way of feeding by slitting open the walls of siphonaceous algae and sucking out the contents. The group radiated by adapting to different species of Siphonales and have spread from warm to temperate seas. Their small size and lack of mobility favoured hermaphroditism. A penis protected the sperm from the harmful effects of the environment which varied considerably in turbidity and salinity as the animals extended their range to top-shore pools, mud-flats, and salt-marshes (Gascoigne, 1974).

3.1.1   Previous Work

Limapontia depressa was first recorded by Alder & Hancock in 1862 and the published description is quoted in full below. Considering that it is well over a century ago, there has been relatively little work done on this fascinating sacoglossan.

> "**Description of a new species of naked Mollusca by Albany Hancock, F.L.S.**
>
> Family **Limapontiidae**
>
> *Limapontia depressa* n. sp. PL. XVII.
>
> *Body*, oblong-ovate, depressed, swelling behind the centre and terminating in blunt point posteriorly, but varying much according to the degree of expansion or contraction; black with minute yellowish-white spot or freckles, not always present, and very inconspicuous. *Head* rounded in front, and slightly angulated at the sides; lateral crests less elevated than in *L. nigra*, with the eyes situated near the centre of a white oblong area at the side of each. Anus

placed in a depression at the posterior extremity of the body. *Foot* yellowish-white, linear, and squared in front.

Length upwards of a quarter of an inch.

A few individuals of the species were obtained, last October, in brackish-water pools at the mouth of Hylton Dene, near Sunderland, associated with *Alderia modesta* on a Conferva (*Vaucheria submarina?*)."

Note: *Limapontia nigra* mentioned in the above excerpt is now known as *Limapontia capitata*, a separate species to *Limapontia depressa*.

Kevan (1934) described *Limapontia depressa* as being a 'chrome yellow colour' and not the black colour previously described by Alder & Hancock (1862). The pale colour allowed the branched hepatic organ of a bright green colour to be clearly visible. A pale area around the eye accentuated its location. When the body was both contracted and extended the green colour allowed effective camouflage amongst the algae. On this basis Kevan (1934) suggested that there was more than one variety of *Limapontia depressa* and proposed the name *pellucida* for this variety.

From his own investigations on *Limapontia depressa*, Quick (1950) observed slugs from 4mm to 6mm long, a black upper body except for the pearshaped white areas on the sides of the head containing the conspicuous round black eyes. Underneath, the grey translucent sole allows the reproductive organs with the yellow follicles of the ovotestis to be seen dimly. The sides of the head are slightly lobed, the body widens from the neck and then narrows again and ends in a blunt extremity beyond which the rounded end of the tail is just visible. The foot is as wide as the body in front then narrows and runs with parallel sides to the blunt tail. The animal crawls by thrusting the front of the body and drawing up the rear, locomotory waves were not observed. Quick (1950) also observed *Limapontia depressa* var. *pellucida*, his description being similar to that of Kevan (1934). Following this work Gascoigne (1978) proposed that *Limapontia depressa* be considered a polytypic species with three subspecies (Fig. 3.1a, b, c), the dominant colour of the animals due to a melanin which is deposited in granules at the base of the epithelial cells. It is possible that the kind of melanin found depends on the species of algae on which the animal feeds (Gascoigne, 1978).

Limapontia depressa depressa which is the estuarine form, possesses melanic granules which are numerous and consequently the animals appear black in colour. *Limapontia depressa olivaria nov.* is dark olive in colour. This form produces a brown melanin and the deposition of the granules is variable. The third subspecies is *Limapontia depressa pellucida*. There are few melanic granules to be found in the green/yellow form. The yellow colour appears to be a fat soluble compound whilst the green hue is probably due to chloroplasts stored in the gut.

The surface of the body is devoid of gills or cerata and has no visible respiratory modification. The renal organ, if visible, may appear opaque (Gascoigne, 1956). The renal opening is to the left of the rectum, anterior to and distant from the anus (Fig. 3.1c).
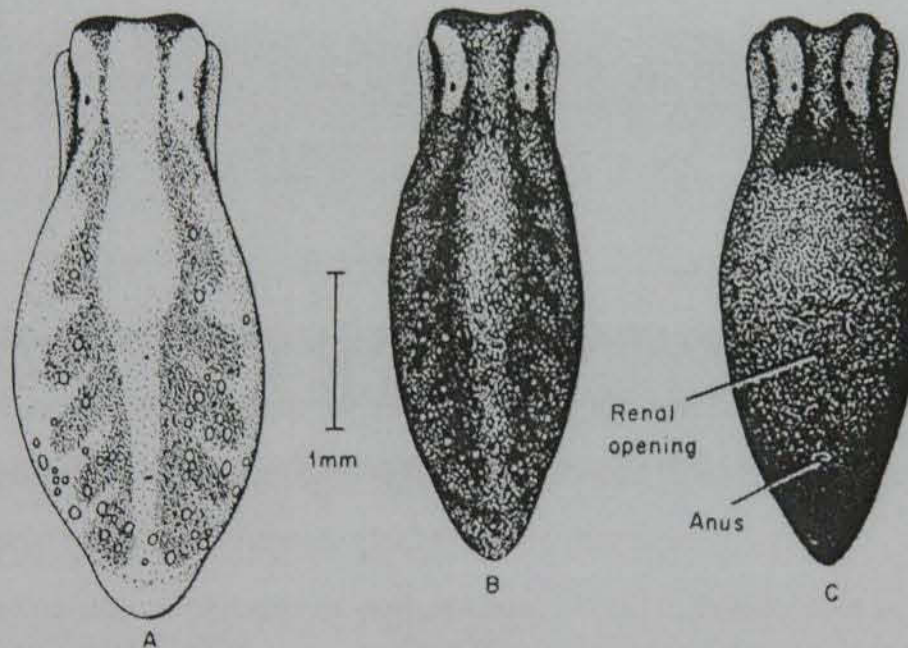
Figure 3.1 Varieties of *Limapontia depressa*: a) *Limapontia depressa pellucida*; b) *Limapontia depressa olivaria*; c) *Limapontia depressa depressa*, this figure also shows the location of the renal opening in relation to the anus (Thompson & Brown, 1976).

3.2 Taxonomy

Phylum	>>>	Mollusca
Class	>>>	Gastropoda
Subclass	>>>	Opisthobranchia
Order	>>>	Sacoglossa
Suborder	>>>	Plakobranchea
Superfamily	>>>	Limapontioidea
Family	>>>	Limapontiidae
Genus	>>>	*Limapontia*

Three species of *Limapontia* exist; *Limapontia depressa* (which is the focus of the present study) *Limapontia capitata* and *Limapontia senestra*.

3.3 Habitat

Since Alder & Hancock (1862) found *L. depressa* in brackish-water pools, habitat descriptions have not greatly varied. Kevan (1934, 1939) described the salt-marsh locations in which he found *L. depressa* and remarked that 'the marsh is only covered by the sea at high spring tides'. Pelseneer (1934) stated that from his study *L. depressa* was living in the same natural conditions at each station; brackish pools more or less isolated from the sea.

L. depressa is a characteristic inhabitant of British saltmarshes, as well as those of the European continent, rarely to be found in pools, but usually on adjacent damp mud (Thompson & Brown, 1976). In general, *Limapontia* occurs only in the N.E. Atlantic, including the Mediterranean and the Baltic, an unconfirmed report exists from the east coast of North America (Jensen, 1997). The habitat in which *L. depressa* occurred during the course of this study has been discussed in detail previously. Figure 3.2 shows the distribution of *Limapontia depressa* around Ireland whilst Table 3.1 holds the descriptive records of these locations.
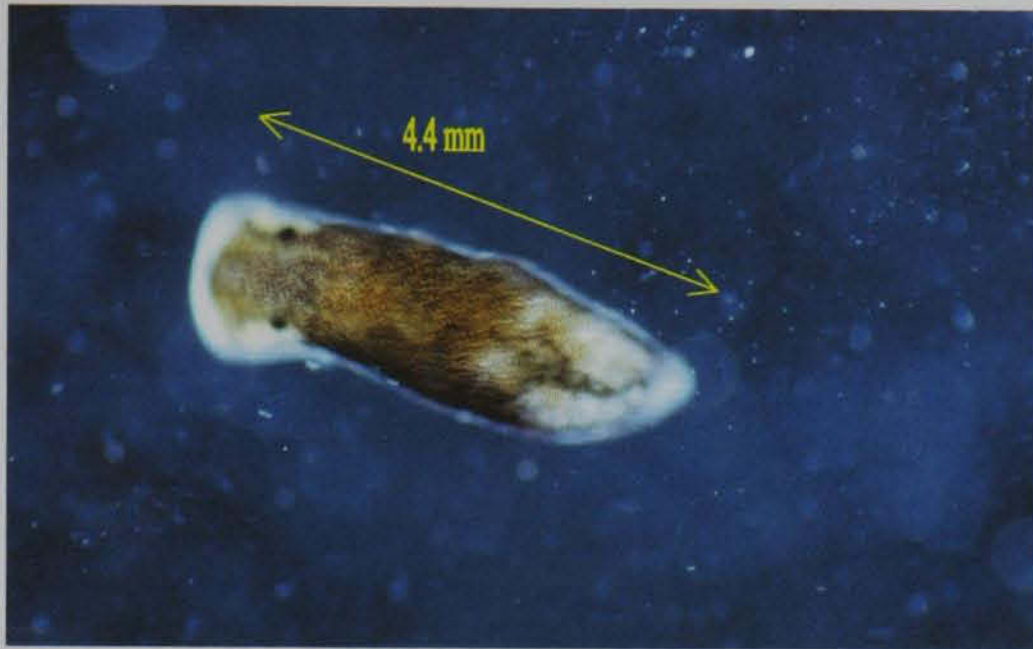
Plate 3.1 *Limapontia depressa* as found at North Bull Island, Dublin Bay.
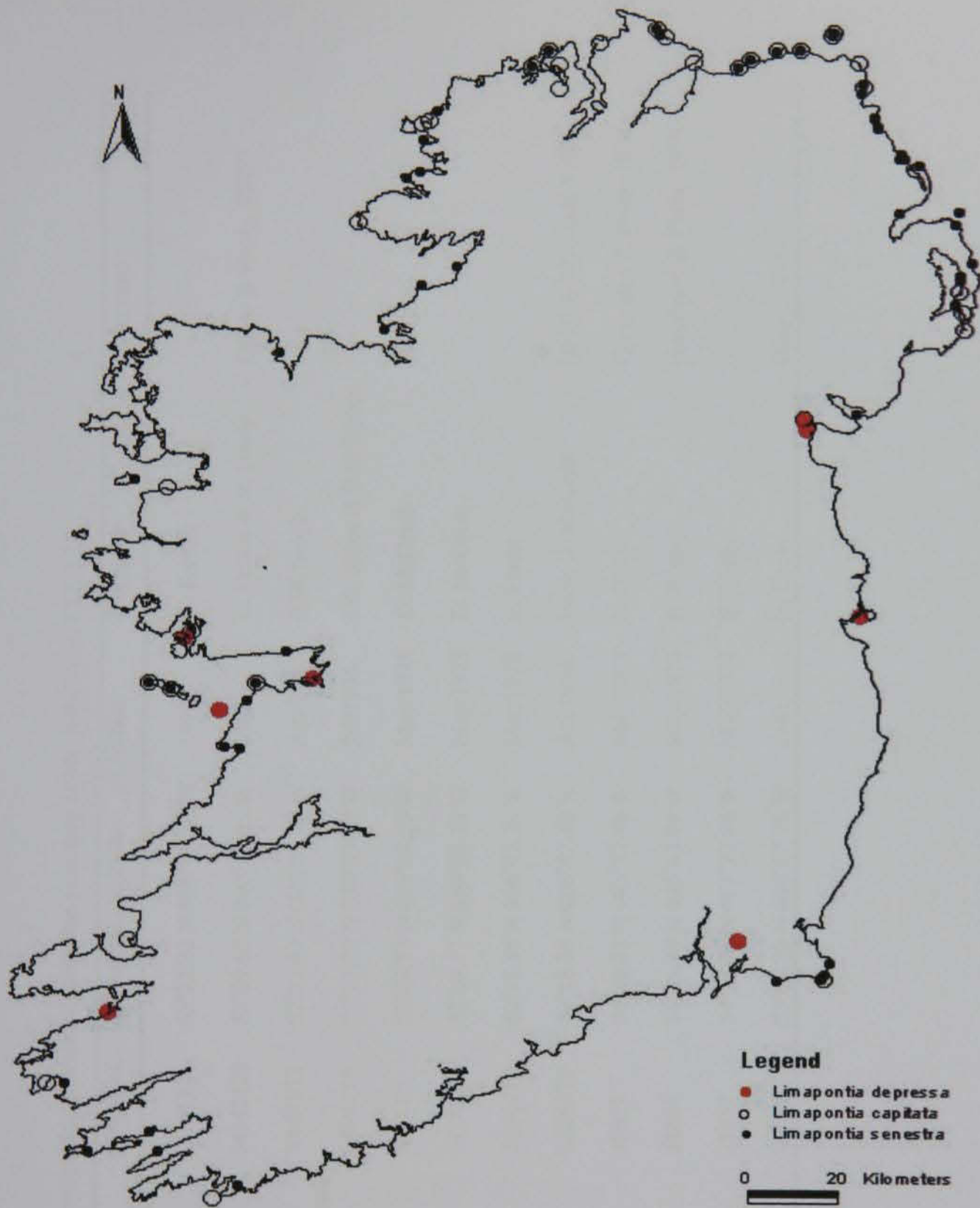
Figure 3.2 Distribution of *Limapontia depressa* around Ireland, the distribution of *Limapontia capitata* and *Limapontia senestra* are included for comparison.

Table 3.1 Descriptive records of *Limapontia depressa* distribution (courtesy of Ms. Julia Nunn, CEDAR).

Site	Grid Ref.	Latitude/Longitude	Date	Recorder	Reference
North Bull, Dublin, Ireland	O244371	53°22.20 N 006°07.75 W	1999	N. Forrest	
Bridge Lough, Galway, Ireland	M342128	53°09.69 N 008°59.05 W	1996	G. Oliver & B. Healy	Oliver & Healy, 1998
Rossbehy salt marsh, Kerry, Ireland	V647913	52°03.40 N 009°58.40 W	Apr/1992	S.M. Smith	
Lettermore Island bridge, Connemara, Galway, Ireland	L896275	53°17.20 N 009°39.30 W	Jul/1986	J.D. Nunn & B.E. Picton	
Carrickadda, Finavarra, Clare, Ireland	M2412	53°09.17 N 009°08.19 W	May/1978	D. McGrath	
Carrickadda, Finavarra, Clare, Ireland	M2412	53°09.17 N 009°08.19 W	May/1978	D. McGrath	
Bannow Island saltmarsh, Wexford, Ireland	S826179	52°18.36 N 006°47.30 W	Mar/1977	E. Platts	
Bannow Island saltmarsh, Wexford, Ireland	S826179	52°18.36 N 006°47.30 W	Jun/1976	Healy & McGrath	Healy & McGrath, 1998
Ardkeen, Strangford Lough, Down, Northern Ireland	J5957	54°26.21 N 005°32.88 W	May/1976	E. Platts	Gascoigne & Platts, 1974
Larne Lough, Antrim, Northern Ireland	J4694	54°46.38 N 005°43.79 W	May/1976	E. Platts	Gascoigne & Platts, 1974
Ardkeen, Strangford Lough, Down, Northern Ireland	J5957	54°26.21 N 005°32.88 W	May/1974	E. Platts	
North Bull, Dublin, Ireland	O244371	53°22.20 N 006°07.75 W	1961	B. Healy	Healy, 1975

3.4 Food and Feeding

In the mouth the number of the teeth is reduced to a row of single teeth, forming a longitudinal series, about a dozen teeth long. This uniseriate radula (Fig. 3.5) is bent in a < shape over the buccal mass (Gascoigne, 1956). The lower limb of the ribbon ends in an ascus, where *L. depressa* retains all its teeth. The buccal mass, a barrel-shaped, muscular pharynx, links the mouth to the oesophagus which is described as being ciliated and glandular. The oesophagus in turn passes to the stomach which receives the slightly branched digestive glands (Fretter, 1941). In *Limapontia depressa* the rectum is long and the anus is subterminal. The backward movement of the anus may be correlated with the fact that *L. depressa* spends considerable time on land where ejection of the faeces from a mid-dorsal position might foul the surface (Gascoigne, 1956) (Fig. 3.3).
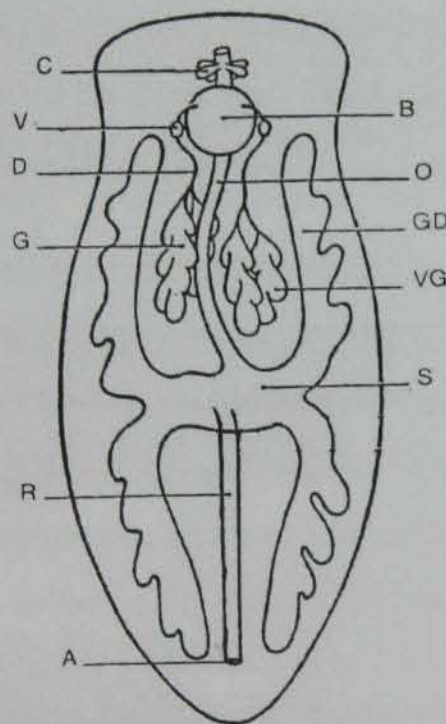
Figure 3.3 Digestive system of *Limapontia depressa*: A, anus; B, buccal mass; C, buccal gland cells; D, salivary duct; G, left dorsal salivary gland; GD, right anterior gut diverticulum; O, oesophagus; R, rectum; V, left salivary vesicle; VG, right ventral salivary gland; S, stomach (adapted from Gascoigne, 1956).

The importance of the relationship between radular anatomy and the structure of food items was pointed out by Macnae (1954) and further stressed by Gascoigne and Sartory (1974). The radula of *Limapontia depressa* (Fig. 3.4) has been described as being

"smooth and sabot-shaped" and presumably represents the highest evolutionary stage of feeding physiology (Jensen, 1980a).
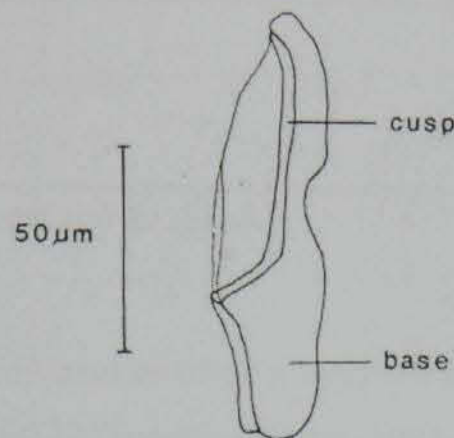
Figure 3.4 The 'smooth sabot-shaped radula' of *Limapontia depressa.*

In general, members of the Sacoglossa feed on algal cell sap (Macnae, 1954). More specifically, *Limapontia depressa* has been described in many instances as a herbivorous, suctorial feeder (Jensen, 1980a, 1981a, 1983a).

Thallus morphology of the food plants is very important in food preference (Jensen 1981b, 1983a). There is a distinct correlation between filament diameter and foot width of the sacoglossan predator in species feeding on filamentous algae (Jensen, 1981b). Apparently structure and chemical composition of the cell wall is the most important factor determining diet width in sacoglossans, and very few species include algae with more than one type of cell wall structure in their diets (Jensen, 1993).

Euryphagy is most common in species occurring in temperate regions. This may have evolved because temporal disappearance of food plants in these regions is associated with low light intensity (Jensen, 1994). Following a thorough review of literature, *L. depressa* has been found to feed on *Vaucheria* (Gascoigne, 1956), *Rhizoclonium* (Hartog, 1959), *Cladophora* (Gascoigne, 1978) and *Chaetomorpha* (Jensen, 1994). Observations made by Jensen (1994) are presented in Table 3.2.

Table 3.2 Summary of foraging behaviour in *Limapontia depressa*. There was only one food patch available (Jensen, 1994).

Species	Food	Initial search time (min)	Feeding time (min)	Meal size (cells)
L. depressa	*Chaetomorpha*	30.7 ± 12.5 n = 6	ca.60*	47.2 ± 23.8 n = 6

* Animals were only allowed to feed for one hour

Feeding behaviour at organism-level involves a sequence of behaviours: (1) arousal, (2) orientation, (3) recognition, and (4) handling (Kohn, 1983). Arousal involves distance chemoreception and usually results in increased locomotory activity. Orientation towards food involves chemotaxis but may also involve visual orientation. The result is directional movement. Recognition of food involves contact chemoreception as well as mechanoreception which may lead to indication of preference. Handling includes positioning of the animal on the food, 'grasping' of food and ingestion (Jensen, 1994).

As *L. depressa* feeds on filamentous algae, the 'grasping' method is used when handling its food. The filament is grasped between the oral and pedal lobes, causing the filament to bend at some point which is where the slug applies its mouth. 'Rasping' involves the active piercing of the algal cell by the radular tooth causing some cell contents to squirt into the buccal cavity. The thick muscular walls of the buccal cavity then act as a modified pumping apparatus to suck out the whole contents of the plant cells referred to as the 'sucking' phase.

Limapontia depressa facilitates buccal regurgitation. This involves reversing the flow of algal cytoplasm, returning material which has been sucked into the pharyngeal cavity and anterior oesophagus to the algal siphon. It has been suggested that the algal cytoplasm is mixed with saliva to reduce viscosity and thus facilitate withdrawal of the remaining cytoplasm (Jensen, 1981a). Buccal regurgitation is probably very important in enabling animals to include non-caulerpan food plants in their diet. These algae often have soft filaments which collapse when the cell wall is punctured as well as wounding responses which prevent loss of cytoplasm through punctures (Jensen, 1993). Mixing the cytoplasm

with saliva may prevent these responses and also facilitate suction by inflating a collapsed filament (Jensen, 1994).

'Chloroplast symbiosis' is the peculiar phenomenon by which certain marine molluscs, under natural conditions, continually acquire and retain functional algal chloroplasts within their digestive cells (Williams & Cobb, 1992). The chloroplasts remain intact, both metabolically and structurally for some time while releasing a vast proportion of their photosynthetic materials to be utilised by their animal host.

Hinde & Smith (1974) investigated chloroplast symbiosis in both pale and dark forms of *Limapontia depressa* which are assumed to be *L. depressa pellucida* and *L. depressa depressa* respectively. The results are discussed and the study summarised in Table 3.3.

The "pale" forms of *Limapontia depressa* presented clear testimony of chloroplast symbiosis. The animals had significantly higher rates of ^{14}C fixation in the light than in the dark, and much more ^{14}C was incorporated into glucose in the light. The lack of chlorophyll b in the June collection provides evidence for the appearance of *Vaucheria* chloroplasts. The presence of some chlorophyll b in the April set suggests that either the animals had been feeding to an extent on algae other than *Vaucheria*, or that *Vaucheria* chloroplasts had been digested and some chlorophyll a degraded to chlorophyll b. The chlorophyll contents were lower in the "dark" *L. depressa* than in "pale" forms and some chlorophyll b was continually present. Rates of ^{14}C fixation were not significantly higher in light than in dark. The absence of photosynthesis in "dark" forms could primarily be due to masking of chloroplasts by the animals' dark brown pigment.

However in 1980, Hinde described the relationships as not being true symbioses in that they are short-lived and apparently wholly biased towards the mollusc and suggested the term 'chloroplast farming'. Kleptoplasty increases "starvation tolerance" which is important in areas of low food density (Jensen, 1994).

Table 3.3 Presence and absence of chloroplast symbiosis in *Limapontia depressa* (after Hinde & Smith, 1974).

Species	Month of collection	Days of starvation	Mean wt. per animal (mg)	Chlorophyll content (mg/g animal)	Ratio Chlorophyll a Chlorophyll b	^{14}C fixation (10^6 counts/min/mg animal)	
						Light	Dark
'pale forms'	April	0	5.25	0.155	7.19	10.9	1.95
	June (1)	0	4.9	0.59	(no b)	24.2	2.55
	(2)	14	4.8	0.52	(no b)	2.2	1.3
'dark forms'	April	0	2.82	0.13	14.5	4.6	3.6
	June	0	1.45	0.29	2.7	0.6	3.7

Intermediates of photosynthetic fixation detected by two-dimensional chromatography of ethanol extracts.

3.5 Reproduction

Limapontia depressa is hermaphroditic and fertilisation is by hypodermic impregnation (Gascoigne, 1956). The main features of its reproductive system (Fig. 3.5) are described as follows: a central canal with a fertilisation region; three ducts enter the fertilisation region - the small oviduct, the vagina and the duct of the albumen gland; two ducts leave the exit region - a short receptacle duct and the large oviduct. The vagina opens to the exterior and a coupling style is present. Consequently, *L. depressa* displays triauly, the condition whereby the reproductive system opens to the exterior in three locations, that is , the male opening, the oviducal opening and the vaginal opening (Fig. 3.5). The penial opening is close and posterior to the patch surrounding the right eye. The vaginal opening is present about a third of the way down the right side.

Limapontia depressa has a coupling style that is distinctive of the species (Gascoigne, 1976). A style consists of a slightly curved shaft, which extends beyond the penis and a base that lies below the thick penial skin. Spines on the inner curve of the shaft help to maintain the shaft in position (Fig. 3.6).

Copulation takes place whilst the animals are lying head to tail. Functionally, the reproductive system (Fig. 3.5) can be interpreted as follows (Gascoigne, 1976).

The sperm pass from the ovotestis (FT) into the hermaphrodite duct (HD). They are then stored temporarily in the ampulla (HA). During copulation the sperm are forced forwards along the vas deferens (VD), whilst continually mixing with prostate secretions (PR). The penis (P) is thrust into the vestibule through the vaginal opening (VO) to allow the sperm to be delivered through the style. The sperm are stored along the vagina until fertilisation.

In the meantime, the eggs move from the follicles into the ampulla and through the small oviduct into the fertilisation region of the canal (F). It is here that the eggs are fertilised and then coated with albumen. They then pass out of the exit region (E) into the large oviduct (LO) to be wrapped in a coat of mucus. The eggmass passes out of the *Limapontia* through the oviducal opening (OO).
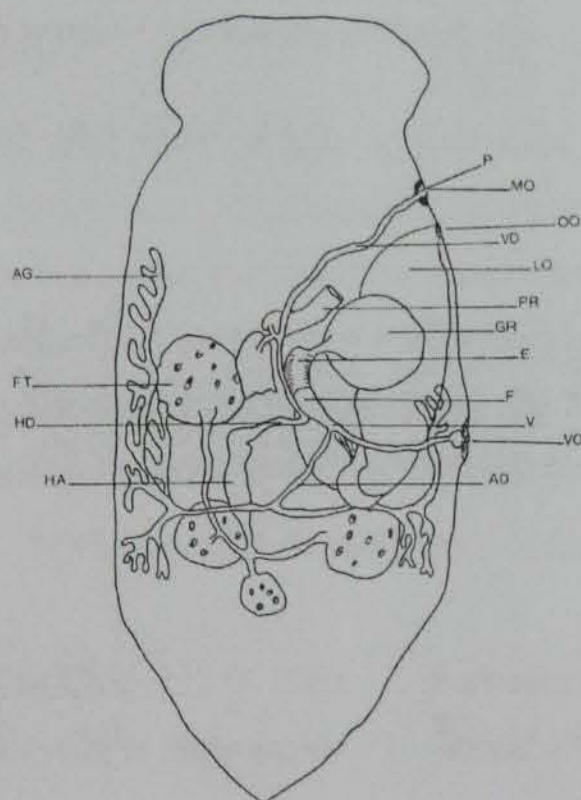
Figure 3.5 Reproductive anatomy of *Limapontia depressa* based on stiligerid reproductive system (adapted from Gascoigne, 1976). Drawing also illustrates the triaulic condition which is characteristic of *Limapontia depressa*. AD, duct of albumen gland; AG, albumen gland; E, exit region of central canal; F, fertilisation region of canal; FT, follicle of ovotestis; GR, genital receptacle; HA, hermaphrodite ampulla; HD, hermaphrodite duct; LO, large oviduct; MO, male opening; P, penis; OO, oviducal opening; PR, prostrate; V, vagina; VD, vas deferens; VO, vaginal opening.
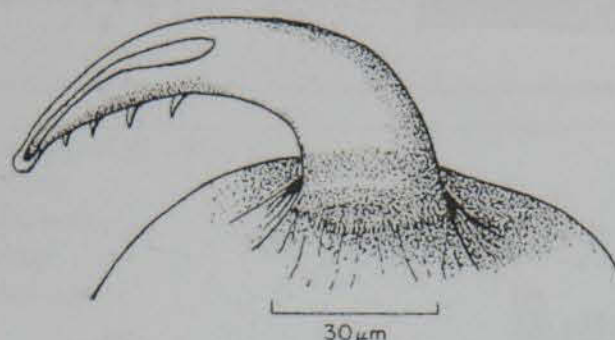
Figure 3.6 The characteristic coupling style of *Limapontia depressa* (after Gascoigne, 1976).

Chia (1971) described the jellylike eggmass as being lamellated, thinner and elastic. The last end of the mass to exit the oviduct is tapered into a fine point in the form of a hook. His studies of the spawn revealed that there was no clear preference as to where the spawn is laid. Spawns were found to be 2 x 5mm in size containing approximately 950 eggs whilst a small spawn - 0.5 x 1mm - yielded just 73 eggs.

Indirect development (a life cycle which includes a larval stage and metamorphosis) is characteristic of *Limapontia depressa*. Planktotrophic larvae are those that obtain at least part of its nutritional needs from either particulate or dissolved exogenous sources (Young, 1999). More specifically, Chia (1971) recorded the planktotrophic development pattern of *L. depressa* and determined that it takes 10 days for *Limapontia depressa* to reach the hatching stage at a temperature of 10 - 14°C (Table 3.4). Hatching time was shortened to 7 days at 19 - 21°C. Essential characteristics of *L. depressa* eggs and capsules
(Table 3.5) were recorded by Chia (1971). Plate 3.2 illustrates what appears to be the veliger stage of *L. depressa* prior to hatching after 14 days at 6°C (found during the course of the present study).

Granular albumen was observed in *Limapontia depressa*, but apparently it has little nutritional value as those eggs without albumen developed equally well. However, the albumen must still play some role as it disappears prior to hatching (Chia, 1971). Pechenik (1999) discussed the advantages of planktonic development and concluded that there is no compelling evidence to suggest that the egg capsule and egg masses protect the embryo from predation. Further research however, may reveal that encapsulated embryos might be spared some pollutant stress even though capsules and masses of a few species have been found to be permeable to water, salts and small organic molecules.

34

Table 3.4 Chronology of development of *Limapontia depressa* at the temperature of 10 - 14°C, (after Chia, 1971).

Developmental Stage	Time
Freshly spawned eggs with intact germinal vesicle.	0
Formation of first polar body	6 hours
Formation of second polar body	9 hours
Completion of first cleavage	12 hours
Completion of second cleavage	15 hours
Young blastula	2 days
Blastula	2 days
Gastrula with open blastopore	3 days
Young veliger with velum rudiments	4 days
Veliger, moving by rotating	4 days
Veliger with well developed shell and gut	5 days
Veliger with well developed ciliated foot and operculum; moving by rocking back and forth	6 days
Veliger with retractable velum	7 days
Hatching; hatched veliger 120µm long	8 days
Hatching completed from one egg mass	10 days

Table 3.5 *Limapontia depressa* egg and capsule characteristics. Albumen: + indicates presence. Developmental pattern: 1 indicates planktotrophic development (after Chia, 1971).

Mean egg diameter (µm)	Mean capsule size (µm)	Capsule volume (mm³)	Albumen	Development Pattern
80	120	0.00090	+	1
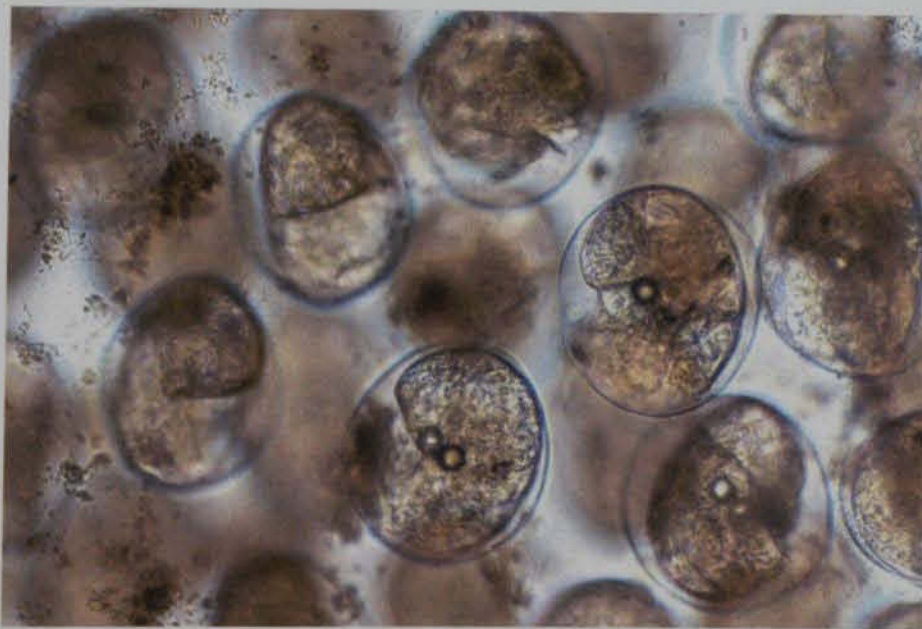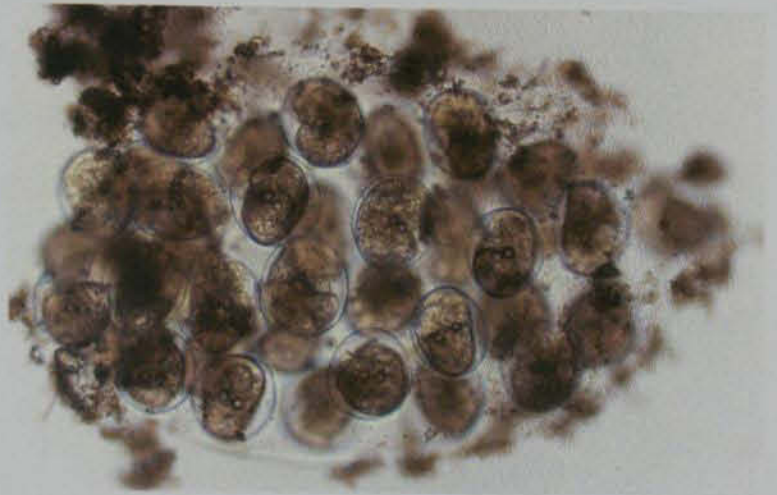
Plate 3.2 An illustration of what appears to be the veliger stage of *Limapontia depressa* following 14 days at 6°C, recorded during the present study.

3.6 Study Aims

Unfortunately due to major problems with regular quantitative sampling, there is little known about the ecology and function of sacoglossans in marine ecosystems. The fact that they exhibit specialisation on the one hand while displaying broad adaptations on the other, makes them unusual among marine animals and warrants investigations that could provide information which would be of interest in marine ecological studies (Clark and DeFreese, 1987). Extrapolations from different geographic regions are not necessarily reliable due to factors such as tidal patterns, water temperature, predators and algal host species. This is particularly true of *Limapontia depressa*. They are unusual animals, possessing several unique characteristics, all of which are previously described. The interest in this sacoglossan was warranted by the fact that it has not been previously studied in Ireland and the fact that such an inconspicuous animal may have an extremely interesting existence. Consequently, the primary focus of this study was to record the presence of *Limapontia depressa* on the saltmarsh at North Bull Island and to investigate certain aspects of its life history.

The main aims are as follows:

- to describe the occurrence of *Limapontia depressa* at North Bull Island, Dublin Bay.

- to record its population dynamics under the conditions imposed by the habitat and climate of the salt marsh.

- to investigate the extent to which *Limapontia depressa* controls the algal mats in the north lagoon.

- to measure the biomass of *Limapontia depressa* in order to provide an indication of the strength of its presence within the ecosystem.

- to investigate the respiration component of the energy budget for the sacoglossan.

Chapter 4

Methods

4.1 Introduction

This chapter reviews the sampling program in its entirety. The determination and location of sampling sites is discussed in order to fully identify the study area of the present investigation. Basic field sampling procedures are outlined. The methods used in laboratory work are described in detail. Practical work for the study commenced in January 1997 and ceased in September 1999.

4.2 Study Sites

The sites chosen for the present study are located in the north lagoon, North Bull Island (Plate 4.1 & 4.2), for which a general description has been provided in the previous chapter. The salt marsh area on the lagoon is within the nature reserve, the status of which has been previously defined.

The sites were marked with stakes at the primary stages of investigation. Access to the sites was gained from the grounds of the golf club as the sites to the east and west are almost equal distances from the clubhouse.

Sites A1 and A2 are to the northeast of the clubhouse while B1 and B2 are 800 metres southwest on the marsh. Sites A1 and B1 are on the upper marsh while A2 and B2 are approximately 100m lower down on the marsh.

North Bull Lagoon

St. Anne's Golf Club
Clubhouse

Dollymount Strand

A2

A1

N

Plate 4.1 Sampling locations A1 & A2 (Image courtesy of The Map & Data Centre, Merrion Square, Dublin 2).

N

North Bull Lagoon

B2

B1

St. Anne's Golf Club
Clubhouse

Dollymount Strand

Plate 4.2 Sampling locations B1 & B2 (Image courtesy of The Map & Data Centre, Merrion Square, Dublin 2).

Two morphological features are seen scattered over the salt marsh. Perhaps the most obvious occurrence across the plain is that of pans, generally a few metres in diameter. These are shallow (10cm), steep sided, sub-circular depressions floored with bare mud (Harris, 1977) (Plate 4.3). Also present are a series of natural drainage creeks which meander generally north-westwards into the lagoons. Slight elevations of the creek beds at the marsh edge prevent them from draining completely. The reduced salinity of the creek water at low tide may be due to additions of rainwater, surface run-off, with the possibility of fresh water trapped from the non-saline ground water table. The marsh is adjacent to the grounds of St. Anne's Golf Club which is bordered by the dunes on the other side. It was noted that the transitional sites between the marsh and the mudflat, A2 and B2, frequently showed signs of anoxic conditions.

Plate 4.3 The pans frequently found on the salt marsh at North Bull Island.

The sites chosen were in close proximity to those used for the Dublin Bay Water Quality Management Plan (DBWQMP) and other studies and therefore water and sediment chemistry, sedimentology, geomorphology and flora and fauna distributions have been investigated and described previously (Harris, 1977; Healy, 1975; Jeffrey, 1977; Pitkin, 1977; Maguire, 1990; Jeffrey *et al.*, 1992; Jennings, 1996).

4.3 Sampling

Samples were taken regularly over spring and neap tidal cycles on a fortnightly basis, occasionally weekly. All sites were visited at low tide. Appendix 1 consists of the general sampling diary.

Samples were taken using PVC handheld corers, 5cm in diameter, to a depth of around 15cm. The cores were taken randomly within 1m of the site stakes.

The temperature (°C) and salinity of the water (when present) at the core location were taken and recorded at each sampling visit using a microprocessor conductivity meter, model WTW LF196. As water was not always present at the sites, further data was sourced from the ESB, Ringsend.

The cores were placed in polythene bags, labelled appropriately and transported back to the laboratory with minimal disturbance to surface layer sediments.

It should be noted that the presence or absence of macroalgae was recorded on each sampling occasion but the actual mass was not measured.

In the laboratory the animals were removed from the sediment after a count had taken place and both animals and sediment were prepared for analysis.

4.4 Sediment analysis

4.4.1 Sample Preparation

Approximately 7.5g of wet sediment was removed from the top 2cm layer of the core and put aside for pigment analysis of microphytobenthos. The bulk of plant material such as stalks and roots were removed from the sample so as not to interfere with actual sediment chlorophyll measurements. Another 20g of wet sediment was taken from the core for moisture content and loss-on-ignition measurements.

4.4.2 Sediment Moisture Content

The subsample from each site was oven dried to a constant weight at 100°C for 24 hours. Samples were cooled in a desiccator and weighed. Percentage moisture content was calculated from loss in weight.

The dried samples were then ground into a fine powder and placed in a desiccator for loss-on-ignition analysis.

4.4.3 Sediment Organic Matter

The organic content of the sediment was determined by the loss-on-ignition (LOI) method. The method is termed approximate as some structural water is driven off from clay minerals at these temperatures and is included in the overall weight loss.

Approximately 1g of dried sediment was placed in a pre-weighed dry crucible. The sediment was combusted in a furnace, gradually reaching 550°C over an hour and then allowed to remain at that temperature for 2 hours (Allen, 1989). The samples were cooled in a desiccator and reweighed.

The loss on ignition was then calculated using the formula:

where weight loss of the sample = (Wt. of crucible + dry sample) - (Wt. of crucible + ashed sample) (g)

% LOI   =   Weight loss of sample (g) x 100

Oven dry weight of sample (g)

4.4.4 Pigment Analysis

Plant pigments mainly consist of chlorophyll, carotenoids and flavonoids. Chlorophyll is a green porphyrin compound containing magnesium as its central atom and is present in photosynthetic tissues of higher plants. It is generally understood that essentially all native sedimentary chlorophyll is degraded to phaeopigments (Swain, 1985). The major degradation products of sedimentary chlorophyll are the phaeopigments, phaeophytin and phaeophoride. Pigment analysis enables estimation of the content of microphytobenthos in the sediment at the time of sampling.

Difficulties such as incomplete extraction, evaporation of the solvent, acidification, formation of degraded pigments by enzyme action and incomplete recovery of the solvent during clarification of the extract must be considered as important sources of error in the extraction of chlorophyll. The pigment content of wet sediment allowed to stand open to air at room temperature has been observed to decrease notably (Fogg & Belcher, 1961), although Fox (1944) found no loss of absorbance on exposure of sediments to light. Vallentyne (1955) found that there was no tangible difference in pigments from cores which had been stored for over a year, and those that had been extracted from cores within 48 hours of being taken. The main source of error in this analysis would arise from the presence and decay of plant and detrital material in the core area. When this was the case, all obvious plant material was removed.

Pigments were extracted from a subsample of mud (approximately 7.5g) in aqueous 90% acetone. Chlorophyll and carotenoids were extracted by shaking for 30 minutes and centrifuging for 10 minutes at 3000rpm with three consecutive 25ml measures of 90% acetone (Sanger & Gorham, 1972a). After each acetone extraction the supernatant was

44

pipetted off. The absorbance of the extract was measured at 665nm and 750nm (to correct for suspended material) using a 1cm cuvette on a Schimadzu UV-visible 1601 spectrophotometer. The sample was acidified using 2 drops of 1% HCl and the cuvette shaken. The absorbance reading was repeated at 665nm and 750nm.

Chlorophyll content was calculated using Lorenzon's (1967) equations so that

$$\text{Chl a } (\mu g \ g^{-1}) \quad = \quad \frac{26.7 \ (665b - 665a) \times 75}{\text{Sed. Wt. (g)} \times l \ (cm)}$$

where 665b is absorbance at 665nm minus absorbance at 750nm before acidification and 665a is absorbance at 665nm minus absorbance at 750nm after acidification.

4.5 *Limapontia depressa* Analysis

4.5.1 Preparation

In the laboratory, the animals were removed from the sediment and remained in similar salinity seawater until analysis. Animal length was measured using an eyepiece micrometer. Trowbridge (1993) recommended using wet weight as a measurement rather than length, however, the animals were too small to provide a reliable weight measurement. Representative samples were preserved in 12% neutral formalin.

4.5.2 Biomass

The "wet oxidation" method for organic carbon analysis was used to measure biomass. This method is an adapted method of one devised by Russell-Hunter *et al.* (1968). It involves the determination of oxidizable carbon by "wet-ashing" using a mixture of potassium dichromate and concentrated sulphuric acid. An increase of organic carbon content is measured using colourimetry that is, the change in colour of the dichromate solution from yellow to clear, after it has been reduced by the organic matter.

The oxidant standard was prepared using 0.817g of potassium dichromate in 20mls of distilled H_2O and brought to 1000ml volume with H_2SO_4. Glucose standard consisted of 7.5g of glucose made up to 100mls, then diluted 1 in 1000 to produce 30 μg ml^{-1}. This glucose solution was used to prepare 'known carbon' standards of 30μg C, 60μg C, 90μg C and 120μg C in 50ml conical flasks. These would result from adding the glucose standard and distilled water in the proportions 1:3, 2:2, 3:1 and 4:0 respectively. Some heat is generated when mixing the solutions so the flasks should be recapped as quickly as possible. The blank contained 4mls of distilled water.

The animals were placed in the digestion tubes. Oxidant was added using an automatic burette which delivers 10mls into the tubes containing the animals, the 'known carbons' and the blanks. Funnels were placed in each tube to allow release of pressure. The tubes were then placed on the digestion block at 105°C for 60 min. After digestion, the tubes were allowed to cool, the dichromate mixture carefully transferred to conical flasks and made up to volume with distilled water. Once cooled, the samples are ready for spectrophotometry. Samples were analysed using the Schimadzu UV-visible 1601 spectrophotometer at 440nm.

4.5.3   Respiration

The method used follows one previously used by McMahon and Russell-Hunter (1977, 1978) and McMahon and Wilson (1981) for small marine gastropods.

Oxygen uptake rates were measured using the YSI model 53 Biological Oxygen Monitor (Fig. 4.1). The essential components of the system are the electronic unit and the YSI 5331 oxygen probe. The probe is a specially designed Clark-type, silver-platinum, polarographic electrode.

The electrode and plunger were placed into glass respiration chambers which contained 4 mls of water. This volume of water was ascertained through trial and error as being the minimum volume required. The water used was fresh millipore filtered (0.2μm) seawater with a salinity value of approximately 25. The electrode was first calibrated in a control chamber and then transferred to the test chambers that had been continuously aerated. The

chambers were kept at a constant temperature (10°C or 20°C) by the water circulating around them from a refrigerated fixed temperature circulator. The muslin 500 μm mesh platform on which the animals rested was placed clear of the magnetic stirrer (Fig. 4.2). Difficulties were encountered in transferring the animals into the chambers whilst ensuring that the exact volume of water was maintained and that all the animals were alive and active after transferral. To counteract this the animals were placed on waxed paper and all excess water removed, they were then transferred using a pipette and the water from the chambers. The chambers contained 30 animals on each occasion.

The oxygen consumption was monitored for a period of 240 mins. The oxygen monitor was attached to a chart recorder so that the linearity of the oxygen consumption could be checked.

The data was entered onto a spreadsheet and was calculated using a series of equations to arrive at a value for respiration in μl O_2 / animal / hour.

4.6 Exclusion Work

It was decided to carry out exclusion experiments at all sites over a six month period during the latter half of the project. PVC cores 30cm in diameter and 60cm long were placed within a metre of each of the stakes. Each corer had holes drilled at regular intervals on its circumference in order to allow the tide to enter the area as normal. A fine mesh was placed over the corer and secured with a PVC brace in order to prevent the birds from feeding in the core at low tide. On each sampling occasion, these areas were investigated and cores taken (Plate 4.4).
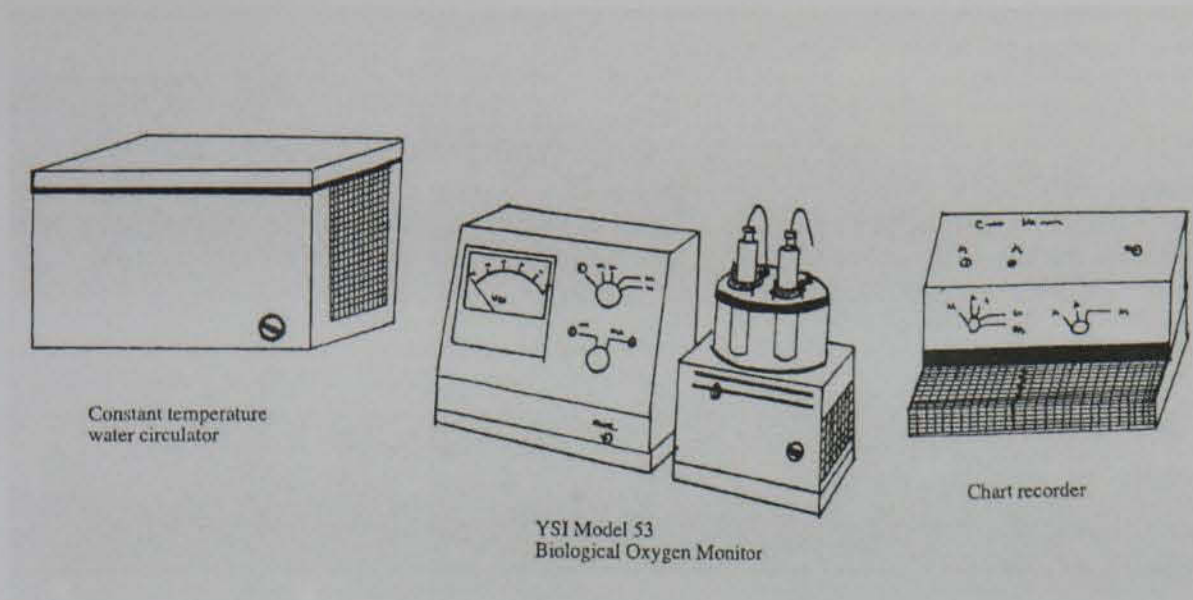
Figure 4.1 The YSI Biological Oxygen Monitor apparatus used to measure respiration.
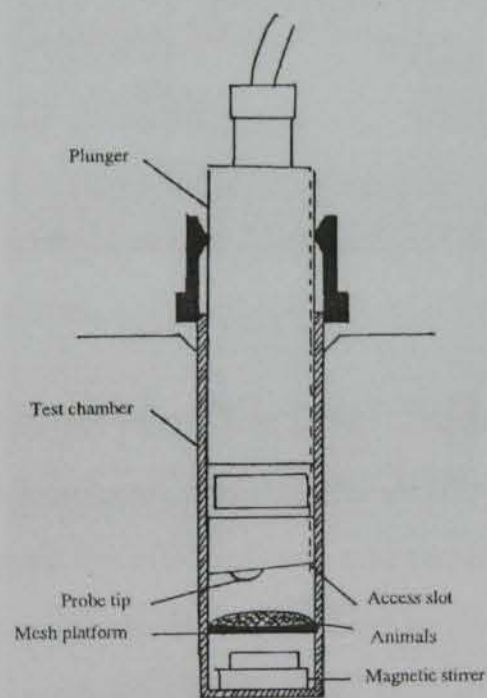
Figure 4.2 Schematic of test chamber showing the position of the animals and probe.

Plate 4.4 Exclusion cores at sampling sites B1 and B2.

4.7   Statistical Analysis

The results were entered onto spreadsheets in Microsoft Excel to be formatted. All figures were created within Microsoft Excel.

All statistical analysis was carried out using Data Desk. The formatted data was analysed for basic summary statistics such as mean, median, etc. A two-way analysis of variance (ANOVA) was used to investigate the effect of time and site on each environmental variable. This was followed by a Scheffe Post-Hoc Test to investigate what difference there was, if any, between sites.

Spearman Rank Correlations were used to determine the effect of the various environmental parameters on animal densities, and lagging was used to investigate time delay effects.

(ANOVA) was used to investigate the effect of time and site on each environmental variable. This was followed by a Scheffe Post-Hoc Test to investigate what difference there was, if any, between sites.

Spearman Rank Correlations were used to determine the effect of the various environmental parameters on animal densities, and lagging was used to investigate time delay effects.

Chapter 5

Results

5.1 Environmental Parameters

5.1.1 Water Temperature

The water temperature data recorded throughout the study is presented in Figure 5.1. The ESB temperature data recorded at Ringsend is included and acts as a control. Water temperature was only recorded when water was present at the site when the sample was being taken, therefore, there were occasions when no measurement was made. This was the case at site A1 during the summer months, whilst measurements were also scarce at sites A2 and B1 between April and September.

Overall, the temperature data closely followed the pattern of the ESB control figures. It must be noted, however, that ESB temperatures are recorded in deep waters in Dublin Bay. On the other hand, measurements taken over the course of this study were from an extremely shallow water column for the most part, such that the temperature of the water would be easily affected by environmental parameters, such as sunlight or wind speed.

An ANOVA test was applied to the data. A strong seasonal trend is evident from the data. All sites recorded values within a narrow range. Highest temperatures were recorded between April and September each year as would be expected. The analysis of variance tests applied to the data supported the seasonal trend ($F_{57,144} = 181.4$, $p \leq 0.0001$). Extremely high temperatures were recorded during June and July of the first year at site B2 that are not supported by ESB data. It is not possible to identify any specific cause for this occurrence. The lowest temperature of $8.2°C$ was recorded at site B2 during January 1998, whilst the maximum temperature, $28°C$ was also recorded at site B2 in June 1997. There appeared to be no significant difference between sites generally ($F_{3,268} = 2.3355$, $p = .0764$), however, to further investigate the variability between sites, Scheffe Post-Hoc Tests (Table 5.1) were carried out and the output fully supports the overall conclusion from the ANOVA.

Table 5.1 Scheffe Post-Hoc Test to test for variability in water temperature (°C) between sites.

Sites	Difference	Probability
A2 – A1	-0.251	0.183
B1 – A1	-0.845	0.908
B1 – A2	0.166	0.528
B2 – A1	-0.247	0.194
B2 – A2	0.004	0.999
B2 – B1	-0.162	0.547
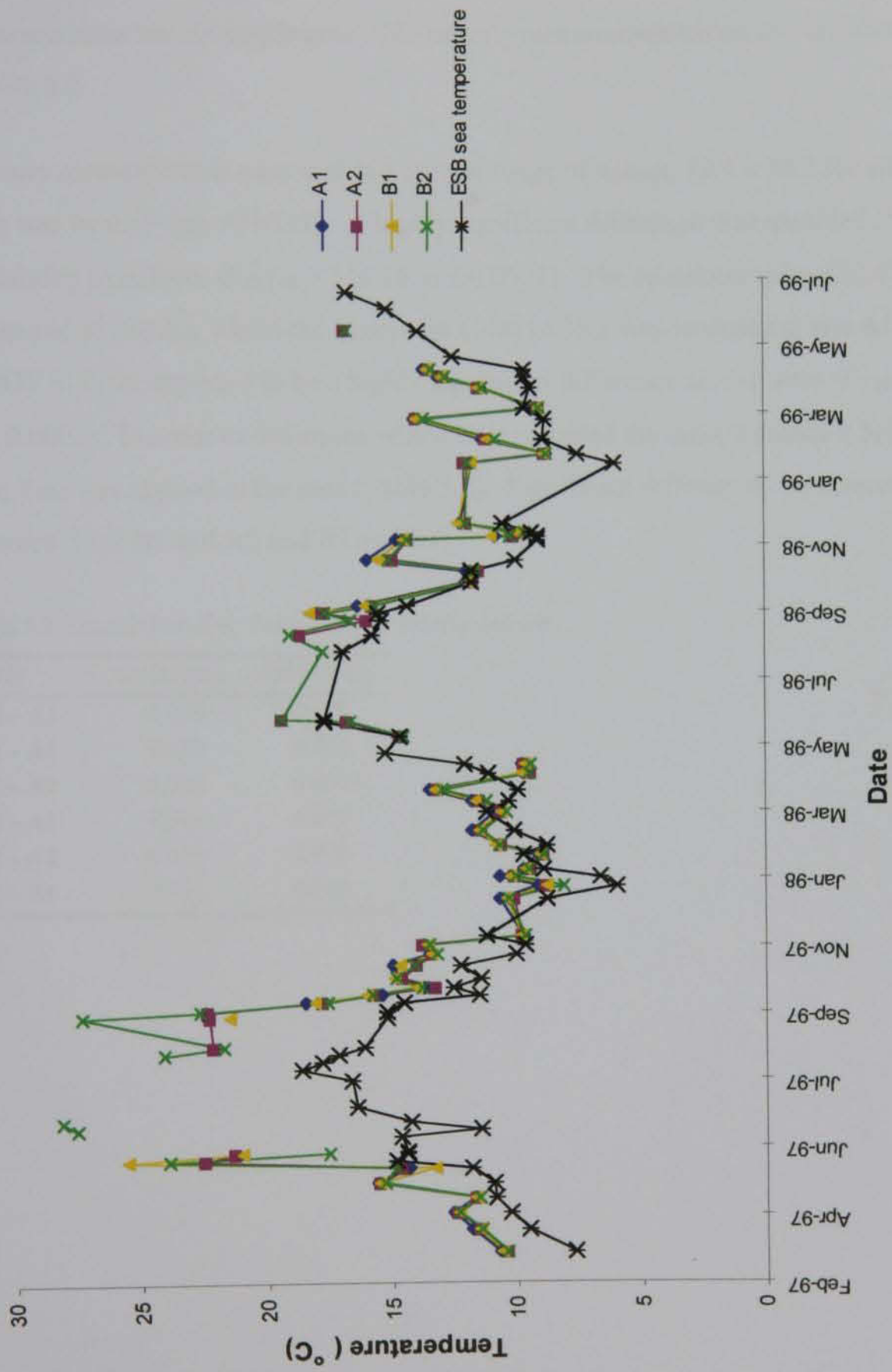
Figure 5.1 Water temperatures (°C) from both field work and ESB data sets.

5.1.2 Salinity

Salinity measurements were also taken throughout the course of the study, all values being recorded at low tide. However, as water was not always present at the sites, salinity measurements are not continuous. The salinity measurements recorded are presented in Figure 5.2.

Salinity measurements were within a narrow range of values, 22.4 – 38.2 for all sites. The data was treated with ANOVA. A highly significant difference was recorded for the variability over time, ($F_{57,144} = 115.16$, $p \leq 0.0001$). The minimum value (22.4) was measured at site A2, whilst the maximum value of 38.2 was recorded at site A1. From the ANOVA, there appeared to be a highly significant difference among sites ($F_{3,268} = 8.6956$, $p \leq 0.0001$). In order to determine which sites recorded the most variance a Scheffe Post-Hoc Test was applied to the data (Table 5.2). Significant differences were recorded between Sites B1 and A2 and B2 and B1.

Table 5.2 Scheffe Post-Hoc Test results for salinity and site.

Sites	Difference	Probability
A2 – A1	0.419	0.015
B1 – A1	-0.139	0.765
B1 – A2	-0.558	0.0003
B2 – A1	0.341	0.072
B2 – A2	-0.078	0.933
B2 – B1	0.481	0.003
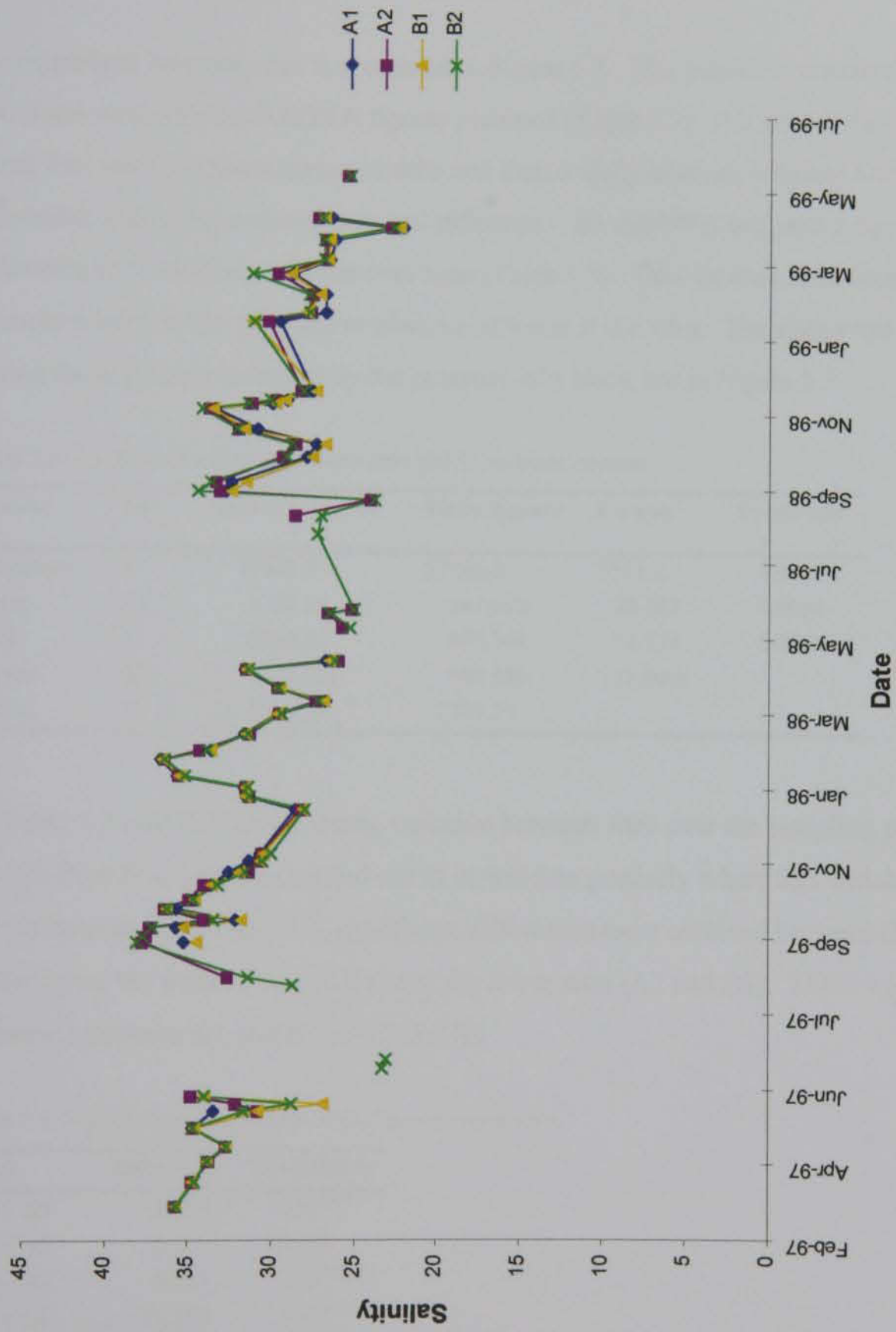
Figure 5.2 Salinity measurements recorded throughout the course of the study at individual sites.

5.1.3 Sediment Moisture Content

The % moisture content values are reported on a monthly basis between April 1997 and June 1998. The raw data is given in Appendix 2.

A comparison between sites is presented in Figure 5.3. The graphic representation correlates well with the ANOVA figures obtained (Table 5.3). All sites follow a similar trend, low values in the summer months and then a sharp increase between October and November indicating a strong seasonal influence – the ANOVA suggests a significant difference in % moisture content over time (Table 5.3). This increase and decrease may be strongly related to the presence or absence of water at the sites. The sites were mostly dry during those periods indicated by the presence of a black bar in Figure 5.3.

Table 5.3 Analysis of variance between time and % moisture content.

Source	DF	Sum of Squares	Mean Square	F-ratio	Probability
Constant	1	87586.5	87586.5	7323.2	0.0001
Date	14	4782.43	341.602	28.562	0.0001
Site	3	2086.03	695.344	58.138	0.0001
Error	42	502.326	502.326	11.9601	
Total	59	7370.79	7370.79		

As Table 5.3 also indicates a strong variation between sites over the sampling period a Scheffe Post-Hoc Test was carried out to investigate precisely where this variability lay. As can be seen from Table 5.4, significant differences were obtained between those sites higher up on the marsh (A1 and B1) and the lower sites (A2 and B2). There was no difference between A1 and B1 or A2 and B2.

Table 5.4 Scheffe Post-Hoc results indicating site variability.

Sites	Difference	Probability
A2 – A1	9.999	1.93^{E-08}
B1 – A1	0.55	0.979
B1 – A2	-9.449	7.59^{E-08}
B2 – A1	13.575	3.98^{E-12}
B2 – A2	3.575	0.06
B2 – B1	13.025	1.39^{E-11}
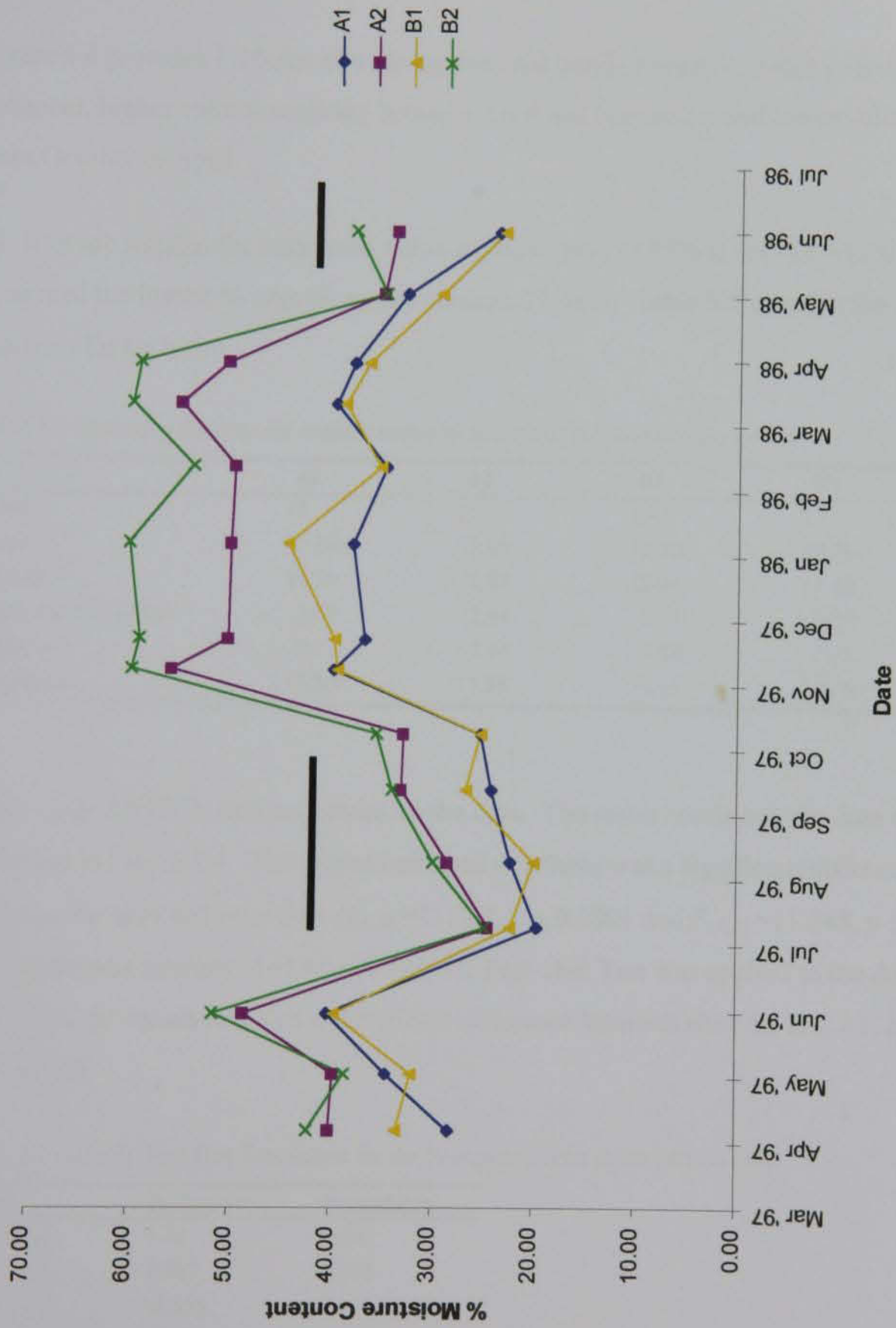
Figure 5.3 % moisture content values for all four sites, A1, A2, B1 and B2. The black bars indicate periods during which there was no water present at the sites.

5.1.4 Sediment Organic Matter

Organic matter was measured between March 1997 and June 1998 on a monthly basis, the raw data is available in Appendix 3

Figure 5.4 provides evidence of a strong seasonal trend of organic matter content in sediment, higher values occurring between April and September and lower values recorded from October to April.

All sites are similar, the maximum value recorded was 17.85% at site A2 whilst site B2 presented the lowest % organic matter content, 13.56%. Table 5.5 contains the descriptive statistics for each site.

Table 5.5 Summary statistics for organic matter % content of the sediment at each site.

	A1	A2	B1	B2
Count	15	15	15	15
Mean	11.04	12.06	11.50	10.70
Median	11.56	12.87	12.54	11.48
Standard Deviation	2.08	2.94	2.71	2.24
Minimum	7.13	7.54	6.98	7.11
Maximum	13.58	17.85	15.15	13.56

A two-way ANOVA was performed on the data. The result confirmed the time effect observed in Figure 5.4. The output indicated that there was a significant difference between the sites and over time ($F_{3,56}$ =11.348, $p \leq 0.0001$ and $F_{14,45}$ =11.348, $p \leq 0.0001$). The result was substantiated when a Scheffe Post-Hoc Test was applied to the data (Table 5.6). The 'p' values revealed a significant difference between sites A2 and A1, as well as B2 and A2.

Table 5.6 Scheffe Post-Hoc Test output for the % organic matter at the various sites.

Sites	Difference	Probability
A2 – A1	1.02	0.002
B1 – A1	0.467	0.325
B1 – A2	-0.553	0.188
B2 – A1	-0.335	0.610
B2 – A2	-1.354	4.15^{E-05}
B2 – B1	-0.801	0.023
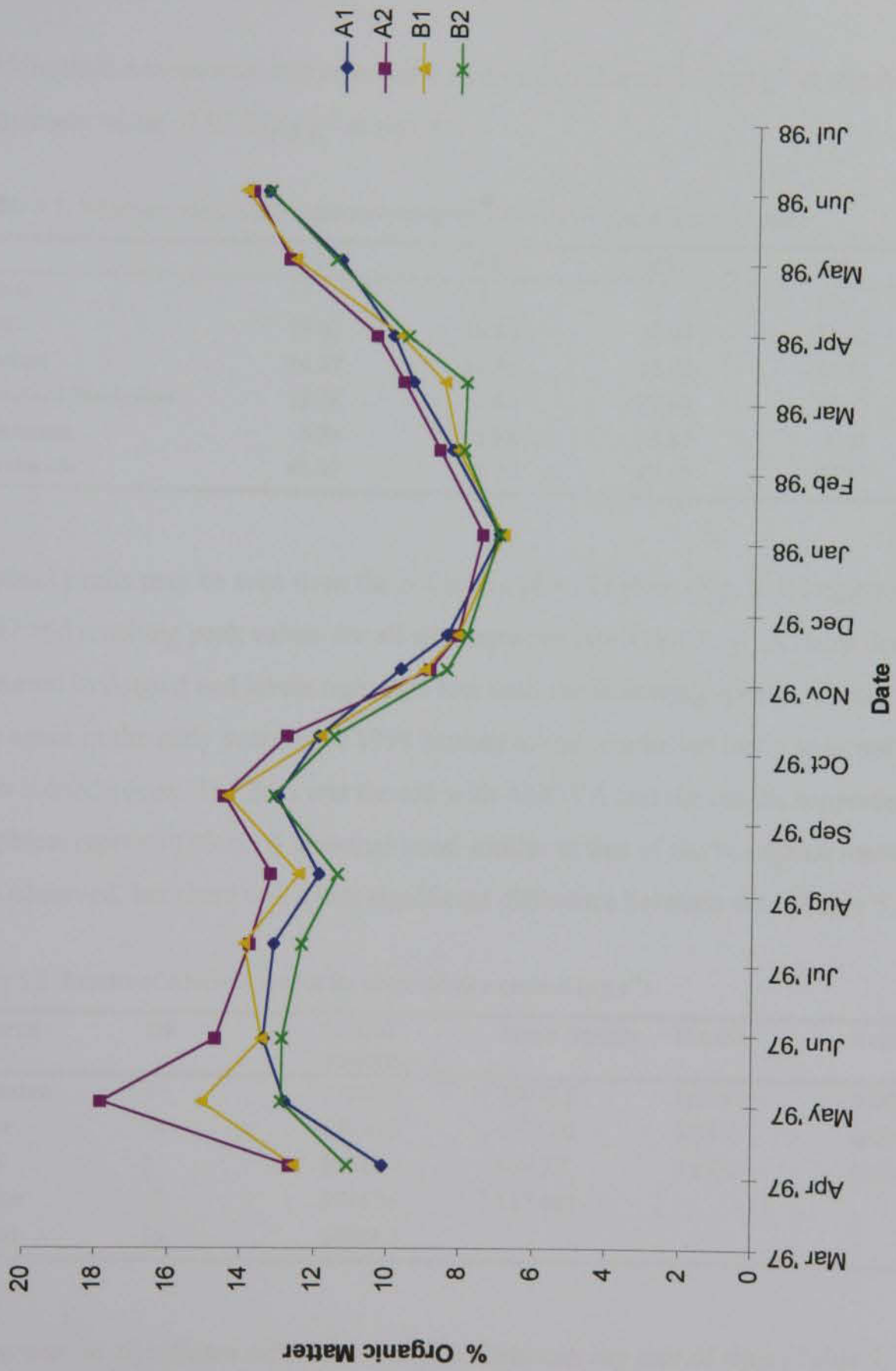
Figure 5.4 Organic matter % content for sites A1, A2, B1 and B2.

5.1.5 Pigment Analysis

Chlorophyll a (μg g^{-1}) measurements and conversions are presented in Appendix 4. The descriptive statistics for this parameter are given in Table 5.7.

Chlorophyll a measurements recorded a minimum value of 5.29μg g^{-1} at site A1 and a maximum value of 83.57μg g^{-1} at site B1.

Table 5.7 Summary statistics for sediment chlorophyll a content (μg g^{-1}) at each site.

	A1	A2	B1	B2
Count	15	15	15	15
Mean	18.87	19.10	30.04	31.42
Median	14.37	16.56	15.49	20.56
Standard Deviation	12.58	11.64	27.64	23.87
Minimum	5.29	5.99	5.87	8.03
Maximum	46.99	43.70	83.57	77.57

Distinct peaks may be seen from the collective plot of values (Fig. 5.5) beginning in April 1997 and reaching peak values for all sites between April and July. A sharp decrease occurred in August and levels remained low until the following spring. Values started to rise again in the early summer of 1998 leading to the conclusion that a seasonal pattern does indeed occur. The data was treated with ANOVA and the results supported the graphical representation. A seasonal trend similar to that of the % organic matter content was observed, but there was a less significant difference between sites (Table 5.8).

Table 5.8 Results of ANOVA output for chlorophyll a content (μg g^{-1}).

Source	DF	Sum of Squares	Mean Square	F-ratio	Probability
Constant	1	37072.2	37072.2	269.64	0.0001
Date	14	17010.3	1215.02	8.8372	0.0001
Site	3	2084.31	694.77	5.0533	0.0044
Error	42	5774.56	137.489		
Total	59	24869.2			

There was no significant difference recorded between any pair of sites (Table 5.9).

Table 5.9 Scheffe Post-Hoc output of site variability for chlorophyll a content ($\mu g\ g^{-1}$).

Sites	Difference	Probability
A2 – A1	0.228	0.999
B1 – A1	11.167	0.095
B1 – A2	10.939	0.105
B2 – A1	12.553	0.048
B2 – A2	12.325	0.053
B2 – B1	1.385	0.991
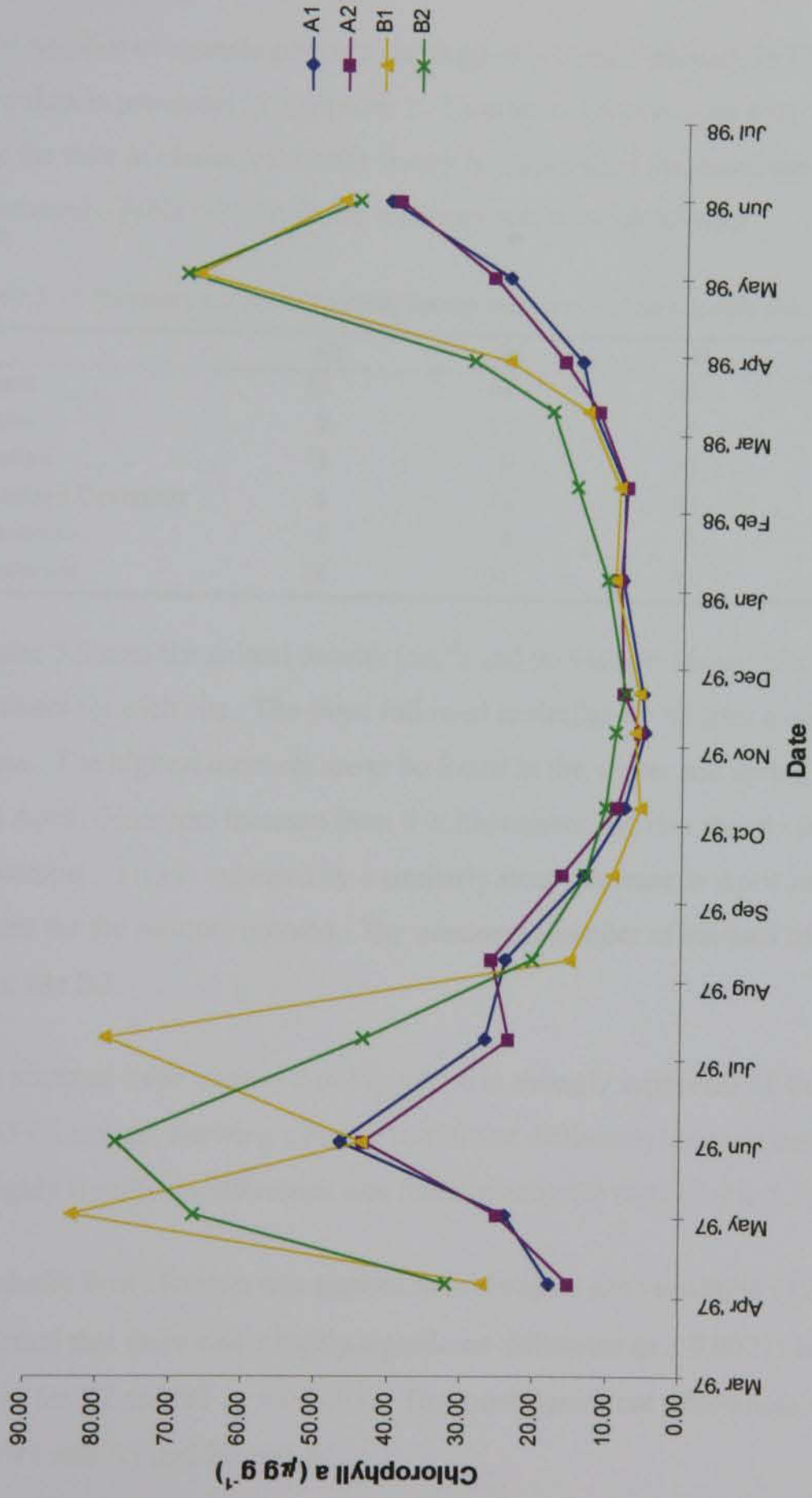
Figure 5.5 Sediment chlorophyll a content (μg g^{-1}) at each site.

5.2 *Limapontia depressa* Analysis

5.2.1 Animal Density

The number of animals per core was logged between February 1997 and August 1999, the raw data is presented in Appendix 5. Numbers of animals per core was used in Table 5.10 for the sake of clarity, otherwise it may be understood that numbers of animals cm^{-2} are discussed. Table 5.10 holds the summary statistics for all sites.

Table 5.10 Summary statistics for animal density per core ($19.6cm^2$) at each site.

	A1	A2	B1	B2
Count	68	68	68	68
Mean	7	11	15	18
Median	5	9	15	19
Standard Deviation	8	11	14	16
Minimum	0	0	0	0
Maximum	28	31	42	45

Figure 5.6 uses the animal density (cm^{-2}) and provides evidence of a strong trend in numbers for each site. The trend followed is similar for all sites over the three sampling terms. The highest numbers are to be found in the winter and spring between November and April. Numbers increase from 0 in September and rise sharply in October and November. This is mirrored by a similarly steep decrease in April and May. Animals are absent for the summer months. The maximum number of animals recorded per core was 45 at site B2.

The seasonal trend observed in Figure 5.6 is strongly supported by the results of the ANOVA output, showing a highly significant difference between dates.
A highly significant difference was found among the sites (Table 5.11) as well.

A Scheffe Post-Hoc test was applied to investigate site variability (Table 5.12). The result indicated that there was a highly significant difference ($p \leq 0.0001$) between all sites except for B2 and B1 ($p = 0.0005$). The most significant differences were found between sites B1 and A1 and B2 and A1.

Table 5.11 Two-way ANOVA observations for variations in animal density between sites (cm^{-2}).

Source	DF	Sum of Squares	Mean Square	F-ratio	Probability
Constant	1	115.951	115.951	2468.5	0.0001
Date	67	96.8918	1.44615	30.787	0.0001
Site	3	11.3123	3.77078	80.275	0.0001
Error	201	9.44157	0.046973		
Total	271	117.646			

Table 5.12 Output following application of a Scheffe Post-Hoc Test to site variability data.

| Sites	Difference	Probability
A2 – A1	0.209	1.82^{E-06}
B1 – A1	0.387	0
B1 – A2	0.178	7.08^{E-05}
B2 – A1	0.547	0
B2 – A2	0.339	5.22^{E-15}
B2 – B1	0.160	0.0005
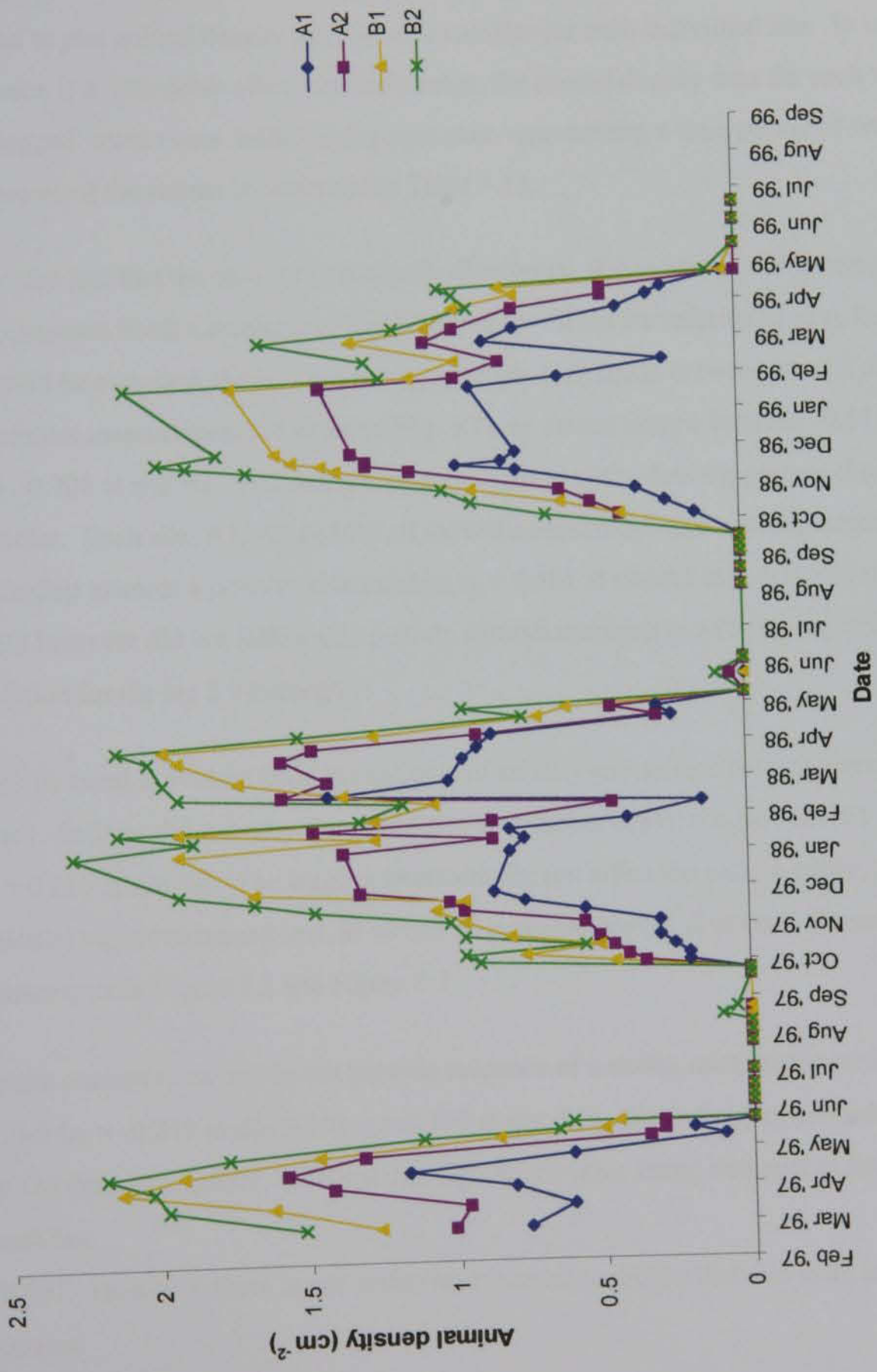
Figure 5.6 Animal density (cm^{-2}) at each site between February 1997 and September 1999.

5.2.2 Correlation Analysis

Animal abundance was plotted against the various environmental parameters, Figure 5.7 – Figure 5.11. As location was extremely influential on the environmental variables, it was decided to plot animal density against each variable for each individual site. In order to determine if a time delay effect was influential, the animal density data for each variable was 'lagged' three times, each lagging operation representing a time period of one month. A synopsis of the results is presented in Table 5.13.

Due to the fact that the data is not normally distributed, it was tested with a non-parametric test, Spearman Rank Correlation. The resulting 'r' values are referred to as r_S hereafter. As would be expected, there was a strong negative correlation between animal density and temperature measurements at all sites (Fig. 5.7), r_S values ranged between -0.411 at site A1 to –0.708 at site B2. Following lagging treatment of the data the picture changed somewhat. Each site, A1, A2 and B1 all moved consistently from a strong negative relationship towards a positive relationship, $r_S = 0.381$ at site A1 to $r_S = 0.572$ at site A2. Site B2 however did not follow this pattern, instead reverting to a strong negative correlation for the lag 2 treatment.

A definite trend is evident from the analysis of salinity and animal density correlations at all sites. Salinity did not record a significant correlation at any site, $r_S = -0.191$ at site B1 to $r_S = 0.210$ at site B2. The lagging treatment did not affect the pattern either, all correlation values remained low, as would be expected having illustrated the salinity measurements in Figure 5.2 and Figure 5.7.

Moisture content r_S values do not provide evidence of a strong relationship with animal densities ($r_S = -0.249$ at site B2 to $r_S = 0.199$ at site A1). Again lagging procedures did not affect the data enormously, with just one significant value being obtained at site B2 after a 1 month lag,
$r_S = 0.507$. However, there is not sufficient evidence to dictate that this is an important occurrence.

The organic matter content of the sediment indicated an unexpected negative correlation with animal density; $r_S = -0.797$ at site A1, $r_S = -0.750$ at site A2, $r_S = -0.680$ at site B1, $r_S = -0.823$ at site B2. Figure 5.10 graphically supports this relationship. The lagging treatments correlated highly in just two cases after a one-month lag, at sites A1 and B2. The remaining lagging treatments shifted towards positive correlations but were not significant at $p = 0.05$.

Chlorophyll a measurements suggested a difference between the A and B sites (Fig. 5.11). The correlation between animal density and chlorophyll a content was strongly negative at the A sites, $r_S = -0.650$ at site A1, $r_S = -0.770$ at site A2, whilst the relationship was weaker at the B sites, $r_S = -0.423$ at site B1 and $r_S = -0.468$ at site B2. The effect of lagging treatments was to shift the relationship from a strong negative relationship to a strong positive relationship after a three-month period, ranging from $r_S = 0.610$ at site A2 to $r_S = 0.867$ at site B2.

Table 5.13 Synopsis of correlation results for each site, 'actual' indicates the result from data obtained during the course of the study; Lag 1 – Lag 3 respectively indicate lagging periods of 1 month to 3 months accordingly. Levels of significance are denoted by *, * = 0.05, ** = 0.01 and *** = 0.001.

Site	Date	Temperature	Salinity	Moisture Content	Organic Matter	Chlorophyll a
A1	Actual	***	NS	NS	***	**
	Lag 1	***	**	NS	*	NS
	Lag 2	NS	NS	NS	NS	NS
	Lag 3	**	NS	NS	NS	***
A2	Actual	***	NS	NS	**	***
	Lag 1	***	NS	NS	NS	NS
	Lag 2	NS	***	NS	NS	NS
	Lag 3	***	NS	NS	NS	*
B1	Actual	***	NS	NS	**	NS
	Lag 1	**	NS	NS	NS	NS
	Lag 2	NS	NS	NS	NS	*
	Lag 3	***	NS	NS	NS	***
B2	Actual	***	NS	NS	***	NS
	Lag 1	***	NS	NS	NS	NS
	Lag 2	***	***	NS	NS	**
	Lag 3	***	NS	NS	Ns	***

(a)
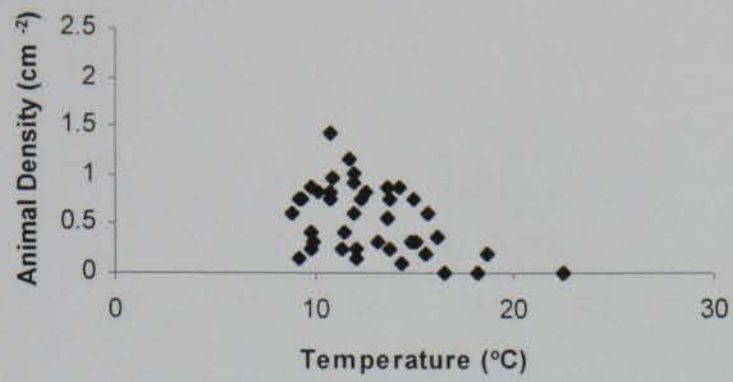
(b)
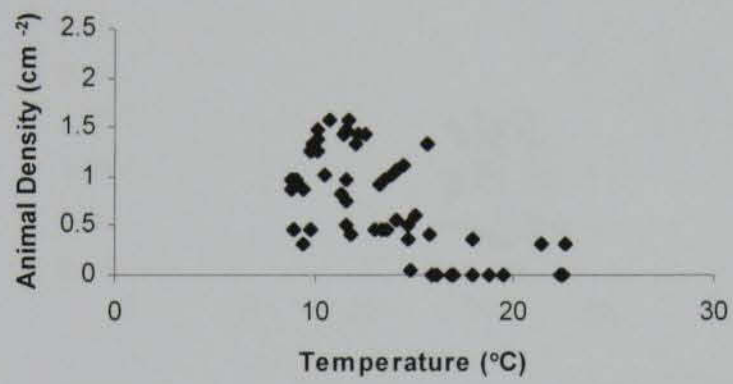
(c)
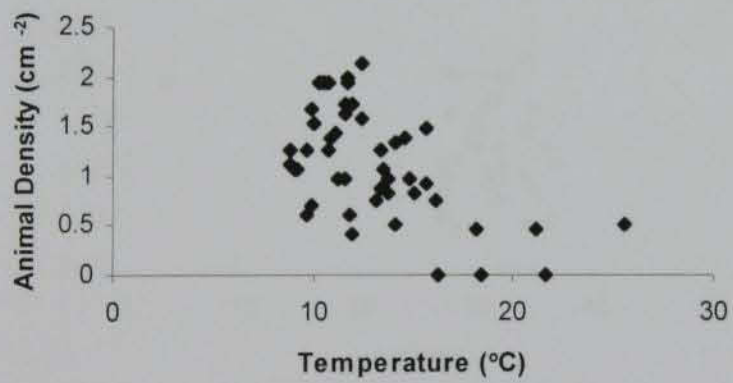
(d)
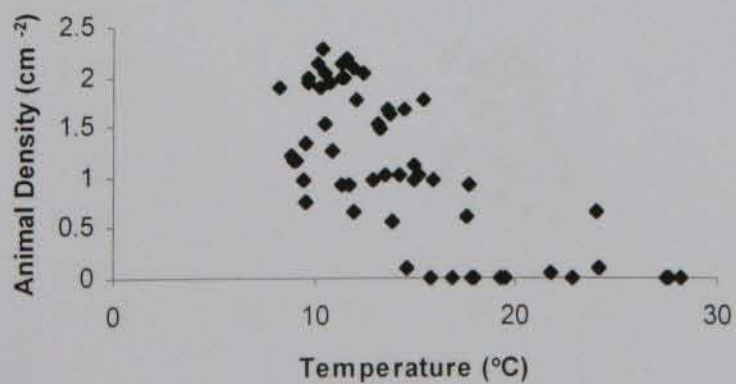
Figure 5.7 Scatterplots illustrating the relationship between temperature ($^{\circ}$C) and animal density (cm^{-2});
(a) A1, (b) A2, (c) B1 and (d) B2.

(a)
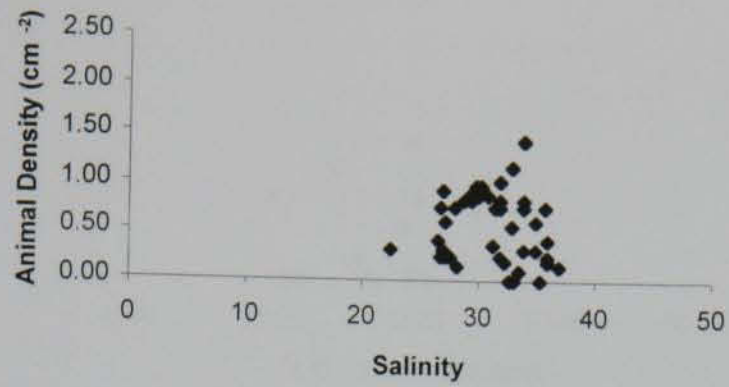
(b)
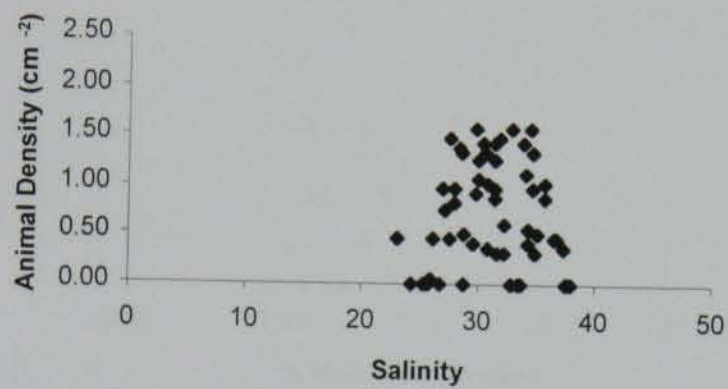
(c)
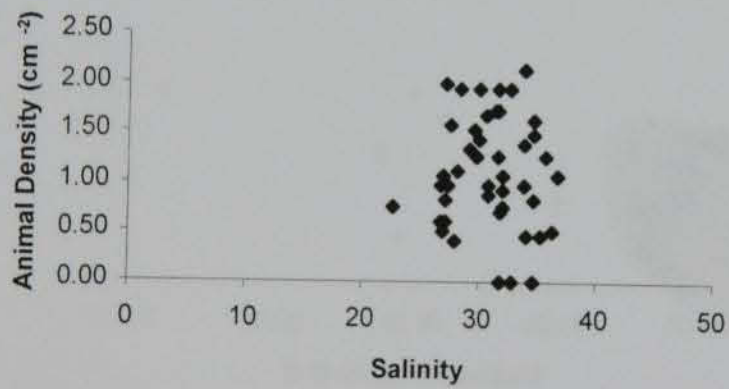
(d)
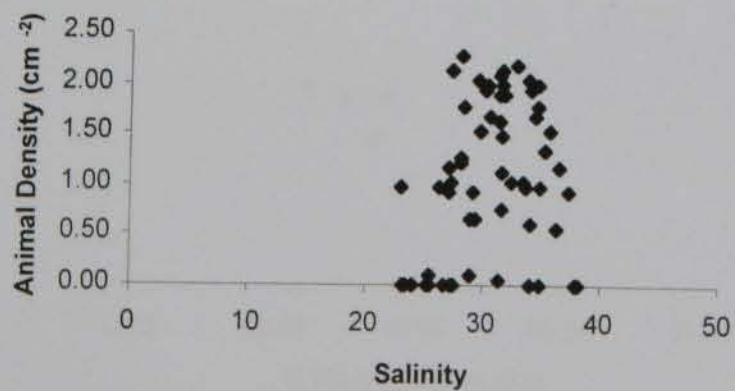
Figure 5.8 Scatterplots illustrating the relationship between salinity and animal density (cm^{-2}); (a) A1, (b) A2, (c) B1 and (d) B2.

(a)
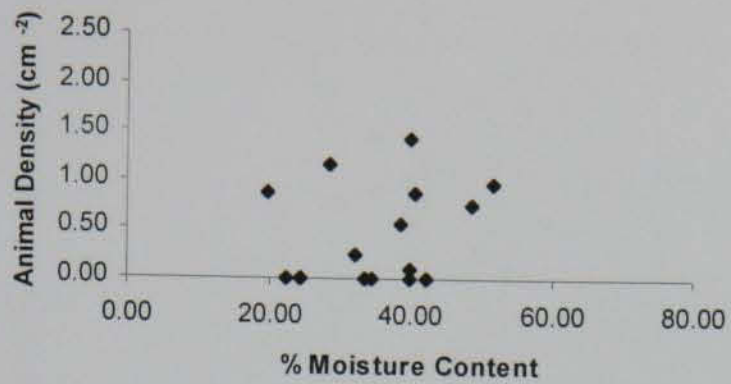
(b)
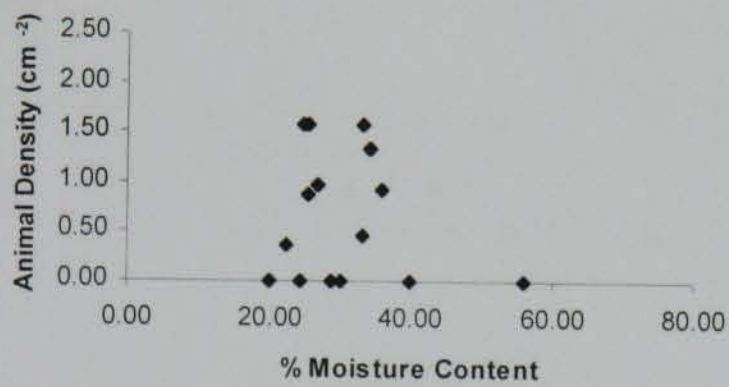
(c)
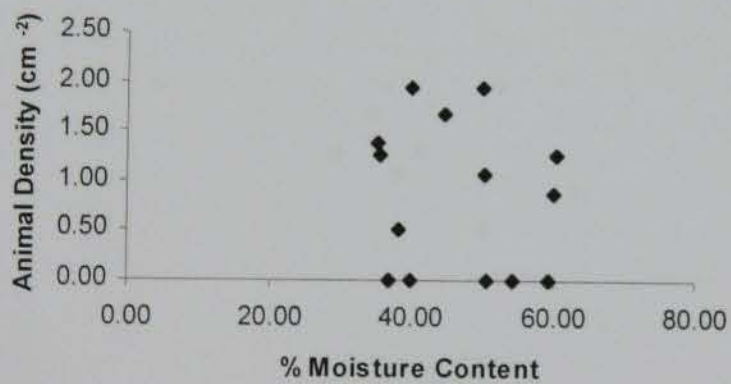
(d)
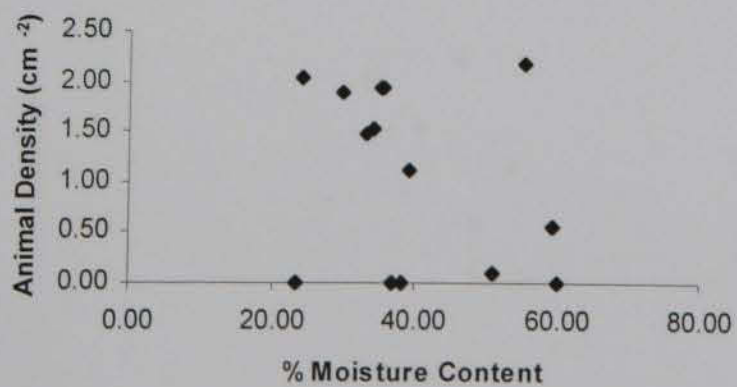
Figure 5.9 Scatterplots illustrating the relationship between % moisture content and animal density (cm^{-2}); (a) A1, (b) A2, (c) B1 and (d) B2.

(a)
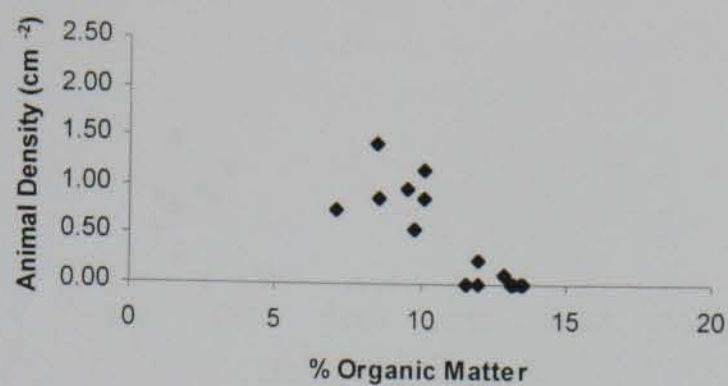
(b)
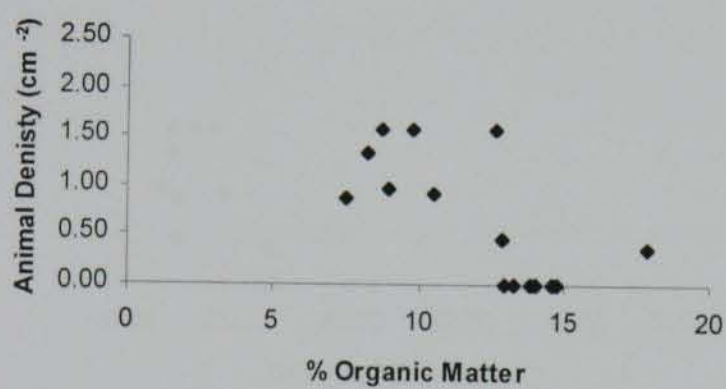
(c)
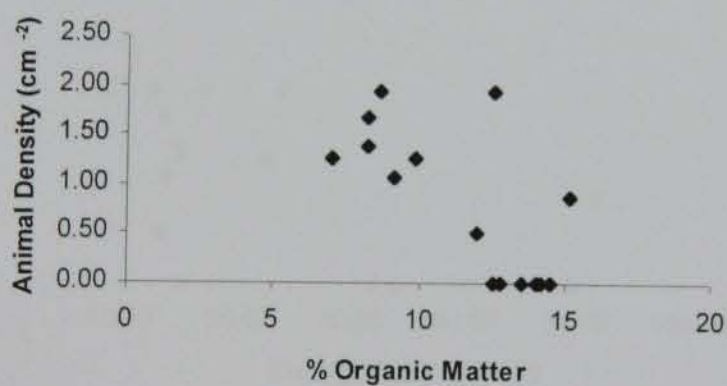
(d)
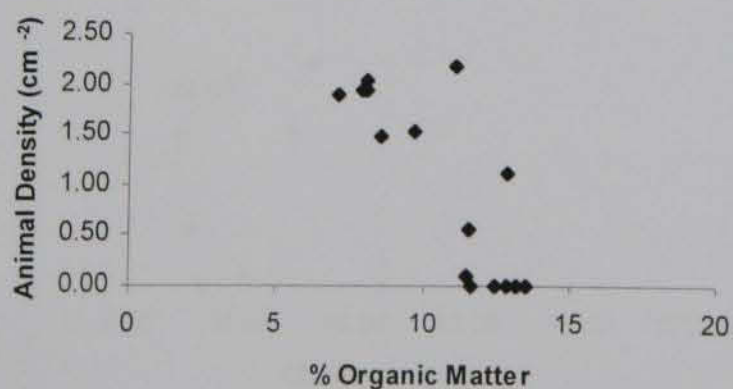
Figure 5.10 Scatterplots illustrating the relationship between % organic matter and animal density (cm^{-2}); (a) A1, (b) A2, (c) B1 and (d) B2.

(a)
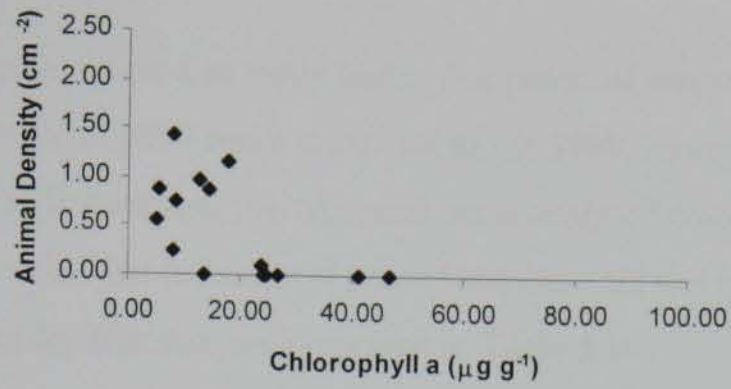
(b)
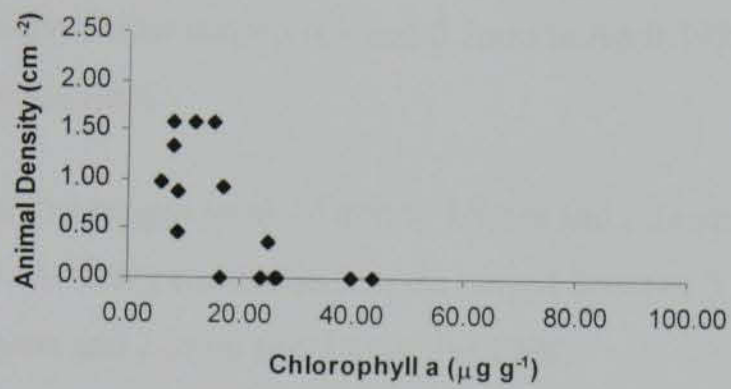
(c)
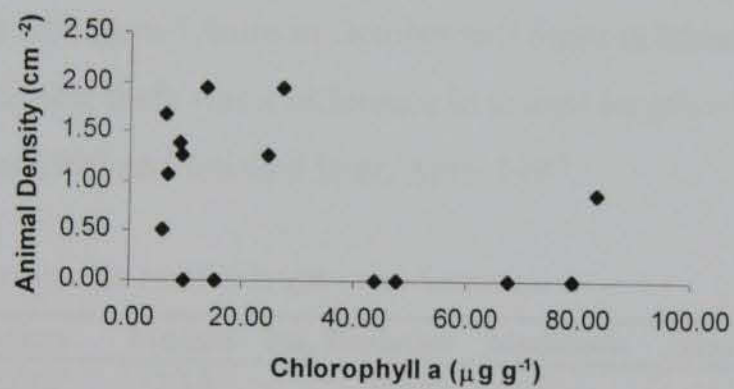
(d)
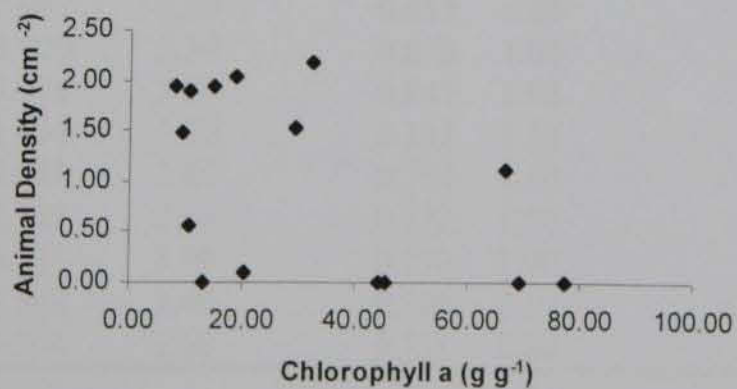
Figure 5.11 Scatterplots illustrating the relationship between chlorophyll a (μg g^{-1}) and animal density (cm^{-2}); (a) A1, (b) A2, (c) B1 and (d) B2.

5.2.3 Population Analysis

Animal length was measured on a monthly basis. For practical reasons sampling commenced in November of 1997 and a month earlier in 1998, however, sampling did continue for six months in both seasons. Animals were analysed cumulatively and not for individual sites. It was felt that insufficient animal numbers did not warrant analysis of individual sites. Summary statistics are presented in Table 5.14.

The minimum length recorded was 1.1mm in November 1997, October 1998 and November 1998. The maximum lengths reached 5.3mm in April 1997 whilst the maximum for 1998 was 5.1mm.

Monthly minimum lengths ranged from 1.1mm to 1.9mm and 1.1mm to 2.2mm for 1997 and 1998 respectively. Monthly maximum lengths ranged between 3.6mm and 5.3mm for the 1997 sampling season and 2.2mm and 5.1mm for 1998.

Mean values increased from 2.1mm to 3.6mm between November and April 1997. In 1998 the mean values rose from 1.4mm in October to 3.6mm in March. From these results, it may be noted that there was a difference in animal length when sampling began earlier, that is, October 1998 and finished later, April 1997.

Table 5.14 Descriptive statistics for monthly length (mm) frequency.

Date	Count	Mean	Median	Std. Deviation	Minimum	Maximum
20-Nov-97	80	2.068	2.10	0.791	1.10	3.60
05-Dec-97	114	2.644	2.50	0.758	1.60	4.00
19-Jan-98	94	3.285	3.25	1.083	1.80	5.00
17-Feb-98	56	2.982	2.90	0.653	1.80	4.10
27-Mar-98	128	3.420	3.30	0.870	1.80	5.20
16-Apr-98	98	3.576	3.60	0.841	1.90	5.30
19-Oct-98	32	1.434	1.30	0.337	1.10	2.20
26-Nov-98	96	2.055	2.00	0.754	1.10	3.60
11-Dec-98	107	2.583	2.40	0.722	1.50	4.00
04-Feb-99	121	3.321	3.30	0.790	1.90	5.10
26-Feb-99	65	3.503	3.40	0.798	2.10	5.00
26-Mar-99	78	3.564	3.50	0.751	2.20	5.10

A growth curve was constructed that included mean, median, minimum and maximum for both sampling seasons (Fig. 5.12). An obvious growth pattern is evident from the data from when the animals appear in October/November to their disappearance in April/May.
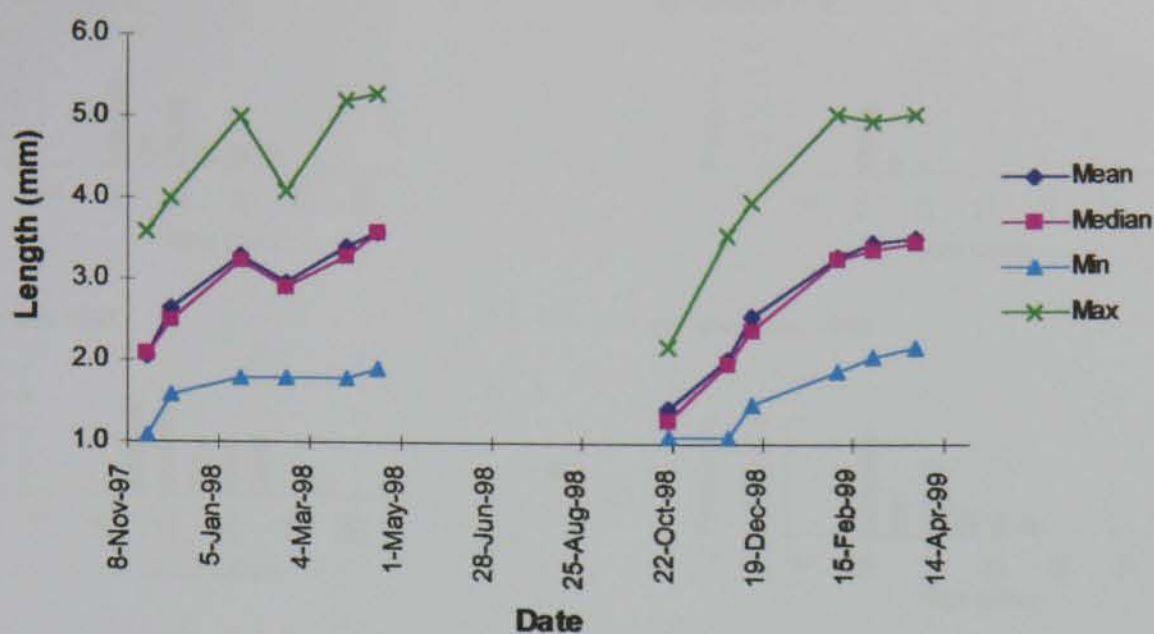
Figure 5.12 Mean, median, minimum and maximum animal lengths (mm) measured monthly between November 1997 and March 1999.

This data is further graphically analysed in Fig. 5.13 in the form of monthly length class frequencies.

The pattern of animal growth is even more evident from these figures. The higher frequencies move resolutely towards the larger length class as the season progresses. At the beginning of the sampling season, there are few or no adults present, (Fig. 5.13a and 5.13g). The growth pattern continues as one would expect, recruits becoming less apparent as adult numbers increase. In the latter months of the season, larger individuals of up to 5.3mm are recorded in much higher numbers (Fig. 5.13f and Fig. 5.13l).

(a) November 1997
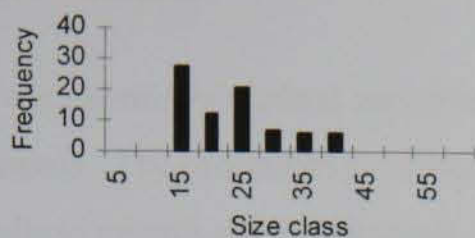
(b) December 1997

(c) January 1998

(d) February 1998

(e) March 1998

(f) April 1998

(g) October 1998
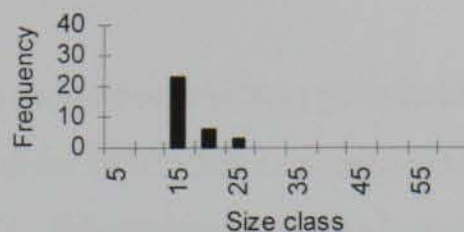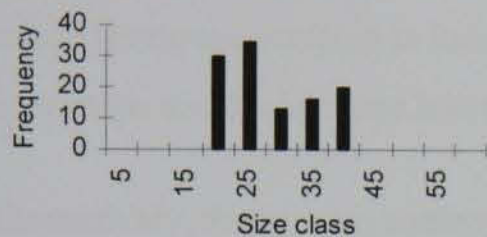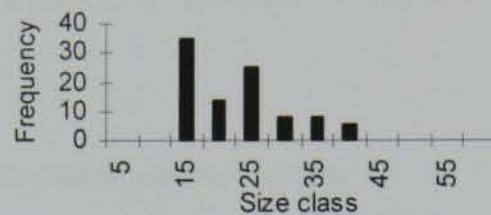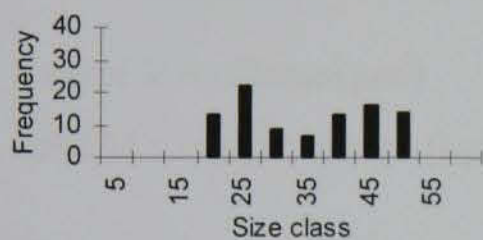
(h) November 1998
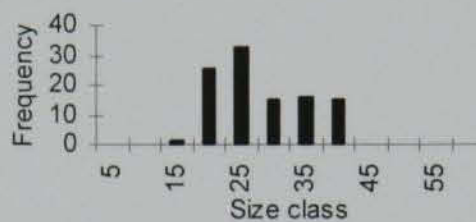
(i) December 1998
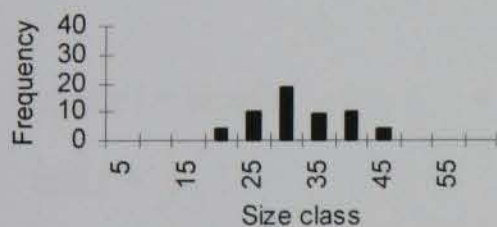
(j) January1999
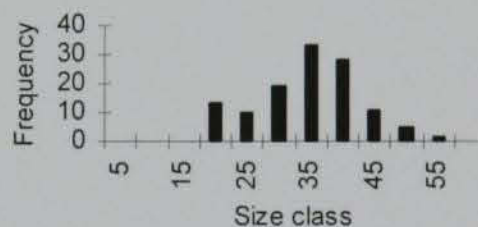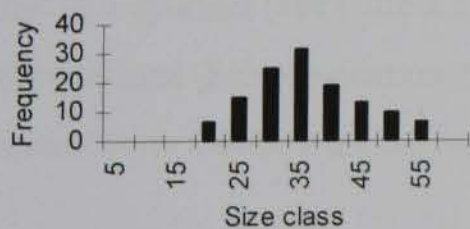
(k) February 1999
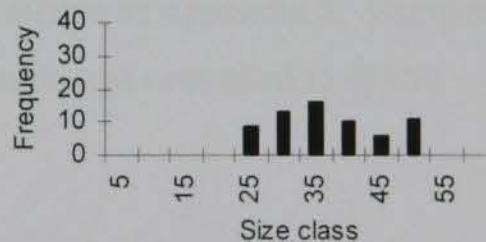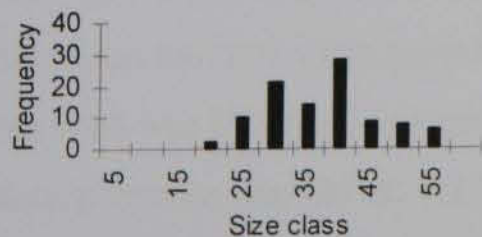
(l) March 1999
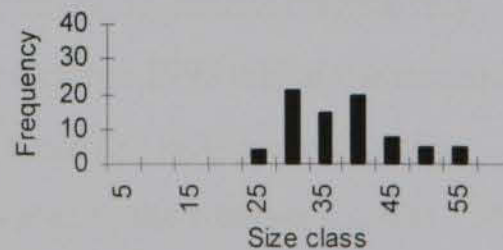
Figure 5.13 Length class frequencies (0.1mm).

5.2.4 Biomass

A wet chemistry method was attempted to calculate the carbon contents of individual animals. The procedure used was based on a method for estimating total organic carbon in mollusc growth studies (Russell-Hunter *et al.*, 1968). Adaptations were made to this method in order to increase its sensitivity for the determination of carbon. However, at the carbon levels encountered in individuals it was not possible to differentiate between individuals and background levels.

Alternatively, the organic content or biomass of *Limapontia depressa* may be approximated using the following equation derived by Strathmann & Vedder (1977):

$$M = 6.05 \times 10^{-6} \times V^{0.747}$$

where V = volume (μm^3)

and M = organic content (μg).

Volume was calculated using the formula:

$$\tfrac{4}{3} \pi r^2 l$$

where l = length

and $r = \tfrac{1}{3} l$

for each individual animal considering the shape of *Limapontia depressa* to be similar to that of a cylinder (see Plate 3.1). The raw data is available in Appendix 5. Using a series of equations (Schwinghammer *et al.*, 1986) the biomass was converted to kj and productivity values were derived.

Figure 5.14 shows the biomass (m^{-2}) for each monthly collection. The average biomass was 322.81kjm^{-2} and 251.64kjm^{-2} for the six month sampling periods respectively. The minimum biomass value recorded was 3.16kjm^{-2} in October 1998 whilst the maximum recorded was 89.8kjm^{-2} in March 1998. There was a marked increase in biomass throughout the year (1998) until the animals disappeared in the summer months. There was a noticeable decrease in biomass in February of each year and this corresponds directly to the animal density, see Figure 5.6.
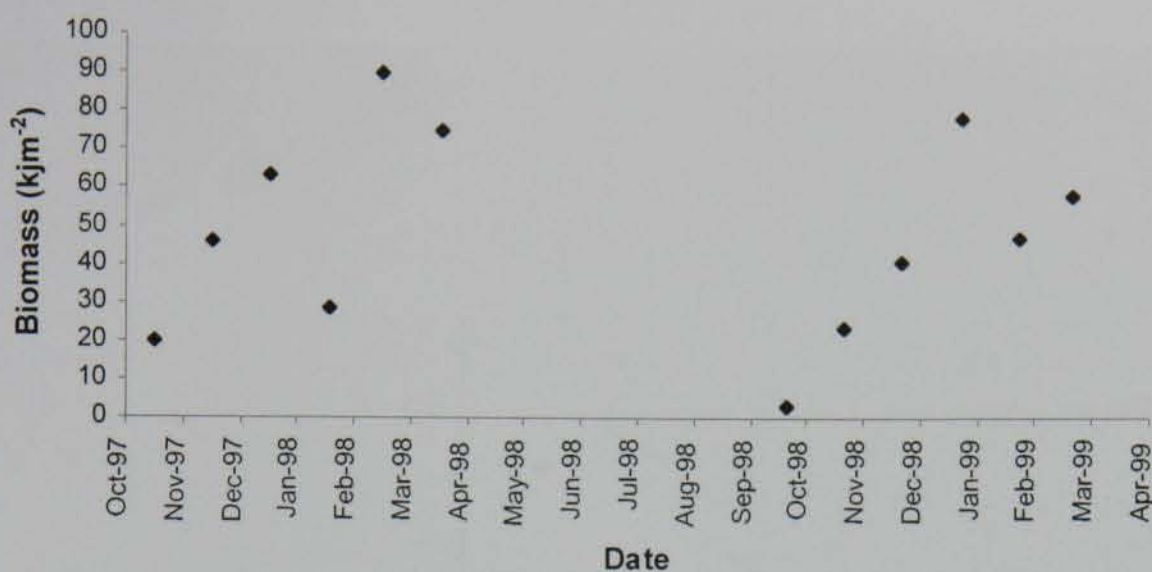
Figure 5.14 Biomass (kjm^{-2}) measurements for each monthly sampling collection.

5.2.5 Respiration

The raw data is available in Appendix 6. An example of the output following an investigation is shown in Figure 5.16.

The data is plotted in bar chart form in Figure 5.17. The initial observation is that the respiration rate is unexpectedly higher at the lower temperature. There are a minority of occasions during which oxygen consumption is greater at 20°C.

Oxygen uptake recorded the lowest level of 0.003 μl O$_2$/animal/hour at 10°C in October 1998 whilst the highest value of 0.340 μl O$_2$/animal/hour was also recorded at 10°C in April 1999. Oxygen consumption values at 20°C ranged from between 0.010 μl O$_2$/animal/hour and 0.079 μl O$_2$/animal/hour.
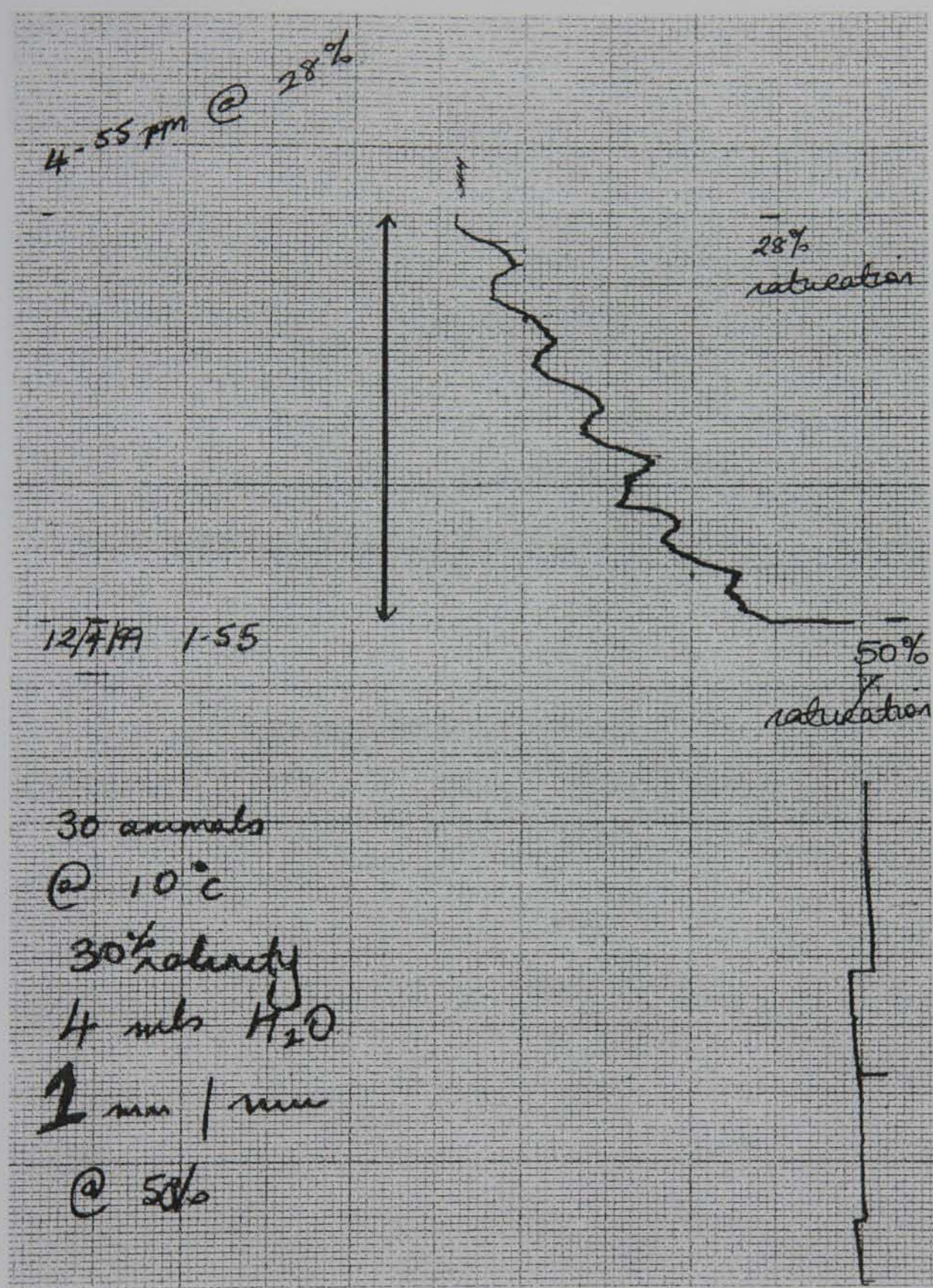
Figure 5.16 Typical output from respiration apparatus.
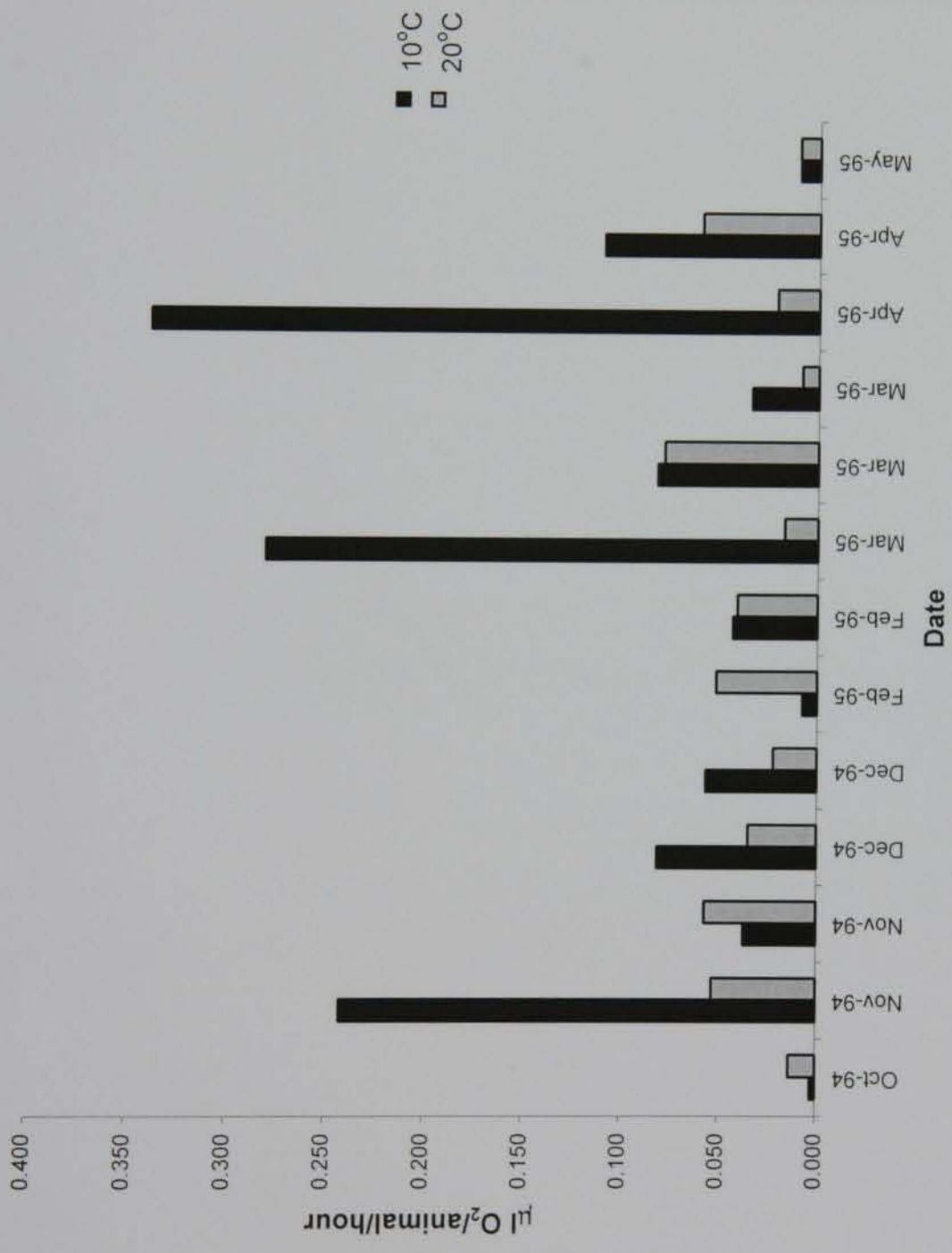
Figure 5.17 Respiration μl O$_2$/animal/hour on a monthly basis.

5.2.6 Exclusion Zone Investigation

The exclusion cores were visited on each sampling occasion for the time period previously discussed. When the zones were inspected, there appeared to be no animals present and an anoxic environment was developing. Cores were taken from within the zone and further inspection revealed that the area was devoid of *Limapontia depressa*, even during the winter months when the animals were to be found in the area surrounding the cores.

Chapter 6

Discussion

6.1 Environmental Variables

6.1.1 Water Temperature

The temperatures at which *Limapontia depressa* was found ranged between 8.2°C and 28°C. The correlation between water temperature and animal density provided evidence of a highly significant negative relationship, a similar trend being apparent over three sampling seasons.

Limapontia depressa occurs only in the temperate zone of the NE Atlantic, including the Mediterranean and the Baltic (Jensen, 1997). Temperate zone temperatures are more variable than polar or tropical waters. The diurnal fluctuation at the surface is rarely more than 4°C, however seasonal fluctuations may be as great as 20°C (Cossins & Bowler, 1987). The water temperature measurements for North Bull Island therefore correlates well with the literature.

Newell (1979) stated that most inhabitants of the salt marsh would be capable of withstanding large variations in salinity, temperature and water loss by burrowing or by finding refuge in available vegetation. The magnitude of thermal stresses is intimately linked to the timing of tidal water movements (Harrison, 1985). The consequent heat exchange mechanisms that operate between water and air and water and substrate following inundation are important and must exert some influence on an organisms behaviour. A temperature profile of a saltmarsh environment is presented in Figure 6.1. The tide provides some stability as regards temperature. Whilst the tide is absent however, there are considerable differences in temperature in a pool.

In the case of *Limapontia depressa*, the relationship between air and water temperatures would be more important as it does not burrow. Surprisingly, there has not been much work carried out as regards temperature tolerances for *L. depressa*. However, Jensen

(1977) determined the optimal growth rate of *Limapontia capitata* to take place at 15°C, based on growth rates, percentage of non-growing animals during experiments, spawning and heart rate measurements. Animals were found to experience heat coma between 38°C and 40°C whilst minimum temperatures tolerated were found to be about 0°C.
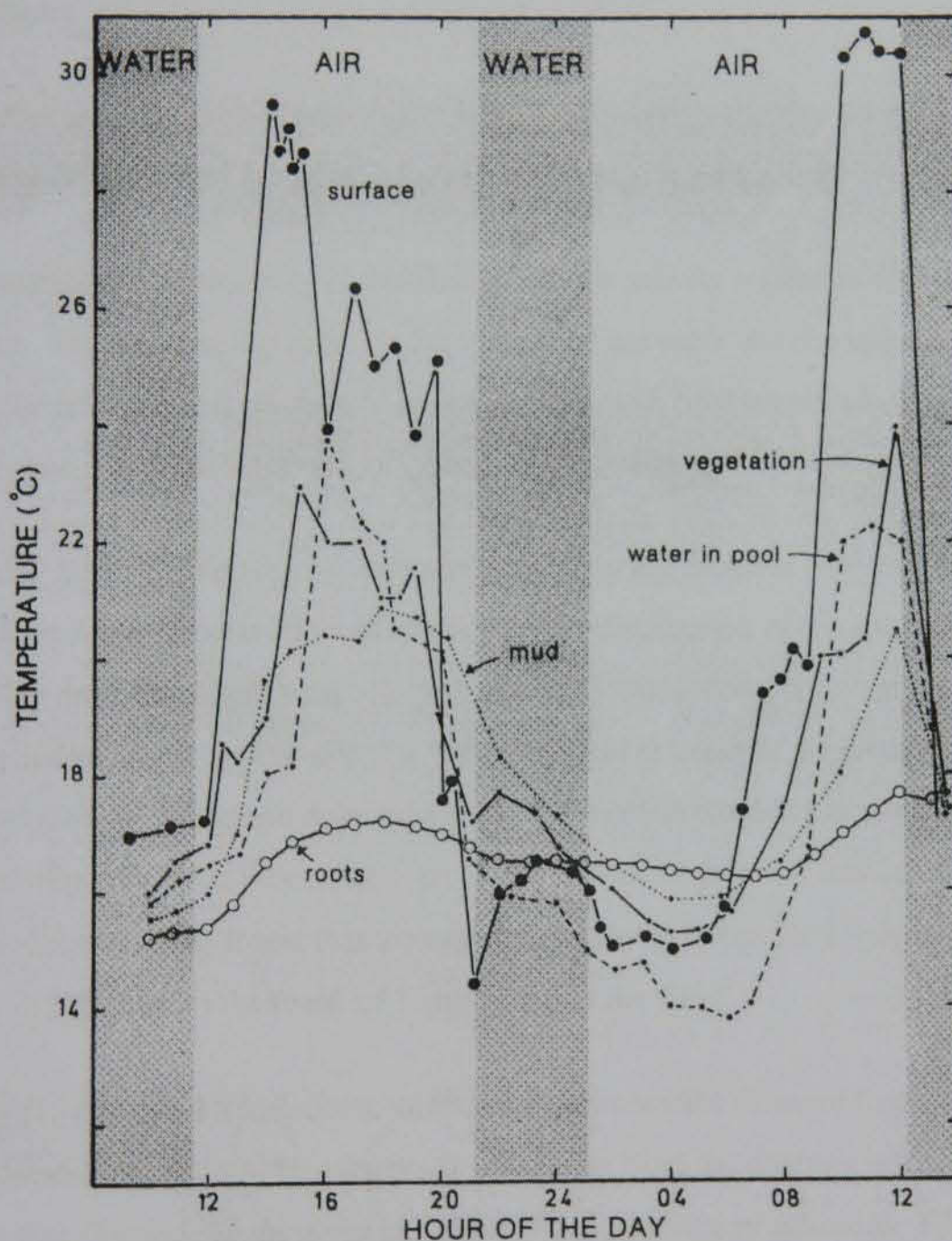
Figure 6.1 A temperature profile of a saltmarsh environment taken over two tidal cycles in the vicinity of a subsaline pool on a saltmarsh in North Kent, U.K. during July 1973 (Newell, 1979).

It has been suggested that animals can physiologically adapt to temperature with a change in season (Jensen, 1977; Cossins & Bowler, 1987). This phenomenon would explain the ability of a sacoglossan to withstand extreme temperature changes and therefore does not

account for the sudden absence of *Limapontia depressa* from the sampling areas during the present study. The extreme range of temperature tolerance for *Limapontia capitata* may be applicable to *Limapontia depressa* if various other factors were taken into account and will be discussed in detail later.

6.1.2 Salinity

Salinity data analysis did not present any significant trends, only that all sites recorded salinities within a narrow range of values on each sampling occasion.

In the estuarine environment of North Bull Island the salinity regime is difficult to generalise. The relationship between the volume of seawater and the volume of freshwater entering the area must be considered in conjunction with tidal amplitude, topography, substrate type and climate (Nicol, 1935; McLusky, 1989).

The salinity range within which *Limapontia depressa* are found at North Bull Island makes it difficult to determine the effect of salinity on the distribution of the slugs, the relationship not being significant. Seeleman (1968) found that *Limapontia depressa* can survive salinities from 5ppt to 40ppt at 14°C while an extreme of 60ppt can be tolerated if introduced slowly. Seeleman determined that the animals would only spawn between 10ppt and 40ppt and that they possess an ability to osmoregulate at low salinities. However, Jensen(1977) found that the optimal salinity of 30ppt for *Limapontia capitata* was very different from the mean of 15ppt found in the field.

McLusky (1989) stated that salinity tolerance determines the distance that a species is capable of penetrating into the estuary. It is obvious from the analysis of data and literature that *Limapontia depressa* can survive a wide range of salinities. On this basis it may be concluded that *Limapontia depressa* is certainly a euryhaline animal.

6.1.3 Sediment Moisture Content

Moisture content values displayed a seasonal trend on the whole. The winter values gave a higher moisture content value than those samples taken during the summer months.

Water content is largely determined by the grain size distribution, grain shape and sediment packing. Figure 6.2 illustrates the relationship between sediment particle size and water content. However, as the grain particle size in the North Lagoon is for the most part, sand, there should not be a large amount of variation due to grain size. Even though samples were taken at low tide for all sites, the water content of surface sediments may vary considerably during the period of exposure at low tide in response to factors such as temperature, wind, rainfall and the slope of the mudflat surface.
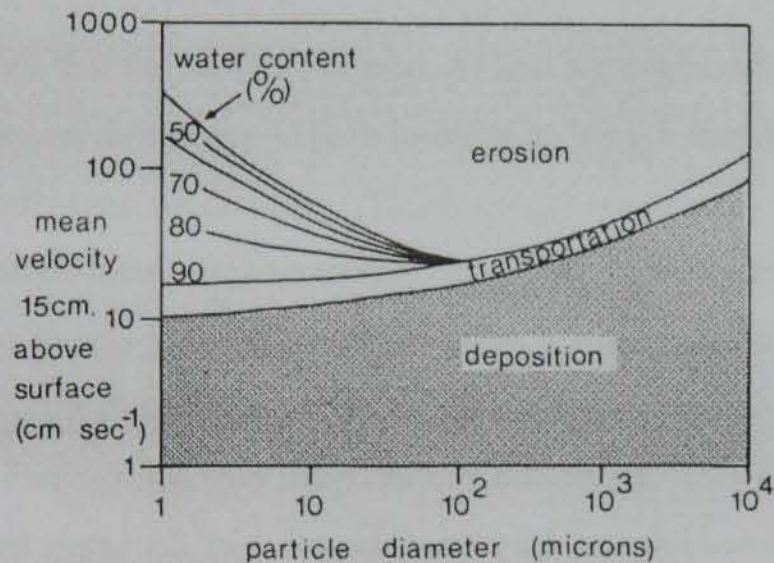
Figure 6.2 Relationship between water content and particle size diameter (McLusky, 1989).

From the analysis there was no evidence of a relationship between animal distribution and moisture content. It must be noted that there may be some bias attached to the samples taken during the course of this study, in that those samples with water coverage would invariably have a higher % moisture content than those without. The sites lower down on the marsh recorded consistently higher values than sites A1 and B1. The effect of tidal inundation must certainly be considered as having an effect as the tides would reach the A2 and B2 sites more frequently.

6.1.4 Sediment Organic Matter

Analysis of sediment organic matter revealed a significant seasonal trend, high values between April and October and low % sediment organic matter from November to March. Following analysis, there is a highly significant negative relationship between the density of *Limapontia depressa* and the sediment organic matter content. Due to the fact that there are essentially two ecotones involved in the study as regards the substrate, the upper sites and the lower sites will be discussed separately for this variable.

Faunal composition is usually negatively related to the organic matter content of the sediment (Newell, 1979). At low organic matter content, the availability of food is generally the limiting factor for the fauna. On the other hand high organic content may imply low oxygen values due to the bacterial decomposition process taking place.

It would be expected that the substrate of sites A1 and B1 would show stronger tendencies towards a homogenous state owing to their location on the salt marsh, where they are least affected by tides and organism diversity. This homogenous trend is reflected in the organic matter content, there being no significant difference between the upper sites. However, the much greater variation expected in the % organic matter of the A2 and B2 sites is evident from the Scheffe Post-Hoc test (Table 5.9). The low organic matter content of site B2 corresponds with a high animal density ($p = 0.001$, Table 5.16). The contrary is observed at site A2, high organic matter content and low animal density($p = 0.01$, Table 5.16). It was noted that the transitional sites between the marsh and the mudflat, A2 and B2 frequently showed signs of anoxic conditions.

6.1.5 Sediment Pigment Analysis

A review of the literature relating to the feeding habits of *Limapontia depressa* was discussed previously in Chapter 3 and concluded that the main food source was macrophytes such as *Vaucheria*, *Rhizoclonium*, *Cladophora* and *Chaetomorpha*. Whilst direct measurements of macroalgal growth were not made, the presence of macroalgae was recorded and supports the findings of the Jeffrey *et al.* (1992), that of higher macroalgal production between May and September.

Microphytobenthos measurements were essentially seen as an approximate measure of the standing crop of primary producers. An unexpected negative correlation with animal density resulted at all sites.

It is possible to suggest that the reduction in microphytobenthos production for the remainder of the year may be due to the grazing effect of *L. depressa*. Some caution must be applied however in interpreting the correlation between primary productivity measurements and animal density. Even though an inverse relationship is observed they may only be related through a common factor and one may not directly influence the other.

According to Reise (1984) there is a general reduction in habitat quality with an increase in algal mat density. Hence, Jeffrey *et al.* (1992) recorded a decrease in infauna diversity and density whilst the epifaunal species favoured this habitat change. It is possible that the conditions such as anoxia created by increased algal production are unsuited to the living environment of *Limapontia depressa*. The notion that adverse habitat conditions may cause the slugs to find a temporary habitat elsewhere should be entertained.

Todd (1991) suggested that the biochemical and nutritive value of the algae *Isochrysis* may change at high temperatures. A similar observation was made by Khan (1999) from algae studied in the North Bull Lagoon, that of a large increase in the C:N ratio during the summer months, resulting in decreased algal quality. The same principle may be applied to the algal diet of *Limapontia depressa*. This phenomenon would also encourage *L. depressa* to migrate towards a habitat where the host plants would be less affected by changes in temperature.

6.2 *Limapontia depressa* Distribution Analysis

The appearance and disappearance of the animals is perhaps the greatest concern, in that it is not expected and raises questions which merit some discussion.
Limapontia depressa appeared in October at relatively low temperatures with some algal presence. The animals density began to decrease when temperatures increase. The disappearance of the animals in May occurred over a very short period, as little as two

weeks. The sites are almost devoid of slug presence over the summer months until the following October, even though a thorough search of the entire habitat was undertaken once a fortnight.

When the animals were most prevalent, the following conditions were observed: temperatures were relatively low, moisture content was at its highest and salinity measurements were within a narrow range, even though *Limapontia depressa* have been found to have a wide salinity range tolerance.. The extremes were observed during the summer months, that is, from May to September: higher temperatures and low moisture contents. This in turn is supported by the finding that the animals disappeared entirely in the summer months when their habitat was devoid of water for long periods. The habitat of *Limapontia depressa* at North Bull Island is such that the areas in which they are found most abundantly are more often covered with water than not, even though the water column on occasion may be quite shallow. When water is absent, the animals are to be found on the sediment surface.

Firstly, having discussed temperature, salinity and moisture content individually, it is now necessary to marry these variables in order to establish a more realistic picture of environmental change. These parameters are linked by factors such as tidal inundation, topography, substrate type and climate. The most obvious outcome and one that epitomises the environmental conditions is the presence or absence of water. During the winter months it is probable that the tides will reach higher levels on the marsh than during the summer ensuring that the influence of water controls the extremes of change in the habitat. Higher levels of precipitation and drainage will also affect the pools. During the summer months after low levels of rainfall, it was observed that there was consistently less water to be found at the A1 and B1 sites, however the reasons for this remain unclear. The tidal and climatic influences allow for gradual and relatively minor changes in temperature and salinity. During the summer months these changes may not be so subtle. High air temperatures are bound to have an effect on the animals as they do not burrow into the safety of the sediment. When high tides occur or there are large amounts of precipitation, there would be sharp salinity gradients. McLusky (1989) remarked that salinity may have a greater effect on larvae or breeding adults than it does on animals at intermediate stages of growth. However, the available literature (Seeleman, 1968; Jensen, 1977) seems to

suggest that *Limapontia depressa* is able to cope with these changes in salinity. Newell (1979) suggested that the animals take cover in the vegetation in order to avoid the harsh environmental changes. It can be seen from Figure 6.1 that there is a decrease in temperature from air to vegetation to water. It may be that the protection offered by the resident vegetation is not enough, perhaps a deeper water column would provide more protection.

The corresponding changes in algal growth are of the utmost importance, primarily because the algae are the food source of *Limapontia depressa*. The effects of termperature must be equally considered when discussing the distribution of algae. If, as Todd (1991) suggested, temperature has an effect on the composition of algae, then it may be that during the summer months the algae is of little or no nutritive value. Khan (1999) found that there was a severe drop in nitrogen levels in the algae during the summer months. A change in algal composition may be a strong indication to *L. depressa* to find a more favourable habitat.

The predation issue was investigated through the use of exclusion zones. It must be noted that there were some problems with the method, which do not allow concrete conclusions. The conditions created were probably inhospitable to the animals over a long period and the effect of tides in the area was restricted.

6.3 Population Study

The population study as a whole revealed a very strong seasonal trend for three sampling periods over a 30 month period, highest densities occurring in the winter and spring months, whilst animals were generally non-existent during the summer months. Analysis of animal length revealed an increase in animal length from a minimum of 1.1mm at the start of the season in October to a maximum length of 5.3mm before they disappeared in April. Chia (1971) calculated the mean egg size as being 80μm in diameter. It is therefore possible to suggest that the animals found at the beginning of the sampling periods in November 1997 and October 1998 were recruit animals.

Limapontia depressa appeared in October at relatively low temperatures with some algal presence. These animals were quite small. They grew continuously without much evidence of further recruitment until April. The animals density began to decrease when temperatures increased. The disappearance of the animals in May occurred over a very short period, as little as two weeks.

Opisthobranch life-history strategies are described as being opportunistic for a number of reasons such as continuous recruitment, rapid growth, the continuous small size of juvenilles and short life-span. Miller (1962) stated that rapid growth and maturation, accelerated by temperature and food supply must allow the production of several generations during the reproductive season. Consequently, Trowbridge (1993) found a fast-growth rate and a high level of fecundity in her study of the sacoglossan *Aplysiopsis enteromorphae* in Oregon, 1990.

Even though Figure 5.13 suggests that the growth rate of *Limapontia depressa* can be described as fast and correlates well with the findings of Trowbridge (1993), there are other factors of its opportunistic life-history which are not so evident. There is no visual proof from Figure 5.13 to suggest that there are two or more cohorts present during the sampling season and there was never any concrete evidence of a reproduction period, even though egg masses were found.

Larval strategies in general have been discussed by several authors (Clark & Goetzfried, 1978; Todd, 1991; Pechenik, 1999). However, the literature referring to nudibranch larvae are limited and Miller (1962) provided a comprehensive review of literature discussing this notion. Moreover, specific literature referring to sacoglossan development is inadequate.

In studying nudibranch annual cycles in a region where there is an intertidal zone, migration theories are popular. Balch (1908) amongst others believed that the animals which suddenly appeared in the intertidal zone had migrated from deep water to the shore for the purpose of breeding. Accordingly, their abrupt disappearance at the end of the spawning season was perceived as the death of spawning adults. Garstang (1890), following his studies on *Goniodoris nodosa*, concluded that larvae metamorphosed off-

89

shore and the early post-larvae travelled towards the shore reaching it at an advanced stage. Garstang suggested that this accounted for the absence of very small animals in his samples. Eliot (1910) and Chambers (1934) suggest that the tidal currents in the habitat may be responsible for the erratic movements of *Limapontia depressa*. Crozier (1917) concluded that the shoreward movement of *Chromodoris zebra* was not connected with breeding but with changes in environmental parameters such as light.

Sacoglossa from Florida show a higher incidence of lecithotrophic and direct development patterns than those of Great Britain or southern New England. This finding contradicts Thorson (1950), who suggested that benthic invertebrate development patterns were geographically correlated with temperature, through control of the period of habitability and surface waters and the larval development rates. Effectively this would mean an increase in direct development from tropical waters to polar regions. However, this is not the case as concluded by Clark and Goetzfried (1978). Although, Todd (1991) stated that evolutionarily, direct development is on the increase, this is not the case for *Limapontia depressa*. Both Clark & Jensen (1981) and Chia (1971) have referred to planktotrophic veliger larval development of *Limapontia depressa*.

There have been some studies on the oviposition and fecundity of *Limapontia depressa* which have been discussed in Chapter 3. Chia (1971) investigated spawn masses of *Limapontia depressa* and the effects of some environmental parameters. Table 6.1 records the egg-laying pattern of the animal within a month.

Table 6.1 Record of egg-laying by 70 animals within a month (Chia, 1971)

Date	April									May		
	11	16	18	20	22	24	26	28	3	5	10	12
No of spawn masses laid	0	2	9	34	59	70	50	34	35	20	23	0

Chia (1971) found that continuous light or dark tended to repress spawning, but throughout his studies the spawning pattern did not change after returning to normal conditions. As temperature increased, the period required for larval development

decreased. The author also found that whilst embryos develop in moist air or water, the veligers will not hatch unless completely covered by water.

It is at this stage that the migration and development pattern theories are considered important. Considering the previous comments on these theories however, it would not be feasible to apply them to the reappearance of *Limapontia depressa* at the sites. It is more conceivable that the adults spawn in April during periods of food host stability and relatively high nutrient value before they gradually die-off. It is possible that the spawn remain in the general area until conditions are suitable for hatching, however it is important to emphasise that despite intensive searches, spawn were not found in the field consistently. On the other hand, if spawn is present throughout the season the larval development period may be substantially reduced. The recolonization of the algal mat habitat may be aided by some animals being carried inwards on the shore due to tidal inundation (Miller, 1962). This is supported by Hiscock (1999) when commenting on recovery potential of species - planktotrophic larvae are assigned a high to very high recovery potential and adult populations are expected to recover within a few weeks or at most six months. There will be an in depth discussion on the population dynamics in the next section.

In the light of the above literature, the observations made between February 1997 and June 1999 must be discussed. From descriptions of the reproduction strategies provided in various literature, it seems unlikely that the slugs would develop a migration pattern as suggested by Balch (1908) and Garstang (1890) when the planktotrophic veliger larval stage itself may be dispersed by water if necessary. It is also not very feasible to suggest that the minute creatures would be able to cover long distances in a definite direction. It may be ascertained that the absence of small animals from the above studies is simply because they are so small, 1.1mm to 5.3mm. The varying coloration of the animals is another obstacle that does not make the sampling protocol any easier. Therefore, it is not surprising that very small animals may have been overlooked in sampling. On the other hand, if the sample is left open to the air, the animals will actually make themselves quite visible in time by crawling out onto the open sediment. On occasion, even though it may be assumed that all animals have been procured, a large number of animals may have been overlooked.

Animals were not seen copulating at any stage of the season during the course of this study. The single egg mass found in April 1998 did not occur in a sample in which animals were present. Furthermore, these spawn could not be encouraged to hatch even though all treatments recorded in the literature were utilised. Either there was a highly specific factor not exercised or there is an inherent variation in the slugs not conducive to the spawning treatments out of their natural environment.

6.4 Energy Budget Measurements

Studies of the flow and allocation of energy in biological systems often have as their ultimate goal the construction of a budget describing the partitioning of energy within an individual, population or community. Such budgets are then used to make inferences about physiology or ecology, in particular explaining why an organism or population does what it is observed to do, assuming that energy allocation is the overriding concern (Davies & Hatcher, 1998). Care should be taken when discussing any values obtained as the data are only strictly applicable to the animal at the exact time of measurement. Attempts were made to calculate two budget variables, respiration and biomass.

6.4.1 Biomass

The link that exists between a population study and an energy budget is most evident when discussing biomass measurements. It is not possible to determine biomass or discuss its significance without reference to the population structure of the organism.

The chemical biomass measurements did not result in any data which would prove useful for statistical analysis. However, the procedure refinement that resulted indicated that the method described by Russell-Hunter *et al.* (1968) is not applicable in its entirety to *Limapontia depressa* and revisions will be required before appropriate data can be recorded. It was determined in the present study that the number of animals required for analysis were such that there were not enough animals in a length class within the samples to allow the procedure to determine organic carbon.

On the other hand, the mathematical model described in Chapter 5 provides approximate values. The biomass of individual *Limapontia depressa* increased sharply over the sampling season as did that of the population untilthey disappeared at the start of the summer.

6.4.2 Respiration

The marine littoral is characterised by extensive gradients of temperature variation and environmental O_2 concentration that are associated with vertical height above the low water mark (McMahon & Wilson, 1981). For the purposes of this study however, the samples were not separated on the basis of site, respiration measurements were recorded cumulatively for all animals found during one sampling trip.

The stresses under which these measurements are made must be taken into account. The act of moving animals from the field to the laboratory may cause stresses that last through experimental procedure. On the other hand, there would also be a large amount of stress involved in placing the animals in the respiration chambers. This was limited as much as possible by slowly introducing the animals to the experimental procedure.

The respiration measurements calculated during the course of experiment provided irregular results. However, it can be concluded that the respiration rate at 10°C is generally higher than that at 20°C. There was no significant difference between measurements as regards season. The fact that oxygen consumption increased at lower temperatures is unusual. The initial reaction would be to suggest that temperature inversely affects oxygen consumption in *Limapontia depressa*. This may be related to the disappearance of animals at high temperatures from the saltmarsh and intertidal zones. It is possible that an effect such as 'heat coma' is observed as the animals would not normally be subjected to such temperatures.

6.5 Conclusions

Limapontia depressa displays a sporadic life history, being absent for most of the summer months and then returning to the saltmarsh habitat in September or October producing the most abundant numbers during the winter months.

The temporal distribution pattern appears to be largely determined by a variety of environmental parameters, with temperature appearing to have most influence.

Limapontia depressa biomass increases sharply throughout the season until the animal disappears in summer. *L. depressa* has a longer turnover rate in relation to its size than that indicated by previous work on other sacoglossans.

Respiration measurements produced results which indicate that the respiration rate is higher at lower temperatures. Oxygen consumption at high temperatures may also be an indicator of temperature stress.

It is not clear whether *Limapontia depressa* actually controls the prevalence of algal mats, but it is likely that it is influenced by algal presence and *vice versa*.

Chapter 7

Future Work

It is important that the gaps that still exist about sacoglossan biology are studied. Recommendations for future studies are as follows:

- A concerted effort should be made to recreate the conditions in which *Limapontia depressa* lives in the laboratory, such as a microcosm study, in order that the conditions in which it is active may be recorded more accurately. One could look into the possibility of colouring the organisms with a luminescent dye, which would consequently be recorded on video. This might provide a more comprehensive picture of the movement of the animals.

- As there is a reasonable spatial distribution of *Limapontia depressa* around the Irish Coast, a population survey similar to that carried out during this study would prove useful. There could follow an analysis of latitude versus population distribution. It would be important to include habitat topography in this study. An environmental analysis of the environment would also be productive, perhaps concentrating on the effects of season and temperature, as these most influenced the findings of the present study.

- The respiration study warrants further work in determining the laboratory tolerances experienced by the animal so that there should be no doubt as to the extent of stresses to the animal.

- It is vitally important that the issue of the food algae be investigated to fully clarify the algae which make up the diet of *Limapontia depressa* at North Bull Island. Analysis of the biochemical and nutritive values of the algal mats, such as C:N ratios, directly from the field may result in significant correlations with *Limapontia depressa* presence.

- An investigation into the possible predators of *Limapontia depressa* would prove very useful but would require strict vigilance in the field. It was observed that there large amounts of birds feeding in the general environment of the slug.

References

Alder, J., and Hancock, A., (1845 - 1855). *A monograph of the British Nudibranchiate Mollusca.* Ray Society, London.

Allen, S.E., (ed.) (1989). *Chemical Analysis of Ecological Materials.* Blackwell Scientific, Oxford.

An Foras Forbatha, (1977). *Inventory of Outstanding Landscapes in Ireland.* An Foras Forbatha, Dublin.

An Foras Forbatha, (1977). *A Study of Bull Island, Co. Dublin.* An Foras Forbatha, Dublin.

Balch F.N., (1908). Two interesting New England nudibranch records. *Nautilus*, 22, 13.

Banse, K., and Mosher, S., (1980). Adult body mass and annual production/biomass relationships of field populations. *Ecological Monograph*, 50, 355 - 379.

Barrett, J., & Yonge, C.M., (1958). *Collins Pocket Guide to the Sea Shore.* Collins, London.

Begon, M., Mortimer, M. & Thompson, D.J., (1996). *Population Ecology, A Unified Study of Plants and Animals.* Blackwell Scientific, Oxford.

Bold, H.C., and Wynne, J., (1985). *Introduction to the Algae.* 2nd edition. Prentice-Hall Inc., New Jersey.

Brennan, M., Wilson, J.G., Jeffrey, D.W. and Dowley, A. (1994). *Particulate nutrient inputs and their role in macro-algal development in Dublin Bay.* Department of the Environment, Dublin.

Brunton, M., (1987). Hydrology of Dublin Bay. **IN** *Managing Dublin Bay*, (Brunton, M., Convery, F.J. and Johnson, A., eds.), pp 19 - 20. Resource and Environmental Policy Centre, University College Dublin.

Burrows, E. M., (1991). *Seaweeds of the British Isles*, Volume 2 Chlorophyta. National History Museum, London.

Chambers, L.A., (1934). Studies on the organs of reproduction in the nudibranchiate molluscs, with special reference to *Embletonia fuscata* Gould. *Bulletin of the American Museum of Natural History*, 66, 599 - 641.

Chia, F.S., (1971). Oviposition, fecundity and larval development of three sacoglossan opisthobranchs from the Northumberland Coast, England. *Veliger*, 13 (4), 319 - 325.

Clark, K.B., and DeFreese, D., (1987). Population ecology of Caribbean ascoglossa (Mollusca: Opisthobranchia): a study of specialised algal herbivores. *American Malacological Bulletin*, 5, 259 - 280.

Clark, K.B., and Goetzfried, A., (1978). Zoogeographic influences on development patterns of North Atlantic ascoglossa and nudibranchia, with a discussion of factors affecting egg size and number. *Journal of Molluscan Studies*, 44, 283 - 294.

Clark, K.B., and Jensen, K.R., (1981). A comparison of egg size, capsule size, and development patterns in the order Ascoglossa (Sacoglossa) (Mollusca: Opisthobranchia). *International Journal of Invertebrate Reproduction*, 3, 57 - 64.

Collins, J.F. and Cummins, T., (1996). *Agroclimatic Atlas of Ireland*. ASMET, Dublin.

Cossins, A.R., and Bowler, K., (1987). *Temperature Biology of Animals*. Chapman & Hall, London.

Crozier, W.J., (1917). On a periodic shoreward migration of tropical nudibranchs. *American Naturalist*, 51, 377 - 382.

Crisp, D.J., (1984). Energy Flow Measurements. **IN** *Methods for the study of Marine Benthos*, 2nd edition, (Holme, N.A. & McIntyre, A.D., eds.), pp.284 - 387. Blackwell Scientific, Oxford.

Daley, R.G. and Brown, S.R., (1973). Experimental characteristics of lacustrine chlorophyll diagenisis. Physiological and environmental effects. *Arch. Hydrobiol.*, 72, 277 - 304.

Davies M.S., and Hatcher, A.M., (1998). The energy budget: a useful tool? *Annales Zoologici Fennici*, 35, (4), 231 - 240.

Davis, J.P., and Wilson, J.G., (1983). Seasonal changes in tissue weight and biochemical composition of the bivalve *Nucula turgida* in Dublin Bay with reference to gametogenesis. *Netherlands Journal of Sea Research*, 17, (1), 84 – 95.

DeFreese, D., and Clark, K.B., (1991). Transepidermal uptake of dissolved free amino acids from seawater by three ascoglossan opisthobranchs. *Journal of Molluscan Studies*, 57, 65 - 74.

Eliot, C., (1910). *A monograph of the British Nudibranchiate Mollusca* (cf. Alder & Hancock). Part VII (Supplementary). London (Ray Society).

Finch, T.F., and Gardiner, M.J., (1993). *Soils of Tipperary North Riding, Soil Survey Bulletin No. 42.* Teagasc, Dublin.

Fogg, G.E., and Belcher, J.H., (1961). Pigments from the bottom deposits of an English lake. *New Phytol.*, 60, 129 - 142.

Fox, D.L., (1944). Fossil pigments. *Scientific Monthly*, 59, 394 - 396.

Fretter, V., (1941). On the structure of the gut of the ascolglossan nudibranchs. *Proceedings of the Zoological Society of London*, series B, 110, 185 - 198.

Garstang, W., (1890). A complete list of the opisthobranchiate Mollusca found at Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, 35, 307 - 325.

Gascoigne, T., (1956). Feeding and Reproduction in the Limapontiidae. *Transactions of the Royal Society of Edinburgh*, 63, 129 - 151.

Gascoigne, T., (1974). A note on some sacoglossan penial styles (Gastropoda: Opisthobranchia). *Zoological Journal of the Linnean Society*, 55, 53 - 59.

Gascoigne, T. and Platts, E., (1974). *Alderia modesta* (Loven) and *Limapontia depressa* (Alder and Hancock) in Down and Antrim: the latter species new to Ireland. *Irish Naturists Journal*, 18, 123.

Gascoigne, T., (1976). The reproductive systems and classification of the Stiligeridae (Opisthobranchia: Sacoglossa). *Journal of the Malacological Society of Australia*, 3, 157 - 172.

Gascoigne, T., (1978). British forms of *Limapontia depressa* Alder and Hancock, 1862 (Opisthobranchia: Ascoglossa). *Journal of Conchology*, 29, 253 - 259.

Gascoigne, T. and Sartory, P.K., (1974). The teeth of three bivalved gastropods and three other species of the order Sacoglossa, with an appendix on *Calliopaea oophaga* n.sp., a new sacoglossan by H. Lemche. *Proceedings of the Malacological Society of London*, 41, 109 - 126.

Graham, A., (1955). Molluscan diets. *Proceedings of the Malacological Society*, 31, 144 - 153.

Harris, C.R., (1977). Sedimentology and geomorphology. **IN** *North Bull Island, Dublin Bay - a modern coastal natural history*. (Jeffrey, D.W. ed.), pp. 13-25. Royal Dublin Society.

Harrison, S.J., (1985). Heat Exchanges in Muddy Intertidal Sediments: Chichester Harbour, West Sussex, England. *Estuarine, Coastal and Shelf Science*, 20, 477 - 490.

Healy, B., (1975. Fauna of the Salt-marsh, North Bull Island, Dublin. *Proceedings of the Royal Irish Academy*, 75, (B), 225 - 244.

Healy, B. and McGrath, D., (1998). Marine fauna of County Wexford, Ireland: the fauna of rocky shores and sandy beaches. *Irish Fisheries Investigations*, 2, 1 – 91.

Healy, B., and Oliver, G.A., (1998). Irish coastal lagoons: summary of a survey. *Bulletin of the Irish Geographical Society*, 21, 116 – 150.

Heip, C., Herman, P.M.J., and Coomans, A., (1984). The productivity of marine meiobenthos. *Academiae Analecta*, 44, (2), 1 - 20.

Hinde, R., and Smith, D.C., (1974). "Chloroplast symbiosis" and the extent to which it occurs in Sacoglossa (Gastropoda: Mollusca). *Biol. Linn. Soc.*, 6, 349-356.

Hinde, R., (1980). Chloroplast "symbiosis" in sacoglossan molluscs. **IN** *Edocytobiology, Endosymbiosis and cell biology. Proceedings of the international colloquium endosymbiosis and cell research*, (Schwemmler, W. and Schenk, H.E.A., eds.), pp 729 - 736. Tübingen, Germany.

Hiscock, K., (1999). Identifying marine 'sensitive areas' - the importance of understanding life cycles. **IN** *Aquatic Life Cycle Strategies, Survival in a variable environment*, (Whitfield, M., Matthews, J., and Reynolds, C., eds.), pp 97 - 104. Marine Biological Association of the United Kingdom.

Jeffrey, D.W. (ed.) (1977). *North Bull Island, Dublin Bay - a modern coastal natural history*. Royal Dublin Society.

Jeffrey, D.W., Madden, B., Rafferty, B., Dwyer, R., Wilson, J., and Allot, N., (1992). *Dublin Bay Water Quality Management Plan, Technical Report No.7, Algal Growths and Foreshore Quality*. Environmental Research Unit, Dublin.

Jeffrey, D.W., Madden, B., and Rafferty, B., (1993). Beach fouling by *Ectocarpus siliculosus* in Dublin Bay. Marine Pollution Bulletin, 26 (1), 51 - 53.

Jeffrey, D.W., Brennan, M.T., Jennings, E., Madden, B., and Wilson, J.G., (1995). Nutrient sources for in-shore nuisance macroalgae: The Dublin Bay Case. *Ophelia*, 42, 147 - 161.

Jennings, E., (1996). Sediment-Water Nitrogen Exchange in the Intertidal Areas of Dublin Bay. Ph.D. Thesis, Trinity College, Dublin.

Jensen, K., (1975). Food preference and food consumption in relation to growth of *Limapontia capitata* (Opisthobranchia, Sacoglossa). *Ophelia,* 14, 1 - 14.

Jensen, K., (1976). The importance of *Limapontia capitata* (Mueller) (Opisthobranchia, Sacoglossa) as a primary producer in the *Cladophora* belt. *Proc. 10th Eur. Symp. Mar. Biol.,* 2, 339 - 350.

Jensen, K., (1977). Optimal salinity temperature intervals of *Limapontia capitata* (Opisthobranchia, Sacoglossa) determined by growth and heart rate measurements. *Ophelia,* 16, 175-185.

Jensen, K., (1980). A review of sacoglossan diets, with comparitive notes on radular and buccal anatomy. *Malacological Review,* 13, 55 - 77.

Jensen, K., (1981a). Observations on feeding methods in some Florida ascoglossans. *Journal of Molluscan Studies,* 47, 190 - 199.

Jensen, K.R., (1981b). Influence of filament diameter on food preference and growth in *Oxynoe azuropunctata* Jensen, 1980 and *Elysia cauze* Marcus, 1957 (Opisthobranchia: Ascolglossa). *Ophelia,* 20, 127 - 135.

Jensen, K., (1983). Factors affecting feeding selectivity in herbivorous ascoglossa (Mollusca: Opisthobranchia). *Journal of Experimental Marine Biology and Ecology,* 66, 135 - 148.

Jensen, K., (1991). Comparison of alimentary systems in shelled and non-shelled sacoglossa (Mollusca, Opisthobranchia). *Acta Zoologica* (Stockholm), 72 (3), 143 - 150.

Jensen, K.R., (1993). Morphological adaptations and plasticity of radular teeth of the Sacoglossa (=Ascoglossa) (Mollusca: Opisthobranchia) in relation to their food plants. *Biological Journal of the Linnean Society,* 48, 135 - 155.

Jensen, K., (1994). Behavioural adaptations and diet specificity of sacoglossan opisthobranchs. *Ethology, Ecology and Evolution,* 6, 87 - 101.

Jensen, K., (1996). Phylogenetic systematics and classification of the Sacoglossa (Mollusca, Gastropoda, Opisthobranchia). *Philosophical Transactions of the Royal Society of London*, 351, 91 - 122.

Jensen, K.R., (1997). *Systematics, phylogeny and evolution of the Sacoglossa (Mollusca, Opisthobranchia)*. Vestjydsk Forlag, Denmark.

Kennish, Michael J., (1986). *Ecology of Estuaries*, Volume 1: Physical and Chemical Aspects. CRC Press Inc., Florida.

Kevan, D.K., (1934). *Limapontia depressa* (A. & H.) var. nov. in Scotland. *Journal of Conchology*, 20, 16 - 24.

Kevan, D.K. (1939). Further notes on *Limapontia depressa* (A. & H.) var. *pellucida* Kevan. *Journal of Conchology*, 21 (6), 160 - 162.

Kevan, D.K., (1941). Notes on *Limapontia depressa* (A. & H.) var. *pellucida* Kevan kept under artificial conditions. *Journal of Conchology*, 21 (10), 301 - 302.

Khan, J., (1998). *Factors Influencing Macroalgal Growth in the Dublin Bay Lagoons*. Ph.D. Thesis, Trinity College, Dublin.

Kohn, A.J., (1983). Feeding biology of gastropods. **IN** *The Mollusca*, Volume 5: Physiology, Part 2, (Saleuddin, A.S.M. and WilburK.M., eds.), pp 1 - 63. Academic Press, London.

Lorenzon, C.J., (1967). Determination of chlorophyll and phaeo-pigments: spectrophotometric equations. *Limnology of Oceanography*, 12, 343 - 346.

Macnae, W., (1954). On four sacoglossan molluscs new to South Africa. *Ann Natal Mus.*, 13, 51 - 54.

Maguire, B., (1990). *The Macroalgae of Dublin Bay: Identification, Spatial and Temporal Distribution*. Unpublished B.A. Mod. Thesis, Trinity College, Dublin.

Marine Institute, (1999). Ireland's Marine and Coastal Areas and Adjacent Seas, An Environmental Assessment. Marine Institute, Dublin.

McHugh, R. and Partners, (1991). *Dublin Bay Water Quality Management Plan, Technical Report No.1, Recreation, Amenity and Wildlife Conservation Study.* Environmental Research Unit, Dublin.

McLusky, D.S., (1989). *The Estuarine Ecosystem.* Blackie, Glasgow.

McMahon, R.F., and Russell-Hunter, W.D., (1977). Temperature relations of aerial and aquatic respiration in six littoral smails in relation to their vertical zonation. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole,* 152, 182 - 198.

McMahon, R.F., and Russell-Hunter, W.D., (1978). Respiratory responses to low oxygen stress in marine littoral and sublittoral snails. *Physiol. Zöol.,* 51, 408 - 424.

McMahon, R.F., and Wilson, J.G., (1981). Effects of temperature and hypoxia on the oxygen consumption of three species of intertidal bivalve molluscs from Dublin Bay, Ireland. *Journal of Thermal Biology,* 6, 267 -277.

Miller, M.C., (1962). Annual cycles of some Manx nudibranchs, with a discussion of the problem of migration. *Journal of Animal Ecology,* 31, 545 - 569.

Newell, R.C., (1979). *Biology of Intertidal Animals.* Marine Ecological Surveys, Kent.

Nicol, E.A.T., (1935). The ecology of a salt marsh. *Journal of the Marine Biological Association of the United Kingdom,* 20, 203 - 261.

Oertli, B., and Dall, P.C., (1993). Population dynamics and energy budget of *Nemoura avicularis* (Plecoptera) in Lake Esrom, Denmark. *Limnologica,* 23 (2), 115 - 122.

Ostergaard, J.M., (1950). Spawning and development of some Hawaiin marine Gastropods. *Pacific Science,* 4, 75 - 115.

O'Sullivan, A.J., (1987). Recreation. **IN** *Managing Dublin Bay,* (Brunton, M., Convery, F.J. and Johnson, A., eds.), pp 112 - 128. Resource and Environmental Policy Centre, University College Dublin.

Pechenik, J.A., (1999). On the benefits of being a larva......or not. **IN** *Aquatic Life Cycle Strategies, Survival in a variable environment*, (Whitfield, M., Matthews, J., and Reynolds, C., eds.), pp 97 - 104. Marine Biological Association of the United Kingdom.

Pelseneer, P., (1934). Bionomics of a Brackish-water Nudibranch: *Limapontia depressa*. *Journal of Conchology*, 20, 54 - 55.

Phillipson, J., (1975). Introduction to ecological energetics. **IN** *Methods for Ecological Bioenergetics*. (Grodzinski, W., Klekowski, R.Z. and Duncan A., eds.), pp 3 - 14. Blackwell Scientific, Oxford,.

Pitkin, P.H., (1977). Distribution and biology of algae. **IN** *North Bull Island, Dublin Bay - a Modern Coastal Natural History*. (Jeffrey , D.W., ed.), pp 32 - 37. Royal Dublin Society.

Quick, M.E., (1950). Observations on *Limapontia*. *Proceedings of the Royal Malacological Society of London*, 28, 134 - 138.

Raffaelli, D., Hull, S., and Milne, H., (1989). Long-term changes in nutrients, weed mats and shorebirds in an estuarine system. *Cah. Biol. Mar.*, 30 (2), 59 - 270.

Reise, K., (1984). Indirect effects of sewage on a sandy tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research*, 10, 148 - 153.

Russell-Hunter,W.D. and McMahon, R., (1968). On the use of a "wet-oxidation" method for estimates of total organic carbon in mollusc growth studies. *Proceedings of the Malacological Society of London*, 38, 1-11.

Sanger, J.E., and Gorham, E., (1972a). Stratigraphy of fossil pigments as a guide to the postglacial history of Kirchner Marsh, Minnesota. *Limnology and Oceanography*, 17, 840 - 854.

Schwinghammer, P., Hargrave, B., Peer, D., and Hawkins, C.M., (1986). Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. *Marine Ecology - Progress Series*, 31, 131 - 142.

Strathmann, R., and Vedder, K., (1977). Size and organic content of eggs of echinoderms and other invertebrates as related to developmental strategies and egg eating. Marine Biology, 39, 305 – 309.

Swain, E.B., (1985). Measurement and interpretation of sedimentary pigments. *Freshwater Biology*, 15, 53 - 75.

Thompson, T.E., and Brown, G.H., (1976). *British Opisthobranch Molluscs, Mollusca: Gastropoda, Keys and Notes for the Identification of the Species*. For the Linnean Society of London by Academic Press, London.

Thorson, G., (1946). Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Medd. Komm. Havundersøg. Kbh. (Ser Plankton)*, 4, 5 - 523.

Todd, C.D., (1991). Larval strategies of nudibranch molluscs: similar means to the same end?. *Malacologia*, 32, (2), 273 - 289.

Trowbridge, C.D., (1993). Population structure of two common species of ascoglossan (=sacoglossan) opisthobranchs on the central coast of Oregon, USA. *Veliger*, 36 (2), 99 - 106.

Trowbridge, C.D., (1995). Hypodermic insemination, oviposition, and embryonic development of a pool-dwelling ascoglossan (=sacoglossan) opisthobranch: *Ercolania felina* (Hutton, 1882) on New Zealand shores. *Veliger*, 38 (3), 203 - 211.

Vallentyne, J.R., (1955). Sedimentary chlorophyll determination as a paleobotanical method. *Can. Jour. Bot.*, 33, 304 - 313.

Wells, M.J., and Clarke, A., (1996). Energetics: the costs of living and reproducing for an individual cephalopod. *Philosophical Transactions of the Royal Society of London, Series B*, 351, 1083 - 1104.

Williams, M.L., and Cobb, A.H., (1992). Chloroplasts in animals: photosynthesis and assimilate distribution in chloroplast 'symbioses'. **IN** *Carbon partitioning within and*

between organisms. (Pollock, C.J., Farrar, J.F. & Gordon, A.J., eds.), pp 32 - 37. BIOS Scientific Publishers, Cambridge.

Wilson. J.G., (1983). The future for the cockle *Cerastoderma edule* in Dublin Bay. *Occ. Publ. Ir. Biogeog. Soc.*, 2, 141 - 149.

Young, C.M., (1999). Marine Invertebrate Larvae. **IN** *Encyclopedia of Reproduction.* (Knobil, E., & Neill, J.D., eds.), Volume 3, pp 89 - 97. Academic Press.

Appendices

Appendix 1: General sampling diary from February 1997 to July 1999.

Appendix 2: Raw data for % moisture content analysis.

Appendix 3: Raw data for % organic carbon analysis.

Appendix 4: Raw data from analysis of chlorophyll a (μg g^{-1}).

Appendix 5: Animal density (cm^2) at each site.

Appendix 6: Biomass (kjm^{-2}) for each monthly sampling collection.

Appendix 7: Respiration analysis data.

Appendix 1: General sampling diary from February 1997 to July 1999.

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (^{0}C)	ESB Temp. (^{0}C)	Salinity
28-Feb-97	59	S	08:24	1.04	A1	10.8	7.7	35.8
28-Feb-97	59	S	08:24	1.04	A2	10.5	7.7	35.8
28-Feb-97	59	S	08:24	1.04	B1	10.7	7.7	35.7
28-Feb-97	59	S	08:24	1.04	B2	10.5	7.7	35.8
19-Mar-97	78	N	14:31	1.24	A1	11.9	9.6	34.8
19-Mar-97	78	N	14:31	1.24	A2	11.6	9.6	34.7
19-Mar-97	78	N	14:31	1.24	B1	11.6	9.6	34.7
19-Mar-97	78	N	14:31	1.24	B2	11.5	9.6	34.6
04-Apr-97	94	N	14:42	0.72	A1	12.6	10.3	33.9
04-Apr-97	94	N	14:42	0.72	A2	12.5	10.3	33.8
04-Apr-97	94	N	14:42	0.72	B1	12.4	10.3	33.9
04-Apr-97	94	N	14:42	0.72	B2	12.4	10.3	33.9
16-Apr-97	106	N	12:49	1.34	A1	11.7	10.9	32.8
16-Apr-97	106	N	12:49	1.34	A2	11.7	10.9	32.8
16-Apr-97	106	N	12:49	1.34	B1	11.7	10.9	32.7
16-Apr-97	106	N	12:49	1.34	B2	11.6	10.9	32.8
30-Apr-97	120	S	10:57	1.06	A1	15.7	11.0	34.8
30-Apr-97	120	S	10:57	1.06	A2	15.6	11.0	34.6
30-Apr-97	120	S	10:57	1.06	B1	15.6	11.0	34.6
30-Apr-97	120	S	10:57	1.06	B2	15.4	11.0	34.7
13-May-97	133	S	09:53	1.14	A1	14.4	11.9	33.5
13-May-97	133	S	09:53	1.14	A2	14.7	11.9	30.9
13-May-97	133	S	09:53	1.14	B1	13.4	11.9	30.9
13-May-97	133	S	09:53	1.14	B2	14.9	11.9	31.7

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (°C)	ESB Temp. (°C)	Salinity
20-May-97	140	N	15:56	0.89	A1		14.9	
20-May-97	140	N	15:56	0.89	A2	22.6	14.9	32.2
20-May-97	140	N	15:56	0.89	B1	25.6	14.9	27.0
20-May-97	140	N	15:56	0.89	B2	24.0	14.9	28.9
26-May-97	146	S	19:53	0.81	A1		14.5	
26-May-97	146	S	19:53	0.81	A2	21.4	14.5	34.9
26-May-97	146	S	19:53	0.81	B1	21.1	14.5	34.1
26-May-97	146	S	19:53	0.81	B2	17.6	14.5	34.1
28-May-97	148	S	09:29	0.77	A1		14.5	
28-May-97	148	S	09:29	0.77	A2		14.5	
28-May-97	148	S	09:29	0.77	B1		14.5	
28-May-97	148	S	09:29	0.77	B2		14.5	
10-Jun-97	161	S	08:30	0.90	A1		14.7	
10-Jun-97	161	S	08:30	0.90	A2		14.7	
10-Jun-97	161	S	08:30	0.90	B1		14.7	
10-Jun-97	161	S	08:30	0.90	B2		14.7	
17-Jun-97	168	N	14:40	1.09	A1		11.5	
17-Jun-97	168	N	14:40	1.09	A2		11.5	
17-Jun-97	168	N	14:40	1.09	B1		11.5	
17-Jun-97	168	N	14:40	1.09	B2	27.6	11.5	23.4
24-Jun-97	175	S	19:39	0.67	A1		14.3	
24-Jun-97	175	S	19:39	0.67	A2		14.3	
24-Jun-97	175	S	19:39	0.67	B1		14.3	
24-Jun-97	175	S	19:39	0.67	B2	28.2	14.3	23.2
07-Jul-97	188	S	18:49	0.89	A1		16.5	
07-Jul-97	188	S	18:49	0.89	A2		16.5	
07-Jul-97	188	S	18:49	0.89	B1		16.5	
07-Jul-97	188	S	18:49	0.89	B2		16.5	

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (°C)	ESB Temp. (°C)	Salinity
29-Jul-97	210	S	13:08	1.23	A1		16.7	
29-Jul-97	210	S	13:08	1.23	A2		16.7	
29-Jul-97	210	S	13:08	1.23	B1		16.7	
29-Jul-97	210	S	13:08	1.23	B2		16.7	
08-Aug-97	220	S	08:06	0.88	A1		18.7	
08-Aug-97	220	S	08:06	0.88	A2		18.7	
08-Aug-97	220	S	08:06	0.88	B1		18.7	
08-Aug-97	220	S	08:06	0.88	B2		18.7	
15-Aug-97	227	S	14:26	1.19	A1		17.9	
15-Aug-97	227	S	14:26	1.19	A2		17.9	
15-Aug-97	227	S	14:26	1.19	B1		17.9	
15-Aug-97	227	S	14:26	1.19	B2		17.9	
22-Aug-97	234	S	07:32	0.29	A1		17.2	
22-Aug-97	234	S	07:32	0.29	A2		17.2	
22-Aug-97	234	S	07:32	0.29	B1		17.2	
22-Aug-97	234	S	07:32	0.29	B2	24.2	17.2	28.9
28-Aug-97	240	N	13:53	1.46	A1		16.2	
28-Aug-97	240	N	13:53	1.46	A2	22.3	16.2	32.8
28-Aug-97	240	N	13:53	1.46	B1		16.2	
28-Aug-97	240	N	13:53	1.46	B2	21.8	16.2	31.5
24-Sep-97	267	S	14:09	1.57	A1	22.5	15.3	35.4
24-Sep-97	267	S	14:09	1.57	A2	22.4	15.3	37.9
24-Sep-97	267	S	14:09	1.57	B1	21.6	15.3	34.6
24-Sep-97	267	S	14:09	1.57	B2	27.5	15.3	38.2
29-Sep-97	272	N	13:55	1.15	A1		15.3	
29-Sep-97	272	N	13:55	1.15	A2	22.5	15.3	37.6
29-Sep-97	272	N	13:55	1.15	B1		15.3	
29-Sep-97	272	N	13:55	1.15	B2	22.8	15.3	37.9

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (^{0}C)	ESB Temp. (^{0}C)	Salinity
07-Oct-97	280	S	00:57	1.07	A1	18.6	14.6	35.9
07-Oct-97	280	S	00:57	1.07	A2	17.9	14.6	37.4
07-Oct-97	280	S	00:57	1.07	B1	18.2	14.6	35.4
07-Oct-97	280	S	00:57	1.07	B2	17.7	14.6	37.3
13-Oct-97	286	N	09:36	1.06	A1	15.5	11.6	32.3
13-Oct-97	286	N	09:36	1.06	A2	15.8	11.6	34.2
13-Oct-97	286	N	09:36	1.06	B1	16.1	11.6	32.0
13-Oct-97	286	N	09:36	1.06	B2	15.9	11.6	33.6
21-Oct-97	294	S	04:48	1.12	A1	13.8	12.6	35.9
21-Oct-97	294	S	04:48	1.12	A2	13.4	12.6	36.5
21-Oct-97	294	S	04:48	1.12	B1	14.1	12.6	36.4
21-Oct-97	294	S	04:48	1.12	B2	13.9	12.6	36.4
28-Oct-97	301	N	07:12	1.24	A1	14.8	11.5	34.8
28-Oct-97	301	N	07:12	1.24	A2	14.7	11.5	35.1
28-Oct-97	301	N	07:12	1.24	B1	15.0	11.5	34.7
28-Oct-97	301	N	07:12	1.24	B2	14.9	11.5	34.9
10-Nov-97	314	N	04:19	1.31	A1	15.1	12.3	33.8
10-Nov-97	314	N	04:19	1.31	A2	14.1	12.3	34.2
10-Nov-97	314	N	04:19	1.31	B1	14.8	12.3	33.8
10-Nov-97	314	N	04:19	1.31	B2	14.2	12.3	33.4
20-Nov-97	324	S	11:31	1.39	A1	13.6	10.1	32.8
20-Nov-97	324	S	11:31	1.39	A2	13.5	10.1	31.5
20-Nov-97	324	S	11:31	1.39	B1	13.5	10.1	32.1
20-Nov-97	324	S	11:31	1.39	B2	13.3	10.1	31.7
28-Nov-97	332	N	01:40	1.10	A1	13.8	9.7	31.5
28-Nov-97	332	N	01:40	1.10	A2	13.9	9.7	30.9
28-Nov-97	332	N	01:40	1.10	B1	13.7	9.7	30.9
28-Nov-97	332	N	01:40	1.10	B2	13.6	9.7	30.7

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (^{0}C)	ESB Temp. (^{0}C)	Salinity
05-Dec-97	339	S	04:04	1.07	A1	9.8	11.3	30.8
05-Dec-97	339	S	04:04	1.07	A2	9.9	11.3	30.7
05-Dec-97	339	S	04:04	1.07	B1	9.9	11.3	30.6
05-Dec-97	339	S	04:04	1.07	B2	9.7	11.3	30.2
08-Jan-98	373	N	07:26	1.27	A1	10.8	8.8	28.7
08-Jan-98	373	N	07:26	1.27	A2	10.2	8.8	28.4
08-Jan-98	373	N	07:26	1.27	B1	10.5	8.8	28.3
08-Jan-98	373	N	07:26	1.27	B2	10.4	8.8	28.2
19-Jan-98	384	S	04:19	1.33	A1	9.2	6.0	31.8
19-Jan-98	384	S	04:19	1.33	A2	8.9	6.0	31.5
19-Jan-98	384	S	04:19	1.33	B1	8.8	6.0	31.7
19-Jan-98	384	S	04:19	1.33	B2	8.2	6.0	31.5
27-Jan-98	392	N	07:26	0.73	A1	10.8	6.7	31.9
27-Jan-98	392	N	07:26	0.73	A2	10.2	6.7	31.8
27-Jan-98	392	N	07:26	0.73	B1	10.3	6.7	31.7
27-Jan-98	392	N	07:26	0.73	B2	10.1	6.7	31.6
04-Feb-98	400	S	09:07	1.21	A1	9.8	9.0	35.9
04-Feb-98	400	S	09:07	1.21	A2	9.5	9.0	35.7
04-Feb-98	400	S	09:07	1.21	B1	9.7	9.0	35.8
04-Feb-98	400	S	09:07	1.21	B2	9.6	9.0	35.4
17-Feb-98	413	S	07:26	1.12	A1	9.2	9.8	36.9
17-Feb-98	413	S	07:26	1.12	A2	9.0	9.8	36.7
17-Feb-98	413	S	07:26	1.12	B1	9.1	9.8	36.8
17-Feb-98	413	S	07:26	1.12	B2	9.0	9.8	36.6
25-Feb-98	421	N	02:24	0.60	A1	10.8	8.8	33.9
25-Feb-98	421	N	02:24	0.60	A2	10.7	8.8	34.5
25-Feb-98	421	N	02:24	0.60	B1	10.9	8.8	33.9
25-Feb-98	421	N	02:24	0.60	B2	10.8	8.8	34.1

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (^{0}C)	ESB Temp. (^{0}C)	Salinity
10-Mar-98	434	N	12:43	0.94	A1	11.9	10.2	31.9
10-Mar-98	434	N	12:43	0.94	A2	11.5	10.2	31.5
10-Mar-98	434	N	12:43	0.94	B1	11.6	10.2	31.7
10-Mar-98	434	N	12:43	0.94	B2	11.4	10.2	31.6
27-Mar-98	451	N	07:26	0.28	A1	10.9	11.3	29.8
27-Mar-98	451	N	07:26	0.28	A2	10.7	11.3	29.7
27-Mar-98	451	N	07:26	0.28	B1	10.7	11.3	29.9
27-Mar-98	451	N	07:26	0.28	B2	10.5	11.3	29.6
06-Apr-98	461	N	10:19	1.22	A1	11.9	10.4	26.9
06-Apr-98	461	N	10:19	1.22	A2	11.6	10.4	27.5
06-Apr-98	461	N	10:19	1.22	B1	11.7	10.4	27.1
06-Apr-98	461	N	10:19	1.22	B2	11.3	10.4	27.4
16-Apr-98	471	S	06:57	0.88	A1	13.6	10.0	29.9
16-Apr-98	471	S	06:57	0.88	A2	13.3	10.0	29.8
16-Apr-98	471	S	06:57	0.88	B1	13.4	10.0	29.7
16-Apr-98	471	S	06:57	0.88	B2	13.1	10.0	29.8
01-May-98	486	S	07:55	0.75	A1	9.8	11.2	31.9
01-May-98	486	S	07:55	0.75	A2	9.5	11.2	31.7
01-May-98	486	S	07:55	0.75	B1	9.9	11.2	31.8
01-May-98	486	S	07:55	0.75	B2	9.6	11.2	31.6
08-May-98	493	N	08:09	0.97	A1	9.9	12.2	26.9
08-May-98	493	N	08:09	0.97	A2	9.8	12.2	26.2
08-May-98	493	N	08:09	0.97	B1	9.7	12.2	26.7
08-May-98	493	N	08:09	0.97	B2	9.5	12.2	26.4
19-May-98	504	S	14:09	1.07	A1		15.4	
19-May-98	504	S	14:09	1.07	A2		15.4	
19-May-98	504	S	14:09	1.07	B1		15.4	
19-May-98	504	S	14:09	1.07	B2		15.4	

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (°C)	ESB Temp. (°C)	Salinity
03-Jun-98	519	N	04:19	1.22	A1		14.8	
03-Jun-98	519	N	04:19	1.22	A2	14.8	14.8	25.9
03-Jun-98	519	N	04:19	1.22	B1		14.8	
03-Jun-98	519	N	04:19	1.22	B2	14.6	14.8	25.5
16-Jun-98	532	S	06:28	0.81	A1		17.8	
16-Jun-98	532	S	06:28	0.81	A2	16.9	17.8	26.8
16-Jun-98	532	S	06:28	0.81	B1		17.8	
16-Jun-98	532	S	06:28	0.81	B2	16.8	17.8	26.7
18-Jun-98	534	N	09:07	0.88	A1		17.8	
18-Jun-98	534	N	09:07	0.88	A2	19.5	17.8	25.4
18-Jun-98	534	N	09:07	0.88	B1		17.8	
18-Jun-98	534	N	09:07	0.88	B2	19.5	17.8	25.3
17-Aug-98	594	N	01:12	1.25	A1		17.1	
17-Aug-98	594	N	01:12	1.25	A2		17.1	
17-Aug-98	594	N	01:12	1.25	B1		17.1	
17-Aug-98	594	N	01:12	1.25	B2	17.9	17.1	27.5
01-Sep-98	609	N	12:57	1.57	A1		15.9	
01-Sep-98	609	N	12:57	1.57	A2	18.8	15.9	28.8
01-Sep-98	609	N	12:57	1.57	B1		15.9	
01-Sep-98	609	N	12:57	1.57	B2	19.2	15.9	27.3
15-Sep-98	623	N	12:00	1.49	A1		15.5	
15-Sep-98	623	N	12:00	1.49	A2	16.1	15.5	24.3
15-Sep-98	623	N	12:00	1.49	B1		15.5	
15-Sep-98	623	N	12:00	1.49	B2	16.8	15.5	24.1
21-Sep-98	629	S	08:09	0.86	A1	18.2	15.7	33.1
21-Sep-98	629	S	08:09	0.86	A2	17.9	15.7	33.4
21-Sep-98	629	S	08:09	0.86	B1	18.4	15.7	32.8
21-Sep-98	629	S	08:09	0.86	B2	17.8	15.7	34.8

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (°C)	ESB Temp. (°C)	Salinity
28-Sep-98	636	S	11:02	1.51	A1	16.5	14.5	32.7
28-Sep-98	636	S	11:02	1.51	A2	15.9	14.5	33.6
28-Sep-98	636	S	11:02	1.51	B1	16.2	14.5	31.9
28-Sep-98	636	S	11:02	1.51	B2	15.8	14.5	34.0
19-Oct-98	657	N	09:21	1.00	A1	12.1	11.9	28.2
19-Oct-98	657	N	09:21	1.00	A2	11.8	11.9	29.6
19-Oct-98	657	N	09:21	1.00	B1	12.0	11.9	27.9
19-Oct-98	657	N	09:21	1.00	B2	11.9	11.9	29.4
29-Oct-98	667	N	09:50	1.67	A1	12.1	11.9	27.6
29-Oct-98	667	N	09:50	1.67	A2	11.6	11.9	28.8
29-Oct-98	667	N	09:50	1.67	B1	11.8	11.9	27.1
29-Oct-98	667	N	09:50	1.67	B2	11.7	11.9	29.1
09-Nov-98	678	S	06:14	0.61	A1	16.1	10.1	31.2
09-Nov-98	678	S	06:14	0.61	A2	15.1	10.1	32.3
09-Nov-98	678	S	06:14	0.61	B1	15.7	10.1	32.0
09-Nov-98	678	S	06:14	0.61	B2	15.2	10.1	32.4
26-Nov-98	695	S	11:16	1.50	A1	14.9	9.2	33.8
26-Nov-98	695	S	11:16	1.50	A2	14.5	9.2	34.1
26-Nov-98	695	S	11:16	1.50	B1	14.6	9.2	33.9
26-Nov-98	695	S	11:16	1.50	B2	14.5	9.2	34.5
30-Nov-98	699	N	01:40	1.14	A1	10.9	9.2	30.3
30-Nov-98	699	N	01:40	1.14	A2	10.2	9.2	31.5
30-Nov-98	699	N	01:40	1.14	B1	11.1	9.2	30.1
30-Nov-98	699	N	01:40	1.14	B2	10.3	9.2	31.8
03-Dec-98	702	N	08:24	0.52	A1	10.2	9.4	29.4
03-Dec-98	702	N	08:24	0.52	A2	9.8	9.4	30.1
03-Dec-98	702	N	08:24	0.52	B1	10.0	9.4	29.5
03-Dec-98	702	N	08:24	0.52	B2	9.7	9.4	30.4

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (^{0}C)	ESB Temp. (^{0}C)	Salinity
11-Dec-98	710	N	02:38	1.67	A1	12.3	10.6	27.9
11-Dec-98	710	N	02:38	1.67	A2	12.1	10.6	28.5
11-Dec-98	710	N	02:38	1.67	B1	12.4	10.6	27.6
11-Dec-98	710	N	02:38	1.67	B2	12.1	10.6	28.4
04-Feb-99	765	S	07:18	0.88	A1	11.9	6.1	29.8
04-Feb-99	765	S	07:18	0.88	A2	12.2	6.1	30.5
04-Feb-99	765	S	07:18	0.88	B1	11.9	6.1	31.5
04-Feb-99	765	S	07:18	0.88	B2	12.0	6.1	31.4
12-Feb-99	773	N	14:49	1.36	A1	8.8	7.6	27.1
12-Feb-99	773	N	14:49	1.36	A2	8.9	7.6	28.0
12-Feb-99	773	N	14:49	1.36	B1	8.9	7.6	28.2
12-Feb-99	773	N	14:49	1.36	B2	8.8	7.6	28.1
26-Feb-99	787	N	14:20	1.11	A1	11.4	9.0	27.1
26-Feb-99	787	N	14:20	1.11	A2	11.3	9.0	27.9
26-Feb-99	787	N	14:20	1.11	B1	11.2	9.0	27.4
26-Feb-99	787	N	14:20	1.11	B2	10.9	9.0	28.1
15-Mar-99	804	N	15:44	0.89	A1	14.2	8.9	29.1
15-Mar-99	804	N	15:44	0.89	A2	14.1	8.9	30.0
15-Mar-99	804	N	15:44	0.89	B1	14.1	8.9	29.2
15-Mar-99	804	N	15:44	0.89	B2	13.8	8.9	31.5
26-Mar-99	815	N	12:56	1.21	A1	9.3	9.7	26.8
26-Mar-99	815	N	12:56	1.21	A2	9.1	9.7	27.0
26-Mar-99	815	N	12:56	1.21	B1	9.2	9.7	26.9
26-Mar-99	815	N	12:56	1.21	B2	9.1	9.7	27.2
12-Apr-99	832	N	15:27	1.05	A1	11.5	9.5	26.5
12-Apr-99	832	N	15:27	1.05	A2	11.6	9.5	27.1
12-Apr-99	832	N	15:27	1.05	B1	11.6	9.5	26.8
12-Apr-99	832	N	15:27	1.05	B2	11.4	9.5	27.2

Date	Julian Day	Tide	Time	Height	Site	Sampling Temp. (^{0}C)	ESB Temp. (^{0}C)	Salinity
22-Apr-99	842	N	11:01	0.97	A1	13.2	9.7	22.4
22-Apr-99	842	N	11:01	0.97	A2	13.0	9.7	23.1
22-Apr-99	842	N	11:01	0.97	B1	13.1	9.7	22.6
22-Apr-99	842	N	11:01	0.97	B2	12.9	9.7	23.0
29-Apr-99	849	N	17:45	0.80	A1	13.8	9.7	26.7
29-Apr-99	849	N	17:45	0.80	A2	13.6	9.7	27.5
29-Apr-99	849	N	17:45	0.80	B1	13.7	9.7	27.2
29-Apr-99	849	N	17:45	0.80	B2	13.5	9.7	27.3
11-May-99	861	N	14:45	0.97	A1		12.6	
11-May-99	861	N	14:45	0.97	A2		12.6	
11-May-99	861	N	14:45	0.97	B1		12.6	
11-May-99	861	N	14:45	0.97	B2		12.6	
03-Jun-99	884	S	08:32	0.94	A1		14.0	
03-Jun-99	884	S	08:32	0.94	A2	17.0	14.0	25.7
03-Jun-99	884	S	08:32	0.94	B1		14.0	
03-Jun-99	884	S	08:32	0.94	B2	16.9	14.0	25.6
23-Jun-99	904	N	14:26	1.20	A1		15.3	
23-Jun-99	904	N	14:26	1.20	A2		15.3	
23-Jun-99	904	N	14:26	1.20	B1		15.3	
23-Jun-99	904	N	14:26	1.20	B2		15.3	
08-Jul-99	919	N	01:32	0.94	A1		16.9	
08-Jul-99	919	N	01:32	0.94	A2		16.9	
08-Jul-99	919	N	01:32	0.94	B1		16.9	
08-Jul-99	919	N	01:32	0.94	B2		16.9	

Appendix 2: Raw data for % moisture content analysis.

Date	Tide	Site	Weight of Sample	Dried Weight	Loss in Weight	% Moisture Content
16-Apr-97	N	A1	80.15	57.35	22.80	28.45
16-Apr-97	N	A2	90.54	54.22	36.32	40.12
16-Apr-97	N	B1	87.32	57.95	29.37	33.64
16-Apr-97	N	B2	101.51	58.56	42.95	42.31
13-May-97	S	A1	94.05	61.55	32.50	34.56
13-May-97	S	A2	90.58	54.47	36.11	39.87
13-May-97	S	B1	96.22	65.28	30.94	32.16
13-May-97	S	B2	100.61	61.60	39.01	38.77
10-Jun-97	S	A1	102.54	60.99	41.55	40.52
10-Jun-97	S	A2	89.78	46.02	43.76	48.74
10-Jun-97	S	B1	90.69	54.53	36.16	39.87
10-Jun-97	S	B2	94.78	45.63	49.15	51.86
21-Jul-97	S	A1	99.84	80.00	19.84	19.87
21-Jul-97	S	A2	95.62	72.13	23.49	24.57
21-Jul-97	S	B1	101.33	78.58	22.75	22.45
21-Jul-97	S	B2	78.56	58.94	19.62	24.97
21-Aug-97	S	A1	85.21	66.08	19.13	22.45
21-Aug-97	S	A2	98.70	70.33	28.37	28.74
21-Aug-97	S	B1	95.26	76.07	19.19	20.14
21-Aug-97	S	B2	95.59	66.80	28.79	30.12
24-Sep-97	S	A1	84.65	63.88	20.77	24.54
24-Sep-97	S	A2	89.44	59.61	29.83	33.35
24-Sep-97	S	B1	90.21	65.88	24.33	26.97
24-Sep-97	S	B2	87.64	57.61	30.03	34.26

Date	Tide	Site	Weight of Sample	Dried Weight	Loss in Weight	% Moisture Content
21-Oct-97	S	A1	84.95	63.32	21.63	25.46
21-Oct-97	S	A2	123.88	82.68	41.20	33.26
21-Oct-97	S	B1	117.04	87.23	29.81	25.47
21-Oct-97	S	B2	98.53	63.14	35.39	35.92
20-Nov-97	S	A1	98.67	59.08	39.59	40.12
20-Nov-97	S	A2	105.69	46.25	59.44	56.24
20-Nov-97	S	B1	110.24	66.32	43.92	39.84
20-Nov-97	S	B2	102.87	41.01	61.86	60.13
05-Dec-97	S	A1	85.36	53.67	31.69	37.12
05-Dec-97	S	A2	80.14	39.44	40.70	50.78
05-Dec-97	S	B1	75.10	44.96	30.14	40.13
05-Dec-97	S	B2	78.49	31.87	46.62	59.40
19-Jan-98	S	A1	196.05	120.67	75.38	38.45
19-Jan-98	S	A2	206.77	102.41	104.36	50.47
19-Jan-98	S	B1	194.44	107.37	87.07	44.78
19-Jan-98	S	B2	247.71	97.65	150.06	60.58
25-Feb-98	N	A1	121.54	78.73	42.81	35.22
25-Feb-98	N	A2	119.87	59.82	60.05	50.10
25-Feb-98	N	B1	124.68	80.07	44.61	35.78
25-Feb-98	N	B2	121.34	55.38	65.96	54.36
27-Mar-98	N	A1	100.24	60.02	40.22	40.12
27-Mar-98	N	A2	105.87	47.03	58.84	55.58
27-Mar-98	N	B1	110.64	67.15	43.49	39.31
27-Mar-98	N	B2	102.33	40.65	61.68	60.28
16-Apr-98	S	A1	107.13	65.93	41.20	38.46
16-Apr-98	S	A2	75.64	37.08	38.56	50.98
16-Apr-98	S	B1	90.55	57.06	33.49	36.98
16-Apr-98	S	B2	103.38	41.70	61.68	59.66

Date	Tide	Site	Weight of Sample	Dried Weight	Loss in Weight	% Moisture Content
19-May-98	S	A1	119.89	80.16	39.73	33.14
19-May-98	S	A2	165.93	106.84	59.09	35.61
19-May-98	S	B1	154.85	108.67	46.18	29.82
19-May-98	S	B2	251.91	162.99	88.92	35.30
18-Jun-98	N	A1	98.64	74.81	23.83	24.16
18-Jun-98	N	A2	129.08	84.91	44.17	34.22
18-Jun-98	N	B1	103.69	79.27	24.42	23.55
18-Jun-98	N	B2	99.70	61.48	38.22	38.34

Appendix 3: Raw data for % organic carbon analysis.

Date	Tide	Site	Crucible No.	Wt. Of crucible	Wt. of sample and crucible	Wt. of sample	Wt. Loss	% LOI
16-Apr-97	N	A1	215	6.7420	7.7500	1.0080	0.1023	10.15
16-Apr-97	N	A2	205	6.7851	7.7901	1.0050	0.1275	12.69
16-Apr-97	N	B1	210	6.7416	7.7416	1.0000	0.1258	12.58
16-Apr-97	N	B2	202	6.7614	7.7614	1.0000	0.1112	11.12
13-May-97	S	A1	215	6.7418	7.7428	1.0010	0.1287	12.86
13-May-97	S	A2	205	6.7852	7.7853	1.0001	0.1785	17.85
13-May-97	S	B1	210	6.7416	7.7418	1.0002	0.1515	15.15
13-May-97	S	B2	202	6.7610	7.7610	1.0000	0.1292	12.92
10-Jun-97	S	A1	215	6.7419	7.7440	1.0021	0.1348	13.45
10-Jun-97	S	A2	205	6.7851	7.7860	1.0009	0.1479	14.78
10-Jun-97	S	B1	210	6.7411	7.7429	1.0018	0.1354	13.52
10-Jun-97	S	B2	202	6.7598	7.7606	1.0008	0.1294	12.93
21-Jul-97	S	A1	215	6.7415	7.7415	1.0000	0.1321	13.21
21-Jul-97	S	A2	205	6.7854	7.7854	1.0000	0.1387	13.87
21-Jul-97	S	B1	210	6.7400	7.7410	1.0010	0.1402	14.01
21-Jul-97	S	B2	202	6.7614	7.7623	1.0009	0.1246	12.45
21-Aug-97	S	A1	215	6.7420	7.7425	1.0005	0.1199	11.98
21-Aug-97	S	A2	205	6.7850	7.7848	0.9998	0.1330	13.30
21-Aug-97	S	B1	210	6.7399	7.7405	1.0006	0.1255	12.54
21-Aug-97	S	B2	202	6.7692	7.7702	1.0010	0.1149	11.48
24-Sep-97	S	A1	215	6.7418	7.7435	1.0017	0.1317	13.15
24-Sep-97	S	A2	205	6.7851	7.7863	1.0012	0.1463	14.61
24-Sep-97	S	B1	210	6.7416	7.7422	1.0006	0.1454	14.53
24-Sep-97	S	B2	202	6.7614	7.7625	1.0011	0.1325	13.24

Date	Tide	Site	Crucible No.	Wt. Of crucible	Wt. of sample and crucible	Wt. of sample	Wt. Loss	% LOI
21-Oct-97	S	A1	215	6.7420	7.7433	1.0013	0.1206	12.04
21-Oct-97	S	A2	205	6.7851	7.7872	1.0021	0.1290	12.87
21-Oct-97	S	B1	210	6.7416	7.7423	1.0007	0.1199	11.98
21-Oct-97	S	B2	202	6.7614	7.7623	1.0009	0.1164	11.63
20-Nov-97	S	A1	215	6.7420	7.7440	1.0020	0.0980	9.78
20-Nov-97	S	A2	205	6.7851	7.7863	1.0012	0.0899	8.98
20-Nov-97	S	B1	210	6.7416	7.7447	1.0031	0.0915	9.12
20-Nov-97	S	B2	202	6.7614	7.7623	1.0009	0.0855	8.54
05-Dec-97	S	A1	215	6.7419	7.7429	1.0010	0.0855	8.54
05-Dec-97	S	A2	205	6.7851	7.7863	1.0012	0.0824	8.23
05-Dec-97	S	B1	210	6.7411	7.7433	1.0022	0.0823	8.21
05-Dec-97	S	B2	202	6.7598	7.7617	1.0019	0.0797	7.95
19-Jan-98	S	A1	215	6.7417	7.7431	1.0014	0.0714	7.13
19-Jan-98	S	A2	205	6.7853	7.7861	1.0008	0.0755	7.54
19-Jan-98	S	B1	210	6.7415	7.7412	0.9997	0.0698	6.98
19-Jan-98	S	B2	202	6.7619	7.7622	1.0003	0.0711	7.11
25-Feb-98	N	A1	215	6.7420	7.7432	1.0012	0.0846	8.45
25-Feb-98	N	A2	205	6.7851	7.7869	1.0018	0.0879	8.77
25-Feb-98	N	B1	210	6.7412	7.7432	1.0020	0.0828	8.26
25-Feb-98	N	B2	202	6.7615	7.7638	1.0023	0.0814	8.12
27-Mar-98	N	A1	215	6.7422	7.7452	1.0030	0.0957	9.54
27-Mar-98	N	A2	205	6.7856	7.7871	1.0015	0.0979	9.78
27-Mar-98	N	B1	210	6.7419	7.7426	1.0007	0.0870	8.69
27-Mar-98	N	B2	202	6.7619	7.7621	1.0002	0.0805	8.05
16-Apr-98	S	A1	215	6.7501	7.7505	1.0004	0.1012	10.12
16-Apr-98	S	A2	205	6.7859	7.7859	1.0000	0.1057	10.57
16-Apr-98	S	B1	210	6.7420	7.7421	1.0001	0.0989	9.89
16-Apr-98	S	B2	202	6.7623	7.7632	1.0009	0.0972	9.71

Date	Tide	Site	Crucible No.	Wt. Of crucible	Wt. of sample and crucible	Wt. of sample	Wt. Loss	% LOI
19-May-98	S	A1	215	6.7418	7.7418	1.0000	0.1156	11.56
19-May-98	S	A2	205	6.7851	7.7859	1.0008	0.1298	12.97
19-May-98	S	B1	210	6.7416	7.7426	1.0010	0.1286	12.85
19-May-98	S	B2	202	6.7614	7.7621	1.0007	0.1172	11.71
18-Jun-98	N	A1	215	6.7420	7.7426	1.0006	0.1359	13.58
18-Jun-98	N	A2	205	6.7854	7.7857	1.0003	0.1402	14.02
18-Jun-98	N	B1	210	6.7416	7.7419	1.0003	0.1423	14.23
18-Jun-98	N	B2	202	6.7614	7.7618	1.0004	0.1357	13.56

Appendix 4: Raw data from analysis of chlorophyll a (μg g^{-1}).

Date	Site	665o	665a	Chl a (μg g^{-1})
16-Apr-97	A1	0.322	0.255	17.83
16-Apr-97	A2	0.125	0.068	15.28
16-Apr-97	B1	1.033	0.931	27.36
16-Apr-97	B2	0.995	0.875	32.14
13-May-97	A1	0.912	0.822	24.03
13-May-97	A2	0.562	0.468	25.10
13-May-97	B1	1.754	1.441	83.57
13-May-97	B2	1.343	1.093	66.87
10-Jun-97	A1	1.320	1.144	46.99
10-Jun-97	A2	1.125	0.961	43.70
10-Jun-97	B1	1.430	1.266	43.81
10-Jun-97	B2	1.751	1.460	77.57
21-Jul-97	A1	0.158	0.057	27.00
21-Jul-97	A2	0.262	0.173	23.79
21-Jul-97	B1	1.212	0.915	79.30
21-Jul-97	B2	1.220	1.055	44.06
21-Aug-97	A1	0.184	0.093	24.41
21-Aug-97	A2	0.271	0.173	26.20
21-Aug-97	B1	0.541	0.483	15.49
21-Aug-97	B2	0.884	0.807	20.56
24-Sep-97	A1	0.134	0.082	13.77
24-Sep-97	A2	0.144	0.082	16.56
24-Sep-97	B1	0.403	0.367	9.61
24-Sep-97	B2	0.784	0.045	13.35
21-Oct-97	A1	0.122	0.091	8.14
21-Oct-97	A2	0.098	0.064	9.14
21-Oct-97	B1	0.192	0.170	5.87
21-Oct-97	B2	0.358	0.318	10.63
20-Nov-97	A1	0.087	0.067	5.29
20-Nov-97	A2	0.081	0.059	5.99
20-Nov-97	B1	0.187	0.161	6.83
20-Nov-97	B2	0.124	0.089	9.39
05-Dec-97	A1	0.081	0.060	5.70
05-Dec-97	A2	0.088	0.057	8.21
05-Dec-97	B1	0.123	0.099	6.28
05-Dec-97	B2	0.098	0.068	8.03
19-Jan-98	A1	0.097	0.064	8.68
19-Jan-98	A2	0.090	0.057	8.92
19-Jan-98	B1	0.103	0.067	9.55
19-Jan-98	B2	0.085	0.045	10.70

Date	Site	665o	665a	Chl a (μg g^{-1})
25-Feb-98	A1	0.092	0.061	8.20
25-Feb-98	A2	0.079	0.049	7.95
25-Feb-98	B1	0.094	0.060	9.13
25-Feb-98	B2	0.154	0.098	15.02
27-Mar-98	A1	0.298	0.250	12.88
27-Mar-98	A2	0.110	0.065	12.06
27-Mar-98	B1	0.250	0.199	13.68
27-Mar-98	B2	0.673	0.604	18.54
16-Apr-98	A1	0.406	0.352	14.37
16-Apr-98	A2	0.403	0.340	16.87
16-Apr-98	B1	0.621	0.529	24.67
16-Apr-98	B2	0.985	0.875	29.37
19-May-98	A1	0.883	0.791	24.63
19-May-98	A2	1.121	1.021	26.82
19-May-98	B1	1.344	1.090	67.82
19-May-98	B2	1.452	1.192	69.50
18-Jun-98	A1	1.284	1.130	41.13
18-Jun-98	A2	1.436	1.287	39.88
18-Jun-98	B1	1.119	0.941	47.59
18-Jun-98	B2	1.115	0.944	45.61

Appendix 5: Animal density (cm²) at each site.

DATE	A1	A2	B1	B2
28-Feb-97	0.76	1.02	1.27	1.53
19-Mar-97	0.61	0.97	1.63	1.99
04-Apr-97	0.81	1.43	2.14	2.04
16-Apr-97	1.17	1.58	1.94	2.19
30-Apr-97	0.61	1.32	1.48	1.78
13-May-97	0.10	0.36	0.87	1.12
20-May-97	0.20	0.31	0.51	0.66
26-May-97	0.00	0.31	0.46	0.61
28-May-97	0.00	0.00	0.00	0.00
10-Jun-97	0.00	0.00	0.00	0.00
17-Jun-97	0.00	0.00	0.00	0.00
24-Jun-97	0.00	0.00	0.00	0.00
07-Jul-97	0.00	0.00	0.00	0.00
29-Jul-97	0.00	0.00	0.00	0.00
08-Aug-97	0.00	0.00	0.00	0.00
15-Aug-97	0.00	0.00	0.00	0.00
22-Aug-97	0.00	0.00	0.00	0.10
28-Aug-97	0.00	0.00	0.00	0.05
24-Sep-97	0.00	0.00	0.00	0.00
29-Sep-97	0.00	0.00	0.00	0.00
07-Oct-97	0.20	0.36	0.46	0.92
13-Oct-97	0.20	0.41	0.76	0.97
21-Oct-97	0.25	0.46	0.51	0.56
28-Oct-97	0.31	0.51	0.81	0.97
10-Nov-97	0.31	0.56	0.97	1.02
20-Nov-97	0.56	0.97	1.07	1.48
28-Nov-97	0.76	1.02	0.97	1.68
05-Dec-97	0.87	1.32	1.68	1.94
08-Jan-98	0.81	1.38	1.94	2.29
19-Jan-98	0.76	0.87	1.27	1.88
27-Jan-98	0.81	1.48	1.94	2.14
04-Feb-98	0.41	0.87	1.27	1.32
17-Feb-98	0.15	0.46	1.07	1.17
25-Feb-98	1.43	1.58	1.38	1.94
10-Mar-98	1.02	1.43	1.73	1.99

DATE	A1	A2	B1	B2
27-Mar-98	0.97	1.58	1.94	2.04
06-Apr-98	0.92	1.48	1.99	2.14
16-Apr-98	0.87	0.92	1.27	1.53
01-May-98	0.25	0.31	0.71	0.76
08-May-98	0.31	0.46	0.61	0.97
19-May-98	0.00	0.00	0.00	0.00
03-Jun-98	0.00	0.05	0.00	0.10
16-Jun-98	0.00	0.00	0.00	0.00
18-Jun-98	0.00	0.00	0.00	0.00
17-Aug-98	0.00	0.00	0.00	0.00
01-Sep-98	0.00	0.00	0.00	0.00
15-Sep-98	0.00	0.00	0.00	0.00
21-Sep-98	0.00	0.00	0.00	0.00
28-Sep-98	0.00	0.00	0.00	0.00
19-Oct-98	0.15	0.41	0.41	0.66
29-Oct-98	0.25	0.51	0.61	0.92
09-Nov-98	0.36	0.61	0.92	1.02
26-Nov-98	0.76	1.12	1.38	1.68
30-Nov-98	0.97	1.27	1.43	1.88
03-Dec-98	0.81	1.27	1.53	1.99
11-Dec-98	0.76	1.32	1.58	1.78
04-Feb-99	0.92	1.43	1.73	2.09
12-Feb-99	0.61	0.97	1.12	1.22
26-Feb-99	0.25	0.81	0.97	1.27
15-Mar-99	0.87	1.07	1.32	1.63
26-Mar-99	0.76	0.97	1.07	1.17
12-Apr-99	0.41	0.76	0.97	0.92
22-Apr-99	0.31	0.46	0.76	0.97
29-Apr-99	0.25	0.46	0.81	1.02
11-May-99	0.05	0.00	0.05	0.10
03-Jun-99	0.00	0.00	0.00	0.00
23-Jun-99	0.00	0.00	0.00	0.00
08-Jul-99	0.00	0.00	0.00	0.00

Appendix 6: Biomass (kjm^{-2}) for each monthly sampling collection.

Date	Biomass(kjm^{-2})
Nov-97	20.060
Dec-97	45.924
Jan-98	63.579
Feb-98	28.396
Mar-98	89.805
Apr-98	75.051
Oct-98	3.162
Nov-98	23.448
Dec-98	40.749
Jan-99	78.610
Feb-99	47.316
Mar-99	58.359

Appendix 7: Respiration analysis data based on 30 animals per chamber, (salinity = 25; volume of water = 4mls; 4 hour period).

Date	Average pressure (hpa)	Temp (^{O}C)	O_2 solubility (μg ml^{-1})	Time (hrs)	% O_2 used	μg/animal/hour
20-Oct-98	50.25	20	0.0775	4	25	0.0135
21-Oct-98	9	10	0.0949	4	23	0.0027
30-Oct-98	189.25	20	0.0775	4	26	0.0530
02-Nov-98	836	10	0.0949	4	22	0.2425
10-Nov-98	212	20	0.0775	4	25	0.0570
11-Nov-98	134.25	10	0.0949	4	21	0.0372
27-Nov-98	163.25	20	0.0775	4	20	0.0351
02-Dec-98	325.5	10	0.0949	4	19	0.0815
14-Dec-98	109.75	20	0.0775	4	19	0.0224
15-Dec-98	215.25	10	0.0949	4	20	0.0568
05-Feb-99	252	20	0.0775	4	19	0.0515
08-Feb-99	31.75	10	0.0949	4	18	0.0075
15-Feb-99	211.25	20	0.0775	4	18	0.0409
16-Feb-99	192.5	10	0.0949	4	17	0.0431
01-Mar-99	63.75	20	0.0775	4	25	0.0172
02-Mar-99	929.25	10	0.0949	4	23	0.2818
16-Mar-99	280.75	20	0.0775	4	26	0.0786
17-Mar-99	283.5	10	0.0949	4	22	0.0822
29-Mar-99	28.75	20	0.0775	4	27	0.0084
30-Mar-99	107.5	10	0.0949	4	24	0.0340
12-Apr-99	70	20	0.0775	4	28	0.0211
13-Apr-99	993	10	0.0949	4	26	0.3404
26-Apr-99	206.25	20	0.0775	4	27	0.0599

Date	Average pressure (hpa)	Temp (°C)	O_2 solubility (μg ml^{-1})	Time (hrs)	% O_2 used	μg/anim/hr
27-Apr-99	320.75	10	0.0949	4	26	0.1100
12-May-99	34	20	0.0775	4	28	0.0102
13-May-99	28.25	10	0.0949	4	27	0.0101