THE INTERTIDAL ECOSYSTEM:
THE VALUE OF IRELAND'S SHORES

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The seminar and book were generously sponsored by
the Marine Institute (Ireland)
and
the Industrial Research and Technology Unit (Northern Ireland)

Royal Irish Academy
Dublin 2005

ROYAL IRISH ACADEMY
19 DAWSON STREET
DUBLIN 2

ISBN 1 904890 09 1

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library.

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FOREWORD: THE INTERTIDAL SYSTEM

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On behalf of the Marine Institute, I would like to commend the initiative by the Royal Irish Academy's National Committee for Biology in organising this exciting Conference on "The Intertidal System" and to say how delighted the Marine Institute is to be one of the sponsors.

The Intertidal Zone is where the sea meets the land. It is, in many cases, our first personal contact with the rich biological diversity and form of marine life. Indeed many a career in marine science can trace its genesis to a youthful experience splashing around in an intertidal pool.

Ireland is fortunate in having a diverse coastline. Extending for over 7,500 km, our coastline encompasses a broad range of intertidal habitats from rocky shorelines to sandy beaches, muddy lagoons and estuarine mud flats. Many of these habitats are of national and/or international importance and warrant conservation whether as Special Areas of Conservation (SACs) or other designations.

While we can appreciate the aesthetic and "*quality of life*" value of the coastal zone, though perhaps not put an economic value on it, we very often overlook the very significant ecological function provided by the intertidal zone. In this context, we look forward to the keynote presentation by Dr Wilson of the Gund Institute for Ecological Economics (Vermont, USA) who are internationally recognised experts in this field.

Intertidal biodiversity provides us with a measure of environmental quality, sentinel species such as the dogwelk (*Nucella*) and the mussel (*Mytilus*) provide a warning of environmental pollution, while species such as the barnacle are being used to monitor climate change. As a laboratory, for educational and experimental purposes, the intertidal is unique. It provides many with their first introduction to taxonomy, and is a natural laboratory for experiments in physiology, form and function.

As to the sustainable economic value of intertidal resources, I was surprised to learn that the lowly periwinkle (*Littorina littorea*) is worth some €6 million/annum to the economy. The Irish Seaweed Centre informs us that intertidal seaweeds contribute another €6 million/annum. The value of intertidal aquaculture is well known and I have no doubt that others will give examples of the economic value of intertidal resources.

And who knows what new developments in marine biotechnology might provide? Perhaps the mussel and barnacle will give up their illusive secret to "*the glue that sets underwater*".

A Conference like this fulfils many functions:

- It provides an opportunity to review existing and on-going work. Many of you will be familiar with the results of the EU Life BioMar project. But how many are familiar with the results of the EU *INTERREG*-II funded SensMap project which has mapped intertidal habitats along the east coast or of the JNCC Directory of the Celtic Seas and Coasts?
- It provides an opportunity to network with colleagues, find out what they are doing and share experiences and approaches to common problems.
- It provides an opportunity to identify gap areas and propose ways to address these.
- In this context, we hope and trust that RIA will produce a Proceedings of this Conference.

This decade, the first decade of the New Millennium, promises to be an exciting era for Irish marine science. Through NDP funding, marine research facilities and capacities in the third level sector and in state research organisations are being strengthened. Competitive research funding is available like it never was before from both European Union–6th Framework Programme (2002–2006), Life, and INTERREGs IIIA (Ireland/Wales) and IIIC (Atlantic Rim) and national sources (National Development Plan). Partnership, both between Irish institutions and with the international scientific community, will be the key to success.

PREFACE

We live in a world increasingly impacted by man's activities. Human population continues to grow, and more importantly perhaps human expectations continue to grow. Since 1950 the population of the world has increased from 2.5 billion to over 5.4 billion. Of the present total, almost three-quarters are accounted for by the developing nations, whose aspirations, not unnaturally, are to raise their lifestyle to the level enjoyed by the developed countries. Over the next three decades not only will another 3 billion people will be added to the world's population, but also this increase will be in those underdeveloped countries striving to raise living standards. Increasing numbers of people combined with demand for a better standard of living will lead inevitably to increasing pressures on natural resources.

These pressures are most acutely felt in the intertidal system. The bulk of the world's population lives near, or on, the coast and it is here that the demands on the system are greatest.

Over the past thirty years or so there has also been an increasing awareness of environmental matters and environmental problems, coupled with a realisation that technology alone is not going to resolve all the problems we are faced with. It is also fair to say that many of the earlier doomsday predictions have not been borne out, and although food supply, to take a popular example dear to all ecologists' hearts, is certainly a problem in some parts of the world, the global system as a whole does still produce enough to go round, and the problem is one of distribution and allocation and local imbalances of supply and demand. Local pressures are often ignored or passed over in the quest for the 'big picture', but these resources are vital elements in the quality of life–or indeed in some cases in the very continuance of life–for those local inhabitants.

The contributions in this volume cover a wide range of interests. Some emphasise the utility of the intertidal ecosystem in elucidating ecological principles and hopefully will stimulate a wider investigation and a deeper understanding of their mechanisms; some consider the system from a socio-economic point of view, with particular attention to the uses and stresses imposed by human activities on the system; and some look at the practical management aspects especially in view of the over-arching EC Directives.

The range of contributions reflects also a range of scales. The bulk of the contributions are intended to reflect, and in places review current knowledge and activities in Ireland, focussing on specific locations and/or processes. The three international contributions have a dual function: firstly to put the Irish research into an international context and secondly to draw attention to some of the current thinking in selected areas. For completeness, and as a record of the meeting, the abstracts of posters are also included.

The opening contribution by Wilson *et al.* builds on Bob Constanza *et al.*'s seminal *Nature* paper on the value of ecosystem goods and services. This is an important and expanding field, in terms of how we think of natural systems, and in particular of how to widen the appreciation of what they contribute to our present lifestyle beyond the immediate economic resource exploitation. Thus the value of a system is linked to the function, and so to understand value, we must understand function. The paper by Costello and Emblow is driven by conservation and biodiversity considerations and categorises the system at the level of the biotope to provide the framework of a classification scheme for Ireland. Such classifications rely on two premises: firstly that the classification units themselves are sufficiently well-defined to serve as surrogates for the properties we wish to measure, such as biodiversity; and secondly that a change in the driving forces, whether it be natural climate change or anthropogenic pollution, will result in a measurable change in designation. Management is the prime consideration in Merne's contribution, which is placed in context of the EU Birds Directive. The Directive places statutory duties on Government in terms of the designations and management of coastal bird populations and is a salutory example of an instance of the value of one particular component ecosystem and the extent to which it is driving current practice.

Several contributors link processes and concepts. Jeffrey and Hayes highlight the basic trophic level, the primary producers, and draw attention to the fragmented nature of much of our knowledge. The primary producers illustrate a major difficulty in understanding function in that minor disruption may actually augment system function (e.g. eutrophication) and this phenomenon is further explored both in Colijn and van Beusekom and in Jennings and Jeffrey. The former draw attention to the fact that various initiatives in the Wadden Sea have resulted in significant changes in nutrient input. However, while they acknowledge that the overall consensus suggests a reduction in eutrophication, but the actual mechanisms of the reduction, and the nature of the link between nutrients and productivity (as opposed to biomass) is still not entirely clear. Jennings and Jeffery provide another good example of this process from Dublin bay, The nutrient delivery fuelling eutrophication is itself a function of another process, namely the remineralisation of particulates, and this illustrates the way in which system processes are interlinked.

Boaden's paper on meiofauna encapsulates many of the limitations imposed in terms of understanding the system. The meiofauna are among the most important contributors to intertidal system function, yet taxonomic data is the best aspect of our knowledge, and even that is severely limited in terms both of the taxa themselves and localities for which lists are available. Quantitative data for the Irish situation is even scarcer and almost nothing has been done in terms of process or function. In many cases we lack even the basis to be able to extrapolate from other work abroad to Ireland.

The intertidal system has provided the inspiration for some fundamentals of ecological science, and in particular through the consideration of population dynamics on the rocky shore. McGrath provides a detailed analysis for the blue-rayed limpet, which shows the importance of its association with the shore algae and of secondary settlement in its life history. The interaction of species within the community is further elaborated by Crowe and by Johnson. Crowe brings together a wide range of examples to consider what happens when species are taken out of a system. Will system function (and by extension system value) be altered? And if so, can we predict how, and by how much, it will be altered? Johnson's paper considers that final question in the light of what we know of community succession of the temperate rocky shore and gives examples of current models of the system. In this he shows the potential of mathematical modelling and how the modelling approach compliments both time series data and experimental studies and how it can be applied to a wider range of contexts

Wilson's paper looks at the link between system properties and sysytem function, with emphasis on the long-term changes in the system, and echoes the queries posed by Crowe (above), for the sand and mud communities. In the context of long-term sustainability, what aspects should we concentrate on preserving and is there anything we can use as an early-warning indicator of system deficiency or malfunction?

The papers are brought to an end by the contribution from Heip *et al.*, which places much of the Irish work presented previously in an international context. The Westerschelde is a well-studied system, and this example illustrates not only the level of information which is a pre-requisite for any interrogation of the system, but also the kinds of questions which can then be posed and the management advantages that derive from it.

This selection of papers is intended to serve several ends. Firstly, they have been brought together to bring out many of our ideas about the scientific worth and also the practical usefulness of intertidal systems as objects of investigation. Secondly, they are intended to highlight the way in which "pure" science underpins much of the "applied" practice and how anthropogenic impacts derive from the responses of the natural environment. Thirdly, they are intended to encourage further investigations in the whole field of intertidal ecology, and of system function in particular. As our understanding of the reactions of organisms to changes in the environment increases, so will our ability to predict and hopefully avert future deleterious ecological changes–which after all is what is at the base of sustainable development. Fourthly, the volume is written as a guide to managers and administrators or others who may not be biologists by training or inclination, but whose work or interests bring them into contact with the sorts of situations described herein. Finally, this volume has been written to encourage. To encourage present and future students with the fascination and the utility of such studies, to encourage our colleagues, to whom due acknowledgement for their encouragement in turn is owed, to continue with such work, and finally to encourage non-specialists that such knowledge and understanding are not only necessities, they also have a rationale and an allure all of their own.

As with all volumes of this kind, it would not have been possible to bring it together without the generous help of many individuals and institutions. Thanks are due to all the participants, not only those who presented papers, and whose contributions are published herein, but those who contributed to discussions, both formal and informal, during the meeting. Many also discovered that their contribution extended well beyond the meeting in their refereeing of these contributions, and their efforts have ensured the standard of this volume. Thanks are also due to the sponsors, and in particular to the Marine Institute and to the IRTU, and to the Royal Irish Academy as hosts without whom we could not have attempted anything on this scale. My personal thanks, as editor, to the organising Committee (listed below), for their ideas, their support, and their intellectual and physical contributions to the organisation and the running of the meeting and to the production of this volume. Above all, thanks are due to Ruth Hegarty of the RIA, who has put in as much work as anyone on the whole thing and especially for keeping it all together.

ORGANISING COMMITTEE

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James G. Wilson
November 2003

PROFESSOR DAVID JEFFREY–AN APPRECIATION

One of David Jeffrey's commonest admonitions was to those who persistently miss-called him and addressed him as "Prof. Jeffreys". This would be politely corrected with the reminder that there was only one of him. This, in a nutshell, is the truth: there is only one of him and he has made a unique contribution to so many aspects of environmental science. Intertidal ecology has been only one of the many arrows to his bow.

His first degree was at Sheffield, which some might say showed remarkable (but typical) broad-mindedness for one born under the red rose, and this was followed by a PhD in Melbourne. Australia clearly inspired him, and he has maintained contact with friends and colleagues there throughout the years. Then followed four years at the fledgling University of Lancaster as a post-doc. Two of these years were spent on coastal ecology of Morecombe Bay, establishing his long interest in the intertidal zone. David Jeffrey came to the School of Botany in Trinity in 1969, although even then he would point out that his brief extended beyond narrow disciplinary boundaries and that he was appointed to teach Biology and not just Botany.

In the early 1970's he was drawn, by An Taisce, into the legal controversies regarding the North Bull Island. This led him to realise both the international value of the site, and the fact that a large amount of unpublished material existed. He proposed that a volume should be prepared bringing this material together. This was eventually published by the Royal Dublin Society in 1977 as "North Bull Island, Dublin Bay–a modern coastal natural history." This episode established an interest in environmental activism and in the value of presenting scientific studies to the public.

One of his plans for the future is an update and expansion of the latter volume in the light of the advances made largely as a result of his efforts. Over the years, David Jeffrey has been involved with Bull Island and its management in many ways, from the science underpinning the decisions, through its designation as a UNESCO Biosphere reserve and other national and international designations, to explaining its unique character and attractions to school children and the general public. That it has now achieved such recognition is due in no small part to his endeavours.

The Irish Estuaries Research Programme was another of David Jeffrey's innovations. Not only was it one of the first of many EC-funded sciences projects to come to Ireland it established an interdisciplinary strand of research that persists to the present day. Arising out of his interdisciplinary interests was the founding of the Environmental Sciences Unit (now the Centre for the Environment) in TCD and the introduction of the first MSc in Environmental Science in Ireland, followed a few years later by an undergraduate Environmental Sciences degree.

He has always been able to appreciate the broad view, and his publications reflect these wide interests with a volume on *Soil-Plant Relationships* (1987), two on *Bioindicators* (1991, 1994) and one on *The Heritage of Clonmacnoise* (1987). The last encompasses so many of David's personal ideals: the scientific and professional knowledge as the basis for education (in its widest sense); the interdisciplinarity, this time bringing in historic and socio-economic expertise; and last but not least the creation of something out of (practically) nothing. Outside his professional life, he is a keen and knowledgeable gardener. His annual plant sale, assisted by his wife Janet, herself a teacher and a keen gardener, was initially on behalf of the local national school, later other charities. It raised such sums as to convince us that he could have done this for a living, and a very handsome one at that.

Over the years I have worked with him, I, like others, have always found him an encouraging and stimulating colleague, never short of new ideas or suggestions. All this he has done with the greatest good humour while never shirking his share, and sometimes more than his share, of the routine and administrative tasks. Although he will (officially) retire in 2003, he leaves a legacy of ideas, of initiatives and of concrete (literally) achievement for which we can all be grateful.

J.G. Wilson

PROFESSOR ALAN MYERS–AN APPRECIATION

Professor Alan Myers is one of the most distinguished zoologists to have worked in Ireland. Based at University College Cork for the last three decades, he worked in the pharmaceutical industry for a while after leaving school, but found routine work on anaerobic vaccines uncongenial, so studied at the Regent's Street Polytechnic (now the University of Westminster) for a part-time evening External University of London Zoology degree in the mid 1960s. That difficult degree had an elegantly simple syllabus–"A general knowledge of Zoology will be acquired". Alan has lived up to that requirement magnificently. From 1965–68 he conducted PhD research on amphipods at University of Wales Swansea under the supervision of Professor Ernest Naylor. Almost all of his thesis on *Microdeutopus* was published. From 1968–70 he lectured at University College Dar es Salaam, Tanzania, then briefly at the Regent's Street Polytechnic, before before moving to Cork in 1971. At University College Cork he has had heavy teaching and administrative commitments for many years, yet has sustained a phenomenal research output. The quality of that research was recognized by the award of a DSc by the University of Wales, Swansea in 1990.

Internationally Alan Myers is generally recognized for his wide experience in marine biology with particular reference to intertidal ecology, crustacean taxonomy and analytical biogeography. However, his range is far wider than this: not only is he a specialist amphipod taxonomist (he is the world's acknowledged authority on the taxonomy of the Aoridae, one of the most difficult amphipod families), he is also no mean lepidopterist, specialising in noctuid moths whilst still at school–to the extent that he had the best collection in the UK. This interest in lepidopterans had been stimulated very early in his life by seeing what he has since found out was a huge migration of Clouded Yellow butterflies in south east England in 1946. I am told that lepidopterans also brought Alan and his wife Pamela together while he was a PhD student in Wales. Pamela has been a great support to Alan's career, helping him with collection of taxonomic material and enthusiastically supporting a lifestyle that includes the constant presence of live animals and amphipod collections around the house.

Alan is also an expert herpetologist, having moved from a childhood fascination for snakes, through work on chameleons in Tanzania, to his present focus on the biology, captive breeding and biogeography of geckoes. He has even published on seal biology–what more could be asked from a zoologist? He has published over 170 refereed papers, monographs and books. His former PhD students are legion and many now occupy senior research and teaching positions. The combination of amphipod and gecko taxonomic research has involved much travel and international collaboration; he is holder of senior research positions at the University of the South Pacific and the Australian Museum in Sydney. He holds Senior Fellowships at the Christensen Research Institute, Papua New Guinea, the Phuket Marine Biological Center, Thailand, and ORSTOM New Caledonia. Within Europe he is renowned for his contributions to international workshops, particularly on amphipods.

Taxonomy, though an unfashionable discipline, is crucial to understanding of biodiversity and evolution. Alan Myers has been, and continues to be a taxonomic pioneer; at present he is involved in programmes to devise interactive electronic keys that can be published on the world-wide web to facilitate identification. Taxonomic studies of the quality produced by Alan Myers demand tremendous painstaking effort. When asked how he managed to produce such voluminous quantities of beautiful amphipod drawings, he said that he used to spend all his lunch-hours drawings amphipods (even when he was up to his eyes in administration and teaching). That speaks volumes for his dedication.

In writing this appreciation I have relied heavily on Alan's many scientific friends for input. Without exception they refer to his great kindness and unselfishness in his professional and personal dealings. I too can testify to these qualities, which have so enriched the Department of Zoology, Ecology and Plant Science of University College Cork.

John Davenport

In: James G. Wilson (ed.) *The Intertidal Ecosystem: The Value of Ireland's Shores*, 1–24. Dublin: Royal Irish Academy.

INTEGRATED ASSESSMENT AND VALUATION OF ECOSYSTEM GOODS AND SERVICES PROVIDED BY COASTAL SYSTEMS

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ABSTRACT

The goods and services provided by coastal systems and the natural capital stocks that produce them are critical to the functioning of the earth's life support systems. They also contribute significantly to human welfare, both directly and indirectly, and therefore represent a significant portion of the total economic value of the global environment. Coastal systems including estuaries, coastal wetlands, river deltas and coastal shelves are particularly rich in ecosystem goods and services. They provide a wide range of highly valued resources including fisheries, open spaces, wildlife habitat, nutrient cycling, and recreational opportunities. In this paper, we present a conceptual framework for the assessment and valuation of goods and services provided by coastal systems. First, we elucidate a formal system based on functional diversity for classifying and valuing coastal ecosystem services, emphasizing that no single ecological or economic methodology can capture the total value of these complex systems. Second, we demonstrate the process of ecosystem service valuation using a series of economic case studies and examples drawn from peer-reviewed literature. We conclude with observations on the future of coastal ecosystem service valuation and its potential role in the science and management of coastal zone resources.

INTRODUCTION

Throughout history, humans have favored coastal locations as desirable places to live, work, and play. Forming a dynamic zone of convergence between land and sea, the coastal regions of the earth serve as unique geological, ecological and biological domains of vital importance to a vast array of terrestrial and aquatic life. Given this abundance, it is perhaps not surprising that the coastal zone (≤ 150km of the coastline) has long served as a focal point for human activity.

Early on, estuaries and inlets served as places of relative shelter that also provided staging areas for harvesting food and fibre. As trading between human settlements developed, ports grew up in those places that offered sea-going vessels protection and provided access to the interior via freshwater river systems. The industrial revolution increased the use of the coastal zone not only for the transport of raw materials and finished goods, but also in new uses such as water extraction and the discharge of waste. With the recent ascendance of post-material society, recreational aspects of the coastal zone have increased in importance, as inland waterways, stretches of beach, coral reefs and rocky cliffs provide opportunities for leisure activity.

Coastal areas around the world are currently undergoing significant human population growth pressures. Approximately 44% of the global population in 1994 lived within 150 km of a coastline (Cohen *et al.* 1997). Today, that trend appears to be accelerating. Already, more than half of the United States population lives along the coast and in coastal watersheds (Beach 2002). Coastal states in the U.S. are among the nation's fastest growing and are expected to experience most of the absolute growth in population in the decades ahead (Beatley *et al.* 2002). The overwhelming majority of Chinese (94%) live in the eastern third of China and over 56% reside in coastal provinces along the Yangtze river valley, and two coastal municipalities – Shanghai and Tianjin (Hinrichsen 1998). In Europe, according to projections worked out by the Mediterranean Blue Plan (*http://www.planbleu.org/indexa.htm*), the Mediterranean Basin's resident population could go as high as 555 million by 2025. These projections clearly show that coastal regions within the Mediterranean could reach 176 million – 30 million more than the entire coastal population in 1990.

Today, there are few, if any, coastal regions that have not been affected in some way by human intervention (Vitousek *et al.* 1997). Just the fact that so many people live in the coastal zone is a form of pressure on the natural structures and processes that provide the goods and services people desire. Moreover, humans are now a major agent influencing the morphology and ecology of the coastal zone either directly by means of engineering and construction works and/or indirectly by modifying the physical, biological and chemical processes at work within the coastal system (Townend 2002).

The population and development pressures that coastal areas are now experiencing raise significant challenges for coastal planners and decision makers. Communities must often choose between competing uses of the coastal environment and the myriad goods and services provided by healthy, functioning ecosystems. Should this shoreline be cleared and stabilized to provide new land for development, or should it be maintained in its current state to serve as a wildlife habitat? Should that wetland be drained and converted to agriculture or should more wetland area be created to provide freshwater filtration services? Should this coral reef be mined for building materials and the production of lime, mortar and cement or should it be sustained to provide renewable seafood products and recreational opportunities?

To choose from among these competing options, it is important to know not only what ecosystem goods and services will be affected but also what they are actually worth to different members of society. When confronting decisions that pit different ecosystem services against one another, decision makers cannot escape making a *social choice* based on values: whenever one alternative is chosen over another, that choice indicates which alternative is deemed to be worth more than other alternatives. In short, "we cannot avoid the valuation issue, because as long as we are forced to make choices, we are doing valuation" (Costanza and Folke 1997 p. 50). Thus, without efforts to assess and quantify *all* the benefits associated with coastal ecosystem goods and services, policy and managerial decisions will ultimately be skewed in favor of environmentally degrading practices by neglecting the diffuse social interests that benefit from the non-use characteristics of such systems.

1. CONCEPTUAL FRAMEWORK

Coastal systems such as estuaries, rivers, wetlands and beaches provide many different goods and services to human society. An ecosystem service, by definition, contains all "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life" (Daily 1997). Ecosystem goods, on the other hand, represent the material products that are obtained from natural systems for human use (DeGroot *et al.* 2002). Ecosystem goods and services occur at multiple scales, from climate regulation and carbon sequestration at the global scale, to flood protection, water supply, soil formation, nutrient cycling, waste treatment and pollination at the local and regional scales (DeGroot *et al.* 2002). They also span a range of degree of direct connection to human welfare, with those listed above being less directly connected, while food, raw materials, genetic resources, recreational opportunities, and aesthetic and cultural values are more directly connected. For this reason, ecologists, social scientists and environmental managers are increasingly interested in assessing the economic values associated with ecosystem goods and services associated with coastal systems (Bingham *et al.* 1995; Costanza *et al.* 1997; Daily 1997; Farber *et al.* 2002).

Figure 1 represents an integrated framework we have developed for the assessment of ecosystem goods and services within the coastal zone, including consideration of ecological structures and processes, land use decisions, human welfare and the feedbacks between them. As the schematic shows, ecosystem goods and services form a pivotal conceptual link between human and ecological systems. Ecosystem structures and processes are influenced by long-term, large-scale biogeophysical drivers (e.g., tectonic pressures, global weather patterns) which in turn create the necessary conditions for providing the ecosystem goods and services people value. The concept of ecosystem goods and services

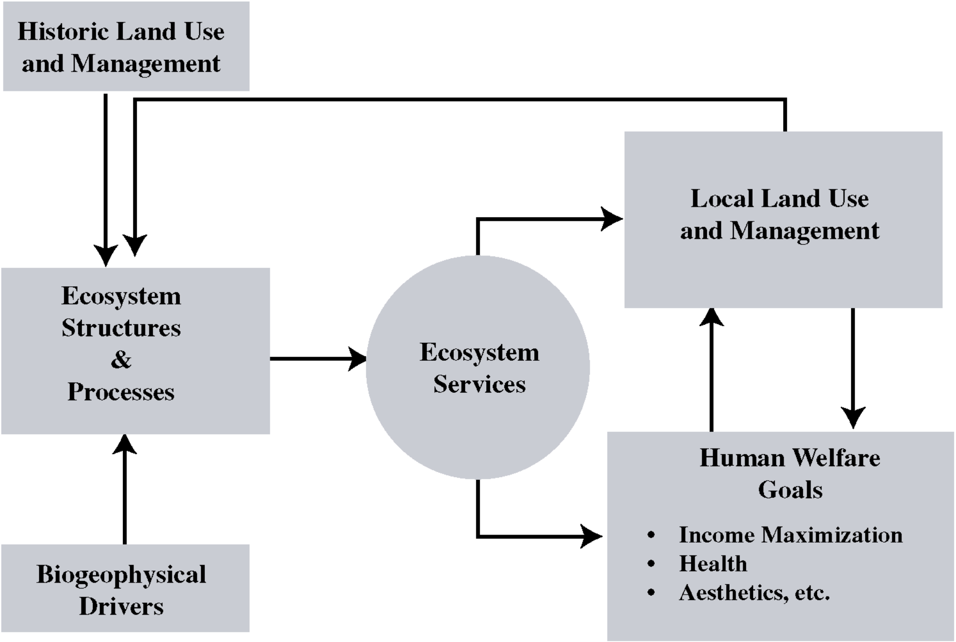

Figure 1. Framework for integrated assessment and valuation of ecosystem functions, goods and services in the coastal zone

used in this paper is inherently *anthropocentric:* it is the presence of human beings as welfare-maximizing agents that enables the translation of basic ecological structures and processes into value-laden entities. Through laws and rules, land use management and policy decisions, individuals and social groups make tradeoffs between these values. In turn, these land use decisions directly modify the structures and processes of the coastal zone by engineering and construction and/or indirectly by modifying the physical, biological and chemical processes of the natural system (Boumans *et al.* 2002).

The concept of ecosystem goods and services is useful for coastal zone science and management for three fundamental reasons. First, it helps us synthesize essential ecological and economic concepts, allowing researchers and managers to link human and ecological systems in a viable and policy relevant manner. Second, it draws upon the latest available economic methods for economic valuation. Third, scientists and policy makers can use the concept to evaluate social and political tradeoffs between coastal land use development and conservation alternatives. In this paper, we use the concept of goods and services to describe a diversity of human values associated with coastal systems. In particular, we focus on the estimation of *economic* values and how these values can be used to inform decisions about the future of the coastal zone.

2. DEFINING THE ECOLOGICAL STRUCTURES, PROCESSES AND HABITATS IN THE COASTAL ZONE

Coastlines around the world exhibit a variety of physical types and characteristics, the result of major differences in geology and biophysical processes. There are also a number of distinct habitat and ecosystem types within the coastal zone, each suggesting unique management and planning needs. As mentioned previously, coastal regions are dynamic interface zones where land, water and atmosphere interact in a fragile balance that is constantly being altered by natural and human influences. When establishing classification schemes for the coastal zone, it is important to remember that critical biological and physical drivers and interconnections extend beyond these areas and that coastal zones can be significantly affected by events that happen great distances (temporal and spatial) from the coast itself.

Accurate land cover/land use definition and classification are essential preliminary steps in the valuation and management of coastal systems. When designing and implementing a classification system, a balance is struck between the use of *a priori* and *post priori* schemas. While the former provides a greater degree of standardization and consistency, the latter provides greater flexibility by allowing the end user to adopt the system to unique spatiotemporal contexts. In this paper, we strike a balance between the two by using a global land use classification system with a high level of standardization and adapt that system to a recently developed typology of ecosystem goods and services (DeGroot *et al.* 2002).

The landscape classification is based on the strategy outlined by the UN's Food and Agricultural Organization Land Cover Classification System (LCCS) for terrestrial systems amended to account for attributes specific to coastal systems (see http://www.lccs-info.org/) (Di Gregorio and Jansen 2000). Coastal attributes were modified using the typologies of the "Land-Ocean Interactions in the Coastal Zone" (LOICZ) program (http://www.nioz.nl/loicz/info.htm) and "The Coastal Systems of Europe" (CSE) developed under the auspices of the European Coastal and Marine Ecological Network (ECMEN) (http://www.coastalguide.org/csm/index.html).

The FAO-LCCS program defines land cover as "the observed biophysical cover on the earth's surface" including vegetation and man-made features as well as bare rock, bare soil and inland water surfaces (Di Gregorio and Jansen 2000). Because most extant land cover classifications in the literature are spotty with respect to quality, scale and nomenclature, and class definitions are often imprecise, ambiguous and/or absent with a limited ability to accommodate the whole range of possible phenomena, the LCCS team designed a system that seeks to provide common, internationally applicable standards. The LCCS program is the first to provide a comprehensive framework for the description, characterization, classification and comparison of all non-oceanic land covers identified anywhere in the world, at any scale.

While terrestrial land covers in coastal zones are readily classified using the existing LCCS system, oceanic features are not. Extending the LCCS objective of a creating a classificatory system that harmonizes and standardizes the collection of land cover data worldwide, we have borrowed from the aforementioned LOICZ typology those attributes that are specific to the coastal zone and merged it with the extant LCCS system. The LOICZ project is one of eleven "Program Elements" in the International Geosphere-Biosphere Project and focuses specifically on the coastal zone. The availability of a global, geo-referenced LOICZ database allowed for the use of several key attributes within the coastal zone: wave heights, tidal type, tidal range, salinity specifications, ocean currents, morphologic characteristics and presence/absence of coral reefs.

Additionally, where necessary, we have employed the classification of coastal systems illustrated by "Coastal Systems of Europe" (CSE). For example, the LOICZ typology only differentiates between narrow and wide coastal shelfs (smaller or wider than 50 km) classifying slope features of the coastline as mountainous, hilly, or plain and identifies the presence/absence of reefs, glacial ice or deltas. The CSE system provides significant additional information about the attributes of predominant *substrates* in the coastal zone. CSE subdivides the littoral zone into (a) hard rocks, (b) soft rocks (c) recent sediments and uses slope features to distinguish between inter-tidal and supra-tidal habitats.

Specific coastal landscape features are identified under this synthesized typology. For example, hard rock on cliffed coasts is most likely represented by sea cliffs, cliff islands, archipelagos, fjords and sea lochs, rias, rocky shores with caves, bay and pocket dunes, river mouths, small estuaries and embayments. Hard rock on coastal plains is more characteristic of skerry coasts, fjords, river mouths, arctic tidal plains, and karstic shores. Once landscape features are identified, it is possible to associate ecological habitats and ecosystem types with them (see Table 1). The general class, "coastal zone" harbors sub and intertidal habitats as well as supra tidal habitats. Because supra tidal habitats such as forests, urban areas and agriculture are not unique to the coastal zone, we do not include them within our analysis. Sub and Intertidal habitat classifications recognized for Europe are: cliffs, stony banks and shingles, kelp forests, estuaries, sea dunes, sandbanks, salt marshes, mud and sand flats, lagoons, and sea grass beds. Additional habitats included for tropical regions are corals and mangrove forests.

Table 1 below presents results from cross-referencing ecosystem goods and services against coastal landscape features and habitats. Following the differentiation between structure and process noted above, we have separated coastal landscape features from their associated habitats because geomorphology and landscape structure provide different ecosystem goods and services than those provided by ecological habitats. For example, mismanagement of a river habitat could devoid the river of living organisms and severely impact those ecosystem services associated with the ecological habitat of the river system – e.g., nutrient uptake and wildlife refugium – while leaving water regulation, flood prevention and transportation values untouched. An accurate land-cover classification needs to be able to delineate whether or not ecosystem services are derived from landscape features or habitat to prevent the danger of double-counting (see below section 4).

The information depicted in Table 1 shows that ecosystem good and service values can be associated with either landscape features or habitats or both. Open circles represent potential ecosystem goods and services provided by landscape features and habitats. Closed circles, on the other hand, represent ecosystem goods and services that have been empirically

Table 1: Landscape Types, Habitats, Goods and Services in the Coastal Zone

	Ecosystem services																			Ecosystem goods				
	Gas regulation	Climate regulation	Disturbance prevention	Water regulation	Water supply	Soil retention	Soil formation	Nutrient regulation	Waste treatement	Pollination	Biological control	Habitat functions	Refugium function	Nursery function	Aesthetic information	Recreation	Cultural and artistic info	Spiritual and Historic info	Science and Education	Food	Raw materials	Genetic resources	Medical resources	Ornamental resources
Landscape features																								
cliffs			○									○	○	○	○	○	○		○		○			○
fjords_lochs_rias			○									○	○	○	○	○		○			○			○
estuaries	○		○	●	●			●	●			○	○	○	○	●				●	●			○
Ice coasts		○										○	○	○	○				○					
tidal plains			○	○				○	○			○	○	○	○	○	○			○				
barrier coast			●									○	○	○	○	○		○		○				○
lagoons	○	○	○	○				○				○	○	○	○	○	○	○		○				○
dunes	○		○		○							○	○	○		○	○		○		○			
deltas	○	○	○	○	○		○	○	○			○	○	○	○	○	○	○	○	○	○			
beaches			●			○						○	○		●	●	○	○						
Habitats																								
Intertidal																								
Cliffs			○										○	○	○	○			○					
Shingle			○										○	○	○	○				○				
Kelp	○		○			○		○			○		○	○					○	○	○			○
Seagrass	○		○			○		○					○	○	○				○	○				
Estuary	○	○	●					●	●		○		○	●	●	●			○	●				
Wetland	○	○	●	○	●		○	●	○		○		○	○	○	●			○	●				
Salt_marsh	○	○	○			○	○	●					○	○					○	●				
Mud_flat			●					○					○	○					○	○				
lagoons	○	○	○					○					○	○	○	○			○	○				
Mangrove	○	○	●	○				○	○				○	○	○	●	○		○	●	●	○	○	○
dunes	○		○	○		○	○	○					○	○	○				○	○	○			
Sandbank								○					○			○			○	○	○			
Coral								○			○		○	○	○	●	○		○	●	●	○	○	○

● = Economic Values Available in Peer-Reviewed Literature

○ = No Economic Values Available in Peet-Reviewed Literature, but Values Probable measured in the economic valuation literature. In this paper, we focus primarily on studies that have measured economic values for ecosystem goods and services.

3. ECONOMIC VALUATION OF COASTAL ECOSYSTEM GOODS AND SERVICES

In economic terms, the ecosystem goods and services depicted in Table 1 can potentially yield a number of important values to humans. When discussing these values, however, we first need to clarify what the underlying concept actually means. The term 'value' as it is employed in this paper has its conceptual foundation in economic theory (Freeman 1993). In this limited sense, value can be reflected in two theoretically commensurate empirical measures. First, there is the amount of money people are willing to pay for specific improvements in a good or service, *willingness to pay* (WTP). Second, there is the minimum amount an individual would need to be compensated to accept a specific degradation in a good or service, *willingness to accept compensation* (WAC) (Bishop *et al.* 1997). Simply put, economic value is the amount of money a person is willing to give up in order to get a thing, or the amount of money required to give up that thing. To date in the literature, WTP has been the dominant measure of economic value. However, WTP is not restricted to what we actually observe from people's transactions in a market. Instead, "it expresses how much people would be willing to pay for a given good or service, whether or not they actually do so" (Goulder and Kennedy 1997).

A central concern in coastal management is one of making social tradeoffs – allocating scarce resources among society's members. For example, if society wished to make the most of its endowment of coastal resources, it should be possible to compare the value of what society's members receive from any improvement in a given coastal ecosystem with the value of what its members give up to degrade the same system. The prevailing approach to this type of assessment in the literature is cost-benefit analysis (Ableson 1979; Kneese 1984; Turner 2000). Cost-benefit analysis is characterized by a fairly strict decision-making structure: "defining the project, identifying impacts which are economically relevant, physically quantifying impacts as benefits or costs" and then, "calculating a summary monetary valuation" (Hanley and Spash 1993). Given this approach, a key question comes down to: what gets counted?

In addition to the production of marketable goods, coastal ecosystems provide natural functions such as nutrient recycling as well as conferring aesthetic benefits on humans (Costanza *et al.* 1997). Coastal goods and services may therefore be divided into two general categories: (1) the provision of direct *market* goods or services such as drinking water, transportation, electricity generation, pollution disposal and irrigation; and, (2) the provision of *non-market* goods or services which include things like biodiversity, support for terrestrial and estuarine ecosystems, habitat for plant and animal life, and the satisfaction people derive from simply knowing that a beach or coral reef exists.

The market values of ecosystem goods and services are the observed trading ratios for services that are directly traded in the marketplace: price = exchange value. The exchange-based, welfare value of a natural good or service is its market price net of the cost of bringing that service to market. For example, the exchange-based value of fresh fish to society is based on its catch rate and "value at landing" which is the market price of fish, minus harvest and time management costs. Estimating exchange-based values in this case is relatively simple, as observable trades exist from which to measure value.

Since individuals can be observed making choices between objects in the marketplace while operating within the limits of income and time, economists have developed several market-based measures of value as imputations from these observed choices. While monetary measures of value are not the only possible yardstick, they are convenient since many choices involve the use of money. Hence, if you are observed to pay $9 for a pound of shrimp, the imputation is that you value a pound of shrimp to be at least $9, and are willing to make a trade-off of $9 worth of other things to obtain that shrimp. The money itself has no intrinsic value, but represents other things which could have been purchased. Time is often considered another yardstick of value; if someone spends 2 hours fishing, the imputation is that the person values the fishing experience to be worth more than 2 hours spent on other activities. Value is thus a resultant of the expressed tastes and preferences of persons, and the limited means with which objects can be pursued. As a result, the scarcer the object is, the greater its value will be on the margin.

By estimating the economic value of ecosystem goods and services not traded in the marketplace, however, social costs or benefits that otherwise would remain hidden or unappreciated are revealed. While measuring exchange values requires monitoring market data for observable trades, non-market values of goods and services are much broader and more difficult to measure. Indeed, it is these values that are have captured the attention of environmental and resource economists who have developed a number of techniques for valuing ecosystem goods and services (Bingham *et al.* 1995; Freeman 1993). When there are no explicit markets for services, more indirect means of assessing economic values must be used. A spectrum of economic valuation techniques commonly used to establish the WTP or WTA when market values do not exist are identified below.

As these brief descriptions suggest, each economic valuation methodology has its own strengths and limitations, thereby restricting its use to a select range of goods and services associated with coastal systems. For example, Travel Cost (TC) is useful for estimating recreation values, and Hedonic Pricing (HP) for estimating coastal property values, but they are not easily exchanged. Rather, a full suite of valuation techniques is required to quantify the economic value of goods and services provided by a naturally functioning coastal ecosystem. By using a range of methods for the same site, the so-called "total economic value" of a given coastal ecosystem can thus be estimated (Freeman 1993).

- **Avoided Cost** (AC): services allow society to avoid costs that would have been incurred in the absence of those services; flood control provided by barrier islands avoids property damages along the coast.
- **Replacement Cost** (RC): services could be replaced with man-made systems; nutrient cycling waste treatment can be replaced with costly treatment systems.
- **Factor Income** (FI): services provide for the enhancement of incomes;

water quality improvements increase commercial fisheries catch and incomes of fishermen.

- **Travel Cost** (TC): service demand may require travel, whose costs can reflect the implied value of the service; recreation areas attract distant visitors whose value placed on that area must be at least what they were willing to pay to travel to it.
- **Hedonic Pricing** (HP): service demand may be reflected in the prices people will pay for associated goods: For example, housing prices along the coastline tend to exceed the prices of inland homes.
- **Marginal Product Estimation** (MP): Service demand is generated in a dynamic modeling environment using production function (i.e., Cobb-Douglas) to estimate value of output in response to corresponding material input.
- **Contingent Valuation** (CV): service demand may be elicited by posing hypothetical scenarios that involve some valuation of alternatives; people would be willing to pay for increased preservation of beaches and shoreline.
- **Group Valuation** (GV): This approach is based on principles of deliberative democracy and the assumption that public decision making should result, not from the aggregation of separately measured individual preferences, but from *open public debate.*

As these brief descriptions suggest, each economic valuation methodology has its own strengths and limitations, thereby restricting its use to a select range of goods and services associated with coastal systems. For example, Travel Cost (TC) is useful for estimating recreation values, and Hedonic Pricing (HP) for estimating coastal property values, but they are not easily exchanged. Rather, a full suite of valuation techniques is required to quantify the economic value of goods and services provided by a naturally functioning coastal ecosystem. By using a range of methods for the same site, the so-called "total economic value" of a given coastal ecosystem can thus be estimated (Freeman 1993).

Figure 2 depicts a model based on the idea of functional diversity, linking different ecosystem structures and processes with the output of specific goods and services, which can then be assigned monetary values using the range of valuation techniques described above.

Here, key linkages are made between the diverse structures and processes associated with the coastal zone, the landscape and habitat features that created them, and the goods and services that result. Once delineated, economic values for these goods and services can then be rationally assessed by measuring the diverse set of human preferences for them. In economic terms, the natural assets of the coastal zone can thus yield direct (fishing) and indirect (nutrient cycling) use values as well as non-use (preservation) values of the coastal system. Once accounted for, these values can then be aggregated to estimate the total value of the entire system (Anderson and Bishop 1986).

In principle, a global picture of the potential economic value associated with the coastal zone can be built up via the aggregation of a number of existing valuation studies. For example, in a preliminary estimate of the total economic value of ecosystem services provided by global systems, Costanza *et al.* (1997) showed that while the coastal zone

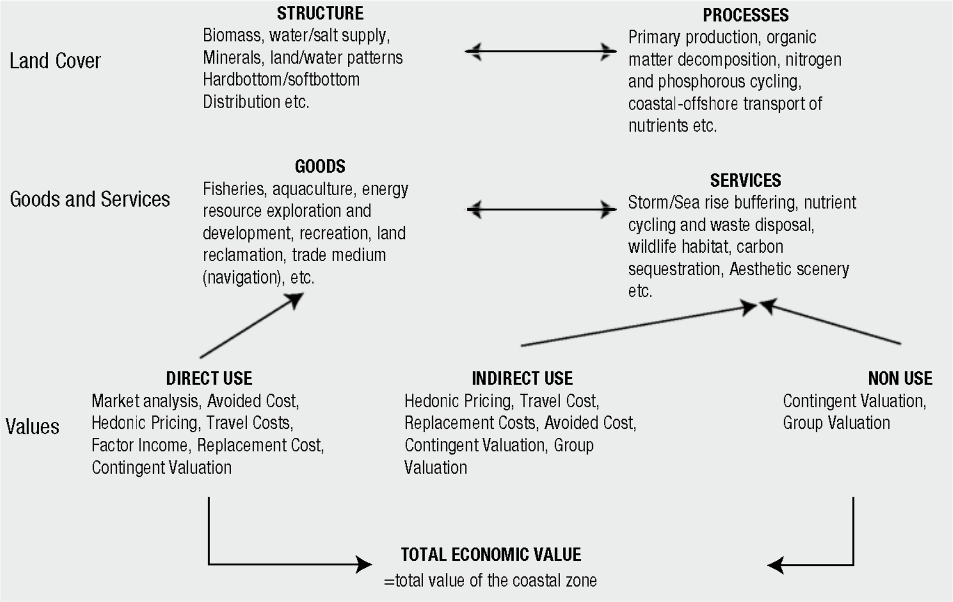

Figure 2: Total economic value of coastal zone functions, goods and services (Adapted from Turner 2000)

covers only 8% of the world's surface, the goods and services provided by it are responsible for approximately 43% of the estimated total value of global ecosystem services: US$ 12.6 Trillion in 1997 dollars. While controversial (Pearce 1998; Pimm 1997), this preliminary study made it abundantly clear that coastal ecosystem services do provide an important portion of the total contribution to human welfare on this planet. Furthermore, it demonstrated the need for additional research and indicated the fact that coastal areas are among the most in need of additional study (Costanza 2000).

On a smaller scale, such 'synthesis' studies often form the bedrock of practical policy analysis because only rarely can policy analysts or managers afford the luxury of designing and implementing an original study for every given ecosystem (Desvouges *et al.* 1998). Instead, we must often rely on the limited information that can be gleaned from past empirical studies that are often quite limited or even contradictory (Desvousges *et al.* 1992; Smith 1992). Primary valuation research, while being a 'first best' strategy, is also very expensive and time consuming. Thus, secondary analysis of the valuation literature is a 'second best' strategy that can nevertheless yield very important information in many scientific and management contexts (Rosenberger and Loomis 2000). When analyzed carefully, information from past studies published in the literature can form a meaningful basis for coastal zone policy and management (Beatley *et al.* 2002; French 1997). In the final section of this paper, we demonstrate our integrative approach to ecosystem service valuation by providing a brief review of case studies drawn from the literature.

4. RESULTS: EXAMPLES FROM THE LITERATURE 1978 TO 2002

Empirical valuation data for coastal ecosystems often appears scattered throughout the scientific literature and is uneven in quality. Despite this unevenness, below we present a brief review of existing valuation literature in order to provide useful insights for further research in the area. Such an exercise provides scientists and coastal managers alike with a sense of where the science of coastal ecosystem valuation has come from, and where it might go in the future. To accomplish this goal, below we have synthesized peer-reviewed economic data on coastal ecosystems depicted above in section 3, Table 1 and delineated a few key examples from the literature for extended discussion. In so doing, we hope to elucidate major findings and gaps in the literature.

All information presented below was obtained from studies that were published between 1978 and 2002. They deal *explicitly* with market and non-market coastal ecosystem goods and services measured throughout the world. To maintain consistency in data quality and findings, only peer-reviewed journal articles were included in this review. The literature search involved an intensive review of databases on the World Wide Web available at the University of Maryland. In total, twelve academic data bases were searched: *Academic Search Premier, ArticleFirst, Business Source Premier, ERIC, ISI Web of Science, JSTOR, OCLC Union Lists of Periodicals, PapersFirst, Proceedings First, USM Authority Database, World Almanac, and WorldCat.* Several keywords – economic value, economics, valuation, management, coastal, wetland, estuary, mangrove, ecosystem goods, and ecosystem service – were combined in various patterns to elicit studies that might be relevant to coastal ecosystem valuation. This search yielded fifty-one citations. Each citation was then located and reviewed by the authors. Twenty-eight citations (55%) were rejected because they were not peer-reviewed or did not explicitly address the economic valuation of coastal ecosystem goods and services.

The literature review yielded a total of twenty-three studies for further analysis and discussion (See Appendix). Results from these studies were then sorted by ecosystem good and service addressed, methodology and empirical data. On this basis, each study was classified as measuring an ecosystem good, service or any combination thereof (several studies report data for more than one good or service). Selected valuation estimates for coastal goods or services are reported in detail below in sections 5.1 and 5.2. The results from each study are reported in their original monetary metric.

5. ECOSYSTEM GOODS

Our review of the literature reveals that coastal ecosystems are among the most productive in the world today, rivaling even tropical rainforests in terms of their overall productivity of materials and goods used by humans (Barbier 1993; Primavera 1991; Spurgeon 1992). Many coastal regions are exploited through market activities that directly support humans – e.g., fishing, hunting, fuelwood and woodchip extraction, harvesting ornamental materials, and the extraction of medical resources.

5.1 Food

Coastal systems generate a variety of seafood products such as fish, mussels, crustaceans, sea cucumbers and seaweeds (Moberg and Folke 1999; Ronnback 1999). These products are vital to subsistence economies and provide a commercial base to local and national economies. For instance, fish and shrimp rank second in the value of export commodities for Bangladesh, and this represents 7% of the total export earnings and contributes 4.7% to GDP (Deb 1998). Given this level of economic productivity, it is perhaps not surprising that overfishing and intensive aquaculture have caused serious ecological and social problems in coastal regions (Jackson *et al.* 2001; Primavera 1991; 1997).

Valuation studies of food directly or indirectly supplied by coastal systems have predominantly focused on the economic value of fishery products (Barbier 2000; Batie and Wilson 1978; Bennett and Reynolds 1993; Buerger and Kahn 1989; Deb 1998; Farber and Costanza 1987; Gilbert and Janssen 1998; Kaoru *et al.* 1995; Lynne *et al.* 1981; Rivas and Cendrero 1991; Ronnback 1999; Ruitenbeek 1994; Sathirathai and Barbier 2001). Most often, the market price of seafood products is used as a proxy when calculating the value of ecosystem goods provided by coastal systems. For example, the annual market value of seafood supported by mangroves has been calculated to range from US$750 to $16,750 (in 1999 dollar) per hectare (Ronnback 1999).

Lynne *et al.* (1981) suggested that the value of the coastal marsh in southern Florida could be modeled by assuming that seafood harvest is a direct function of salt-marsh area. The authors then derived the economic value of a specified change in marsh area through the marginal productivity of fishery harvest. For the blue crab fishery in western Florida salt marshes, a marginal productivity of 2.3 1b per year for each acre of marshland was obtained. By linking the market price of harvested blue crab to this estimate, the authors were able to estimate of the total present value of a marsh acre in human food (blue crab) production at $3.00 for each acre (with a 10% capitalization rate).

5.2 Raw Materials

Raw materials refer to renewable biotic resources such as wood and fibers for building, biochemicals or biodynamic compounds for all kinds of industrial purposes (DeGroot *et al.* 2002). According to Costanza *et al.* (1997), for example, the net value of raw materials provided by coastal systems worldwide is approximately $4/ha/year (1994 dollars). Surprisingly, however, when compared to the number of valuation studies that measure the market value of seafood products, fewer studies on raw materials were gleaned from the literature. From the literature, we were able to identify three empirical studies dealing with the raw material productivity of mangrove areas (Bennett and Reynolds 1993; Ruitenbeek 1994; Sathirathai and Barbier 2001). Here, local direct uses derived from mangrove areas were valued by determining the net income generated from harvesting timber, fuel wood, and other wood products as well as nonwood resources, such as birds and crabs.

For example, by conducting household interviews with 44 households in the Tha Po Village, Southern Thailand, Sathirathai and Barbier (2001) estimated the average annual net income per household by collecting data on the amount of raw materials (e.g., wood for fishing gear) gathered by the household. The direct use value of mangrove resources was assumed to be equivalent to the net income generated from the forests in terms of various wood and nonwood products. Based on the estimated net income from all mangrove products (fuelwood, honey, wood for fishing gear, molluscs etc.) the authors report the mean annual value per household at around $924 (1996 dollars). In another similar study, Bennett and Reynolds (1993) estimated the value of timber products provided by Sarawak mangroves to be worth $123,217.

5.3 Genetic, Medical and Ornamental

Besides food and raw materials, at least three other types of ecosystem goods are provided by coastal systems – genetic resources, medical resources and ornamental resources. While we were unable to locate reliable economic estimates for these products in the peer-reviewed literature, we were able to identify studies that document their social significance and potential economic value. For example, the coastal marine environment (e.g., reefs) has been shown to be an exceptional reservoir of bioactive natural products, many of which exhibit structural features not found in terrestrial natural products (Carte 1996). The pharmaceutical industry has discovered several potentially useful substances among the seaweeds, sponges, molluscs, corals, sea cucumbers and sea anemones of the reefs (Carte 1996; Moberg and Folke 1999). Furthermore, many coastal products are collected not only as food but also to sell as jewellery and souvenirs. Mother-of-pearl shells, giant clams, and red coral are collected and distributed as part of the worldwide curio trade (Craik *et al.* 1990). The marine aquarium market is now a multi million dollar per year industry trading in live reef-dwelling fishes that are collected and shipped live from coral reef communities (Moberg and Folke 1999).

6. ECOSYSTEM SERVICES

In addition to marketable goods and products, our analysis of the literature reveals that landscape features and habitats in the coastal zone also provide critical natural services that contribute to human welfare, and thus have significant economic value (Farber and Costanza 1987). As the aforementioned pattern of data in Table 1 suggests, much of what people value in the coastal zone – natural amenities (open spaces, attractive views), good beaches for recreation, high levels of water quality, protection from storm surges, and waste assimilation/nutrient cycling – are provided by coastal systems. Below, we review a select published group of these economic value estimates.

6.1 Recreation and Nutrient Regulation

Stretches of beach, rocky cliffs, estuarine and coastal marine waterways, and coral reefs provide numerous recreational and scenic opportunities for humans. Boating, fishing, swimming, walking, beachcombing, scuba diving, and sunbathing are among the numerous leisure activities that people enjoy worldwide and thus represent significant economic value (Farber 1988; Kawabe and Oka 1996; King 1995; Morgan and Owens 2001; Ofiara and Brown 1999). Both travel cost (TC) and Contingent Valuation (CV) methods are commonly used to estimate this value. For example, the Chesapeake Bay estuary on the eastern seaboard of the United States has been the focus of an impressive amount of research on nonmarket recreational values associated with coastal systems. When attempting to estimate the monetary worth of water quality improvements in Chesapeake bay, Bocksteal *et al.* (1989) focused on recreational benefits because it was assumed that most of the increase in well-being associated with such improvements would accrue to recreationists (p.2). The authors estimated the average increases in economic value for beach use, boating, swimming, and fishing with a 20% reduction in total nitrogen and phosphorus introduced into the estuary. Using a combination of CV and TC methods, the annual aggregate willingness to pay for a moderate improvement in the Chesapeake Bay's water quality was estimated to be in the range of $10 to $100 million in 1984 dollars (Bocksteal *et al.* 1989). In a similar study, Kawabe and Oka (1996) used TC to estimate the aggregate recreational benefit (viewing the bay, clam digging, bathing, sailing, bathing, snorkeling and surfing) from improving organic contamination of Tokyo Bay by nitrogen at 53.2 billion yen. Using the CV method, the authors also estimated the aggregate value of improving chemical oxygen demand to reduce the reddish-brown color of the bay at 458.3 billion yen (Kawabe and Oka 1996).

As discussed previously in section 3, in addition to habitat services, humans can value the landscape features of the coastline directly. For example King (1995) conducted a CV study to estimate the value of beach quality in Southeast England. The main survey was conducted in August 1993 in the town of Eastbourne off the Dover Straits during peak tourist season (King 1995). By asking respondents to state the maximum amount that they would be willing to pay for a daily entrance fee to use the seafront and beaches, the author estimated the mean WTP per visitor at £1.78. Using existing information on the total annual number of visitor days, the aggregate annual value of Eastbourne's beaches and seafront were calculated to be approximately £4.5 million.

6.2 Aesthetic Information

Open space, proximity to clean water, and scenic vistas are often cited as a primary attractor of residents who own property and live within the coastal fringe (Beach 2002). Hedonic pricing (HP) techniques have thus been used to show that the price of coastal housing units vary with respect to characteristics such as ambient environmental quality (e.g., proximity to shoreline, water quality) because buyers will bid up the price of units with more of a desirable attribute (Johnston *et al.* 2001). For example, Leggett and Bockstael (2000) use hedonic techniques to show that water quality has a significant effect on property values along the Chesapeake Bay, USA. The authors use a measure of water quality – fecal coliform bacteria counts – that has serious human health implications and for which detailed, spatially explicit information from monitoring is available. The data used in this hedonic analysis consists of sales of waterfront property on the western shore of the Chesapeake Bay that occurred between 1993 and 1997 (Leggett and Bockstael 2000). The authors consider the effect of a hypothetical localized improvement in observed fecal coliform counts – 100 counts per 100ml – on a set of 41 residential parcels. The projected increase in property values due to the hypothetical reduction totals approximately $230,000. Extending the analysis to calculate an upper bound benefit for

494 properties, the authors estimate the benefits of improving water quality at all sites at $12.145 million (Leggett and Bockstael 2000, p.142).

6.3 Disturbance Prevention

A critically important service provided by coastal landscapes such as barrier islands, inland wetlands areas, beaches and tidal plains is disturbance prevention. Significant property damages have been attributed to flooding from tidal surges and rainfall as well as wind damage associated with major storm events (Farber 1987; Farber and Costanza 1987). For example, Farber (1987) has described an "Avoided Cost" method for measuring the hurricane protection value of wetlands against wind damage to property in coastal Louisiana, USA. Using historical probabilities for storms and wind damage estimates in Louisiana, an expected wind damage function was derived and from this, expected reductions in wind damage from the loss of 1 mile of wetlands were estimated. Based on 1983 US dollars, the expected incremental annual damaged from a loss of 1 mile of wetlands along the Louisiana coastline was $69,857 which, when extrapolated to a per-acre estimate, amounts to $.44 per acre (Farber 1987).

In another study, Parsons and Powell (2001) measure the cost of land and capital loss, especially in housing, associated with beach retreat in the State of Delaware, USA. The costs associated with beach retreat are grouped into four primary categories: land loss, capital loss (structures) proximity loss, and transition loss (Parsons and Powell 2001). As the vast majority of developed land in coastal Delaware is residential housing, the authors focus on the residential land and housing market as a baseline estimate of the cost of beach retreat. Using a hedonic regression analysis, the authors estimate the cost of beach retreat in Delaware over a 50 year period to be about $291 million in yr 2000 dollars.

6.4 Habitat and Nursery Functions

As mentioned previously in this paper, the coastal zone is one of the most productive ecological habitats in the world (Gosselink *et al.* 1974; Turner *et al.* 1996). Eelgrass, salt marsh and intertidal mud flats all provide a variety of services to the public associated with their nursery and habitat functions. As we have already reported, improvements in the ecological integrity of these habitats may ultimately lead to measurable increases in the production of market goods such as fish, birds and wood products. In other cases, however, ecological productivity itself can represent a unique class of values not captured by traditional market-based valuation methods. Instead, these values represent an increase in the production of higher trophic levels brought about by the increased availability of habitat (Gosselink *et al.* 1974; Turner *et al.* 1996). Here, it is critical to realize that one may not, in general, add productivity value estimates to use values estimated using other market-related methodologies (e.g., hedonic and travel cost) because to do so would risk double counting some aspects of value, or measuring the same benefits twice (Desvouges *et al.* 1992, 1998).

In an example of coastal wetland productivity analysis, Johnston *et al.* (2002) use a simulation model based on biological functions that contribute to the overall productivity of the food web in the Peconic Estuary System (PES) in Suffolk County NY, USA. Based on habitat values for fin and shellfish, birds and waterfowl, an average annual abundance per unit area of wetland habitat in the PES is estimated by summing all relevant food web values and habitat values for a year (Johnston *et al.* 2002). The value of fish and shellfish is based on commercial harvest values. The marginal value of bird species usage of the habitat is based on the benefits human receive from viewing or hunting waterfowl. Using these values as input data, the simulation model result in annual marginal asset values for three wetland types: Eelgrass ($1,065 per acre/year); Saltmarsh ($338 per acre/year); and Inter-tidal mud flat ($67 per acre/year).

In an earlier study, Farber and Costanza (1987) estimated the marginal productivity of a coastal system in Terrebonne Parish, Louisiana, USA by attributing commercial values for several species to the net biomass, habitat, and waste treatment of the wetland ecosystem (Farber and Costanza 1987). Arguing that the annual harvest from an ecosystem is a function of the level of environmental quality, the authors chose to focus on the commercial harvest data for five different native species – shrimp, blue crab, oyster, menhaden, and muskrat – to estimate the marginal productivity of wetlands. The annual economic value (marginal product) of each species was estimated in 1983 dollars: shrimp $10.86/acre; blue crab $.67/acre; oyster $8.04/acre; menhaden $5.80/acre; and muskrat pelts $12.09/acre. Taken together, the total value marginal productivity of wetlands in Terrebonne Parish, Louisiana was estimated at $37.46 per acre.

DISCUSSION

Ecosystem goods and services form a pivotal conceptual link between human and ecological systems. In this paper, we have shown how ecosystem goods and services are critical to the functioning of coastal systems and that they also contribute significantly to human welfare, representing a significant portion of the total economic value of the coastal environment. Using an integrated framework developed for the assessment of ecosystem goods and services within the coastal zone, we have considered how ecological structures and processes, land use decisions, and human values interact in the coastal zone. The concept of ecosystem goods and services has thus allowed us to analyze how human beings as welfare-maximizing agents actively translate basic ecological structures and processes into value-laden entities.

The literature reviewed here demonstrates both the opportunities and the challenges inherent in estimating the economic value of coastal ecosystem goods and services. As the pattern of data in Table 1 suggests, one of the major insights from our analysis is the discrepancy between the ecosystem goods and services that have been documented in the published valuation literature and those that could potentially contribute significantly to human welfare, both directly and indirectly. Accounting for these missing economic values represents a significant challenge for scientists, planners and decision makers involved in coastal zone research and management.

The diversity of studies reviewed here suggests that methodological guidelines and standards are still evolving. However, it is evident that within specific contexts, defensible dollar estimates can be obtained and thereby add to the information base for coastal management and decision making. These estimates may require considerable creative research and have substantial uncertainties. Yet, despite these limitations, the available data suggest that humans do indeed attach substantial positive economic values to the many market and non-market goods and services coastal systems provide.

Through laws and rules, land use management and policy decisions, individuals and social groups ultimately will make tradeoffs between these values as they continue to live, work and play in the coastal zone. In turn, these land use decisions will directly modify the structures and processes of the coastal zone through engineering and construction and/or indirectly by modifying the physical, biological and chemical processes of the natural system. Resource managers and ecologists should therefore be aware that non-use values have been shown to comprise a sizable portion of total economic value associated with coastal ecosystems. One important conclusion that follows is that if such values are left out of policy analysis, resulting policy decisions will tend to overestimate the role of use values, and underestimate the role of non-use values. Without efforts to quantify the non-use benefits associated with freshwater ecosystem goods and services, policy and managerial decisions could potentially be skewed in favor of environmentally degrading practices by neglecting the diffuse social interests that benefit from the many non-use oriented characteristics of such systems.

The science of ecology must play a crucial role in bringing concepts like *ecosystem goods and services* to the foreground of the valuation debate (Costanza *et al.* 1997; Daily 1997; Wilson and Carpenter 1999). As we have shown, assigning economic values to landscape features and habitat functions of coastal ecosystems requires a full understanding of the nature of the natural systems upon which they rest. Ecosystem structures and processes are influenced by long-term, large-scale biogeophysical drivers (i.e., tectonic pressures, global weather patterns) which in turn create the necessary conditions for providing the ecosystem goods and services people value. Ecological information must therefore be thoroughly integrated into an integrative conceptual framework before a meaningful assessment of economic value can be made. This is a formidable challenge, but we believe that the landscape classification system presented in section 3 of this paper provides a critical first step.

We conclude with the observation that most valuation studies to date have been performed for relatively few coastal ecosystem goods and services at a limited number of sites in the world. Hence, our ability to generalize from studies presented in this review is limited (Desvouges *et al.* 1998). Nevertheless, the results presented here do provide valuable insights into the challenges and limitations of ecosystem service valuation as it is currently being practiced. The experiences summarized here should be useful to ecologists, managers, and social scientists as they collaborate to estimate the total value of coastal ecosystem goods and services.

ACKNOWLEDGEMENT

The research for this chapter was sponsored in part by the Land-Ocean Interaction in the Coastal Zone (LOICZ) Project of the International Geosphere-Biosphere Programme.

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A CLASSIFICATION OF INSHORE MARINE BIOTOPES

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ABSTRACT

The greatest benefit of using habitat classifications is that the results from surveys of one or more sites can be directly compared with other studies. Such comparisons are difficult where *ad hoc* classifications peculiar to particular surveys or surveyors have been used. The development of a standard classification thus provides an invaluable standard where evaluation of the nature conservation importance or long term monitoring of sites is required.

The habitat classification developed as part of the BioMar project by the Joint Nature Conservation Committee in Britain, funded under the European Union LIFE Environment programme, is the first and only classification of all inshore littoral and sublittoral biotopes applicable to the north-east Atlantic.

This classification aims to provide a standard nomenclature and guide for describing and mapping marine biotopes. It covers all marine habitats from the high tide seaward, with the exception of salt marshes. Its development involved 12 meetings and 2 workshops with over 100 scientists from over 50 organisations throughout Europe to ensure the resulting structure would be widely applicable in the north-east Atlantic, and analysis of field data from about 1,600 sampling stations at 900 sites in Ireland, and over 10,000 sites in Britain to provide an empirical basis for the biotope descriptions.

This BioMar classification thus encompasses and complements related systems, including the European Union Habitats Directive, CORINE, European Palaearctic, Baltic HELCOM, French ZNIEFF-MER, and European Environment Agency EUNIS (European Nature Information System).

It has already been used in the identification of areas of nature conservation importance in Ireland and Britain. It has also been used in producing

Environmental Impact Statements and mapping areas of sensitivity during the SensMap project. It should also be used for mapping and inventorying areas of nature conservation importance (e.g. Natural Heritage Areas, Special Areas of Conservation, Special Protection Areas).

INTRODUCTION

Marine habitat classifications aim to provide a standard nomenclature and guide for describing and mapping marine biotopes (Costello 2000, 2001). The BioMar biotope classification (Connor *et al.* 1997a, b) covers all marine habitats from the high tide seaward, with the exception of salt marshes. Salt marshes are best characterised by terrestrial vascular plants and thus included in the terrestrial classifications.

Marine "habitats" by definition must be related to certain species. Benthic species habitats (e.g. boulders) vary on a scale of metres, whereas the habitats of pelagic and plankton species, and of marine birds and cetaceans, operate at larger areas, typically kilometres. These larger areas, here called seascapes, include bays, inlets, fjords, lagoons, estuaries, and harbours. Seascapes are the units used in environmental management, and are thus of practical importance. However, they contain a range of benthic marine habitats and biotopes that will vary from bay to bay. For this reason, seascapes were defined separately from biotopes and were excluded from the BioMar classification. If seascapes are to be classified, this requires an comparative analysis of the relationship of geo-morphological features to pelagic, plankton, and megafaunal species distributions. Different methods are used to map seascapes and biotopes. Mapping at a seascape level typically uses coastlines, bathymetric charts, and perhaps oceanographic, satellite or acoustic seabed data. In contrast, biotopes are usually identified by direct visual observation while walking on the seashore or scuba diving, or by sampling using video, still photography, grabs or cores. However, it is necessary to use biotopes to describe, map and evaluate the features of seascapes. Thus, the BioMar biotope classification complements any future developments of classifying seascapes.

The classification was developed as part of the BioMar project by the Joint Nature Conservation Committee in Britain, funded under the European Union LIFE Environment programme (Costello 1995, Picton & Costello 1998). It is the first and only classification of all inshore littoral and sublittoral biotopes applicable to the north-east Atlantic (see review by Hiscock 1991), and has been distributed to over 200 organisations in over 15 countries. Its development involved 12 meetings and two workshops with over 100 scientists from over 50 organisations throughout Europe to ensure the resulting structure would be widely applicable in the north-east Atlantic. An analysis of field data was made from about 1,600 sampling stations at 900 sites in Ireland, and over 10,000 sites in Britain to provide an empirical basis for the biotope descriptions. This BioMar classification thus encompasses and complements related systems, including the European Union Habitats Directive, CORINE (Commission of the European Communities 1991), European Palaearctic (Devilliers and Devilliers-Terschuren 1996), Baltic HELCOM, French ZNIEFF-MER (Dauvin *et al.* 1994), and

European Environment Agency EUNIS (European Nature Information System) (see Connor *et al.* 1997a, b for a more detailed linking of these systems). In this paper, we outline the benefits of using a marine biotope and habitat classification, describe the BioMar classification, and give some examples of the current and potential applications of this standardised ecological nomenclature and framework.

WHY USE THE MARINE BIOTOPE CLASSIFICATION?

The greatest benefit of using the BioMar classification is that the results from surveys of one or more sites can be directly compared with other studies (e.g. in Connor *et al.* 1997a, b). Such comparisons are difficult where *ad hoc* classifications peculiar to particular surveys or surveyors have been used. The classification is thus an invaluable standard where evaluation of the nature conservation importance or long term monitoring of sites is required. It has already been used in the identification of areas of nature conservation importance in Ireland and Britain. It is also being used in producing Environmental Impact Statements and mapping areas of nature conservation importance (e.g. Natural Heritage Areas, Special Areas of Conservation, Special Protection Areas).

Secondly, the classification can save time in the field and in data analysis. In the field, it is possible to rapidly label a sketch map of an area with the biotopes present. It is not necessary to map the distribution of each habitat and species and then subject this data to complex analyses in order to produce such maps. The classification can thus provide benefits in conducting surveys and interpreting their results. The upper levels (physical habitats) of the classification (Table 1) can generally be identified from existing information on marine charts. Thus a third use of the classification is that it can provide the basis of a methodology to predict the distribution of marine biotopes from existing data.

BIOTOPES

A biotope is the combination of the physical habitat (a place where animals and/or plants live) and its community of animals and plants. The three upper levels of the BioMar classification are listed in Table 1, and details of the 4th (biotopes) and 5th (sub-biotopes) are in Connor *et al.* (1997a, b). For the purpose of this classification, biotopes were only defined when they were recognisable in the field, and when the same combination of habitat and community was repeated in several different localities. The species used to characterise a biotope tend to be visually conspicuous by virtue of their size, lack of mobility, and/or dominant growth over the seabed. The presence of other species (not used to characterise biotope) will vary in a biotope over time, and between examples of a biotope in different places. Often, these will be species which are rare, inconspicuous, or need to be identified in the laboratory and/or by specialists. However, even characterising species will vary in abundance between areas. While a habitat and environmental conditions may not change, species abundance and occurrence will vary over time due to natural biological forces (e.g. grazing, predation, or disease). Biotopes can not be treated as a form of 'super-species' because their constituent species will

Table 1. Checklist of the upper three levels (major habitat, habitat complex, biotope complex) of the BioMar marine biotope classification of Connor *et al.* (1997a, b). Species on rock may also occur on other hard substrata (e.g. shells, piers, shipwrecks). Number of biotopes and sub-biotopes indicated in parentheses.

Littoral rock

- Lichens or algal crusts (9)
- Exposed (mussel/barnacle shores)
  - *Mytilus* (mussels) & barnacles (7)
  - Robust fucoids & red seaweeds (3)
- Moderately exposed (barnacle/fucoid shores)
  - Barnacles & fucoids (7)
  - Red seaweeds (5)
  - Ephemeral green or red seaweeds (freshwater or sand-influenced) (3)
  - *Mytilus* (mussels) & fucoids (3)
  - *Sabellaria* (honeycomb worm) reefs (1)
- Sheltered (fucoid shores)
  - Dense fucoids (stable rock) (10)
  - Fucoids, barnacles or ephemeral seaweeds (mixed substrata) (8)
  - *Mytilus* (mussel) beds (mixed substrata) (1)
- Rockpools (9)
- Overhangs & caves (3)

Littoral sediments

- Littoral gravels & sands
  - Shingle (pebble) & gravel shores (2)
  - Sand shores (7)
  - Estuarine coarse sediment shores (1)
- Littoral muddy sands
  - Muddy sand shores (4)
  - Littoral *Zostera* (seagrass) beds (1)
- Littoral muds
- Salt marsh (26 +)
- Sandy mud shores (4)
- Soft mud shores (3)
- Littoral mixed sediments (2)

Circalittoral rock

- Exposed
- Faunal crusts or short turfs (3)
  - *Alcyonium*-dominated communities (tide-swept/vertical) (4)
  - Barnacle, cushion sponge & *Tubularia* communities (very tide-swept/sheltered) (5)
  - Moderately exposed
  - Mixed faunal turfs (4)
  - Bryozoan/hydroid turfs (sand-influenced) (9)
  - Circalittoral *Sabellaria* reefs (1)
  - Mussel beds (open coast circalittoral rock/ mixed substrata) (3)
  - Brittlestar beds (2)
  - Grazed fauna (moderately exposed or sheltered rock) (2)
  - Ascidian communities (silt-influenced) (3)
  - Soft rock communities (2)
- Sheltered
  - Brachiopod & solitary ascidian communities (8)
  - Sheltered *Modiolus* (horse-mussel) beds (2)
  - Faunal turfs (deep vertical rock) (2)
  - Caves & overhangs (deep) (1)

Circalittoral offshore rock

- *Lophelia* (coral) reefs (1)

Sublittoral sediments

- Infralittoral gravels & sands
  - Maerl beds (open coast/clean sediments) (4)
  - Shallow gravel faunal communities (2)
  - Shallow sand faunal communities (5)
  - Estuarine sublittoral gravels & sands (3)
- Circalittoral gravels & sands (3)
- Infralittoral muddy sands

Table 1 (continued)

Infralittoral rock

- Exposed
  - Kelp with cushion fauna, foliose red seaweeds or coralline crusts (13)
  - Robust faunal cushions & crusts (surge gullies & caves) (10)
- Moderately exposed
  - Kelp with red seaweeds (11)
  - Grazed kelp with algal crusts (3)
  - Sand or gravel-affected or disturbed kelp & seaweed communities (7)
- Sheltered
  - Silted kelp (stable rock) (14)
  - Estuarine faunal communities (shallow rock/ mixed substrata) (3)
  - Submerged fucoids, green & red seaweeds (lagoonal rock) (4)
  - Other fauna & seaweeds (shallow vertical rock) (3)

Sublittoral sediments (continued)

  - Seagrass beds (2)
  - Shallow muddy sand faunal communities (4)
- Circalittoral muddy sands (5)
- Infralittoral muds
  - Angiosperm communities (lagoons) (2)
  - Shallow marine mud communities (4)
  - Estuarine sublittoral muds (7)
- Circalittoral muds (3)
- Infralittoral mixed sediments
  - *Laminaria saccharina* (sugar kelp) & filamentous seaweeds(4)
  - Maerl beds (muddy mixed) (3)
  - Oyster beds (1)
  - Shallow mixed sediment faunal communities (3)
- Estuarine sublittoral mixed sediments (3)
- Circalittoral mixed sediments (3)
- Circalittoral offshore sediments (3)

vary between and within an area over time. Areas of transition between recognisable biotopes (sometimes called ecotones) may be large in area, and contain a mixture of biotopes and species. Indeed, they may be richer in species than the more 'typical' biotopes. Such transitional areas are a natural feature of the environment and cannot be viewed as of greater or lesser importance than better known communities. Indeed, the presence of many species in the transitional area is probably dependent on colonisation from the adjacent biotopes. Making such decisions about whether a sampling station represents an already described biotope, is a transition between biotopes, or is a new biotope, requires a wide knowledge of marine community ecology and experience in using the classification.

The relationship between biotopes and the main habitat features can be illustrated in matrices (Figure 1). Many environmental factors influence the distribution and abundance of species, but only those recognisable on a single visit to a site have been used in the classification. However, the influence of other factors, such as temperature, salinity, siltation, turbidity, currents, human disturbance, pollution, and species interactions (e.g. predation, grazing, competition for space), may be indicated or inferred from observations at a site. In the classification, 'exposure' refers to both wave and current action. However, these forces can have significantly different effects on species distribution, but the former is generally the important factor in littoral biotopes and sublittorally on open coasts. Current exposure is more important in narrow channels and straits, and in offshore deep waters (> *c.* 100 m depth).

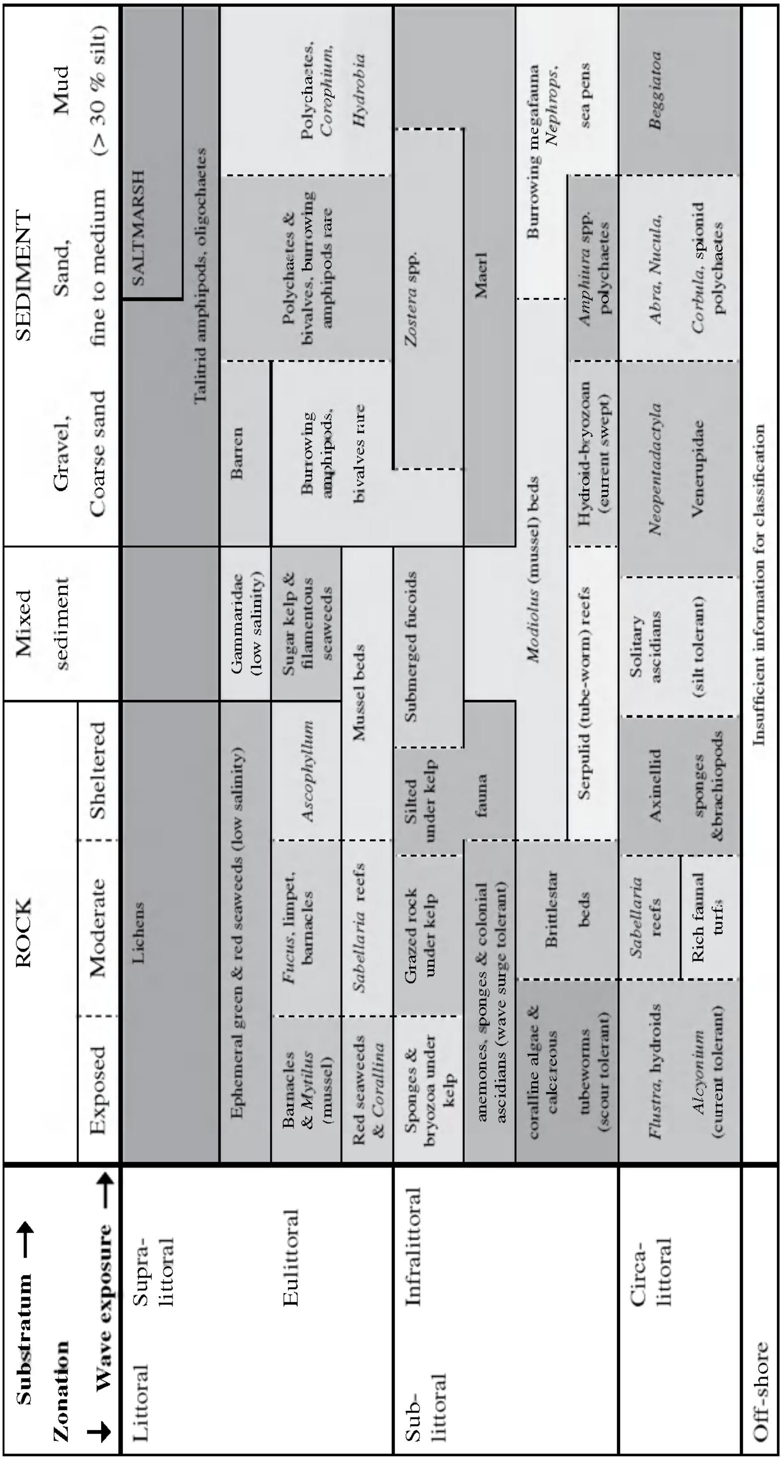

Figure 1. A matrix with the most important habitat features on the axes. This illustrates the relationship of shore height (littoral) and sea depth (sublittoral, offshore), with substratum (rock and grades of sediment), and the exposure of rocky habitats to wave action. These factors distinguish biotopes at the upper levels of the classification. Within the matrix the characteristic species of the communities occurring in the habitats are indicated (but see detailed classification for full definitions and details).

UPPER LEVELS OF THE CLASSIFICATION

The marine biotope classification firstly distinguishes seashores (littoral) from the seabed which is permanently submerged by the sea (sublittoral). Seashores are next divided into rock and sediments. The upper limit of the littoral (supralittoral) is the spray or splash zone on rocky shores, and the strandline on sediment shores. Many seashores may contain areas where boulders are associated with sand and mud, and such mixed sediments are a special category (Table 1 under Littoral sediments). The sublittoral is similarly divided on the basis of substratum being rock or sediment, but also on whether it is dominated by plants with animals (infralittoral) or only animals (circalittoral). The lower limit of the sublittoral is not defined, and offshore (including circalittoral) rock and sediment biotopes have not been sufficiently studied to be classified. However, a deep-sea coral reef biotope which occurs in Irish waters has been included because it is distinct and threatened by deep water trawling.

Littoral rock biotopes have been further divided on the basis of the well known distribution of species according to wave exposure. The uppermost biotopes are dominated by yellow (e.g. *Xanthoria*), grey (e.g. *Ramalina*) and black (e.g. *Verrucaria*) lichens on all rocky shores (Figure 1). The isopod *Ligia,* snails *Littorina saxatilis* and *Melarhaphe neritoides,* seaweeds (algae) *Enteromorpha, Porphyra, Prasiola, Ulothrix* are also common in this zone. The mid-shore (eulittoral) is dominated by either barnacles (*Semibalanus, Chthamalus* spp.), limpets, mussels and/or robust algae such as the coralline alga *Corallina* on wave exposed shores, to dense beds of fucoid algae such as *Ascophyllum* on wave sheltered shores. Moderately exposed shores contain beds of *Fucus* species, associated snails, mussels, amphipods, crabs, red algae, and many other species, and mixtures of species depending on the influences of local scale topography, freshwater, and sand scour. Features such as rock pools, crevices, overhangs (typically characterised by sponges and ascidians), and honeycomb worm (*Sabellaria*) reefs, may be large enough to map as distinct biotopes.

Littoral sediments are classified according to sediment size because this is a readily identifiable feature. It also reflects the wave exposure and water-holding properties on the sediment which influence species distributions. The upper shore, above, on and below the strandline, is characterised by several species of talitrid amphipods with differing microhabitats. In the eulittoral, the coarsest sediments (gravels) may have no species present. The fauna of coarse sand beaches is characterised by amphipod (e.g. *Pontocrates, Bathyporeia, Haustorius*) and isopod (*Eurydice pulchra*) crustaceans, often with certain polychaete worms (*Scolelepis, Nephthys, Lanice*) and the bivalve *Angulus tenuis,* which become progressively rarer in the more widespread muddy sand beaches. The muddy sand beaches are characterised by bivalve molluscs (e.g. *Macoma balthica,* cockle *Cerastoderma edule*), polychaete worms (e.g. *Arenicola, Lanice*), and shrimp *Crangon crangon.* A rich diversity of polychaete worms may occur on muddier beaches, and sea grass *Zostera* species may form beds which stabilise sediments and provide a surface of other species. Very muddy sand and sandy mud shores are dominated by polychaete worms (e.g. *Hediste diversicolor, Nephthys hombergii,* and *Pygospio elegans*), bivalves (e.g. *Macoma balthica, Abra tenuis, Cerastoderma edule, Scrobicularia plana*), snail *Hydrobia,* and amphipod *Corophium* species. Fine mud and muddy sands with a freshwater influence are characterised by oligochaete worms. Sediment shores may extend into salt marsh which is dominated by flowering plants (angiosperms), but will often have fucoid brown algae (e.g. *Pelvetia canaliculata, Fucus* spp.), and talitrid amphipods (e.g. *Orchestia* species) present. Because of the dominance of salt marshes by angiosperms their biotopes have already been classified in terrestrial phytosociological classifications (e.g. Commission of the European Communities 1991) and are not considered further in this marine classification.

Infralittoral rock is usually dominated by kelp species along the sublittoral fringe, ranging from *Alaria esculenta* in the most wave exposed, to *Laminaria digitata* in moderately exposed, and *Laminaria saccharina* in sheltered areas. Mixtures of these kelp species are common, and a rich under-storey of red algae, sponges, bryozoans and ascidians may occur. Immediately below these species the kelp *Laminaria hyperborea* may form a forest with a variety of associated fauna and flora forming a range of biotopes. The effects of sea urchin (e.g. *Echinus esculentus*) grazing may significantly impoverish the under-storey community.

Circalittoral rock is often characterised by some of the fauna which occurred under *L. hyperborea* forest, depending on the wave exposure, current, and sand scour conditions. The soft-coral *Alcyonium,* large sponges *Pachymatisma johnstonia* and *Cliona celata,* and hydroids (e.g. *Tubularia indivisa*), characterise vertical rock and tide swept biotopes. Wave exposed biotopes are characterised by the jewel anemone *Corynactis viridis,* cup coral *Caryophyllia smithii,* feather star *Antedon bifida,* and a range of bryozoans, anemones, sponges and hydroids. Current swept and sand scoured biotopes are usually characterised by hydroids (e.g. *Flustra foliacea, Sertularia* spp.), bryozoans, anemone *Urticina felina,* barnacles (e.g. *Balanus crenatus*), and calcareous tubeworms (e.g. *Pomatoceros triqueter*). Solitary ascidian species, brachiopods, and sponges characterise more wave and current sheltered conditions, such as occur in deeper waters. Some species may form particular biotopes, such as reefs of the honeycomb worm *Sabellaria spinulosa,* beds of mussels (i.e. *Mytilus edulis, Musculus discors, Modiolus modiolus*) and brittlestars (e.g. *Ophiothrix fragilis, Ophiocomina nigra*).

Sublittoral sediments represent an extension of the lower shore fauna into the sublittoral, with less distinct zonation of biotopes than occurs on rock. Beds of seagrass (*Zostera* species), *Ruppia maritima,* oysters *Ostrea edulis,* or maerl (e.g. *Phymatolithon calcareum, Lithophyllum* spp.), may occur on a range of sediments from coarse to very muddy sands. Other shallow sublittoral sand habitats may also be characterised by the urchin *Echinocardium cordatum* and razor shell (*Ensis*) species. Gravel with 'clean' and coarse sand habitats are characterised by bivalves (e.g. *Spisula elliptica*), anemones (e.g. *Halcampa, Edwardsia, Aureliania*), polychaetes (e.g. *Nephthys cirrosa, Lanice conchilega*) and amphipods (e.g. *Bathyporeia* spp.). In more stable and muddier sediments, anemones, seapens (*Virgularia mirabilis*), polychaetes, bivalves (e.g. *Pecten maximus, Fabulina fabula, Chamelea gallina*), characterise the biotopes. Very muddy sand biotopes are characterised by bivalves (e.g. *Abra* spp.), small brittlestars (e.g. *Amphiura* spp., *Ophiura* spp.), urchin *Brissopsis lyrifera,* Dublin Bay prawn *Nephrops norvegicus,* seapens (e.g. *Virgularia, Pennatula*) and polychaetes.

USING THE CLASSIFICATION OF MARINE BIOTOPES

The use of the marine biotope classification generally requires people with a first degree in an ecological science (e.g. botany, zoology, environmental science), some weeks field experience in sampling marine habitats, and skill in identifying species using specialist texts. Less skilled surveyors can limit their definition of biotopes to higher levels in the hierarchy (Table 1). More skilled surveyors, as would be required to assess the nature conservation importance of an area, would need to use the more detailed classification of over 200 biotopes published by Connor *et al.* (1997a, b), and identify more species than used to characterise biotopes. This detailed classification defines biotopes equivalent to the plant communities in the CORINE classification (Commission of the European Communities 1991). Connor *et al.* (1997a, b) also provide a biotope coding system based on abbreviations of the characterising habitat features and species. This is useful shorthand for use in map presentation and is linked to a colour code system for mapping. It should be noted that the classification is never final, and will be expanded as more information and results of analyses of existing data become available. For example, analysis of data from strandline habitats on seashores in Ireland showed that at least two biotopes could be characterised by common talitrid amphipod crustacean genera (Costello *et al.* 1999).

Biotopes less than 5 × 5 m in area, such as rockpools on the seashore, crevices in rock, or occasional stone on a sediment seabed, are not mapped but their presence is noted in the description of that biotope because such microhabitats can significantly increase the number of species in an area. The sampling of marine habitats is usually 'stratified' by limiting sampling to certain zones and/or biotopes. This greatly reduces the variation between replicate samples. The seashore is probably the most narrowly banded range of biotopes in the world due to the varying sensitivity of species to exposure to the air and submersion by the sea. Here biotopes may be only centimetres wide but kilometres long. Selected suites of biotopes can be combined for mapping purposes depending on the map scale, proposed readership, and data quality.

Field notes provide a standard indication of the abundance of species. This is helpful in biotope identification, desirable to compare the same biotopes in different areas, and essential to monitor change in a biotope over time. All conspicuous fauna and flora should be identified to species level and assigned to a semi-quantitative ($\log_{10}$) abundance scale following the methods described in Hiscock (1996). Where identification of species is uncertain or may be questioned later, representative specimens should be collected and/or photographed, and retained in a voucher collection. Where there are insufficient conspicuous species to identify a biotope, as usually is the case on mobile sediments (e.g. sandy beaches), then replicate sediment samples must be taken and the fauna identified microscopically. The naming of species should follow a standardised list (Costello *et al.* 2001, www.marbef.org/data/erms.php) unless otherwise stated, and of biotopes should follow Connor *et al.* (1997a, b). Ecological terminology should be used with care (Table 2).

Methods for biotope mapping have been developed in Ireland by the SensMap project (Emblow *et al.* 1998, Ecological Consultancy Services 2000, Davies *et al.* 2001). Field studies which mapped seabed habitats and communities in Wales were developed into an integrated methodology for mapping in the field, linking marine and terrestrial maps. This methodology was transferred to Ireland and adapted through collaborative fieldwork (Emblow *et al.* 1998). These methods and the biotope classification have already been used in producing Environmental Impact Statements. It should also be used for mapping and inventorying areas of nature conservation importance (e.g. Natural Heritage Areas, Special Areas of Conservation, Special Protection Areas).

The length of seashore occupied by the major habitats in the classification has been determined for each county of Ireland (Neilson and Costello 1999). This data could be used to consider how representative existing and candidate marine protected areas are of the habitats along the 7,500 km coastline, and could be expanded to aid prediction of the occurrence of biotopes and biodiversity (Neilson and Costello 1999).

The BioMar biotope classification provides a readily available (http://www.marlin.ac.uk/baski/baski_bio_home.htm), well-defined, ecological framework for use in environmental management, research and education. This standards-based system facilitates data management and exchange, and mapping at different spatial scales, such that comparisons of biodiversity between studies is possible. Future developments should include expanding the biotope classification beyond inshore waters and the North-East Atlantic, using it more as a management tool, and research into the potential of the classification to act as a surrogate for measures of biodiversity (e.g. species richness, complementarity, beta-diversity).

Table 2. A glossary of marine terminology used here. Some terms may be used slightly differently in other contexts. A useful dictionary of ecological terms is that by Lincoln *et al.* (1998).

Term	Definition	Alternative named
Biota	all living organisms, including fauna and flora	
Biotope	a habitat with a characteristic community	facies
Boulder	stones > 25 cm diameter	
Circalittoral	seabed dominated by animals, algae rare or absent, seasonally stratified, effect of wave action limited to storms	
Cobble	stones 64 to 256 mm diameter	
Community	group of different species which occur together	
Epibenthos	animals (epifauna) and plants (epiflora) living on the surface of the seabed or on other animals and plants	
Eulittoral	Between the supralittoral and sublittoral fringe	mediolittoral, hydrolittoral

Table 2 (continued)

Gravel	sediment grains 4 to 16 mm diameter	
Infauna	animals living within sediments	
Infralittoral	Rock dominated by algae, water column temperature and salinity variable,	Nearshore
Inshore	generally within 5 km of coastline and < 50 m depth	Coastal seas
Littoral	Between upper and lower tidemarks, exposed to air at the lowest tides	Intertidal
Mud	sediment grains < 0.063 mm diameter	silt, clay
Offshore	Stable water column characteristics (stenothermal, stenohaline), permanently stratified, beyond zone of freshwater influence, no benthic algae, generally > 5 km from the coastline	
Pebble	sediment grains 16–64 mm diameter	
Reefs	hard substrata raised from the seabed to provide cover for mobile fauna (e.g. fish, crustaceans). May be formed by rocks, coral, and tubeworms.	
Rock	with epibiota and infauna absent or rare	Hard substrata
Sand	sediment grains 0.063–4 mm diameter	
Sediment	with infauna, and usually some epibiota	Soft substrata
Spray zone	area of upper seashore not submerged at high tide but sprayed at high tide by seawater	Splash zone
Strandline	area of upper seashore where loose seaweed and other floating debris is deposited by the falling tide	
Sublittoral	Below the littoral, never exposed to air	Subtidal
Sublittoral fringe	Transition zone where littoral and sublittoral species occur	infralittoral fringe
Substrata	surfaces (plural) to which an organism grows on or amongst	
Substrate	substance used as a food source by organism or enzymes	
Substratum	surface (singular) to which an organism grows on or amongst	
Supralittoral	Uppermost part of shore affected by wave splash but not regularly submerged by the sea	Strandline, splash zone, spray zone, epilittoral, littoral fringe, supratidal
Zone	Horizontal area of vertical height above, and depth below, sea level which has characteristic fauna and flora	étage (French)

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COASTAL WETLAND BIRDS AND THE EU BIRDS DIRECTIVE

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THE BIRDS DIRECTIVE

On 2nd April 1979 the European Communities published a Council Directive on the conservation of wild birds (79/409/EEC), which has become known as the Birds Directive (Official Journal of the European Communities, 1979). Ireland, being a Member State of the European Union, is obliged to implement the Birds Directive here. This Directive is quite short, containing 19 Articles, some of which relate to procedural, administrative and legal matters, e.g. the setting up of a Committee for Adaptation to Technical and Scientific Progress (known as the ORNIS Committee), triennial reporting requirements, amendments to national laws and regulations to ensure compliance with the Directive. There are also Articles relating to the regulation of hunting and trade in wild birds, and to derogations from provisions of the Directive.

The Directive relates to the conservation of all species of wild birds naturally occurring in the Member States, and there is a strong emphasis on maintaining a favourable conservation status for these species and their various habitats. Annex I of the Directive lists species which, because of their rarity or vulnerability, require special conservation measures concerning their habitat. Article 4 of the Directive requires that Member States establish a network of Special Protection Areas (SPAs) for the needs of these species.

The SPA network should apply also to regularly occurring migratory species not listed in Annex I and to internationally important bird concentrations, and particular emphasis is placed on the need to protect wetlands, especially those of international importance for birds. The SPAs must be protected from significant pollution, deterioration of habitat and disturbance to birds. The Directive has been transposed into Irish law.

IRELAND'S COASTAL BIRDS

Ireland, being an island with an indented coastline, has many intertidal bays and estuaries which are important for a wide variety of bird species. These birds utilise the intertidal zone primarily for feeding (mainly on invertebrates, small fish, green algae, saltmarsh plants, etc.), and also for roosting. The largest numbers and diversity of birds occur during the winter months, and during spring and autumn passage migration periods. The great majority are migrants from breeding grounds to the north, ranging from north-east arctic Canada to Siberia. A number of them are included in Annex I of the Birds Directive, while some occur in internationally important concentrations at individual sites. The main species which occur regularly, and in significant numbers, at Irish intertidal wetlands are listed in Table 1, and those which are included in Annex I of the Directive are indicated.

Table 1 Main bird species for which intertidal Special Protection Areas (SPAs) have been designated in the Republic of Ireland and Annex I listing

Great Crested Grebe	*Podiceps cristatus*	
Cormorant	*Phalacrocorax carbo*	
Grey Heron	*Ardea cinerea*	
Whooper Swan	*Cygnus cygnus*	Annex I
Greenland White-fronted Goose	*Anser albifrons flavirostris*	Annex I
Greylag Goose	*Anser anser*	
Light-bellied Brent Goose	*Branta bernicla hrota*	
Shelduck	*Tadorna tadorna*	
Wigeon	*Anas penelope*	
Teal	*Anas crecca*	
Mallard	*Anas platyrhynchos*	
Pintail	*Anas acuta*	
Shoveler	*Anas clypeata*	
Red-breasted Merganser	*Mergus serrator*	
Oystercatcher	*Haematopus ostralegus*	
Ringed Plover	*Charadrius hiaticula*	
Golden Plover	*Pluvialis apricaria*	Annex I
Grey Plover	*Pluvialis squatarola*	
Lapwing	*Vanellus vanellus*	
Knot	*Calidris canutus*	
Sanderling	*Calidris alba*	
Dunlin	*Calidris alpina*	
Black-tailed Godwit	*Limosa limosa*	
Bar-tailed Godwit	*Limosa lapponica*	Annex I
Whimbrel	*Numenius phaeopus*	
Curlew	*Numenius arquata*	
Redshank	*Tringa totanus*	
Greenshank	*Tringa nebularia*	
Turnstone	*Arenaria interpres*	
Black-headed Gull	*Larus ridibundus*	
Common Gull	*Larus canus*	

Lesser Black-backed Gull	*Larus fuscus*	
Herring Gull	*Larus argentatus*	
Great Black-backed Gull	*Larus marinus*	
Sandwich Tern	*Sterna sandvicensis*	Annex I
Common Tern	*Sterna hirundo*	Annex I
Arctic Tern	*Sterna paradisaea*	Annex I

SELECTION OF SITES SUITABLE FOR DESIGNATION AS SPECIAL PROTECTION AREAS

Much is known about the occurrence and distribution of coastal wetland birds from the middle of the 19th century, but the historic information is almost entirely non-quantitative. This made it difficult to establish the relative importance of the wetlands for the various bird species which utilised them. The situation improved greatly from 1960, when systematic censusing of waterbirds began with national censuses of Light-bellied Brent Geese *Branta bernicla hrota* (Merne *et al.* 1999). In the mid-1960s the then Irish Wildfowl Committee (now BirdWatch Ireland) began to encourage the censusing of all wintering waterfowl in Ireland, and Hutchinson (1979) reported on the results of systematic waterfowl censusing in the early 1970s. Based on these it was possible, for the first time, to identify the relative importance for birds of a large number of Irish wetlands. At the same time An Foras Forbartha embarked on a programme of identifying Areas of Scientific Interest in Ireland and all the important waterfowl wetlands were included in the ASIs (Anon. 1981).

Because of the great mobility of migrant waterbirds, changes in their distribution, and the fluctuations in their populations over time, it is necessary to monitor them at regular intervals. The survey and censuses reported by Hutchinson (1979) were repeated in the mid-1980s by Sheppard (1993), and these showed some significant changes in the status and distribution of some species, leading to re-evaluation of the importance of some wetland sites. It was recognised that the survey/census interval of about ten years was too long to identify changes in numbers and distribution as they occurred and so a new, permanent, annual waterbird census was established in 1994/95. This was called the Irish Wetland Bird Survey (I-WeBS) and is a joint project of BirdWatch Ireland, Wildfowl and Wetlands Trust (UK) and Dúchas The Heritage Service. I-WeBS prioritises monthly counts from September to March at the internationally and nationally important wetlands, and the results appear in an annual report (Delany 1996, 1997; Colhoun 1999, 2000, 2001).

The combined results of these surveys and censuses over about thirty years have enabled us to identify with confidence the internationally and nationally important wetlands for waterbirds in Ireland, and, in turn, these wetlands qualify as candidate Special Protection Areas. The main criteria used for selecting wetlands for SPA designation are as follows:

1. An area which is internationally important because it is regularly used by 1% or more of the biogeographical population of a regularly occurring migratory waterbird species.

2. An area which is internationally important because it is regularly used by over 20,000 waterfowl in any season.
3. An area which is nationally important because it is regularly used by 1% of the all-Ireland population of a species, particularly of an Annex I species.

The first two criteria arise from the Ramsar Convention on Wetlands of International Importance especially as Waterfowl Habitat (1971).

SPA DESIGNATION PROCESS

The first stage, described above, is the collection of sufficient data to establish the range of bird species, their numbers, and the regularity of their usage of a wetland. The numerical criteria can then be applied and when it is deemed a site qualifies for SPA designation it is formally proposed. Once a site reaches this stage it must be protected as if legally designated, according to case law (EU Commission *vs.* Spain – Santona Marshes) of the European Court of Justice.

The next stage is to produce a definitive large-scale map showing the proposed boundary of the site. There follows a consultative stage where relevant government departments, local authorities, the public and other parties may comment, appeal or object to the SPA proposal, on scientific grounds. Once this stage has been concluded the site (with boundary modifications if appropriate) is formally designated by Statutory Instrument, and the EU Commission is notified. SPAs are included with Special Areas of Conservation in the EU-wide Natura 2000 network set up under the Council Directive 92/43/EEC (the Habitats Directive).

INTERTIDAL SPAS FOR COASTAL BIRDS IN IRELAND

To date Ireland has designated 110 Special Protection Areas, of which 80 are coastal. Of these, 40 are islands and mainland cliffs which are important sites for breeding seabird colonies. Of the remaining 40, 34 are intertidal bays and estuaries, which are internationally or nationally important habitats for migratory waterfowl (swans, geese, ducks, waders, gulls, terns, etc.) (Figure 1, Table 2). Work is continuing on the SPA network and it is envisaged that the total number of SPAs in Ireland will be c.160 within the next few years. A number of the new SPAs will be coastal sites. In addition, a number of coastal SPAs will be extended significantly as a result of a review which established the importance of additional areas adjacent to the originally designated sites.

With the I-WeBS project continuing indefinitely, and gradually expanding its geographical coverage, it can be anticipated that new information on waterbird numbers and distribution may lead to the identification of additional candidate SPAs in the medium and long terms. It is also possible that future changes in numbers and distributions of waterbirds at the biogeographical or flyway scale will give rise to the identification of new candidate SPAs. Clearly there is an on-going need for monitoring and periodic review to ensure that our network of SPAs adequately meets the conservation needs of our migratory waterfowl.

It should be mentioned that coastal wetlands which do not meet the quantitative criteria for SPA designation may, individually or collectively, make an important contribution to waterbird conservation. These sites can receive protection under national legislation (Wildlife Act, 2000) by designation as Natural Heritage Areas.

Figure 1. Location of intertidal Special Protection Areas for coastal birds in the Republic of Ireland. See also Table 1.

Table 2 Intertidal Special Protection Areas for coastal birds in the Republic of Ireland: see also Figure 1

SPA	County
Carlingford Lough	Louth/Down
Dundalk Bay	Louth
Boyne Estuary	Louth/Meath
Rogerstown Estuary	Dublin
Malahide/Swords Estuary	Dublin
Baldoyle Bay	Dublin
North Bull Island	Dublin
Tolka Estuary	Dublin
Sandymount Strand	Dublin
Kilcoole/Newcastle	Wicklow
Broad Lough	Wicklow
The Raven	Wexford
Wexford Harbour	Wexford
Tacumshin Lake	Wexford
Ballyteige/The Cull	Wexford
Bannow Bay	Wexford
Tramore Back Strand	Waterford
Dungarvan Harbour	Waterford
Blackwater Estuary	Waterford/Cork
Ballymacoda	Cork
Ballycotton	Cork
Cork Harbour	Cork
Castlemaine Harbour/Rossbehy Creek	Kerry
Tralee Bay/Barrow Harbour/Banna Strand	Kerry
Shannon/Fergus Estuary	Kerry/Limerick/Clare
Inner Galway Bay	Clare/Galway
Blacksod Bay/Broadhaven	Mayo
Killala Bay	Mayo/Sligo
Ballysadare Bay	Sligo
Cummeen Strand	Sligo
Drumcliff Bay	Sligo
Lough Swilly	Donegal
Trawbreaga Bay	Donegal
Lough Foyle	Donegal/Derry

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NET PRIMARY PRODUCTIVITY OF INTERTIDAL SYSTEMS: THE DUBLIN BAY EXAMPLE

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ABSTRACT

Reasons for the determining of intertidal primary production are explained, and methods for so doing described. Data are presented for a *Salicornia* bed, a *Zostera* bed, a salt marsh, macroalgae and microphytobenthos from Dublin Bay. *Spartina* production is reviewed. It is concluded that organic production in the intertidal zone is effectively removed, and no sequestration of carbon occurs. However the resources for secondary production may now be readily quantified, and changes in primary production from season to season used in quality monitoring.

INTRODUCTION

Many studies of intertidal primary production in Dublin Bay have been carried out over the last 30 years. These have included substantial investigations of macroalgae regarded as a nuisance, for example Jeffrey *et al.* (1992), curiosity-driven studies of mudflat angiosperms (Madden 1984, Jennings 1991), and ecosystem studies of salt marsh (McNamee 1976). This experience has led us to develop and employ simple methods. We also have a data bank of interest, which is sufficiently robust to be applied to other similar sites in north-western Europe.

Why should efforts be made to determine the primary productivity of intertidal systems? There are five principal reasons:

1. As a fundamental component of the carbon cycle, enabling the estimation of the comparative contribution of species and communities to production (Biomass × 0.45 = C). In the context of global change, C sequestration is an issue and enhanced carbon dioxide concentrations may drive increased primary production.
2. To allow the quantification of all materials cycles, especially major nutrients and pollutants (g biomass m^{-2} × mg g^{-1} of element or substance).

Nitrogen, phosphorus, sulphur, metals, pesticides are all substances of interest both fundamentally and for the biomonitoring of pollutants. Studies of eutrophication are especially important.

3. To determine potential resource levels for secondary production. During the period of growth grazing certainly occurs; and it is also assumed that exudates from living plants enter the environment. After natural senescence of whole annual plants or portions of root and shoot in perennials, dissolved organic matter (DOM) and particulate organic matter (POM) are released. Accumulated biomass disappears rapidly after the summer growing season, and it is assumed that this material subsidises the offshore marine ecosystems.
4. To compare with input of detrital organic matter, and thus determine whether the system is autotrophic or heterotrophic. All estuaries and most other coastal sites receive inputs of organic matter from elsewhere. In urbanised situations sewage is a major contributor to organic loading. It is of interest whether studying the change from autotrophic to heterotrophic state can be an approach to management.
5. To assist management of intertidal environmental quality generally. It has been established that an index based on the ratio of intertidal area occupied by stable communities, opportunist communities, and abiotic areas may be used as a quality indicator (Wilson & Jeffrey 1994)

DEFINITIONS

Concept of net primary production

Net primary production is biomass produced in a season of growth, not correcting for respiratory losses but adding calculated herbivore consumption and other losses from senescence and transfers to non-living litter.

The usual formula for net primary production, as applied to a grassland (Milner & Hughes 1968) is:

$$P_n = \Delta B_{T2\text{-}T1} + G + L$$

Where: P_n is net primary production, $\Delta B_{T2\text{-}T1}$ is change in dry biomass from time 1 to time 2, G is biomass grazed and L is lost biomass.

This means that the *modus operandi* is to determine dry biomass at intervals during the growing season, and to estimate grazing and other losses for similar time periods. This concept is certainly applicable to saltmarsh (Dalby 1987), and has been readily applied to dune systems (Fay & Jeffrey 1995). Whilst measuring biomass is straightforward, the difficult technical problem is estimating grazing and miscellaneous losses. Expression of productivity on a strictly annual basis is often an aspiration, as sample collection is often not possible for a 12 month period. One expedient is to determine biomass at maximal and minimal values.

Organic matter and fixed carbon

The key characteristic of intertidal areas is that, unlike terrestrial grasslands, they are tidally swept. Thus debris, detrital material and planktonic organisms are passively swept in and out of the system. Flux of carbon-containing material, decomposition of organic matter and incorporation of material into sediment are all more difficult to determine.

Intertidal

The definition of 'intertidal' used in this paper is the amplitude of highest astronomical tides. This may be found by inspection from the Admiralty Tidal Chart entry for a given port. In Dublin Bay, this is from +4.5m O.D. to +0.4m O.D. The upper boundary includes the slightly saline fore dunes at the front of dune systems, the whole of the rocky shore algal sequence, excluding the spray zone with its lichens, and the upper salt marsh to its abrupt transition to a non-halophytic community.

The lower edge is less ecologically critical, with no abrupt community boundaries between the lowest intertidal and truly benthic communities.

METHODS: COMPARISONS AND SCALING ISSUES

Simple, robust, methods must be used for biomass determination in the intertidal zone. They are derived from terrestrial methods and should ultimately yield data expressed as dry weight yields per metre square per annum ($m^{-2}.y^{-1}$). The intertidal environment is very variable and a range of yield classes will inevitably be encountered. It is necessary to be aware of this and to design a stratified random sampling system, which samples each yield class consistently.

Algal biomass

An individual sample of an *Enteromorpha* mat may be taken using a square quadrat from 0.0625m^2 to 1m^2, cutting the mat with a sharp knife and lifting it clear of the substrate. For large quadrats with low cover values, it is worth using a wire rake to gather dispersed filaments. The wet and sediment-contaminated material is weighed in the field using a spring balance. Only a small sub-sample is weighed and transferred to the laboratory. Here it is cleaned, dried and fresh weight:dry weight ratios determined.

Scaling issues arise from the patchiness and pattern of intertidal systems. For example in the 75 ha of the south lagoon of the Bull Island system, the range of biomass presented and the areal extent of each range class are known (Jennings 1996). Another good example is the Narragansett Bay study of Valiela and Teal (1979). Here it is seen that the intensities of production-driven processes in the nitrogen cycle are spatially separated. In order to arrive at a good system analysis, it is vital that a thorough cartographic survey is available. This should have an appropriate level of resolution and accuracy to match that of laboratory-based measurements.

Rooted plants

Examples of intertidal rooted plants include *Salicornia* spp., *Zostera* spp., *Spartina anglica* and saltmarsh vegetation. *Salicornia* and *Zostera* were both sampled using a

10 cm diameter corer. The cores were washed in the lab, and individual components separated where appropriate, e.g. roots, rhizomes, shoots, leaves, flowers, fruits and non-living biomass.

In the case of vegetation samples, aboveground biomass may be harvested and sorted using a quadrat as a guide. Roots can be conveniently sampled with a corer, taking one or more cores per quadrat.

Microphytobenthos

Microalgae, on sediment surfaces, consist mainly of diatoms, with green algae and cyanobacteria also present. Microphytobenthos biomass is estimated using sediment chlorophyll *a* concentrations. Samples are taken using a syringe, modified by cutting off the end of the barrel. It is used as a corer, sampling to a depth greater than 5 mm, in order to protect the top layer of sediment, and returned to the laboratory. The syringe is then cut and the top 5 mm is used for pigment determination. Microphytobenthos can only actively photosynthesise when situated in the photic zone, which is usually less than 2 mm in depth (Paterson *et al.* 1998). Pennate diatoms, the most abundant component of microphytobenthos in intertidal sediment, migrate vertically in and out of the photic zone (Heip *et al.* 1995) linked with both diel and tidal cycles (Underwood and Kromkamp 1999). Although diatoms are present at greater depths they would not be actively photosynthesising and could have been buried for some time. It is for this reason only the top 5 mm is used.

RESULTS

Salicornia dolichostachya (Madden 1984)

The data presented relate to a study, undertaken in 1983, of the 24.1 ha *Salicornia dolichostachya* bed to the north of the Bull Island Causeway. Ten replicate samples were collected regularly from a specific 250m^2 area using a PVC corer approximately 10 cm in diameter, and processed as described above. Sampling commenced in April and ended in November and the results are expressed in Figure 1a, b, and c. The number of seedlings germinated by April is in the order of 4000 to 5000.m^{-2} but by July this has declined to about 3000.m^{-2}. Seedling density at the end of the season is approximately one tenth of the initial density (Figure 1a). The constant disappearance between harvests is not easy to explain, but may be attributed to grazing by fish such as the mullet (*Crenimugil labrosus).* *Salicornia* biomass attained a maximum value in September of approx 400g DW.m^{-2}. This value halved over the next 30 days, suggesting that a pulse of DOM and POM had been released into the intertidal area. In the context of this lagoon, the magnitude of this release is estimated at 241000 m^2 × 200g.m^{-2} = 48200 kg dry matter.

In the first part of the growing season, production by *Salicornia* was accompanied by green algal growth, with a peak biomass of approximately 100 g DW by day 160 (8th June). This had declined to negligible values in September.

Salient features of this production system are:

- Decreasing density of this intertidal annual, hypothetically attributable to grazing by fish.

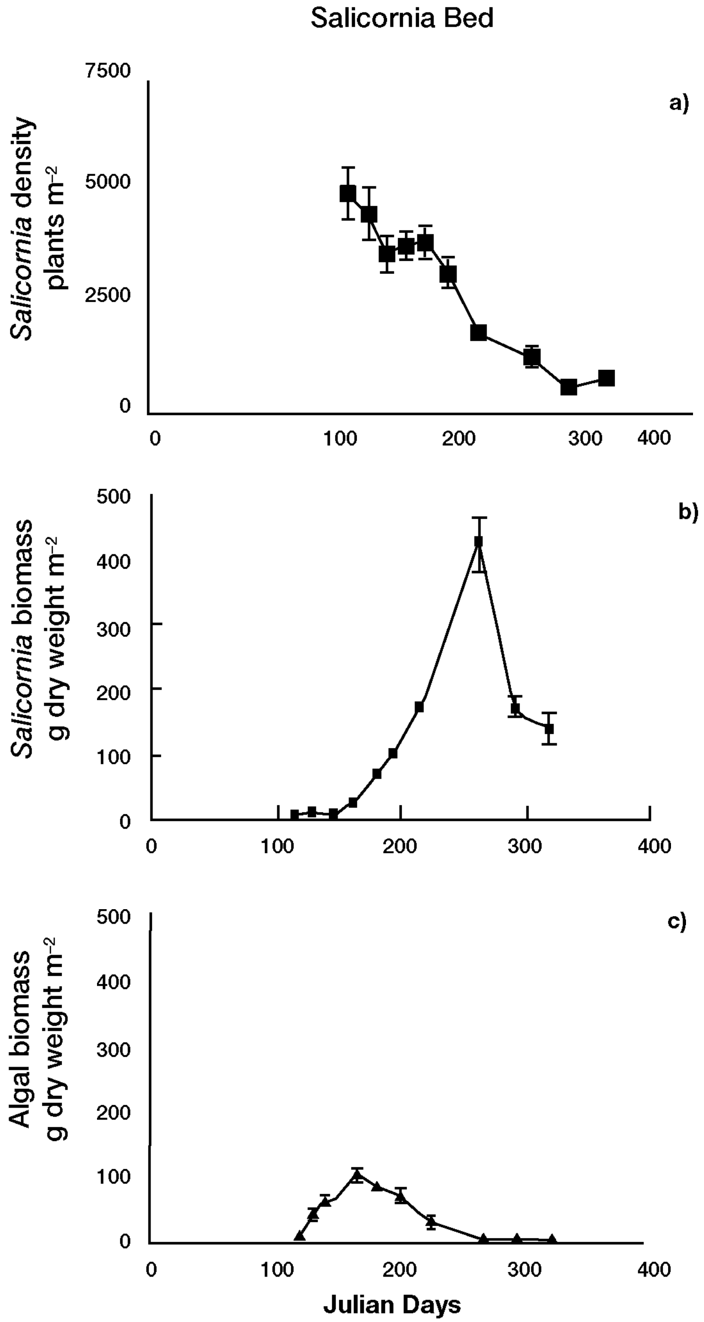

Figure 1. Characteristics (mean, standard deviation) of the North lagoon, Dublin Bay *Salicornia* community: a) *Salicornia dolichostachya* density (number.m^{-2}); b) biomass (gDW.m^{-2}); and c) biomass (gDW.m^{-2}) of *Enteromorpha* spp. in the *Salicornia* bed.

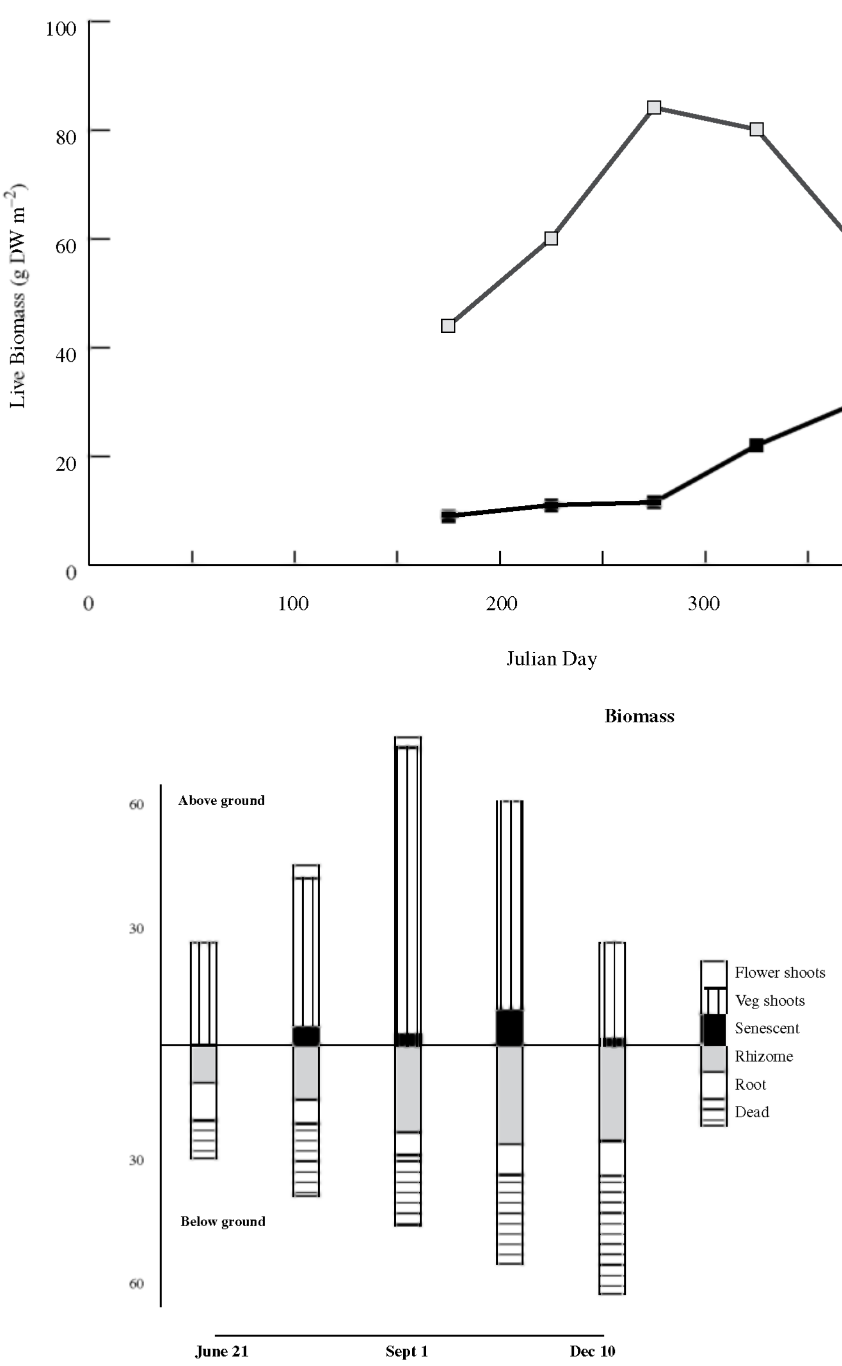

Figure 2. Seasonal (date and Julian day) biomass (gDW.m^{-2}); in the *Zostera noltii* bed; a) live biomass (*Zostera* solid line, algae dotted line); b) partitioning of total *Zostera* biomass among flowering shoots, vegetative shoots, senesced leaf, rhizome, root and dead below-ground material.

- Dual production by *Salicornia* and algae (note that in early June algal biomass is approximately equal to that of *Salicornia*. By September, *Salicornia* has achieved four times this value).
- Rapid disappearance of biomass in autumn.

Zostera noltii (Jennings 1991)

This species was investigated in the period June-December 1991, using the *Zostera* bed north of the Merrion Gates. This bed, one of several in the intertidal of south Dublin Bay, has an area of 1.5 ha. A 50m × 20m plot was used to contain the sample collected. At a resolution of $1m^2$, 52% of the squares contained *Zostera* plants.

Sample collection was designed by randomly selecting 10 vegetated squares, and removing cores as above. Sediment was washed away in the laboratory and the vegetation sorted into six components, namely vegetative shoots; generative shoots, senesced leaves, rhizomes, roots and dead below ground material. Dead root and rhizome were grouped.

Data are presented in Fig 2, where a familiar terrestrial pattern of summer biomass being translocated to below ground in the autumn, may be observed. Rhizome tissue is a key reserve for this apparently long lived perennial. A very small investment is made in flowering tissue, and unlike *Salicornia,* seedlings are not observed.

Grazing by Brent Geese in this locality has been investigated by O'Briain (1989, 1991) and Carton (1993). Carton (1993) used an exclosure to determine grazing by Pale-Bellied Brent Geese *(Branta bernicula hrota)* at this site. Her work showed that biomass close to $100gDW.m^{-2}$ in early October was reduced to about $20gDW.m^{-2}$ in December by goose grazing. Leaves were taken first, followed by rhizomes down to 5 cm.

Saltmarsh (Hayes 1999)

Bull Island saltmarsh was sampled in August 1998 and early January 1999, to determine the biomass at the end and start of the growing season. Five transects were taken along the saltmarsh, two between Bull Bridge and the causeway and three from the causeway to the end of the island. All transects were divided into three zones according to saltmarsh vegetation types, the lower, middle and upper zones defined by McNamee (1976) (see also Jeffrey 1977). A vertical distance of just over 1 metre separated the lowest from the highest zones. At each sampling station three replicate 0.0625 m^2 quadrats were taken of the above ground vegetation and three cores of below ground vegetation were taken per quadrat and processed as described above.

The average above ground biomass of the saltmarsh as a whole in summer was 0.7 $kg.m^{-2}$ while below ground it was 6.1 $kg.m^{-2}$. By January the biomass had fallen by more than half to 0.38 $kg.m^{-2}$ above ground and to 2.91 kg m^{-2} below ground. The fate of the below ground biomass lost from the system is unclear but loss of large amounts of below ground production has been noted elsewhere (Schubauer & Hopkinson 1984). The most probable explanation of winter disappearance in this case is root respiration, combined with decomposition. The total net productivity of Bull Island saltmarsh was 3.5 $kg.m^{-2}.y^{-1}$ of which the below ground portions contributed 3.2 $kg.m^{-2}.y^{-1}$. This high proportion of underground production is within the range of below ground productivity estimates for saltmarsh species (0.3–7.6 kg.m^{-2}.y^{-1}) compiled by Good *et al.* (1982).

Macroalgae (Jeffrey *et. al.*, 1992)

An extensive survey of intertidal macroalgal biomass in Dublin Bay was undertaken in 1989 and 1990. Eleven sampling stations were investigated to represent the main sub-environments in Dublin Bay. *Enteromorpha* spp. were found to be the most dominant group of green algae. Green algae were more extensive in North Dublin Bay with over 95% of the intertidal green algae occurring in these more sedimentary areas. Details are given in Jeffrey *et al.* (1992). The value quoted in Table 1 represents the total mean algal biomass in late June 1989 for the South Lagoon, over an area of 46.4 ha of cover, out of a total of 75ha (61.8% cover).

In Dublin Bay, green algal cover was closely related to sediment containing particulate organic matter, and mineralising nitrogen, expressed as an ammonium flux (Jeffrey *et.al.* 1995).

Coverage of brown fucoid algae was very heterogenous at most stations and biomass was higher in South Dublin Bay. Fucoid distribution was more localised than green algae but had a higher standing biomass. Yearly intertidal macroalgal dry weight biomass for the Bay as a whole was 185000 kg, with green algae contributing 69000 kg and fucoid algae 116000 kg. Green algal production ranged from 0.06–0.4 kg.m^{-2}.y^{-1}, and fucoid algae from 0.2–0.3 kg.m^{-2}.y^{-1}.

In Nauset Marsh, New England, maximum annual macroalgal biomass occurs in summer with *Fucus* producing 0.4 kg.m^{-2}.y^{-1} and *Ascophyllum* producing 1.2 kg.m^{-2}.y^{-1}

Table 1. Comparison of green algal biomass data. A: Estimates of mean maximum biomass (g DW. m^{-2}); B: Biomass (g DW. m^{-2}) calculated for larger system

A	**Site Location**	**Mean Max. Biomass (g DW. m^{-2})**	**Author**
	North Bull Lagoon	404	Walsh (1988)
	Lynher Estuary	196	Joint (1978)
	Two Indian Estuaries	540	Pandey & Masao (1986)
B	**Site Location**	**Mean Overall Biomass (g DW. m^{-2})**	**Author**
	North Bull Island	147	Walsh (1988)
	North Bull Island	84.5	Jeffrey *et al.* (1992)
	Langstone Harbour	39	Lowthion *et al.* (1983)
	Eden Estuary	34	Owens & Stewart (1983)

(Roman, *et al.* 1990). In the west coast estuaries of North America estimates of macroalgal productivity range from 0.2–1.3 kg.m^{-2}.y^{-1} (Emmett *et al.* 2000).

Microphytobenthos (Hayes, unpublished)

The microphytobenthos inhabit the intertidal and subtidal sediments of estuarine and shallow coastal systems and are a primary source of fixed carbon in estuarine food webs and of special importance in unvegetated areas. Microphytobenthos biomass was sampled every two weeks between April 2000 and September 2001 at two intertidal sites, the mudflat in the South Bull Island Lagoon on the Northside of the Bay and a sandflat at Blackrock strand on the southside. Productivity was higher at Bull Island than Blackrock, as expected, as this site is not as exposed. Production was calculated as 0.03–0.1 kg.m^{-2}.y^{-1} at Bull Island and 0.02–0.04 kg.m^{-2}.y^{-1} at Blackrock (Hayes, unpublished), using the model of Colijn and de Jonge (1984). These values are within the range of productivity estimates reported for estuarine flats but most other sites have higher production, (MacIntyre *et al.* 1996; Underwood and Kromkamp 1999; Emmett *et al.* 2000).

Spartina

The most important difference between North American and European saltmarshes is the dominance in the lower marsh zone of *Spartina alterniflora* along with other *Spartina* species such as *Spartina patens* in North America. *Spartina* is well known for its ability to filter out waterborne particles, so in Europe was used in extensive planting programmes for land reclamation (Hemminga *et al.*, 1998). Many European saltmarshes contain *Spartina anglica* and it has been identified in most saltmarsh sites in Ireland (Curtis and Sheehy-Skeffington 1998). To the best of our knowledge, no production estimates have been undertaken in Ireland.

The Flax Pond ecosystem study, an extensive project undertaken in the US in the late 1970s, showed production of *Spartina* was 1.1 kg.m^{-2}.y^{-1} including roots and shoots (Woodwell *et al.* 1979). In a 1979 review of *Spartina,* estimates of net annual primary production for *S. alterniflora* were shown to range from 0.2–6.0 kg.m^{-2}.y^{-1} (Long and Woolhouse 1979). Since then, the most productive *Spartina* marsh recorded was in Georgia, US with *S. alterniflora* producing 7.6 kg.m^{-2}.y^{-1} and *S. cynosuroides* 7.7 kg.m^{-2}.y^{-1} and below ground biomass contributing 68% and 60% respectively (Schubauer and Hopkinson 1984). More recent studies in Brazil, (da Cunha Lana *et al.* 1991) and The Netherlands (Hemminga *et al.* 1996) gave productivity values of 1.6 kg.m^{-2}.y^{-1} and 1.7 kg.m^{-2}.y^{-1}, respectively.

Fate of fixed carbon

- Senescence

The natural death of plant tissue is readily observable in intertidal angiosperms. In the annual *Salicornia* the plant population senesces simultaneously, loses biomass, but continues standing. The seeds remain embedded in the standing lignified tissue. The fate of the green tissue may be autolysis and presumably microbial consumption.

- Grazing

Grazing (*Zostera; Enteromorpha*) by birds has already been referred to, but the taking of nutrient rich *Salicornia* seed by Teal, Mallard and Pintail is also well known (Ferns 1992). There are no quantitative studies to indicate carbon balance or protein nitrogen contribution to diet for this specialised form of grazing. The postulated grazing of *Salicornia* seedlings by mullet is another topic worth study.

- Decomposition

We assume that microbial decomposition is a continuous process that rapidly reduces biomass of non-living plant tissue. It would be worth making estimates of microbial biomass to judge the season of most activity, which we assume is early autumn, following plant senescence. Partial decomposition is probably a prerequisite to removal by the tide.

- Tidal dispersal

In the Flax Pond study, tidal dispersal was seen to be a major fate for biomass. (Woodwell *et al.* 1979). The marsh complex makes a significant particulate carbon contribution to near-shore coastal ecosystems. We assume that this is a generally applicable observation.

- Sequestration

There is no evidence of long term carbon sequestration by burial of estuarine primary production.

COMPARISONS AND CONCLUSIONS

The estimates for intertidal net primary production, expressed in summary in Table 2, bear comparison with the well-known table for the world (Lieth 1975). The range for saltmarsh is as high as that cited for many terrestrial communities, including cultivated land. Algal production is at most a tenth of the saltmarsh value.

The intertidal system serves as an energy source for inshore and offshore secondary production. Virtually all production is consumed and standing crop of perennial angiosperm communities is close to constant. In the whole intertidal area,

Table 2. Synopsis of intertidal primary production for communities in Dublin Bay. Values are expressed in kg dry weight.$m^{-2}.y^{-1}$

Compartment	Production kg DW m^{-2} y^{-1}
Mudflat Fucoid algae	0.2–0.3
Green Algae	0.07–0.4
Microphytobenthos	0.03–0.1
Salicornia	0.5
Spartina[1]	1.0
Zostera	0.1
Saltmarsh	3.0–4.0

[1] Extrapolated value

dynamic changes in the area a community occupies are well known. These changes may be systematic and seral, as in the formation of salt marsh, and must entail sediment accumulation. Alternatively, explosive invasion by *Spartina* spp., especially *S. anglica*, has transformed some intertidal areas in production terms. In the case of saltmarsh development the escalation of production is from the 0.5 $kg.m^{-2}.y^{-1}$ of the *Salicornia* bed to the 3.0–4.0 $kg.m^{-2}.y^{-1}$ of the Saltmarsh (Table 2). In the case of *Spartina*, the change is a gain in the order of 0.5 $kg.m^{-2}.y^{-1}$ in production, with a consequent increase in sediment accumulation. Vegetation changes of this kind are readily determined by aerial survey and may be translated into system production values. This kind of management tool will be useful in managing all anticipated scenarios of intertidal change.

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EFFECT OF EUTROPHICATION ON PHYTOPLANKTON PRODUCTIVITY AND GROWTH IN THE WADDEN SEA

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ABSTRACT

As in most estuarine areas and coastal seas the growth of phytoplankton in the Wadden Sea is regulated by underwater irradiance and nutrient concentrations. The Wadden Sea shows clear signs of eutrophication. It has been documented by the high nutrient concentrations due to the large inputs of nutrients in this area by several European continental rivers (Rhine, Ems, Weser and Elbe), by an increased phytoplankton primary production and by the observations of black spots, areas where anaerobic sediment horizons reach the sediment surface. Other indications of eutrophication are the mass occurrence of green algae (*Ulva* and *Enteromorpha* spp.) and the dominance of specific phytoplankton species like the bloom forming Prymnesiophyte *Phaeocystis* sp. In the stratified parts of the German Bight lowered oxygen values are regularly observed.

To check the validity of the presumption that both irradiance and nutrients are important for the growth of phytoplankton, methods developed by Cloern (1999) were tested for different sites in the Wadden Sea and their effects on the growth of phytoplankton tested. In this review data are presented from another study where nitrogen was tested.

Based on literature data on the Wadden Sea it can be shown that a clear increase in both phytoplankton and microphytobenthos primary production has occurred from the early-70s till the mid-80s. During the same period nutrient inputs increased several fold. It is unlikely that the underwater irradiance has changed substantially, so that most changes can be directly related to the increased nutrient inputs. The efforts to reduce the phosphate input from the European continent has been successful with regard to the objectives set during the second international Ministerial conference on the North Sea, where a 50% reduction of the anthropogenic load had been agreed upon. However, the productivity in the Wadden Sea does not seem to be affected proportionally. This is probably due to two factors: the less intensely studied role of irradiance, and the role of nitrogen as the main limiting nutrient.

INTRODUCTION

The ecology of the Wadden Sea has been studied for more than a century. Due to the presence of nearby research institutes and universities our knowledge of the Wadden Sea has greatly improved during the last 3 decades. Among these institutes are the Netherlands Institute of Sea Research at Texel (the Netherlands), the University of Groningen, Department of Marine Biology, several German Universities and Institutes like the University of Oldenburg (Institute for Chemistry and Biology of the Sea), Bremen and Hamburg Universities, the Research and Technology Institute in Büsum (a branch of the Kiel University), the Biologische Anstalt Helgoland at Helgoland and the Wadden Sea Station Sylt. The latter two now operate under the Alfred Wegener Institute for Polar and Marine Research in Bremerhaven.

Together with several governmental institutes a very large amount of hydrographical and sedimentary data is available for the Wadden Sea. The amount of biological information, however, is limited and just exists for a few sites where long term studies were performed (Texel: Marsdiep area, Norderney, Sylt, Helgoland, Büsum, *cf.* Figure 1). Even these sites are not always representative for the Wadden Sea proper due to the sampling locations which are in the main inlets and therefore may represent coastal North Sea water as well.

Information on the ecological status of the Wadden Sea has been compiled in two so-called Quality Status Reports (QSR) on the Wadden Sea in 1993 (de Jong *et al.* 1993) and in 1999 (de Jong *et al.* 1999). In a recent publication (van Beusekom *et al.* 2001) Wadden Sea specific eutrophication criteria have been developed and critically assessed. So apart from numerous single papers on different aspects of eutrophication of the Wadden Sea the reader is referred to these three different compilations.

In this paper one aspect of the eutrophication of the Wadden Sea is discussed in detail: is the growth of phytoplankton affected by the nutrient levels in the Wadden Sea and which role does irradiance play in the expression of eutrophication?

Most of the analysis will be based on literature references, on work done at the Research and Technology Centre in Büsum, which was established in 1988 to perform multidisciplinary studies in the Wadden Sea, and at the Wadden Sea Station Sylt. Although the Wadden Sea should be treated as a unity as stressed by the trilateral agreement by the governments of the Netherlands, Germany and Denmark, data from different sites in the Wadden Sea will be compared. Large parts of the Wadden Sea are now under nature protection and all together form a very large international nature reserve. A recent description of the main characteristics of the Wadden Sea can be taken from van Beusekom *et al.* (2001). A map indicating the locations mentioned in this paper is presented as Figure 1.

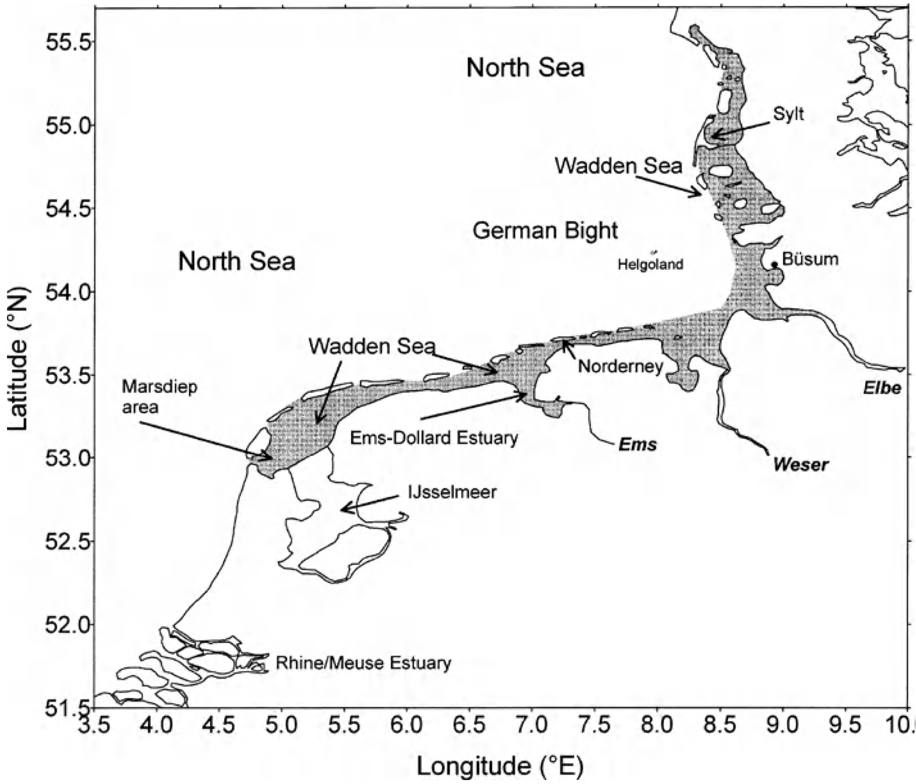


Figure 1: Map of the international Wadden Sea (hatched area) with locations mentioned in the text.

NUTRIENTS IN THE WADDEN SEA

The numbers of papers and reports on the concentrations of the dissolved inorganic macro-nutrients phosphate, nitrate, nitrite, ammonium and silicate is large. For the Dutch western parts of the Wadden Sea studies already started in the late forties (for dissolved phosphate: Postma 1954) and early sixties (for dissolved nitrogen compounds: Postma 1966). During the seventies detailed information in the western part and less frequent observations for the whole of the Dutch Wadden Sea, up to the Ems-Dollard estuary are given by Helder (1974) on nitrogen compounds and de Jonge and Postma (1974) on dissolved phosphate. Recent overviews were published by van der Veer *et al.* (1989), Philippart *et al.* (2000) and Philippart and Cadée (2000). In the German part of the Wadden Sea studies were performed by Hickel (1989), Martens (1992), Hesse *et al.* (1992) and Hanslik *et al.* (1998). Van Beusekom *et al.* (2001) give an overview of nutrient concentrations in the entire Wadden Sea.

In a recent paper (Ladwig *et al.* 2003) the development of nutrient concentrations in a part of the German Wadden Sea was described over the last decade. This study showed that in areas which are under the direct influence of main river outflows (cf. Elbe river) no change in the phosphate and nitrogen concentrations could be observed over the last decade. This is consistent with the main conclusions from the QSR 1999 (de Jong *et al.* 1999). It was noted that nutrient concentrations in the Wadden Sea during winter depend to a large extent on salinity levels. Therefore, actual concentrations cannot be directly compared unless they are standardised to a certain salinity. Details of the concentration salinity method, based on conservative behaviour of nutrients in winter, are given in de Jong *et al.* (1993). The analyses in the 1993 and 1999 QSRs are based on winter concentrations normalised to standard salinities of 10 and 27 psu. The clearest decrease was observed for phosphate which decreased by about 50% in most of the Wadden Sea. Phosphate input via the IJsselmeer (Figure 1) even decreased by 90%. In the western Wadden Sea and Danish Wadden Sea winter phosphate concentrations of about 1 μM are observed which gradually increase towards the estuaries of Weser and Elbe where concentrations of 2–4 μM prevail. No equivalent decrease was observed for nitrogen, although ammonium showed a clear downward trend in the Ems, Weser and Elbe estuaries, presumably due to the progressive implementation and technical improvement of waste water treatment plants. Nitrate showed an upward trend in the western Dutch Wadden Sea and a downward trend in the Ems, Weser and Elbe estuary. Winter nitrate concentrations in the Wadden Sea (27 psu) range between 20–110 μM but are about 50 μM in most parts. These concentrations are clearly higher than the background concentrations of 3 μM dissolved inorganic nitrogen (DIN) and 0.2–0.3 μM PO_4 in summer and 7 μM DIN and 0.4–0.5 μM PO_4 in winter (van Raaphorst *et al.* 2000).

Most studies on the eutrophication focus on winter nutrient concentrations (e.g. de Jong *et al.* 1999). An alternative approach to assess the eutrophication status of the Wadden Sea was proposed by van Beusekom *et al.* (2001). They used the shape of the seasonal cycle of ammonium and nitrite as a measure of eutrophication (remineralisation intensity) and focused on the autumn values. The above authors showed that during the eighties and nineties the major part of the variability in ammonium and nitrite was attributable to variations in riverine nitrogen input. Van Beusekom *et al.* (1999, 2001) stressed the importance of organic matter import from the North Sea into the Wadden Sea as a major nutrient source for the eutrophication of the Wadden Sea.

Despite the import of organic matter into the Wadden Sea and the high remineralisation rates in summer, the seasonal cycle of nitrogen compounds shows minimum values during summer and maximum values during winter (van Beusekom and de Jonge, 2002). This shows that the balance between nitrogen uptake by phytoplankton and phytobenthos and nitrogen release by remineralisation processes is shifted towards the primary producers. In autumn, when light conditions deteriorate, an ammonium maximum develops, indicating a shift in the balance towards remineralisation.

TURBIDITY IN THE WADDEN SEA

Long term data sets on turbidity in the Wadden Sea are only available from the NIOZ Station in the Marsdiep tidal inlet (Cadée and Hegeman 1991). Information on suspended loads is available from several governmental and research institutes in the Netherlands, Lower Saxony and the Island of Sylt. For the area of the Wadden Sea which is influenced by the Ems estuary, frequent data are available from the mid-seventies till the early eighties (Colijn 1982). Mostly simultaneously with the nutrient measurements (see previous section) SPM (suspended particulate matter) has been measured. Several authors have shown the effects of tidal currents and phases on the SPM concentrations (Postma 1954; Colijn 1982). The importance of SPM for the regulation of underwater irradiance is obvious in tide-influenced areas where fine sediments are transported by tidal currents, and resuspended by currents and wind/wave effects (Colijn 1982; de Jonge and van Beusekom 1995). Therefore euphotic zones are limited to a few metres at most, but more often with improved under-water light conditions in summer as opposed to winter with much more wind-driven resuspension of sediments (de Jonge and van Beusekom 1995, Tillmann *et al.* 2000). An overview of euphotic depths in the Schleswig-Holstein part of the Wadden Sea was presented by Ladwig (1997). Calculations showed that the euphotic depth ranged between 1.5 to 6.6 metres depth (May–July 1994, May–August 1995), thereby considerably affecting the primary production in the northern German Wadden Sea.

PRIMARY PRODUCTION OF PHYTOPLANKTON IN THE WADDEN SEA

As compared to nutrient measurements the number of measurements on primary production of phytoplankton is relatively small. At a few sites measurements have been performed such as at the NIOZ pier at Texel in the Marsdiep area of the western Wadden Sea (Cadée and Hegeman 1993), in the Ems-Dollard estuary (Colijn and Ludden 1983), in the eastern German Wadden Sea at two locations: Büsum (Tillmann *et al.* 2000) and the Sylt–Rømø Wadden Sea (Asmus *et al.* 1998). However the only long-term time series available is the one measured at the NIOZ pier because it covers, albeit with different methods, a period of about 30 years. The data series shows that during the seventies the annual primary production of phytoplankton amounted to approximately 150 $gC.m^{-2}$. In the 1980s and 1990s this primary production increased about twofold to more than 300 $gC.m^{-2}$. These high values are consistent with the high values measured in the outer part of the Ems estuary where occasionally values up to 400 $gC.m^{-2}$ were observed (Colijn and Ludden 1983). In the German Wadden Sea at Büsum approximately 150 $gC.m^{-2}$ was measured (Tillmann *et al.* 2000), whereas in the Sylt–Rømø area annual values increased from about 50 to 160 $gC.m^{-2}$ between 1980 and 1995 (Asmus *et al.* 1998).

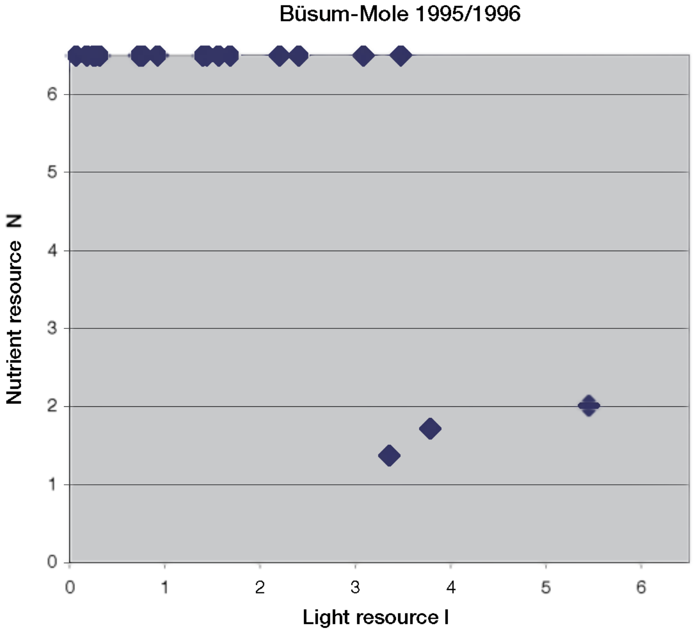
The information available strongly suggests that nutrient concentrations may have played a crucial role in the enhancement of primary production in the Wadden Sea. However this does not imply that a simple nutrient reduction will result in a proportional change in primary production, due to the complexity and non-linearity of the relationships between nutrients, phytoplankton growth and productivity and species composition (Philippart and Cadée 2000). Moreover, until now only phosphate inputs have been reduced substantially, whereas input of nitrogen compounds has been stabilised and slightly decreased (de Jong *et al.* 1999).

A COMPARISON BETWEEN NUTRIENT AND IRRADIANCE REGULATED GROWTH OF PHYTOPLANKTON

Investigations on the light regime in the Wadden Sea and the increased eutrophication of the Wadden Sea suggest that nutrients and light regime are the main factors regulating growth of phytoplankton (and microphytobenthos) in the marine environment (Colijn 1982). Especially in turbid regions the role of irradiance gets more and more important, i.e. becomes the main limiting factor for the growth of phytoplankton. In a direct comparison between light and nutrient regulated growth of phytoplankton in the German Wadden Sea Tillmann *et al.* (2000) showed that during most of the year, except during very few days in summer, light availability in the water column is the limiting factor for phytoplankton growth. In his study on limiting factors Cloern (1999) has developed a simple empirical model which enables a test on the growth conditions of a generalised phytoplankton community. Based on growth dependency from underwater irradiance levels and nutrient concentrations and assumed half saturation constants for nutrient uptake and light dependent phytoplankton growth, he calculated the ranges of nutrient and irradiance where one of both factors gets limiting. This procedure was also used for growth of phytoplankton in the Wadden Sea and tested for several sites with nitrogen (nitrate) and irradiance as parameters (Colijn and Cadée 2003) (Figure 2). The results of this analysis showed that over large areas of the Wadden Sea underwater irradiance levels limit the growth of phytoplankton and that only occasionally nitrogen reaches levels low enough to limit the phytoplankton growth. The different sites showed small differences: at the most western part (Marsdiep inlet) over a two-year period only two of 23 observations showed a potential nutrient limitation; in the turbid part of the Ems estuary (the Dollard) no signs of nutrient limitation could be recognised; in the outer more transparent part of the Ems estuary two values showed nutrient limitation during 1994; data from the German part of the Wadden Sea show comparable results: the station at the island of Norderney showed signs of a more intensive nutrient (nitrogen) limitation: four values during 1990 were indicating nutrient limitation. Again the more turbid station Büsum only showed three values over a two-year period which indicated nitrogen limitation. This is in close agreement with the results presented in Tillmann *et al.* (2000).

CONCLUSIONS

Long term observations at a few sites in the Wadden Sea show that a long term increase in nutrient concentrations (especially nitrate and phosphate) and in phytoplankton and phytobenthos production has taken place. Values increased in the seventies and stabilized in the eighties. After phosphorus reduction measures a decline towards values recorded during the fifties was observed. However, a decline in primary production of phytoplankton has not yet been observed at the only long term monitoring location in the Marsdiep (Dutch Western Wadden Sea). This might well be due to the effects of the still high nitrogen values and the relatively high turbidity in the Wadden Sea. At present, limiting factors for the growth of phytoplankton are primarily the high turbidity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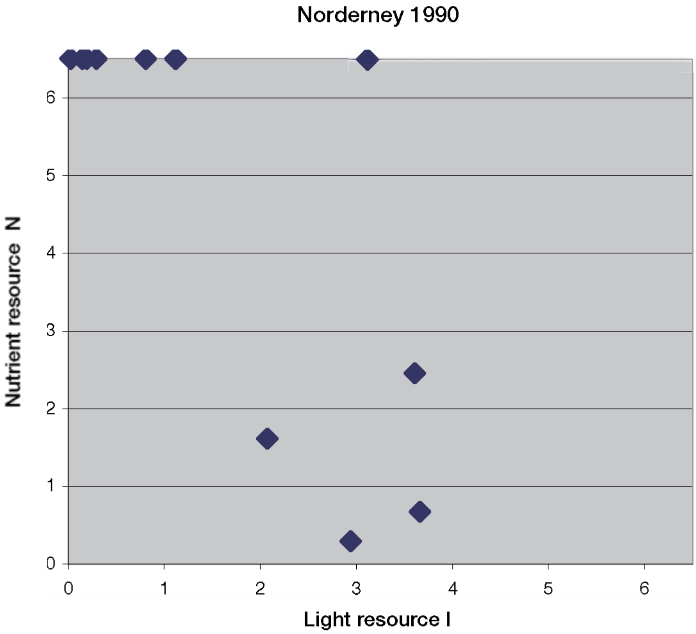
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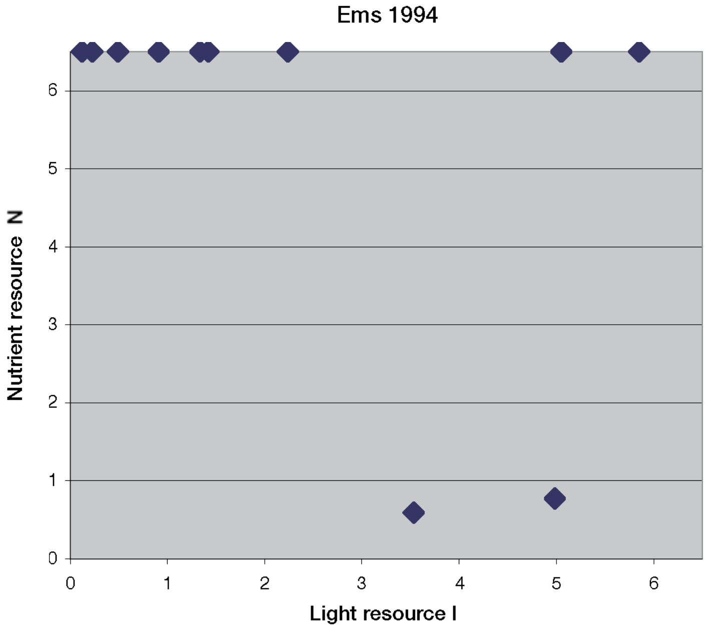
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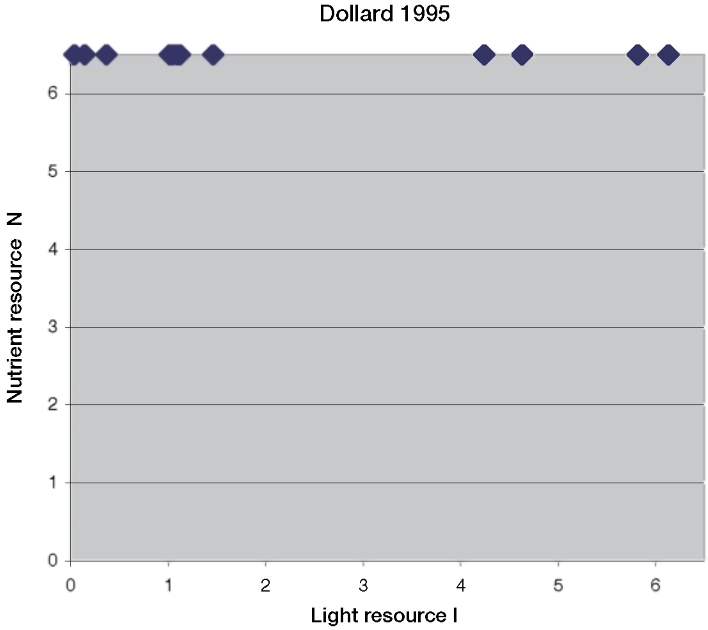
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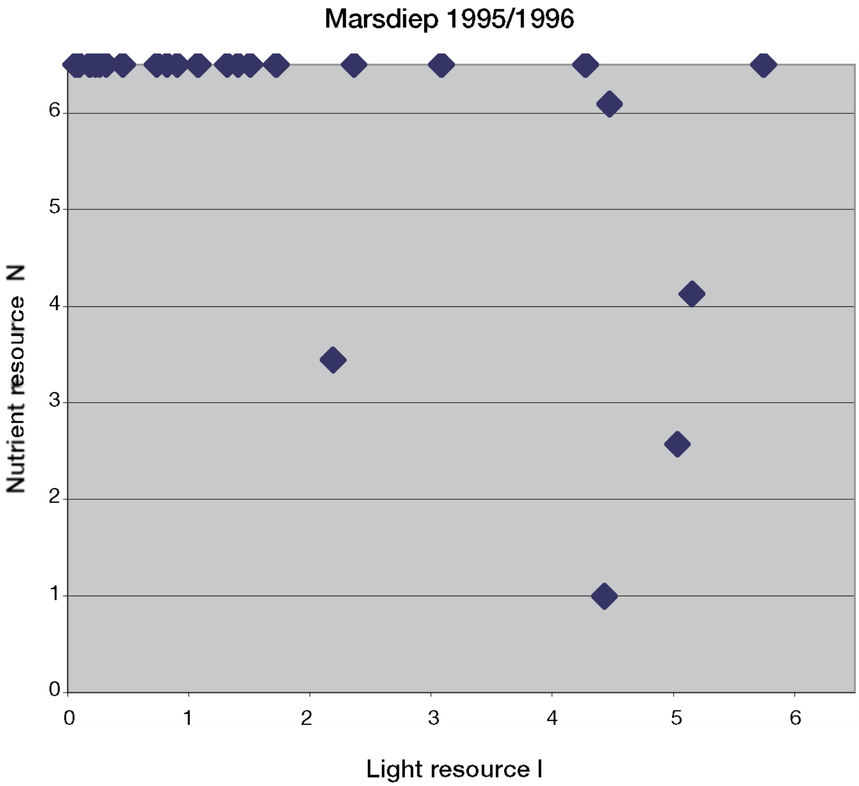

Figure 2: Irradiance and nitrogen limited growth of phytoplankton based on Colijn & Cadée (2003). For every month the mean dissolved nitrogen concentration and the mid-month irradiance has been calculated. The factor nutrient resource is the ratio of the dissolved nitrogen concentrations and an assumed Ks value for growth of phytoplankton on nitrate. The factor light resource is calculated as the ratio of surface global irradiance and the vertical attenuation coefficient (recalculated from SPM-values or secchi disc observations using conversions by Tillmann *et al.* 2000) (for further details see Cloern, 1999. (all nutrient resource values > 6.5 are plotted as 6.5).

and secondarily the availability of nitrogen compounds. Still, primary production is high enough to reduce the nutrient concentrations to levels far below the winter concentrations. This indicates that on an annual level, a decreased nutrient input will decrease the annual primary production, but that the effect will be damped by the light regime.

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THE LINK BETWEEN BIOGEOCHEMICAL NITROGEN CYCLING AND INTERTIDAL GREEN MACROALGAE IN DUBLIN BAY

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ABSTRACT

Biogeochemical nitrogen cycling plays a critical role in the nutrient dynamics of intertidal zones. High denitrification rates in intertidal sediments, together with a lack of comparable nitrogen fixation rates, are considered to be causal factors in the nitrogen limitation of these systems. In addition, inorganic nitrogen efflux from the sediment can make a significant contribution to the nutrient requirements of primary producers, particularly where sediments receive high inputs of organic matter in the incoming tide. In the intertidal zones of Irish coastal systems, sediment ammonium efflux has been found to contribute up to 850 μmol NH_4^+ m^{-2} h^{-1} to the overlying water. The rate of ammonium release is highly dependent on the quality and quantity of sediment organic nitrogen and on temperature. It has been proposed that this source of nitrogen is linked to temporal and spatial patterns in the occurrence of intertidal green macroalgae in Dublin Bay. This paper reviews the literature on the occurrence of green macroalgae in the intertidal areas of the bay and provides an overview of a series of studies that have investigated this relationship.

INTRODUCTION

Although intertidal sediments and the overlying water column can be viewed as two separate systems, they are linked though fluxes of both organic and inorganic nutrients. When tidal waters cover the sediment, particulate organic matter may be deposited onto the sediment surface, recharging the sediment organic matter pool. Following mineralisation of this organic matter by the sediment bacterial and faunal populations, inorganic nutrients may diffuse upwards into the water column. Inorganic nutrients may also diffuse downwards from the water column into the sediment to be used by the sediment biota.

While nutrient cycling occurs in both phases, processes within the sediment occur at rates that are several orders of magnitude higher than those in the water column. This reflects, in particular, the high numbers of bacteria found in surface coastal sediments, with typical numbers in the order of 4×10^9 cm^{-3} (Zobell and Feltham 1943; Fenchel 1992).

Biogeochemical nitrogen cycling plays a critical role in the nutrient dynamics of intertidal zones. High denitrification rates in intertidal sediments, together with a lack of comparable nitrogen fixation rates, are considered to be causal factors in the nitrogen limitation of these systems (Billen and Lancelot 1988; Howarth 1988; Seitzinger 1988). In addition, inorganic nitrogen efflux from the sediment can make a significant contribution to the nutrient requirements of primary producers. The role of sediment bacterial mineralisation in explaining patterns in intertidal productivity was recognized by Zobell and Feltham as early as 1943 when they stated that 'detailed observations of the numbers and kinds of bacteria in localised areas may help to explain presence or absence of flora and fauna' (Zobell and Feltham 1943). Ammonium efflux from sediments has since been consistently identified as an important source of nitrogen for phytoplankton productivity (Klump and Martens 1983; Billen and Lancelot 1988). Maximum ammonium release rates are usually recorded at sites which have significant organic nitrogen inputs, with highest rates at temperate sites occuring in summer in response to seasonal temperature rise (Raine and Patching 1980; Klump and Martens 1983; Pomroy *et al.* 1983; Jeffrey *et al.* 1992; Forja *et al.* 1994; Jennings 1996; Jennings and Jeffrey 1998).

However, in addition to seasonal and diurnal cycles, temperature in intertidal sediments is influenced by the semi-diurnal lunar tidal cycle. This dictates the duration of exposure of intertidal flats to solar radiation and is reflected in a unique 14.76-day cycle with highest summer temperatures occurring when low tide and midday coincide (Vugts and Zimmerman 1975; de Wilde and Berghuis 1979; Pinckney and Zingmark 1991). High uptake of ammonium by sediment microalgae has been reported following exposure to daylight during low tide, decreasing the amount released from the sediment during the subsequent immersion period (Pinckney and Zingmark 1991; Rysgaard *et al.* 1995). Extended periods of exposure to solar radiation at low tide may also induce cracking in the sediment surface and increase oxygen diffusion. This can lead to high nitrification rates of mineralised ammonium and further reduce the efflux of inorganic nitrogen to the water column during the next tidal cycle (Laima *et al.* 2002).

In Ireland, sediment inorganic nitrogen efflux rates have been measured at only a few sites. These include Roskeeda Bay in Galway (Raine and Patching 1980), the Shannon estuary (Brennan 1991; Brennan and Wilson 1993) and Dublin Bay (Jeffrey *et al.* 1992; Brennan *et al.* 1994; Jeffrey *et al.* 1995; Jennings 1996; Jennings and Jeffrey 1998). Low ammonium release rates were recorded at the two western sites. The highest rates (up to 850 mmol NH_4^+ m^{-2} h^{-1}) have been recorded in parts of Dublin Bay at sites impacted by moderate levels of organic pollution.

Investigations in Dublin Bay have indicated that nitrogen released from the sediment can play an important role in explaining seasonal and spatial patterns in the occurrence of green macroalgal mats (Jeffrey *et al.* 1992, 1995; Brennan *et al.* 1994; Jennings 1996,

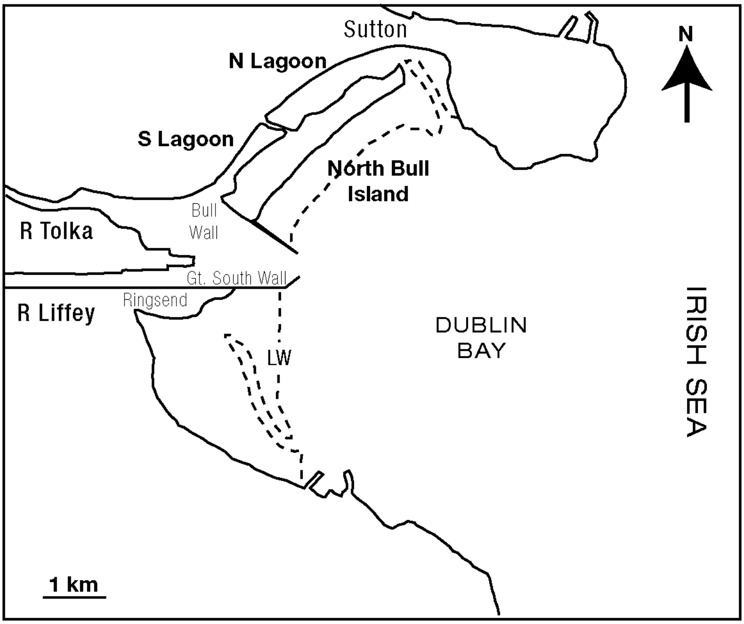

Figure 1. Map of Dublin Bay

Jennings and Jeffery 1998). This paper reviews the literature on the occurrence of green macroalgae in the intertidal areas of Dublin Bay. It also provides an overview of the series of studies that investigated the hypothesis proposed by Jeffrey *et al.* (1992). This hypothesis linked the occurrence of green macroalgae in the bay to the release of ammonium from the sediments following the mineralisation of sedimented sewage particulates.

DUBLIN BAY

Dublin Bay is a large shallow bay on the east coast of Ireland with an extensive intertidal zone that encompasses approximately one third of its area (53° 21' N, 6° 13' W) (Figure 1). The entire perimeter of the bay is urbanised and the inner section of the port has been particularly modified by human activity. These modifications included the building of the Great South Wall and the Bull Wall in the late eighteenth and nineteenth centuries to increase the effect of tidal scouring and deepen the shipping channel (Flood 1977). The River Liffey flows into the area between these two walls. The only other major freshwater input is from the River Tolka, which flows into the bay to the north of the River Liffey.

Much of the sediment in the bay consists of well-sorted, fine, clean sands (Harris 1977). These originate from glacial debris that was deposited as sandbanks in the Irish Sea at the end of the last Ice Age and are brought into the bay on each tide. One of the main features of Dublin Bay is a large island, North Bull Island, which runs parallel to the northern shore. The island is relatively young and its growth was accelerated by the building of the Great South Wall and the Bull Wall (Figure 1). The area between the island and the coast consists of two shallow lagoons, the North Lagoon and the South Lagoon, which are separated by a causeway built in the 1960s. While the sediments in the outer bay consist almost exclusively of sand, those in the intertidal areas and in the lagoon areas behind North Bull Island have a higher percentage of smaller silt and clay size particles, which have originated mainly from river discharge (Harris 1977; ERU 1992).

North Bull Island and its intertidal areas are recognised as the most important section of Dublin Bay in terms of environmental and conservation value. The island, which is now owned and managed by Dublin City Council, received international recognition in 1988 when it was designated a UNESCO Biosphere Reserve. It is also a registered site under the Ramsar Convention and a Special Protection Area under Section 4 of the EC Birds Directive 79/409/EEC. In addition, in 1988, the island and the adjacent lagoons were designated as National Nature Reserves, while in 1995 a Special Amenity Order was adopted for the island by Dublin Corporation (now Dublin City Council).

The main sewage treatment plant for the city is situated at Ringsend, at the mouth of the Liffey. Until the treatment facility was upgraded, the sewage received only primary treatment, which included screening, grit separation and primary sedimentation (ERU 1992). Although the bay has relatively good dispersion and flushing characteristics, particulate material from the treatment plant tends to be moved towards and deposited in the northern sections of the inner bay (Mansfield 1992). This deposition of organic wastes from the Liffey mouth in the intertidal area behind Bull Island was noted as early as 1804 (Flood 1977). These wastes were described at the time as soft ooze from the sewers of the city and were said to be covered with a green slime.

Off-shore nutrient concentrations and productivity in Dublin Bay are usually low (ERU 1992; EPA 2001). However, the consensus of studies of the ecology of the bay has been that, although it is largely unaffected by pollution, organic contamination resulting from sewage discharge has affected some areas, particularly in the northern section (Jeffrey *et al.* 1978, 1985, 1992; Brennan *et al.* 1994, 1998; EPA 2001). Excessive levels of total coliforms were reported in the waters in the Bull lagoons during the Dublin Bay Water Quality Management Plan (DBWQMP) study in the late 1980s confirming that sewage discharge was reaching the intertidal area behind Bull Island (Mansfield 1992). The DBWQMP study also reported that, while the outer intertidal areas of the bay were relatively pristine, the lagoons behind North Bull Island were considered moderately polluted and the Tolka Estuary heavily polluted (Jeffrey *et al.* 1992).

DUBLIN BAY ALGAL STUDIES

Some of the earliest literature on the algal ecology of the bay arose from studies initiated during the redevelopment of the port in the nineteenth century. Bailey (1886) noted the occurrence of green algae on the foreshores of Dublin Bay, stating that 'the seaweed consists mainly of the Chlorosperma appearing as a verdent green on all the sloblands'. The link between the occurrence of large quantities of green algae and excess nutrients arising from sewage discharge to the bay was referred to by Letts and Adeney

(1907) who demonstrated the capacity of *Ulva* and *Enteromorpha* growing in the intertidal area to utilise 'ammonium salts and nitrate' in the tidal waters. This study reported that the main species of green algae occurring in the channels beside the developing North Bull Island were the green algal species, *Ulva* and *Enteromorpha.*

The first comprehensive study of the ecology of North Bull Island was published in 1977 (Jeffrey 1977). This included a history of the development of the island, together with detailed accounts of the flora and fauna and of its various habitats. The distribution of green algae in areas surrounding the island was detailed by Pitkin (1977). The study noted that green algae, mostly of the order Ulvales, were almost ubiquitous in the intertidal area from the Tolka Estuary to Sutton Creek. Species of *Enteromorpha* were found to be particularly common, while other filamentous algae, such as *Cladophora* and *Chaetomorpha,* were also recorded (Pitkin 1977). Measurements along the northern shoreline showed that the highest biomass occurred in the South Lagoon. In contrast, algal mats occurred less frequently in the North Lagoon. The whole of the South Lagoon was described as being covered by large areas of lush green, while the area north of the causeway had noticeably less growth (Pitkin 1977). A subsequent study, undertaken a decade later, also recorded large quantities of algal biomass in the South Lagoon, with biomass measurements comparable to the highest values in the literature (Walsh 1988).

The studies of algal growth and distribution which were undertaken as part of the DBWQMP investigations still recorded *Enteromorpha* as being the dominant species in the lagoons (Jeffrey *et al.* 1992). The scoping study for these investigations identified the occurrence of large quantities of green algae in the intertidal zone, and the odours released when the algae decomposed, as areas of particular public concern. The highest green algal biomass in the entire bay was again recorded in the South Lagoon. High biomass values were also recorded in some outer areas of the Tolka Estuary and in the inner areas of the North Lagoon. However, the heavily polluted soft muds of the main Tolka Estuary had little algal cover.

The study found that biomass had increased in both the North and South Lagoons since Pitkin's initial study of the algal biomass in the 1970s. Pitkin (1977) recorded a maximum biomass measurement of 120g DW.m^{-2} in the South Lagoon. The values recorded during the DBWQMP study were frequently over 200g DW.m^{-2} with some values of 400–500g DW.m^{-2} (Jeffrey *et al.* 1992). Khan (1998) reported that the species distribution in the lagoons in the mid 1990s was similar to that reported by Pitkin in 1977 and was characteristic of eutrophic intertidal areas. Biomass measurements indicated that growth in the late 1990s was approaching optimal levels, with a maximum biomass at one site in the South Lagoon of 501g DW m^{-2} and some individual measurements ranging up to 833g DW.m^{-2} (Khan 1998).

The DBWQMP study noted that the distribution of algae in the bay was relatively consistent from year to year (Jeffrey *et al.* 1992). However, the timing of peak biomass varied. This variation was not related to differences in temperature. Based on the observations in the DBWQMP and other studies, a hypothesis was formulated to explain the temporal and spatial patterns of algal biomass accumulation in the intertidal areas of the bay (Jeffrey *et al.* 1992, 1995). This stated that mineralisation of sedimented sewage particulates provided a major source of nitrogen for macroalgae. The spatial and temporal patterns of algal growth could be explained by variation in the availability of nitrogen from this source. However, the temperature regime in any year would play a key role in temporal patterns. When higher than normal temperatures occurred in the early summer, sediment organic nitrogen would be utilised at a faster rate. This would lead to a cessation in the supply of inorganic nitrogen to the algae and subsequent nitrogen limitation of algal production. This hypothesis was investigated in a series of subsequent studies (Brennan *et al.* 1994; Jeffrey *et al.* 1995; Jennings 1996; Jennings and Jeffrey 1998; Khan 1998)

INVESTIGATION OF THE HYPOTHESIS RELATING ALGAL GROWTHS TO A SEDIMENT NITROGEN SOURCE

A study of particulate nutrient inputs to Dublin Bay in 1992/1993 included the first measurements of the particulate component of the river and sewage effluent nutrient loads (Brennan *et al.* 1994). The results confirmed that the sewage treatment plant was the main contributor of particulate nitrogen to Dublin Bay (Brennan *et al.* 1994). Tidal cycle water column studies carried out also indicated that the South Lagoon received a much greater quantity of both particulate and dissolved nutrients than the North Lagoon, reflecting its closer proximity to both the main rivers and the sewage treatment plant (Brennan *et al.* 1994, 1998; Jeffrey *et al.* 1995).

Measurements of sediment inorganic nitrogen efflux, using sediment-water incubations, were carried out in conjunction with the particulate nutrient input study (Jennings 1996). These demonstrated that a substantial quantity of ammonium was released from some intertidal sediments in Dublin Bay and that both seasonal and spatial variation occurred in these release rates (Jeffrey *et al.* 1995; Jennings 1996; Jennings and Jeffrey 1998). The highest rates were measured in the South Lagoon at sites where high algal biomass measurements had been recorded. The rates were at the higher end of the ranges reported in other literature and were significantly related to monthly temperature. However, other nearby sites had consistently low release rates. Little or no algal biomass occurred at these sites. High rates were also recorded in some sites in the heavily polluted Tolka estuary but these sites had little or no algal biomass (Brennan *et al.* 1994, 1998). This was attributed to the anoxic nature of the sediments and to high water column turbidity.

A positive relationship was noted in the particulate input study between high rates of sediment ammonium efflux and the occurrence of algal biomass at sites in the North Bull Island lagoons (Brennan *et al.* 1994). Sediment ammonium release was calculated to account for an increase of *c.* 70% in the availability of inorganic nitrogen in the water column of the South Lagoon in late summer (Jennings 1996). This contribution was an order of magnitude higher than that from any other source within the lagoon. An estimate of the quantity of inorganic nitrogen released at sites with green macroalgal mats was equivalent to 96–98% of the nitrogen content of the biomass that accumulated in that season. The total amount of nitrogen estimated to have been released by the sediments in the South Lagoon was three times that in peak algal biomass. While Khan (1998) illustrated the importance of light intensity and temperature as limiting factors for

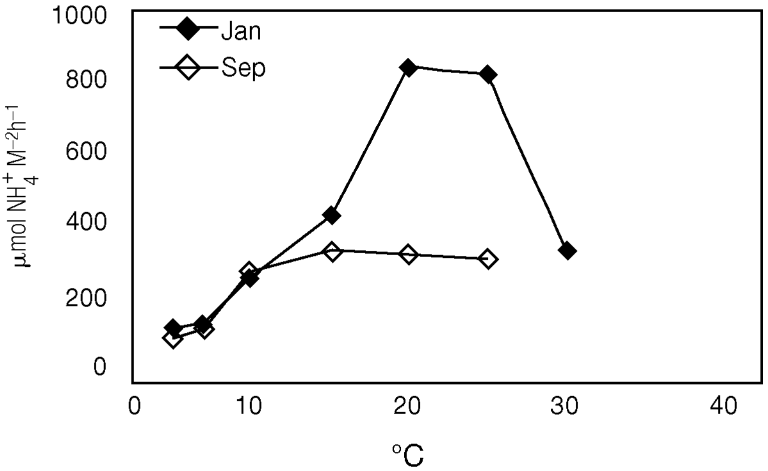

Figure 2. Sediment ammonium release rates (μmol $NH_4^+.m^{-2}.h^{-1}$) from Dublin Bay sediments incubated at a range of temperatures (5°C–30°C) in January and September (after Jeffrey *et al.* 1995).

macroalgal growth in the bay in spring, these results indicated that sediment nitrogen release could play a role in the patterns of macroalgal biomass over the summer, as proposed by Jeffrey *et al.* (1992). This nitrogen source would be of particular importance when water column inorganic nitrogen concentrations in the bay become depleted as often occurs in late summer (Jeffrey *et al.* 1992; Brennan *et al.* 1994; EPA 2001).

Sediment ammonium efflux rates from cores collected in the lagoons during the winter and incubated at a range of temperatures were found to be highly correlated with temperature, with an apparent optimum temperature of 200°C (Figure 2) (Jeffrey *et al.* 1995; Jennings, 1996). However, in autumn a significantly lowered temperature dependence was observed (Jeffrey *et al.* 1995; Jennings 1996). This appeared to confirm the proposal in the hypothesis that the availability of nitrogen *via* sediment release might be decreased in the late-summer/autumn and indicated that factors other than temperature contributed to the observed seasonal patterns. In addition, this lowered response was found to have a significant inverse relationship with the occurrence of high sediment temperatures in the preceding period, possibly as a result of changes in the sediment organic nitrogen pool following high rates of bacterial decomposition (Jennings 1996).

Experimental addition of particulate material, extracted from sea water in the North Bull lagoons, to sediment cores resulted in an immediate response in nitrogen efflux rates, confirming that these particulates represented a labile organic nitrogen source to the sediment (Jeffrey *et al.* 1995; Jennings 1996). Investigation of the sediment organic nitrogen pool indicated that ammonium efflux was also significantly dependent on the C: N ratio of the sediment (Jennings 1996; Jennings and Jeffrey 1998). The relationship with sediment C:N ratio was negatively exponential, with highest release rates occurring at sites with lowest ratios. This relationship reflects the fact that bacteria have a high nitrogen requirement and will only excrete nitrogen when the C:N ratio of the substrate is lower than their own (*c.* 6:1) (Goldman *et al.* 1987).

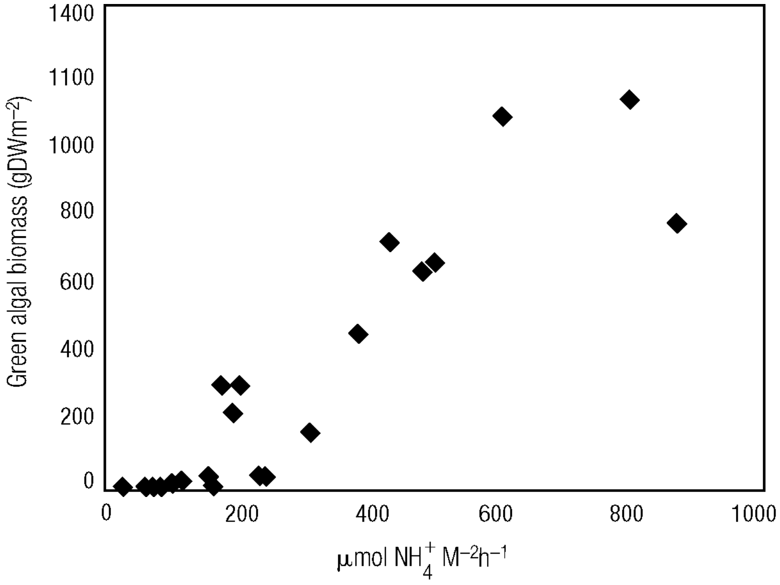

Figure 3. Sediment ammonium release rates (µmol $NH_4^+.m^{-2}.h^{-1}$) at an incubation temperature of 200°C measured in the February/March 1998 at 35 sites in the intertidal area of Dublin Bay plotted against green algal biomass (g $DW.m^{-2}$) measured in July 1998.

Sites in the bay with high ammonium efflux rates also had higher concentrations of hydrolysable protein in surface sediments. The measurement of hydrolysable protein estimates the fraction of the organic nitrogen pool that is easily decomposed by sediment bacteria (Mayer *et al.* 1986). Protein is the main form of nitrogen contained in sewage particulates. The high labile protein concentrations recorded at these sites indicated that they were subject to high deposition rates of particulates from the water column, most probably from sewage treatment. A further investigation into sediment organic matter characteristics at sites throughout the bay in 1997–8 confirmed a highly significant positive relationship between ammonium efflux and the concentration of hydrolysable protein in the sediment (Jennings 1999).

SEDIMENT NITROGEN EFFLUX AND MACROALGAL BIOMASS

During the 1997/1998 study an experiment was carried out to investigate the relationship between sediment inorganic nitrogen efflux and the occurrence of green macroalgae at 35 sites throughout the bay. These sites included the North Bull lagoons, the intertidal areas off North Bull Island, the Tolka estuary and the south bay. Sediment-water incubations were carried out at a temperature of 200°C, the apparent optimum temperature for ammonium release, on one core from each site, in the period February/ March 1998. These measurements were considered to be representative of the potential for nitrogen release from the sediment prior to the commencement of macroalgal growth. Macroalgal biomass was measured at these sites in July of that year.

The results indicated a positive relationship between the amount of nitrogen released from the sediment in the early spring and the accumulation of green macroalgal biomass at those sites later in the growing season (Figure 3). The relationship between nitrogen availability and green macroalgal biomass was generally linear above *c.* 200 µmol $NH_4^+.m^{-2}.h^{-1}$ but appeared to plateau at 600 µmol $NH_4^+.m^{-2}.h^{-1}$. It was considered from field observations that some of the algal biomass recorded at sites with higher weights may have represented stranded material. While this experiment does not prove a direct coupling between macroalgal growth and sediment ammonium efflux, it adds further weight to the hypothesis that the availability of a sediment nitrogen source can be important in sustaining green macroalgal productivity.

SUMMARY

The series of studies initiated to investigate the hypothesis of Jeffrey *et al.* (1992) confirmed that biogeochemical cycling plays a key role in the supply of inorganic nitrogen to macroalgae in the bay. The input of organic matter from sewage treatment was shown to represent the main source of organic nitrogen in Dublin Bay. It was also shown that the South Lagoon area, in particular, received high concentrations of this material. High efflux rates of ammonium were measured from sediments in those areas that consistently had high green algal biomass in summer months. Other areas with little or no algal biomass had low sediment nitrogen efflux rates. The highest algal biomass was recorded at sites with the greatest stores of labile organic nitrogen as measured by hydrolysable protein content and measurements of sediment nitrogen efflux in the spring. While light and temperature are the main factors controlling algal biomass production in the early season, a dependence on a sediment nitrogen source as the growth season continues may contribute to eventual nitrogen limitation if sediment efflux rates decrease. The quantity of nitrogen released from sediments is related to the supply of labile organic matter and thus is highly sensitive to anthropogenic inputs. The dependence of macroalgae on a sediment nitrogen source may help explain patterns in the distribution of primary producers at other sites, particularly those with significant inputs of labile organic nitrogen.

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IRISH INTERTIDAL MEIOFAUNA: A MODICUM OF PROGRESS

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ABSTRACT

Sporadic records of meiofauna on Irish shores appear from the 1860s onwards. These and more recent records of metazoan meiofaunal taxa are reviewed. Meiofaunal abundance and diversity are related to the habitats' structural complexity.

Overall abundances of up to two hundred individuals below each square centimetre of sand beach surface and of one thousand per gram wet weight of plant have been recorded on Co. Down beaches. Distributions and abundances of meiofauna vary with sub-habitats as for example shown by work on Oligochaeta and Acari. An example of sub-habitat differences in abundance is given for flatworms in a sand beach with *Arenicola* burrows. Biomass data is absent from the literature but data for one Co. Down beach is presented.

In spite of the paucity of information on our beach meiofauna, Irish work led to the first published EM pictures illustrating meiofaunal adaptation at the ultrastructural level and to the elaboration of the concept of the thiobios.

A small amount of work has been conducted on behaviour and physiology of meiofauna from Irish beaches but very little is known of their energetics. Some work on meiofaunal respiration has illustrated the foolhardiness of applying laboratory algorithms to field populations unless population density and adaptation to environmental temperatures are considered. Although meiofauna may provide a very good means of monitoring pollution, to date there appear to be only five Irish studies considering possible anthropogenic affects; these relate to oil spill detergent, Pb, sewage discharge, the presence of intertidal oyster trestles and seaweed harvesting respectively.

In conclusion some progress has been made but it is clear that a great deal of work on faunistics, population ecology, species interaction and energetics remains to be done before the role of meiofauna in Irish beaches can be properly assessed.

INTRODUCTION

The history of meiobenthic research extends forward from mid-nineteenth and early twentieth century taxonomic descriptions, for example of Kinorhyncha (Dujardin 1851) and acochlid opisthobranch Gastropoda (Kovalevsky 1901), to present-day studies which range from ultrastructure to community energetics. The paper on the distribution and organisation of the 'microfauna' of the Bay of Kiel by Remane (1933) can be taken as the foundation stone of present studies. This paper compared the distribution, abundance, morphology and feeding of major taxa in three main biotopes – namely phytal, sand and mud. Remane's (*l. c.*) descriptions included a number of biocoenoses (i.e. characteristic habitats and their fauna) which could be found intertidally; these included sand with the gastrotrich *Turbanella hyalina* Schultze, *Arenicola marina* (L.) detritus-rich sand, the seaweed *Fucus vesiculosus* L. and *Zostera marina* L. plants. After Remane's seminal paper, work continued mainly in Europe, on a taxonomic and morphological basis until the 1960s (see Swedmark 1964) when further ecological (reviewed by McIntyre 1969) and experimental studies (Boaden 1962) began. By this time the term 'meiofauna', apparently first used by Mare (1942), had come into general use to describe the fauna which generally passed through the 1 or 2 mm mesh used in sorting the macrofauna from benthic samples.

In Ireland as elsewhere the earliest studies composed of or incorporating meiofaunal records were on a taxonomic and/or faunistic basis such as Brady and Robertson (1869), Halbert (1920) on Acarina and Southern (1910, 1912) on Annelida and Turbellaria respectively. The latter paper resulted from part of the Royal Irish Academy's Clare Island Survey, as did several other papers cited in the references (those from Volume 31 of the Proceedings). In the 1960s meiofaunal studies began to include behavioural and experimental work (e.g. Boaden 1968). The volume edited by Higgins and Thiel (1988) remains a good manual for sampling, preservation and other techniques. Giere (1993) provides an excellent introductory text to the history and status of meiobenthic biology at the end of the twentieth century; this book cites about nine hundred and forty references of which nine are mainly based on work from Ireland. It may be said that our knowledge of Irish meiofauna remains sparse. It is the purpose of the present paper to summarise what is known about the island's intertidal meiofauna to date and to help stimulate work which may help fill the considerable gaps in our knowledge.

THE MEIOFAUNA

The following list must not be taken as exhaustive since it does not, for instance, include various meiofaunal records mentioned incidentally among more general faunal lists – an example could be the polychaete *Dinophilus taeniatus* Harmer often found in rock-pools and recorded in Williams (1954).

Protista

The Protista in general and the Ciliata in particular provide an extremely important component of meiofaunal biotopes. Mulisch *et al.* (1986) list six species of folliculinid (Ciliata Heterotrichida) found intertidally on spirorbid polychaete shells from Strangford

Lough, Co. Down, but there appears to be no other work on the Irish coastline citing free-living ciliate species. Giere (1993) and Patterson *et al.* (1988) should be consulted for further information about the role of Protista in the meiofaunal community.

Foraminiferans have been neglected in many meiofaunal studies but are important in some habitats such as intertidal mud (Ellison 1984). The great Irish naturalist Joseph Wright published many papers on foraminiferans including littoral and deep water species from about 1870 to the early 1900s. The reader is referred to the list in Heron-Allen and Earland (1913) who list many species occurring in shore sand and from shallow-water dredgings in the Clare Island area. The occurrence of some Foraminifera in Bull Island (Dublin) sediment is cited by Healy (1975).

Cnidaria

There are relatively few meiofaunal cnidarians. *Protohydra leukarti* Greef is common in high-shore muddy sands in Strangford Lough and, being of world-wide distribution, is presumably common in similar and brackish-water sediments elsewhere in Ireland. *Halammohydra schulzei* Remane has been found intertidally at Black Island in the Strangford Lough Narrows (Boaden 1966). A curious medusoid form, probably a species of *Eleutheria,* was found to be common on low-shore red algae in the Lough Narrows in September 2000; it 'walked' on the weed thalli using the ventral branches of its capitate tentacles (pers. obs.). A few more meiofaunal cnidarian species probably remain to be found on our beaches.

Gnathostomulida

Sterrer (1971) described the 'new' gnathostomulid *Austrognatharia boadeni* from detritus-rich shell gravel at Green Island in the Strangford Lough Narrows and Sterrer (1969) listed six species of the genus *Pterognathia* from various localities near Portaferry, Co. Down. *Gnathostomula paradoxa* Ax is common in intertidal fine sand in Strangford Lough (pers. obs.). Further investigations of detritus-rich sands could easily double the number of species known from Irish shores.

Platyhelminthes

The marine turbellarians are common in littoral sediments and in low-shore phytal habitats where they are often the third or fourth most common metazoans. Knowledge of their ecology was summarised by Boaden (1995). Acoel species sometimes have population blooms particularly in mud and muddy sands and in phytal habitats. Rhabdocoels especially the Kalyptorhynchia are particularly common in tidal flats and Seriata, especially the Otoplanidae, may dominate in coarse wave-swept sediments. Southern (1912) listed eleven turbellarian species of meiofaunal size occurring intertidally at Clare Island and twenty nine at Blacksod Bay – with seven species in common. His posthumous paper on Turbellaria of Ireland (Southern 1936), which gives thirteen earlier references to Irish Turbellaria, includes records for fifty eight species which had been found intertidally. Boaden (1966) lists fifty turbellarian species from Strangford beach sediments. There are further Co. Down records of some of these and seven other identified species in Maguire (1977). The 'red acoel' in the latter paper has subsequently been identified as *Paratomella* *rubra* Dörjes. The type locality for the retronectid *Retronectes terpsichore* Sterrer and Rieger (1974) is at Green Island, Strangford Lough. An estimation is made that the known number of species on Irish beaches is less than a fifth of those actually occurring.

Gastrotricha

There appear to be no records of marine Gastrotricha in Ireland prior to 1966 when Boaden listed twenty-eight species from Strangford Lough. All but one of these (*Tetranchryoderma coeliopodium* Boaden) have been found intertidally in the area, albeit some at ELWS. Maguire (1977) described three new species from intertidal sand from the Strangford area. The world database for marine gastrotrichs prepared by Hummon (details from hummon@ohio.edu) gives various Irish west coast localities where the gastrotrich fauna has been sampled but does not give further details yet other than the number of species (e.g. at Castlegregory six chaetonotoids and six macrodasyoids). Marine gastrotrichs are more or less limited to marine sands and gravels and are often the third to fourth most abundant metazoans in sand beaches. A general account of the biology of gastrotrichs is presented by Boaden (1985). The number of currently known species on Irish beaches probably represents less than a third of those occurring.

Nematoda

Nematoda are often the most abundant metazoans in the benthos; Platt and Warwick (1980) stressed their significance in the littoral ecosystem. Little is known of their distribution in Ireland in spite of excellent early work by Southern (1914b) who, commenting on his extensive records from the Clare Island Survey, stated that species found on weed or under stones on the shore usually belonged to well-known species but those in sand and mud 'were usually either new or very rare'. Platt (1973) described nine new species from the northern fine-sand flat of Strangford Lough from where he also reported on the ecology of these and a further seventy-five species (Platt 1977). He also described two new species from South Bay on the Outer Ards Peninsula coast (Platt 1983). Our current knowledge probably represents less than a tenth of species occurring on Irish shores.

Annelida

Meiofaunal polychaetes are common in intertidal sediments and on rocky shores but are not commonly recorded in the literature. Southern (1910, 1914a) lists polychaetes from the Dublin bay area (with shore records mostly from Sandymount and Howth) and from the Clare Island area. Littoral meiofaunal species included the so-called 'archiannelids' *Nerilla antennata* Schmidt and *Protodriloides flavocapitatus* (Uljanin) and *Fabricia sabella* Ehrenberg. Boaden (1966) listed eight species from shell gravel and five (those not given a specific location) from fine intertidal sand in Strangford Lough. Healy (1975) listed various annelids, some of meiofaunal size, from North Bull Island. She also studied the intertidal distribution of Oligochaeta in Co. Wexford (1979, 1996a) stating that both meiofaunal and macrofaunal oligochaetes are dominant between HWN and HWS in all but one of the sand beaches studied; three main habitat types for exposed rocky shore oligochaetes, namely rock crevices and cracks, algal and animal 'mats' and pools were described at Carnsore Point where 12 species were found. Two of the new species encountered were described later (Healy 1996b). Healy and Bolger (1984) included references to species occurring in salt marshes. Present knowledge probably represents less than a quarter of our meiofaunal annelid species.

Crustacea

Meiofaunal crustaceans, particularly copepods and ostracods, are often the second or third most abundant metazoans in shore sediments and among seaweed. However, as is the case with other taxa, relatively little is known of their occurrence on Irish shores. Farran (1912) working on Clare Island survey material, listed some ostracods (mainly from earlier records by Norman 1905) and a hundred and twenty species of copepods, many from intertidal habitats. A paper by Roe (1958) listed one hundred and six species of harpacticoid copepods including 6 new species and two she had previously described (Roe 1955) from a variety of habitats on the shore at Dalkey, Co. Dublin. Roe (1960) also listed copepods from Lough Ine from where she described two further species. Holmes (1980, 1981, 1984, 1987) has extended the list of crustaceans from the Lough with records which include many copepods from a wide variety of intertidal habitats including weed and gravel. O'Riordan (1971) studied harpacticoids on the Irish east coast at twelve littoral stations in Counties Louth and Dublin; fifty-three of the sixty species found were meiobenthic. There is little recent information about the west coast although Bodin and Jackson (1987) described a new harpacticoid from intertidal sand at Mweenish Island, Galway. Wells (1963) gave a number of intertidal records of meiobenthic copepods plus the interstitial isopod *Microcharon harrisi* Spooner from low-water shell gravel in Strangford Lough.

The biology of meiobenthic harpacticoids was excellently reviewed by Hicks and Coull (1983). Since this review and that on algal meiofauna by Hicks (1985), Jarvis and Seed (1996) have published data from North Wales on the abundance and diversity of meiofauna, particularly harpacticoids, in the algae *Pilayella* and *Polysiphonia* growing on *Ascophyllum*. Holmes and O'Connor (1990) have published a checklist of harpacticoids currently known from Ireland and Holmes and Gotto (2000) one of the cyclopoids; the former group is particularly common in sand and the latter in phytal and muddy habitats.

It has not been usual to consider commensal forms as part of the benthic meiofauna, however the reader is referred to the numerous papers by Gotto and various co-workers for some account of commensal copepods (see Gotto 1993) including many occurrences in Ireland.

Various Irish records of Ostracoda are included in the classic work by Brady and Norman (1889). Many species occur in littoral mud and the group is abundant in phytal habitats. Athersuch *et al.* (1990) is excellent for identification and general distribution records although there is little specific reference to Ireland rather than the British Isles because of the widespread distribution of many species. Our current knowledge in Ireland may represent less than a sixth of the occurring intertidal meiofaunal crustacean species.

Acari

Early reviews of marine mites including records of species in Ireland are given by Brady (1875) who recorded one littoral species and Halbert (1915, 1920), the latter papers recording twenty species. Bartsch (1985) incorporated these species and twenty-one others from the Strangford Lough Narrows and adjacent Irish Sea in her list of Halacaridae recorded from Ireland. Somerfield and Jeal (1995) compared the distribution of mites on exposed and sheltered Irish shores and found that the range of species were essentially similar on the two shore types. The same authors (1996) investigated the distribution of halacarids among macroalgae in Mulroy Bay and the Strangford Narrows and found different genera were characteristic of the upper and lower shores. Somerfield (1991) gives further distributional data. This is probably the best-studied major taxon of Irish intertidal meiofauna, so only a few species may remain to be found.

Mollusca

The young of many gastropod species may be found among algae in the low intertidal zone but a number of species, for example *Skeneopsis planorbis* (Fabricius) and many members of the Rissoidae and Rissoellidae remain of meiofaunal size throughout their life. Southgate (1982) studied a population of *Rissoa parva* (da Costa) in red algal turf in Bantry Bay; most specimens were less than 3 mm in height and they occurred in 'a rich and varied cryptofauna'. Colgan (1930) recorded various small prosobranchs from the shore of Co. Dublin. Three interstitial opistobranch species including abundant *Hedylopsis brambelli* Swedmark and the prosobranch *Caecum glabrum* (Montagu) were recorded from low-water coarse shell sand in the Strangford Narrows by Poizat (1979). Boaden (1966) also recorded three aplacophorans including two unidentified species from Narrows shell gravel. *H. brambelli* is abundant in many small patches of shell sand with pebbles between *Laminaria* zone boulders in the Narrows and emerges to feed on hydroids on the pebble surfaces when samples of the biotope are placed in aquaria (pers. obs.). Nunn has produced checklists of the molluscan fauna of localities including Strangford Lough (1994) and Clare Island (2002) which include data for meiofaunal sized species. The majority of Irish intertidal meiofaunal molluscans are probably known except for a few low shore interstitial forms such as species of *Pseudovermis,* acochlidiaceans and aplacophorans. A checklist of all the currently known Irish marine molluscs is to be published as a CD ROM (Nunn *et al.* in prep.).

Others

Meiofaunal representatives of some other taxa, fairly well known elsewhere, have single or occasional littoral records from Ireland. Murray (1911) recorded the marine tardigrade *Echiniscoides sigismundi* (Schultze) among sediment washed from algae under Achill Bridge, Co. Mayo and Boaden (1966) records *Batillipes mirus* (Richter) from intertidal fine sand: thus, at least for marine forms, Murray's comment 'Irish water-bears appear to have no history' remains apt. The sipunculoid *Golfingia minuta* (Keferstein) has been recorded by Southern (1910) from Sandymount, Howth and by Boaden (*l.c.*) in Strangford Lough where it is common in detritus rich shell gravel. Kinorhynchs are fairly common in intertidal muds and muddy sand but the only Irish littoral records known to the author are by Southern (1914b) for *Echinoderes dujardinii* Claparède in intertidal algae from Blacksod Bay and Boaden (1966) for *Echinoderes* sp. in Strangford Lough fine sand.

The latter paper also records the meiofaunal holothurian *Leptosynapta minuta* (Becher) from Strangford Narrows shell gravel. One would expect some twenty or more meiofaunal species from these major taxa to be found on Irish beaches, particularly if more muddy habitats are investigated.

Habitats and meiofaunal abundance

Meiofaunal abundance and diversity are broadly related to the structural complexity of the habitat. This is well established for algal habitats (Myers and Southgate 1980; Gibbons 1991) and is also the case for the small animals living in mussel clumps (Tsuchiya and Retière 1992). This is discussed by Hicks (1985) and by Healy (1996a) who also demonstrated that increased cryptofauna diversity resulted from increased structural complexity of barnacle populations at Carnsore Point, Co. Wexford. It is also true on the County Down coast that medium to coarse shell gravels (providing that they do not dry out) provide a greater size range of interstices than finer sediments and have a correspondingly species-rich, but not necessarily more abundant, meiofauna than finer sediments (pers. obs.). Eleftheriou and Nicholson (1975) demonstrated increased meiofaunal densities with decreased wave exposure in some Scottish beaches. It has also been shown, for example by Reise (1981) that biogenic structures in sediment increase faunal diversity and abundance. The general rule that meiofaunal species diversity increases with habitat complexity is therefore hypothesised.

Values for meiofaunal abundance in the literature are sometimes difficult to compare because of the different and sometimes ambiguous units used, for example ind. 10 cm^2 has been used both for the number of individuals from sand beneath a surface area measuring 10 × 10 cm (*i.e.* 100 cm^{-2}) and for the number from a core of 3.57 cm diameter *i.e.* from beneath a 10 cm^{-2} area of sediment surface. It is far better to express densities as per 1 m^2 or 1 cm^2 to avoid such ambiguity.

Table 1 reports densities of meiofauna from some Irish beach sediments and Table 2 from some algae. Data on abundance of nematode species from Strangford Lough (Platt 1977) was later re-used by Lambshead *et al.* (1983) in the verification of cumulative percentage species abundance versus species rank graphs (that is *k*-dominance curves) as the most appropriate way to assess species diversity.

Within habitat distribution

Habitats such as intertidal seaweeds and sand flats provide a number of sub- or micro-habitats. It is clear, for example, that zonation of meiofauna may occur according to height on the shore in relation to tidal parameters (e.g. Giere and Pfannkuche 1982), however even at one tidal height there will be horizontal and vertical patterns of distribution. Thus Boaden and Platt (1971) working at South Bay, Co. Down, showed that dominant species of nematodes had population centres at different depths within the sand column. This has also been shown for turbellarians and gastrotrichs in the beach at Ballymaconnel, Co. Down by Boaden (1977). Such patterns of vertical distribution have often been linked to sediment oxygenation as measured by redox potential. Examples are the important work by Fenchel (1969) on ciliates and Boaden's (1981) discussion concerning the within-sediment

Table 1. Meiofaunal density in some Co. Down sand beaches. Densities have been recalculated from original data and expressed as number of individuals below 1cm^{-2} of the sediment surface. Poizat's samples were to 5cm depth and ice extracted. All others were $MgCl_2$ or Ludox extracted and of sufficient depth to include the surface, RPD and upper black sand layers. Abbreviations such as HWN½MTL mean half way between the indicated tidal levels. M_d is median grain size in microns

Locality	Tidal level	M_d µm	Ind.cm^{-2}	Source
Strangford and Adjacent Area				
Narrows	LWN	687	1.1	Poizat 1979
Narrows	LWN	1160	6.2	Poizat 1979
Doctor's Bay	MTL½LWN	140	148.5	Maguire 1977
Hanna's Mill	MTL½LWN	122	128.5	Maguire 1977
South Bay	MTL½LWN	150	73.1	Maguire 1977
South Bay	HWN½MTL	220	74.0	Boaden and Platt 1971
Greyabbey	HWN½MTL	150	29.5	Boaden and El-Hag 1984
Ballymaconnel	MTL½LWN	165	134.5	Maguire 1977

depth distribution of turbellarian taxa on various Co. Down beaches. The situation is made more complex by tidal and seasonal vertical migrations which for example have been linked to conditions of oxygenation (Fenchel and Riedl 1970) or depth of the RPD layer (Platt 1977 – working on the north Strangford tidal flat) and to disturbance by waves (Boaden 1968, Rieger and Ott 1970).

Work by Johnston (1981) at Doctor's Bay Kircubbin, Co. Down showed that different sand flat subhabitats such as *Arenicola* burrow head shafts or undisturbed sediment from surface pools had different population densities of the various taxa – see Table 3. This can easily lead to errors in determining overall abundance unless the sampling regime ensures that the subhabitats are represented by their correct proportion. For example calculation of the overall mean density of Copepoda from the measured percentage occurrence of each subhabitat gives a mean of 6.1 individuals per 1 cm^{-2} but random sampling (48 cores in the area) gave a mean of 11.2. In addition to the different abundances in sediment subhabitats it is characteristic for sediment meiofauna to occur in small patches (Heip 1975). This has been reported for two gastrotrich and one turbellarian species in Northern Ireland beaches by Boaden (1985, 1995 respectively).

Meiofauna in phytal habitats also can display different subhabitat distribution, for example Hicks (1985) gave a) within holdfasts, b) the base of fronds in association with sediment and c) the frond surface as the main areas of meiofaunal occurrence on intertidal algae. On the other hand Somerfield and Jeal (1996) working on marine mites from Ireland cited four main types of occurrence on emersed plants namely a) on the dry surface layer of fronds, b) on damp fronds, c) on the lower stipe and among the holdfasts and d) on the surface substratum between holdfasts.

Boaden *et al.* (1995) and Boaden (1996) working on *Fucus serratus* L. meiofauna from

Table 2. Abundance and density of meiofauna on intertidal algae from Strangford Lough. *Fucus serratus* data (except weight) from Boaden (1995). Other data from author's records. *Polysiphonia* samples consisted of individual tufts scraped from *Ascophyllum*.

Locality	Algal Species	Total in sample	Plant area (m^{-2})	Plant dry wt (g)	Plant wet wt (g)	Density (individuals per unit)
Narrows LWN						
'Site 9A'	*Fucus serratus* L.	900323	4.01	7571	–	2.25 ind.cm^{-2} frond
						12.1 ind.g^{-1} dry wt.
Opposite Walter Rock	*Scytosiphon lomentaria*	95	–	0.48	0.03	Mean of the samples
	(Lyngybe)	63	–	0.65	0.06	121.7 ind.g^{-1} wet wt.
		73	–	1.04	0.09	2997.6 ind.g^{-1} dry wt.
..	*Cladophora sp.*	14800	–	15.25	3.17	970.5 ind.g^{-1} wet wt.
						4668.8 ind.g^{-1} dry wt.
Kircubbin MTL	*Polysiphonia lanosa (L.)*	722–866			0.045–0.031	Mean of the 5 tufts
	5 tufts					761,0 ind.g^{-1} wet wt.

the Strangford Lough Narrows showed that the presence of epifauna greatly enhanced the meiofaunal abundance and that, at some sites, this was related positively to the amount of silt retention due to the surface configuration (spinosity) of the epifaunal colonies. These papers also showed that the density of meiofauna (per cm of the epifaunal surface) increased from the basal through mid to distal portion of the *Fucus* plants but, since there was much more epifauna in the central parts of the plant, meiofaunal density per unit thallus area was highest in the mid-region (Boaden 1996).

The Thiobios

Fenchel and Riedl (1970), mainly using distributional data from the east coast of the United States, drew attention to the occurrence of metazoan meiofauna in the sulphide-rich layers of sandy marine sediments. Boaden and Platt (1971) reporting on temporal changes in vertical distribution of meiofauna at South Bay, Co. Down, coined the term 'thiobios' for the redox potential discontinuity (RPD) and black (anaerobic) sand layers and their inhabitants as a convenient expression for these layers and 'the living system of the sulfide biome' as they had been called by Fenchel and Riedl (*l.c.*). Four groups of

Table 3. Comparison of mean densities (shown on diagonals as individuals.cm^{-2}) of major taxa between four subhabitats on a fine sand beach inhabited by *Arenicola marina*. The% occurrence of each habitat was measured by mapping twelve 25 × 25 cm quadrats. ME emersed sediment (plain or rippled surface) 52%, MP sediment from surface pools samples 40%, MH sediment from head-shafts 2.5% and MT sediment from tail mounds 5.5%. Results are from thirty-nine to forty-nine 2 cm depth 2.9 cm diameter core samples for each subhabitat. Significant differences are shown as $p < 0.05$*, $p < 0.01$** and $p < 0.001$*** **according to the Mann-Whitney U-test, ns is non-significance. (Data from Johnston 1981).**

Nematoda

	ME	MP	MH	MT
ME	48.3			
MP	ns	59.3		
MH	***	***	30.9	
MT	***	***	ns.	28.6

Copepoda

	ME	MP	MH	MT
ME	3.3			
MP	***	9.9		
MH	***	*	161	
MT	***	***	***	9

Ostracoda

	ME	MP	MH	MT
ME	1.0			
MP	ns	1.2		
MH	**	***	0.4	
MT	*	***	ns	0.5

Gnathostomulida

	ME	MP	MH	MT
ME	1.3			
MP	ns	2.2		
MH	ns.	ns.	3.4	
MT	**	***	***	0.3

Turbellaria

	ME	MP	MH	MT
ME	0.8			
MP	***	3.4		
MH	***	***	8.3	
MT	***	ns	***	3.2

Annelida

	ME	MP	MH	MT
ME	2.6			
MP	*	4.5		
MH	ns	ns	4.8	
MT	***	***	***	0.5

species were defined according to their vertical distribution within sand on Co. Down beaches by Maguire (1977); two of these groups citing particular gastrotrich and flatworm species were characteristic of the thiobios. Maguire and Boaden (1975) used one of these species, the gastrotrich *Megadasys* (*Thiodasys*) *sterreri* (Boaden), to explore features of thiobiotic biology and demonstrated this species' ability to exist anaerobically for a period of at least four months and to respire anaerobically using carbon dioxide in a reversed Krebs cycle sequence. Boaden (1980) found thiobiotic population density equivalent to 78.8 individuals below 1 cm^{-2} of surface sand at Millin Bay, Co. Down – this has led the author to suspect that the thiobiotic component has often been under-represented in samples taken elsewhere. Information on the ecology and adaptations of thiobiotic meiobenthos has been summarised by Giere (1992, 1993).

Behaviour and tolerances

Remane (1933) gave some limited information on the salinity tolerances of meiofauna but little further information emerged until the 1960s when a number of authors began to relate behaviour and tolerances of species to their intertidal distribution (e.g. Boaden 1963; Gray 1966; Jansson 1966). Factors investigated included bacteriology, granulometry, light, temperature and water flow. The initial papers of this type concerning Irish beaches were those by Boaden (1968) and Boaden and Erwin (1971) which described responses of meiofauna at South Bay, Co. Down to various factors. The first of these papers was particularly concerned with responses to tidal movement mediated *via* currents and vibration; it also contained the first published pictures of meiofaunal ultrastructural adaptation. The second paper was principally concerned with the gastrotrich *Turbanella hyalina* Schultze and its avoidance of sand inhabited by the polychaete *Protodriloides symbioticus* (Giard) – a response to a heat-labile substance produced by the latter species; it also summarised responses of the *T. hyalina* to current, temperature, oxygenation, contact, light, vibration, pressure fluctuation and granulometry as well as a gregarious response and attraction to sand mediated *via* bacteria. Johnston (1981, also see Boaden 1995) working with material from Doctor's Bay, Strangford Lough, showed that the flatworm *Monocelopsis otoplanoides* Ax was attracted to *Arenicola marina* (L.) head shaft sand by a heat-labile substance emanating from *Arenicola*.

The responses of the seriate flatworm *Monocelis lineata* (Müller) occurring in the meiofauna on *Fucus serratus* plants from the Strangford Lough were studied by Boaden (1996) who showed that it would select damaged in preference to undamaged *Flustrellidra hispida* (Fabricius) colonies and the latter in preference to *F. serratus* thallus without such epifauna; *M. lineata* also showed negative phototaxis, positive rheotaxis and movement to areas of 17–18°C within a temperature gradient.

Respiration and energetics

In order to assess the overall importance of meiofauna within the littoral ecosystem it is necessary to investigate factors such as food preferences, energy assimilation and population turnover. Unfortunately, relatively little is known about some of these and several of the assumptions made in the literature may be unwarranted (Coull and Bell 1979). It is generally understood that meiofauna can contribute 30–50% of sediment biomass but only about 10% in the phytal. The first biomass data including both macrofauna and meiofauna for an Irish beach is presented in Table 4. McLachlan and co-workers have made extensive studies of sand surf-dominated beaches in South Africa (see McLachlan and Romer 1990) and in Europe work has been carried out on sand- and mud-flats (e.g. Kuipers *et al.* 1981, Warwick and Price 1979). These papers give a production-to-biomass ratios for meiofauna plus microfauna as 65:1 and for meiofauna alone as 8.4:1 respectively.

The general proportion for the meiobenthic contribution to the total energetic budget of an average benthic biotope is estimated as about one quarter (Giere 1993). The only paper that begins to address the energetics of meiofauna in Irish beaches is by Boaden and El-Hag (1984) who produced a partial oxygen budget for a fine sand beach at Greyabbey, Co. Down, which calculated meiofaunal respiration at $40\text{ml.h}^{-1}\ \text{m}^{-2}$ of beach. This was

Table 4. Calculated biomass for major meiofaunal groups and macrofauna in the medium sand beach at Rossglass, Co. Down, March 1985. Five replicate meiofaunal core samples of 3.2 cm diameter were taken to a depth of 10 cm at five approximately equally vertically spaced stations. Macrofauna was from 1 mm sieving of two 50 × 50 cm, 50 cm deep, quadrats at each beach level. The sampled area between mid- and low-tide was affected by a small beach stream. Biomass was calculated from average length and breadth dimensions of specimens in each major taxon assuming animals to be cylindrical and having a specific gravity of 1.33 (Wieser and Kanwisher 1961). From original data.

	Estimated biomass wet weight g.m^{-2}					
	HWN	**HWN½MTL**	**MTL**	**MTL½LWN**	**LWN**	**Mean**
Nematoda	0.56	0.84	0.31	0.24	1.56	0.702
Polychaeta	0.00	0.06	0.45	0.22	0. .22	0.190
Turbellaria	0.00	0.18	0.32	0.03	0.08	0.122
Copepoda	0.01	0.05	0.06	0.01	0.46	0.118
Insecta	0.45	0.00	0.00	0.00	0.00	0.090
Nemertea	0.00	0.22	0.00	0.00	0.11	0.066
Ostracoda	0.00	0.00	0.00	0.00	0.07	0.014
Gastrotricha	0.01	0.01	0.01	0.01	0.01	0.010
Acarina	0.00	0.00	0.01	0.00	0.00	0.002
All meiofauna	**1.03**	**1.36**	**1.35**	**0.51**	**2.51**	**1.352**
Macrofauna	**2.12**	**5.14**	**6.36**	**2.10**	**11.66**	**5.476**

only about 15% of the macrofaunal value. This paper illustrated that the meiofaunal taxa considered all had a minimum respiration rate at between 12–14°C which corresponded to the annual average ambient sand temperature, and furthermore that the respiration rate per animal decreased with the number of individuals being used for each oxygen uptake determination. Further details of this are given by Boaden (1985, 1989, 1995). The work implies that it is unwise to extrapolate laboratory data showing Q_{10} type responses of respiration with temperature change to field conditions where the fauna has been 'conditioned' by the ambient temperature; furthermore the density of the species and any gregarious response affecting activity must be considered.

ANTHROPOGENIC EFFECTS

Pollution

Coull and Chandler (1992) have reviewed laboratory and field studies concerning pollution effects on meiofauna. There are two fully published Irish studies. Boaden and Bleakley (1974) conducted laboratory experiments on harpacticoid copepods and the polychaete *Protodriloides symbioticus* from Ballymaconnel, Co. Down and treated part of this beach with an oil spill remover; concentrations in excess of 100ppm were found to give persistent toxic effects. Roberts and Maguire (1976) using material from Co. Down found limited interaction of lead with intertidal sediment and its meiofauna, probably because of absorption onto particle surfaces. Some unpublished work by Johnston (1981) partly reported by Boaden (1978, 1995) indicated decline in meiofaunal abundance and diversity caused by a sewage-polluted beach stream at Doctor's Bay, Strangford Lough.

Other causes

Unpublished work by Skjaeggestad (1997 and Skjaeggestad and Boaden (2005)) has shown that oyster culture on intertidal trestles affected the abundance of meiofauna in the underlying sediment and in sediment between the trestle rows when compared with the adjacent control site. All the major taxa studied other than the Turbellaria had significantly lower densities under the trestles (Table 5).

The relationship between sediment parameters and the variations in abundance at and between the sites in the course of a year were analysed by multiple linear regression using stepwise variable selection. The most important factors were found to be Chl*a* content for nematodes, temperature and Eh for copepods, temperature for turbellarians, sediment mean grain size and Eh for kinorhynchs and organic carbon content for tardigrades.

Boaden and Dring (1980) in studying the effects of harvesting *Ascophyllum* demonstrated a subsequent coarsening of shore sediment which led to an apparent doubling of meiofauna to about 70 ind.cm^{-2} with a significant increase of crustaceans (mainly copepods) from about 2 to 8 ind.cm^{-2}.

CONCLUSIONS

Our knowledge of the meiofauna of Ireland is rather limited. Although there were some early faunistic studies which included meiofaunal organisms, most of our current knowledge of the distribution of metazoan meiofauna around Ireland is limited to Strangford Lough and the adjacent Co. Down coastline, Dublin Bay and Co. Wexford, although somewhat more is known about the distribution of phytal mites. There is thus a need for more meiofaunal survey work, particularly on the Atlantic coastline. Studies

Table 5. Mean sediment meiofaunal abundance (ind.cm^{-2}) over one year at Paddy's Point, Strangford Lough in low water control (C), between oyster trestle (B) and under oyster trestle sites (T). Cores were of 1 cm^{-2} surface area taken to 5cm depth. $F_{2,40}$ values and probabilities are from three way repeated anovas. Differences between sites are indicated as for example T<B, T<C meaning trestle sites had lower abundance than both between-trestle and control sites. (Data from Skjaeggestad 1997)

	Control C	Between B	Trestles T	F value	p <	Differences
Nematoda	390	300	160	143	0.001	T<B T<C
Copepoda	13.0	13.5	2.0	58	0.001	T<B T<C
Turbellaria	4.7	4.7	4.8	2	0.14	ns
Kinorhyncha	4.1	2.2	0.9	38	0.001	T<C B<C
Tardigrada	2.1	3.0	1.5	23	0.001	T<B

of muddy habitats are also required. Some information is available about the general abundance of the meiofauna (and in particular gastrotrichs and turbellarians) in Co. Down beaches and about Oligochaeta and Acari elsewhere. There is also some information about habitats and sub-habitats on rocky shores, in seaweeds and in sand. Work on vertical distribution of sediment meiofauna on Co. Down beaches has led to the concept of the thiobios and to a little consideration of the biochemistry and ultrastucture of meiofaunal species. There is extremely little information relating to meiofaunal energetics and the role of meiofauna within the intertidal ecosystem of Irish shores. It is clear from work elsewhere that meiofaunal organisms, although of little size, are a major component of the littoral ecosystem. Without their consideration we cannot be really pleased with the state of our knowledge of Irish shores.

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SETTLEMENT AND RECRUITMENT OF THE BLUE-RAYED LIMPET, *PATELLA PELLUCIDA* L. IN GALWAY BAY, WEST COAST OF IRELAND

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ABSTRACT

The seasonal occurrence, density and population structure of the blue-rayed limpet, *Patella pellucida,* on crustose coralline algae (CCA) and *Mastocarpus stellatus* are described from an exposed rocky shore at Ballynahown, Galway Bay, Ireland during 1990–1993. Recently settled recruits of *P. pellucida,* i.e. individuals with larval shells still attached, were found on CCA each year and in virtually every month of the year. A marked annual cycle in the abundance of *P. pellucida* on CCA is described, with the largest densities occurring during winter/spring, of up to 15 cm^{-2}, falling to minima in the summer months.

Analysis of population structure shows that this pattern is due to a winter/early spring settlement peak. Data from *M. stellatus* suggest that *P. pellucida* may settle directly on this alga, but, if so, at densities two orders of magnitude less than on CCA. The pattern of density change and the population structure on *M. stellatus* support the hypothesis that *P. pellucida* migrates to this alga following settlement on CCA. The larval and developing adult shells are described using SEM photographs.

INTRODUCTION

The blue-rayed limpet, *Patella pellucida* L., is a mesoherbivorous gastropod which is particularly associated with laminarians (Fretter and Graham 1976; Toth and Pavia 2002), but is also found on a range of other macroalgae (Vahl 1971; McGrath 1992, 1997) and on open rock (McGrath 1997). It is found on all Irish and British coasts (Seaward 1982) and on all Atlantic coasts between Portugal and northern Norway (Graham 1988). The species occurs in the intertidal zone only near LWST and extends sublittorally to 27 m (Fretter and Graham 1976).

Two forms of the species exist. The *pellucida* form, which makes up two thirds of the population of this limpet, is found on the algal frond while the *laevis* form excavates the base of the kelp stipe within the holdfast (Fretter and Graham 1976). *P. pellucida* are annual: two-year-old limpets are mostly the *laevis* form which have recruited to *Laminaria* holdfasts (Fretter and Graham 1976).

P. pellucida probably breeds throughout the year at Plymouth (Lebour 1937) and exhibits peak spawning in spring with a short larval life of a few weeks (Fretter and Graham 1976). Azevedo *et al.* (1984) have noted that female *P. pellucida* have early meiotic prophase oocytes in their ovaries by October-December and vitellogenic oocytes in February on the Atlantic coast of Portugal. The shelled larvae are to be found in the plankton at Plymouth in almost any month, sometimes occurring in numbers, and the shell of the late larva is 0.16–0.18 mm across (Lebour 1937). Lebour (1937) figures this late larval stage and notes that there are some differences between it and that of other *Patella* species.

According to Fretter and Graham (1976), the larvae of *P. pellucida* settle all over the shore but only those settling on *Laminaria* spp. survive into adulthood. However, Vahl (1971) failed to find the earliest benthic stages on *Laminaria hyperborea* (Gunn.) Foslie and concluded that settlement of *P. pellucida* occurs on another substratum and is followed by migration to *L. hyperborea.* McGrath (1992) found recently settled *P. pellucida,* with larval shells still attached, on crustose coralline algae (CCA) on the lower shore between February and April at Carnsore Point in south-east Ireland. Analysis of the population structure and density of the species on a range of algae at this site, including *Laminaria digitata* (Huds.) Lamour, *L. hyperborea,* and *Himanthalia elongata* (L.) S.F.Gray, led to the hypothesis that settlement did not occur on these algae but that the juvenile limpets recruited to them following settlement on CCA (McGrath 1992). The situation on *Mastocarpus stellatus* (Stackh.) Guiry was not so clear-cut and McGrath (1992) did not exclude the possibility of settlement on this alga. *P. pellucida* appears to undergo multiple phases of recruitment. Settlement on CCA is followed by recruitment to *Laminaria* spp. and *M. stellatus* (at *c.* 2 mm shell length) and later to *Himanthalia elongata* (at *c.* 3 mm shell length) (McGrath 1992). It also migrates from the frond of Laminaria into the holdfast, generally at 3–6 mm shell length (Graham and Fretter 1947). These phases of recruitment imply a high level of mobility in this species and this has been confirmed by a series of field experiments (McGrath 1997, 2001). However, while the seasonal cycles in the density of *P. pellucida* were described quantitatively for *H. elongata* and *M. stellatus* to support the recruitment model described by McGrath (1992), very little data were supplied on the population dynamics of the limpet on CCA. Furthermore, settlement *per se* was not examined in McGrath's study; he found recruits, which were first encountered when they became visible in the field at a shell length >375 µm (McGrath 1992).

The present study set out to investigate in greater detail the relationship between the earliest study benthic stages of *P. pellucida* and CCA. Sampling by removal of patches of CCA for later microscopic analysis allowed for the detection of earlier recruits than those reported by McGrath (1992). The seasonal occurrence, density and population structure of *P. pellucida* on CCA on the lower intertidal of an exposed rocky shore in Galway Bay, west coast of Ireland over a three-year period 1990–1993 is quantitatively described. Simultaneous examination of the density and population structure of *P. pellucida* on *M. stellatus* was carried out in 1993 to examine the hypothesis that larvae settle on this alga (McGrath 1992).

The generic allocation of this species to *Patella* follows recent molecular and morphological analyses (Ridgway *et al.* 1998, Koufopanou *et al.* 1999).

METHODS

Samples of CCA were collected at approximately two-weekly or monthly intervals during October 1990 to April 1992 from an exposed rocky shore at Ballynahown in Galway Bay, west coast of Ireland (Irish National Grid Reference L9920). Each sample was composed of a number of small patches of the alga removed haphazardly (Krebs 1989) from the rocky substratum using a knife. Sampling was, however, restricted to relatively thick patches of CCA, often of coarse topography. Three samples were taken on each occasion with two exceptions, when bad weather allowed for the collection of only two. Collection was at or just below the low water spring tide of the day in the upper *Laminaria digitata* zone. The samples were examined under a stereo microscope within twelve hours of collection at a magnification of ×15–×20 and the *P. pellucida* counted, removed and stored in 70% alcohol. The area of CCA examined from each sample was estimated by drawing around each patch on graph paper and numbers found on each sampling trip are expressed as the mean cm^{-2} of CCA. Sample size ranged from 7 cm^2 to 42 cm^2, mean 21.7±S.D.7.8 cm^2.

Three samples of CCA were also examined from the same area of shore at Ballynahown at approximately monthly intervals from February to May 1993. These were either frozen or stored in 70% alcohol prior to examination. The area of each sample was estimated by image analysis. Otherwise samples were treated in the same way as above. Sample size ranged from 14.4 to 67.0 cm^2, mean 31.2±S.D.16.6 cm^2.

Five samples of *Mastocarpus stellatus* were collected, generally at fortnightly intervals, in 1993, during February to May by cutting the alga from the substratum with a knife. The samples were stored damp in plastic bags at 4°C (up to three days) or at –20°C prior to examination. Sample wet weight (surface blotted dry) ranged from 5.3 to 16.1g, mean 11.2±S.D.3.2g. The algae were scanned microscopically and attached *Patella pellucida* removed and stored in 70% alcohol. Each algal sample was then dried to constant weight (±<2%) at 60°C. The relationship between dry weight and algal surface area was estimated by measuring the surface area of a series of algal samples using image analysis and determining their dry weight as above. A regression analysis of algal dry weight against frond surface area was calculated and used to estimate the surface area of the routinely collected samples. The calculated regression equation was as follows:

Area of frond (cm^2) $= 31.2 * DW$ (g) $+ 37.92$, $r = 0.55$ ($p<0.05$), $N = 25$.

P. pellucida density on *M. stellatus* could therefore be expressed as numbers g^{-1} dry weight or numbers cm^{-2} surface area.

All *Patella pellucida* collected were measured for shell length (maximum dimension) of developing adult shell only to the nearest 25µm below using a calibrated eyepiece in a stereo microscope and were classed into three benthic life history stages:

(i) limpets with larval shell only, or with a developing adult shell
(ii) limpets which had lost the larval shell, but had not developed blue rays
(iii) limpets without a larval shell and with blue rays.

Notes on the identification of the *P. pellucida* recruits:

The smallest recruits found did not have the diagnostic features of the adult shell, *i.e.* characteristic brown colour with blue rays, and are presently presumed to be this species following a number of lines of argument:

- a continuous size series from larval shell only through the various developmental stages has been observed and no discontinuity discerned.
- the larval shell in the smallest stages is similar to that seen on larger shells where some adult shell features are present.
- no other limpet species which might have developed from these larval shells is found as recruits in numbers comparable to *P. pellucida* on the CCA.

In the absence of diagnostic descriptions of the larval shells of all limpet species which might be found in this habitat, proof that *P. pellucida* settles on CCA must await the successful ongrowing of the smallest field collected recruits in the laboratory until the features of the adult shell develop, a diagnostic description of *Patella* species larval shells, or genetic typing of the recruits.

Patella ulyssiponensis Gmelin, *P. vulgata* L. and *Tectura virginea* (Muller) are found as adults on the lower shore at Ballynahown in the upper *L. digitata* zone. Observations suggest that recently settled *T. virginea* are readily separable from *Patella*. Single individuals of presumed *P. vulgata* or *P. ulyssiponensis* recruits, with some of the adult shell and colour patterns developed, have been found very rarely on CCA in the lower shore habitat sampled.

The larval shell of *Patella pellucida* appears to be very similar to the light microscope descriptions of *Patella vulgata* (Smith 1935; Lebour 1937) including the presence of minute granulations. Lebour (1937) notes, however, that the larval shells of *P. pellucida* and *P. vulgata* are distinguishable in that those of the former species are smaller, smooth and more symmetrical at the outer lip, the margin overlapping at both sides. This latter feature was not observed in the specimens from Galway Bay and it may be that it is not obvious by the time of settlement. There is, therefore, some disparity between the description of the larval shell of *P. pellucida* as described by Lebour (1937) and the appearance of the larval shell of the recent recruits from Galway Bay.

RESULTS

The density of *P. pellucida* on CCA during the period October 1990 to April 1992 is shown in Figure 1. A distinct annual cycle is evident. Peak densities occurred in late winter/spring and fell to minima during the summer and autumn. The mean density of *P. pellucida* in the samples ranged from a maximum of 6.84 cm^{-2} in January 1992 to a minimum of 0.01 cm^{-2} in August/September 1991. The maximum density recorded was 15 cm^{-2} on patches of 0.48 and 1.20 cm^{2} in March 1991 and February 1992 respectively.

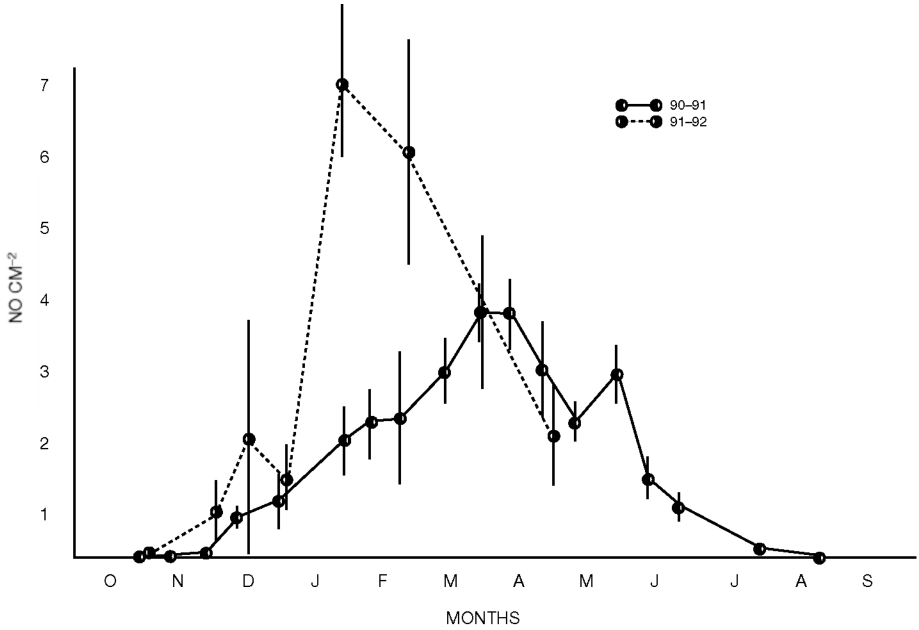

Figure 1: The density of *Patella pellucida* on the crustose coralline alga, as numbers cm^{-2}, from October 1990 to April 1992, on the lower shore at Ballynahown, Co Galway, Ireland. Vertical bars are standard deviations.

The percentage occurrence of the three benthic life history stages of *P. pellucida* on CCA is shown for 1990–1992 in Figure 2. Recently settled recruits, *i.e.* individuals with larval shells attached, were found each year and in virtually every month of the year, the one exception being September 1991, when only one limpet was found. The highest percentages (>90%) of recent recruits occurred between November and February. The proportion then fell steadily until the summer months when these made up less than 15% of the collections. The number of limpets which had lost the larval shell but had not developed the blue rays characteristic of the adult was at its lowest (<10%) from November to February, increased thereafter and peaked in May (62%) and then decreased again. Individuals with blue rays reached their maximum in July with very low abundances (<5%) from January to April.

Individuals with the adult shell yet to be developed were found in low numbers in the months of October to May on CCA. A mean number of 5 individuals month^{-1} was found over this period. Numbers larger than the mean number were restricted to the months of January to March with a maximum density of 0.47 cm^{-2} in January 1992. The larval shell of these specimens ranged in length from 228 to 252 μm with a mean of 241.35 ± S.D. 6.62 μm (N = 20). The larval shell was generally lost at an adult mean shell length of *c.* 550μm and the blue rays developed at a mean length of *c.* 1 mm shell length. These two length values are calculated as the mean lengths of those limpets in a sample lying between the smallest and largest with a larval shell and without blue rays respectively. Exceptionally, an individual of 450 μm shell length with no larval shell was found on 28 December 1991. The largest limpets on CCA were in the range 1.4 to 2.3 mm.

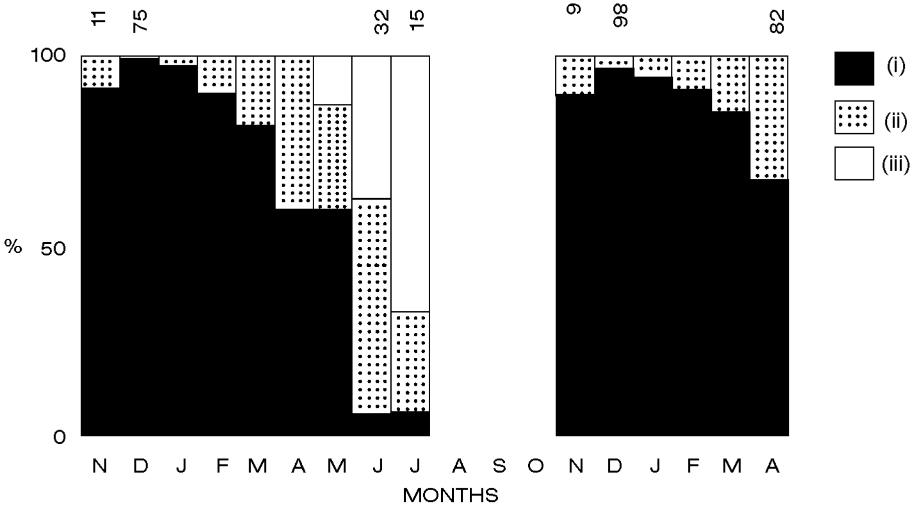

Figure 2: The relative abundance of three benthic stages of *Patella pellucida* on the crustose coralline alga on the lower shore at Ballynahown, Co Galway, Ireland, November 1990 to April 1992.

(i) recruit with larval shell attached.

(ii) without larval shell and without blue rays.

(iii) with blue rays present.

Numbers from sampling sessions in the same month are combined. Where <100 individuals were assessed, the sample number is shown. No data are available for August to October 1991 as <3 specimens were taken on each occasion.

The larval shell of *P. pellucida* is shown in Plate 1. It is involute with little external evidence of spiral growth and consists of one and a half whorls. The surface is smooth but with numerous scattered pores or pits (Plate 1). Growth of the adult shell is patelliform and markedly asymmetric with the shell flaring outward to the larval right and the larval shell being displaced from the centre of the growing adult shell before being lost (Plate 1). Following loss of the larval shell, there is a clearly visible shell plate and an indentation on the adult shell posteriorly where the larval shell rested (Plate 1). The growing adult shell differs from the larval shell in that the pores/pits are fewer and there is a suggestion of growth checks (Plate 1).

The length frequency data for *P. pellucida* on the CCA during 1990–1992 are shown in Figure 3 for selected months when more than 60 individuals was collected. The population was generally comprised of a single mode but this tended to be skewed to the right later in the year as the numbers of larger animals increased. Growth is obvious in the population during April/May 1991 with the mode shifting to the right. The population structure was also similar in 1993 with growth in April/May (Figure 3). Growth rates were not estimated from these length data as, given that recruitment was probably prolonged and migration occurred to other macroalgae with increase in size (McGrath, 1992), such rates would be of doubtful value.

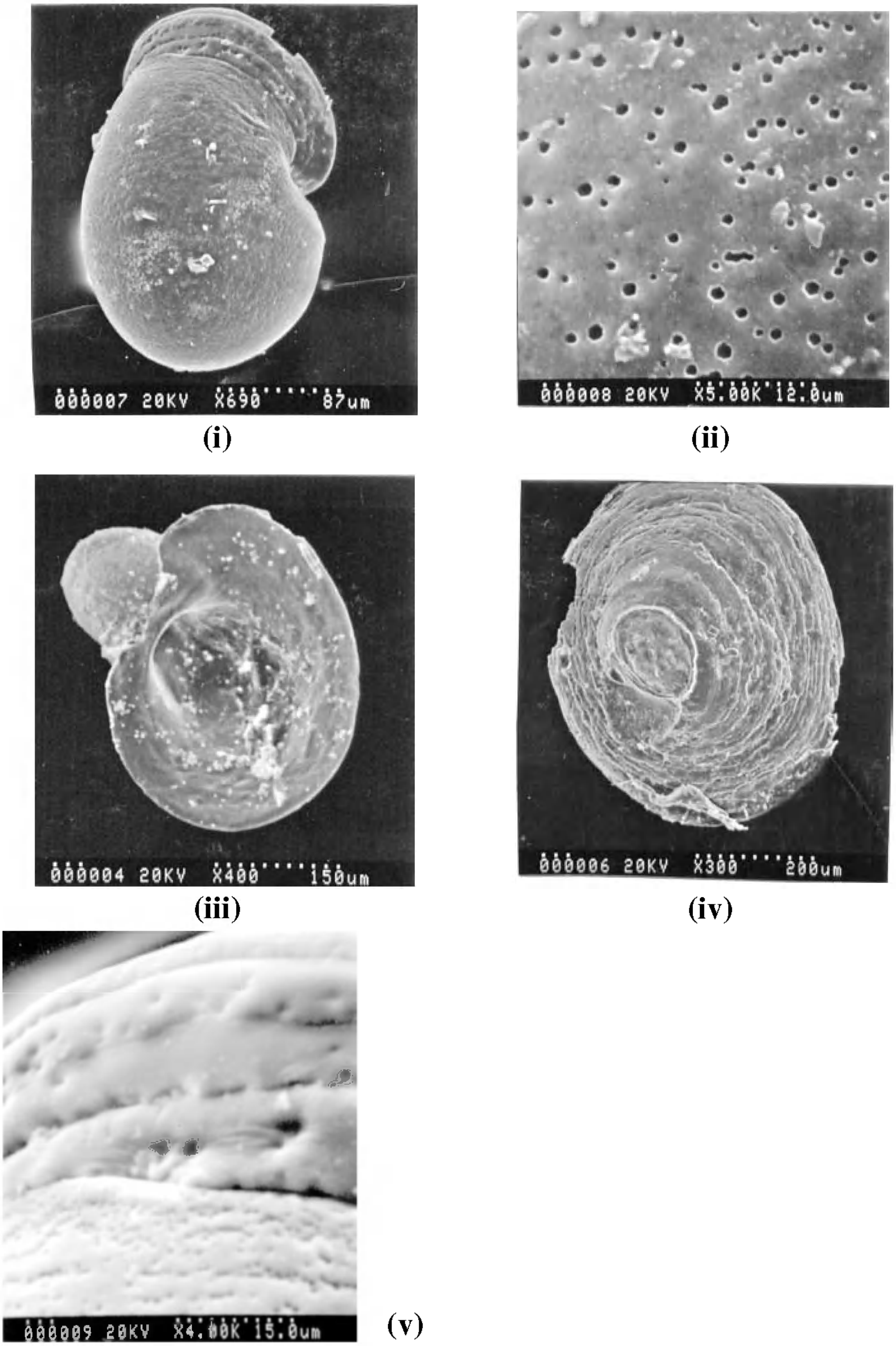

Plate 1: SEM photomicrographs of the juvenile shell of *Patella pellucida*. Magnification used and scale are indicated on each photograph. i) The newly settled recruit to show the larval shell: ii) Pits on the shell surface of the larval shell: iii) The developing juvenile shell: iv) The shell plate and larval shell scar: v) The junction between the larval and juvenile shell.

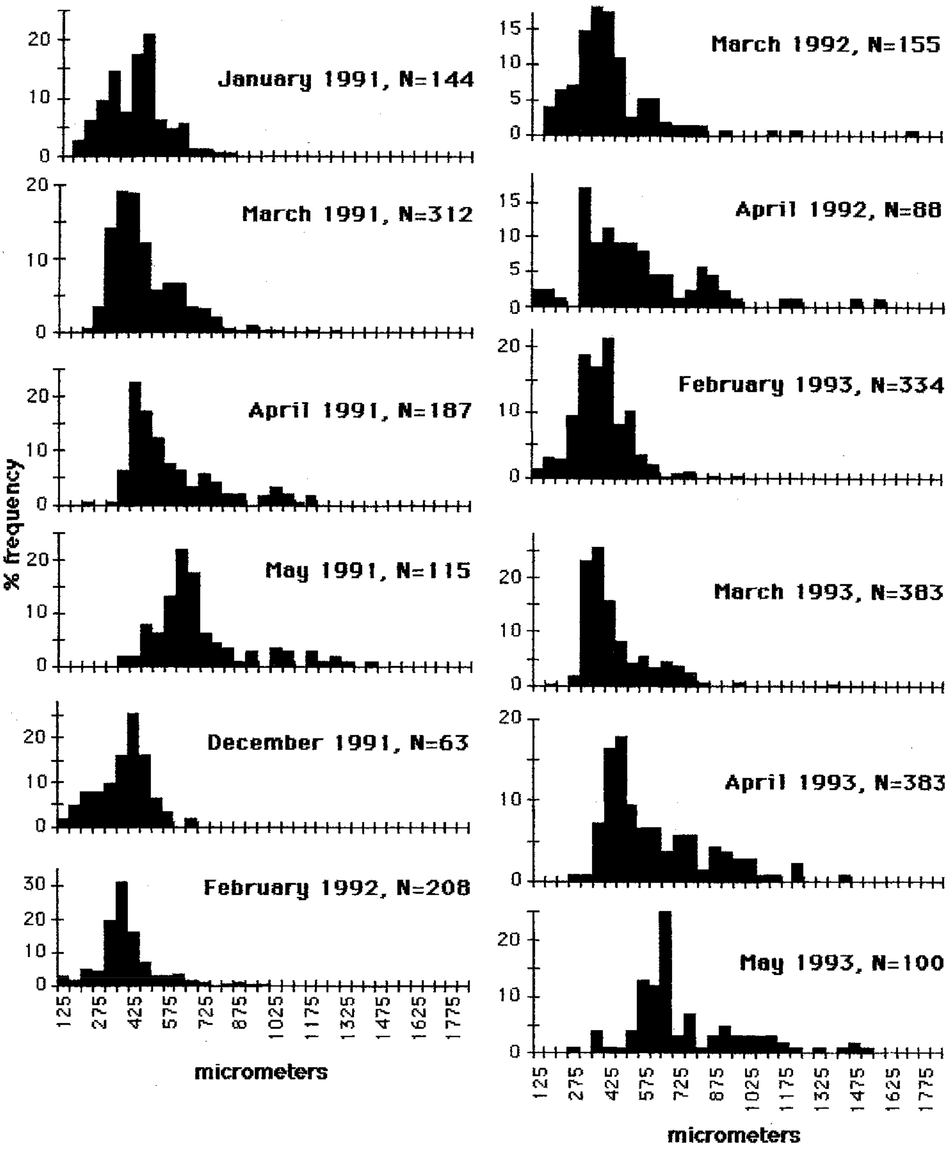

Figure 3: Length frequency data for *Patella pellucida* sampled on the crustose coralline alga on the lower shore at Ballynahown, Co. Galway, Ireland, January 1991 to May 1993 for selected months where >60 individuals were collected.

The density of *P. pellucida* on CCA and *M. stellatus* during February to May 1993 is shown in Figure 4. A mean density of 2.37 cm^{-2} on CCA rose to a peak of 4.36 cm^{-2} in March then fell over the following two months to 1.83 cm^{-2}. Densities on *M. stellatus* were very low compared to those on CCA with a maximum density of 0.12 cm^{-2} over the four month period. The mean densities over the period on CCA and *M. stellatus* were 2.73±S. D.1.12 and 0.03±S.D.0.04 cm^{-2} respectively. A fall in density on *M. stellatus* from early to late February was followed by a progressive rise from March with the peak density in May. Numbers of *P. pellucida* g^{-1} DW *M. stellatus* ranged from 0.27±S.D.0.24 to 14.48±S.D.4.57, mean 3.62±S.D.5.01.

The occurrence of the three benthic life history stages of *P. pellucida* on *M. stellatus* and CCA for the period February to May 1993 is shown in Table 1. Individuals with larval shells attached were found on *M. stellatus* during March to May, but in very low numbers making up 2.4% of the total found on that substratum (Table 1). This contrasts sharply with the situation on CCA where specimens with larval shells were abundant throughout the period, making up on average 76.9% of the population, while showing a decline in relative abundance from 96.4% to 12.9% from February to May (Table 1). Recruits on *M. stellatus* were dominated by individuals which had lost the larval shell. A comparison between the two substrata shows that recruits on *M. stellatus* were less dense than those on CCA, increased in density when the density on CCA decreased, and were generally composed of more advanced benthic life history stages (Figure 4, Table 1).

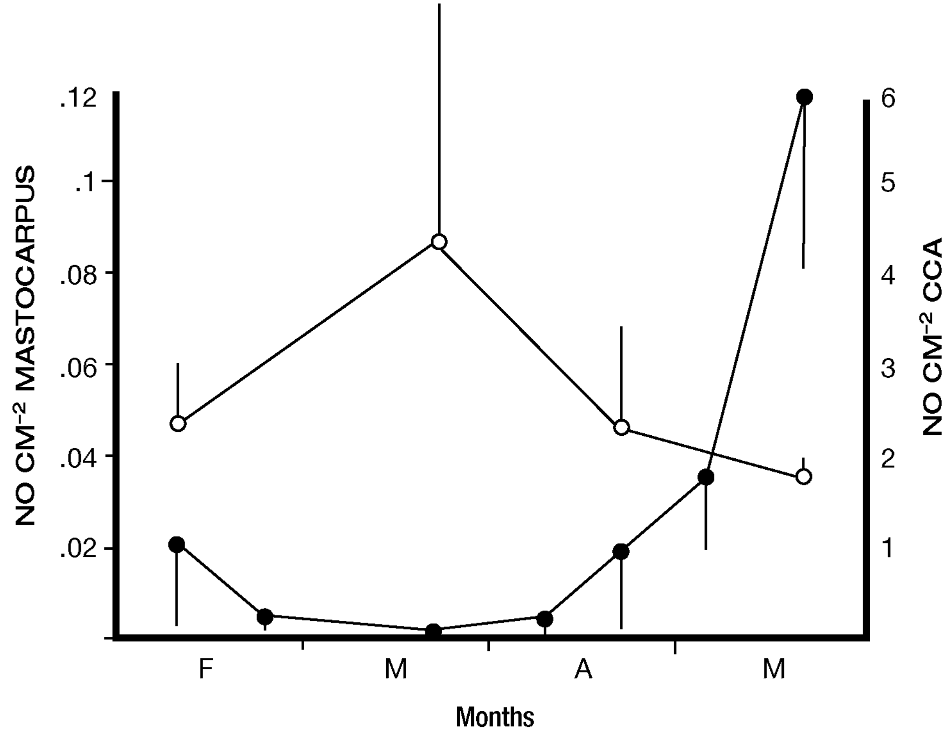

Figure 4: The density of *Patella pellucida* on the crustose coralline alga (CCA) (o) and *Mastocarpus stellatus* (●) on the lower shore at Ballynahown, Co Galway, Ireland, February to May 1993, as numbers cm^{-2} surface area

The mean sizes of *P. pellucida* on *M. stellatus* during the months February to May 1993 are listed in Table 2. The range was 375–7360 µm shell length with a mean of 1413.19±S.D.863.66 µm. Mean size fell from February to March, then showed a tendency

Table 1. Percentages of *P. pellucida* on CCA and *Mastocarpus* during February to May 1993 (February, April, May the replicate *Mastocarpus* samples are combined), on the lower shore at Ballynahown, Co. Galway, Ireland in the three developmental categories as follows:

i) With larval shell;
ii) Without larval shell and without blue rays
iii) Without larval shell and with blue rays

	Mastocarpus				**CCA**			
	N	i	ii	iii	N	i	ii	iii
February	53	0	0	100	362	96.4	3.3	0.3
March	4	25	75	0	390	82.8	16.9	0.3
April	52	9.6	67.3	23.1	141	56	35.5	8.5
May	310	1.3	41	57.7	101	12.9	70.3	16.8
Total	419	2.4	39.4	58.2	994	76.9	20	3.1

to increase until May. The relatively high density of recruits in early February (Figure 4) was composed of larger animals. The data confirm the trend seen in the life history stages in that limpets on *M. stellatus* were larger in any month compare with those on CCA.

DISCUSSION

Patella pellucida recruits were found each year from 1990 to 1993 at Ballynahown on CCA. Later observations also confirm recruitment to CCA in 1994. The smallest recruits encountered during the study were limpets which consisted of larval shells only and these were found during October to May at a maximum density of 0.47 cm^{-2} (January 1992). These had a mean shell length of 241.35±S.D.6.62μm, were involute and consist of one and a half whorls, with a punctate sculpture. Recruits comprised of a larval shell only were rare in the CCA samples. The largest number found was twenty and this made up only 5% of the sample. This may be due to very rapid development of the adult shell. Kay and Emlet (2002) observed that the patellogastropod limpets *Lottia digitalis* (Rathke) and *L. asmi* (Middendorf) initiated adult shell growth 2–4 days after settlement in the laboratory.

McGrath (1992) reported the presence of "recently" settled *P. pellucida,* i.e. limpets with larval shells still attached, at Carnsore Point in south-east Ireland. McGrath (1992) collected visible individuals of *P. pellucida* in the field and the smallest individuals found were 375μm in shell length. These individuals should, more correctly, be termed recruits, settled individuals which have survived some post-settlement time until recorded by an ecologist (Keough and Downes 1982; Connell 1985; Pawlik 1992). In his study, McGrath (1992) gave no data on the length of time these recruits had spent on the shore after settlement and therefore did not define the term recent. Settlement in field situations is

Table 2. Number (N), density (g^{-1} and cm^{-2}), mean size (μm) of *P. pellucidum* on *M. stellatus* February to May 1993 on the lower shore at Ballynahown, Co. Galway, Ireland.

Date	**N**	**N.g^{-1}**	**SD**	**N.cm^{-2}**	**SD**	**Mean size μm**	**SD**
10/2/93	41	2.47	2.04	0.021	0.017	2447	614
24/2/93	12	0.66	0.42	0.005	0.004	2861	1460
21/3/93	14	0.27	0.24	0.002	0.002	769	241
9/4/93	9	0.59	0.36	0.005	0.003	943	577
21/4/93	39	2.43	2.12	0.02	0.018	865	212
5/5/93	96	4.43	1.7	0.037	0.014	1142	476
20/5/93	205	14.48	4.57	0.121	0.038	866	162

often inferred from recruitment data measured in days or even weeks after settlement has taken place (Seed and Suchanek 1992). While settlement itself was not observed in the present study, the discovery of individuals with only larval shell, considerably narrows the gap between settlement proper and recruitment.

The larval shell of *P. pellucida* from Ballynahown was lost at *c.* 550μm and the blue rays developed at *c.* 1 mm shell length respectively. These figures are similar to those reported by McGrath (1992). In *Patella vulgata* the shell cap of the post-larva is cut off when the limpet is about 0.5 mm long (Smith 1935). The larval shell of *P. pellucida* appears similar to that of *P. coerulea* (L.). The post-larval shell of the latter species also shows a distinct scar where the larval shell was attached and a second impression where the larval shell lay (Waren 1988). Recent recruits (with larval shell) of *P. pellucida* peaked in relative abundance during November to February. This was followed by a peak in the number of limpets without larval shells or blue rays, which had a maximum in May, then in turn by those with blue rays present which reached their peak abundance in July.

The density of *P. pellucida* on CCA showed a marked seasonal cycle increasing from October/November and peaking in January or March. Analysis of the population structure of the limpets indicates that this density increase was a result of a recent settlement of larvae. The peak abundance of recent recruits coincided with the first months of the density increase. With the decline in density, older life stages became relatively more abundant. The combination of the density data and the information from population structure analysis suggests that the main settlement is a winter/early spring event, peaking in January to March with, perhaps, some differences in timing from year to year. This finding would also suggest a winter/early spring spawning peak in this species. The occurrence of recent recruits in virtually all months of the year on CCA, albeit at times in very low densities, suggests that some settlement occurs throughout the year. While this contrasts with the view of McGrath (1992) who concluded that settlement was completed by May, the main peak of settlement at Ballynahown was complete by May when recent recruits made up <25% of the population. It must also be noted that the studies were done in different years and in different locations. Fretter and Graham (1976) have observed that, while breeding occurs throughout the year in *P. pellucida,* it is maximal in spring. Larvae of this species have been reported from the inshore plankton at Plymouth in February, August, September, November and December (Fretter and Graham 1962). These observations are consistent with the results of the present study.

Because numbers of recruits accumulate following settlement on natural substrata (King *et al.* 1990) and since data on growth rates is lacking, it is not possible to define the settlement peak more precisely. The maximum densities of recruits seen on CCA at Ballynahown of 15 cm^{-2} are of a similar order to those reported by McGrath (1992) of 4 cm^{-2}, though predictably larger, because microscopic examination of the Ballynahown samples would discover individuals which would have been overlooked visually in the field at Carnsore Point. The maximum mean densities seen on CCA were of a similar order in the three years 1991–1993 respectively, 3.5, 6.8 and 4.4 cm^{-2} respectively. The possible effect of the non-random sampling method used on estimates of density on CCA is not known.

McGrath (1992) did not exclude the possibility that *Patella pellucida* settles on *M. stellatus.* Recruits with larval shells still attached were found in the present study on this alga in 1993, although in small numbers. Thus, either *P. pellucida* settles on *M. stellatus* or can migrate to it from CCA during the earliest benthic life history stages. If the species settles on *M. stellatus,* then it would appear to be a much less favoured substratum than CCA given the very low densities of recent recruits on this alga during the settlement peak on CCA. In summary, however, the data do not allow rejection of the hypothesis that *P. pellucida* settles on *M. stellatus.* It is possible that the recruits on this alga are "desperate larvae" with reduced settlement substratum specificity (Toonen and Pawlik 1994). McGrath (1992) suggested that *P. pellucida* settled on CCA and then migrated to *M. stellatus,* based on the analysis of the population structure of the limpets on the two algae and the fact that a density decrease on CCA following recruitment was followed by an increase on *M. stellatus.* A similar pattern was observed at Ballynahown. The density decrease on *M. stellatus* in February was comprised of larger animals and was not associated, therefore, with a settlement event. The maximum density of *P. pellucida* on *M. stellatus* at Ballynahown is of a similar order to that seen by McGrath (1992) at Carnsore Point.

Settlement of benthic invertebrates with a planktonic larval stage may be by passive deposition or by active habitat selection, though these processes may not be mutually exclusive, and may both operate in a life history at different spatial and temporal scales (Butman 1987). Passive deposition might result in non-random distribution of recruits intertidally due to differing times of immersion (Minchinton and Scheibling 1991), other hydrodynamic effects (Jeffrey and Underwood 2000) or other factors such as predation (see Ross 2001, for a review). Active habitat selection may involve both positive or negative cues (Woodin 1991). Differential mortality of settlers in different habitats may lead to recruit distribution being trimmed to that of the adult (Connell 1985). Also, the observed distribution of recruits may be established by migration after settlement in another habitat, for example, in some *Mytilus edulis* populations (Bayne 1964).

For *P. pellucida,* settlement is clearly not random, as originally proposed by Fretter and Graham (1976), in that the earliest recruits are absent from habitats occupied by the adult (Vahl 1971; McGrath 1992). Given the very small size of recruits found in the present study on CCA, migration from an earlier settlement site appears unlikely and this strengthens McGrath's (1992) hypothesis that settlement occurs on CCA. The data for *P. pellucida* indicate a non-random process, but whether this is due to larval selection, with CCA as a positive settlement cue, is caused by hydrodynamic delivery of larvae to CCA, or other factors is unknown. The ecology of the earliest benthic stages of the other Irish species of *Patella* is very poorly known. However, *P. ulyssiponensis* recruits also appear to have a close, but non-obligative relationship with CCA, while those of *P. vulgata* appear to be indifferent to it (Delany *et al.* 2002). *P. ulyssiponensis,* however, remains associated with CCA throughout life, while *P. pellucida* uses this habitat as a nursery area prior to migration to adult habitats (McGrath 1992; Delany *et al.* 2002).

ACKNOWLEDGEMENTS

We wish to thank Martin McNulty for his help with the image analysis, Donncha McGrath for his assistance with computer work and Dr. David Reid, The Natural History Museum, London, for helpful comments on an earlier draft of this paper.

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WHAT DO SPECIES DO IN INTERTIDAL SYSTEMS?

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ABSTRACT

There is a surprising lack of targeted research into the effects of loss of biodiversity on functioning of marine ecosystems. General theoretical models have been developed and these have been tested in terrestrial systems, particularly grasslands, and in mesocosms. Findings have been controversial, however, with debate focussing on the role of species diversity *per se* as opposed to the role of particular species from specific functional groups (functional diversity). Marine systems process materials and energy quite differently from terrestrial systems and have a high degree of functional diversity. Specific models may therefore need to be developed for marine systems, and marine tests of general models could be valuable in resolving current ecological debates. Although targeted research is lacking, there is a considerable body of relevant work in intertidal systems and some of this research is reviewed here. Idiosyncratic effects of loss of species appear to be prevalent in intertidal systems, and removals of more than one species often result in interactive effects, suggesting a high degree of complexity and unpredictability. However, it is thought that idiosyncratic effects are more likely to occur in systems with 'keystone' species than in systems with weak or diffuse effects of consumers. Intertidal systems, particularly rocky shores, provide an ideal model system for research into effects of loss of diversity on ecosystem function. In addition to distinguishing the roles of species and functional diversity, intertidal research could also characterise intertrophic effects and relationships between the diversity of ecosystems and their stability and invasibility.

INTRODUCTION

The title of this review is derived from an influential paper by John Lawton which summarised some of the theories predicting what may happen to the functioning of ecosystems as species are lost from them (Lawton 1994). Given the currently high rate of loss of species, this issue has become one of the key areas of debate in ecology (Schwartz *et al.* 2000; Tilman 2000). In this paper, I will first outline the sorts of ecosystem functions that have been considered in this context and present the main theories predicting how their rates are related to the numbers of species present. A case will be made for tests of these theories in marine systems and evidence from intertidal systems will be reviewed. Finally, I will discuss one attempt to provide a general predictive framework into which to fit these findings and will suggest some avenues for research in intertidal systems.

EFFECTS OF LOSS OF SPECIES ON ECOSYSTEM FUNCTION

The functioning of ecosystems can be defined in many ways, but may broadly be thought of as the rate at which they process materials and energy (e.g. Díaz and Cabido 2001). Processes of interest thus include productivity (primary, secondary, etc.), decomposition, transfer of energy between trophic levels, nutrient retention, nutrient cycling, etc. Martinez (1996) sought to expand that definition to include ecological processes, such as recruitment, predation, etc., but such processes have not usually been considered in this context and will generally be omitted from the current review.

From a human perspective, the functioning of ecosystems has become a focus of ‘sustainability science’, which supports conservation based on the value of ‘goods and services’ that ecosystems provide to mankind (Costanza *et al.* 1997). International conventions such as the Rio Convention on Biodiversity oblige signatories to protect the biodiversity of systems, in part to maintain the integrity of their functions. This is based on the premise that the functioning of systems is related to their biodiversity, and it is this premise that has been intensely scrutinised in recent years.

Three main hypotheses are commonly cited to predict the relationship between biodiversity and ecosystem function (Figure 1). The redundancy hypothesis (Walker 1992), suggests that the loss of a large proportion of species in an ecosystem would have no effect on its functioning because many species are ‘redundant’ in terms of ecosystem function and their loss would be compensated for by other, similar species. However, a critical point would eventually be reached, at which all functional analogues would have been lost and there would then be a catastrophic decline in ecosystem function (Figure 1). This theory has been particularly controversial, with calls by conservationists for the abandonment of the term ‘redundancy’ due to the implication that some species are of no value and could be lost without consequence (e.g. Gitay *et al.* 1996). Naeem (1998) and Yachi and Loreau (1999) have argued instead that we should think positively about the retention of redundant species as an essential component of ‘biological insurance’ against future changes in environmental circumstances.

Ehrlich and Ehrlich (1981) proposed the ‘rivet hypothesis’ that likens the species in an ecosystem to rivets in an aircraft – the loss of each one would have a small effect on the efficiency of the machine – and predicts a gradual decline in ecosystem function as species are lost until a critical point is reached and the aircraft (ecosystem function) crashes (Figure 1). This change in function is sometimes drawn as a step function, but is distinguished from the redundancy hypothesis by progressive change as species are

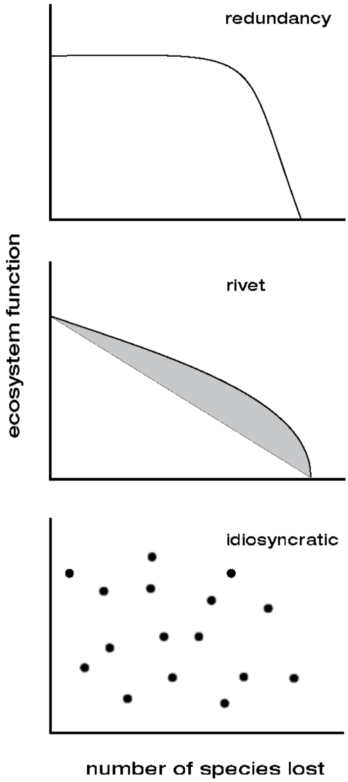

Figure 1. Models of effects of loss of biodiversity on ecosystem function (modified from Lawton 1994)

lost, rather than no change until the critical point. It should also be noted that although these models are illustrated with a negative relationship between number of species and ecosystem function, this does not imply that the relationship is always negative (e.g. see Wardle *et al.* 1997).

Finally, Lawton (1994) proposed that there would not be a smooth relationship between number of species and ecosystem function, but rather that the effects of losing a species would depend on the identity of the species lost and would vary 'idiosyncratically' from species to species (Figure 1).

Diverse systems are also thought to be more stable than less diverse systems and less vulnerable to invasion. These are long-standing ideas, which have again come to the fore in recent years and which have been the subject of renewed experimental research (e.g. McCann 2000; Naeem *et al.* 2000; Prieur-Richard and Lavorel 2000; Lyons and Schwartz 2001). As with other aspects of research in this field, findings have been controversial and no consensus has yet been reached.

EVIDENCE TO DATE

Much of the field evidence for and against these ideas has been derived from terrestrial systems, including grasslands, soils and streams. This evidence has been reviewed elsewhere (e.g. Naeem *et al.* 1999; Schläpfer and Schmid 1999; Tilman 1999; Bolger 2002; Waide *et al.* 1999; Wardle *et al.* 2000; Ekschmitt *et al.* 2001) and will not be considered in any detail here except to note some key findings and controversies. Among the most influential studies have been those of Tilman *et al.*(1996) and Hector *et al.*(1999), which showed positive relationships between number of species of grasses and herbs and primary productivity, in apparent support for the rivet hypothesis. 'Complementarity' was proposed as a key mechanism to explain how more diverse assemblages can be more productive than monocultures; a diverse range of species with slightly different niches make fuller use of available resources than any one species could (Hector 1998).

These findings have provoked considerable controversy, however, with suggestions that the experimental designs and inferences are flawed (Aarssen 1997; Grime 1997; Huston 1997; Huston *et al.* 2000). These authors argued that significant increases in productivity may not be attributable to diversity *per se,* but rather to one or two extremely productive species, which function very differently from the others. Probability dictates that the chances of including such species are increased in the high diversity treatments. This has been termed the 'sampling' (Tilman 1999) or 'selection' effect (Huston 1997). If it is indeed the underlying cause of the observed effects, then the evidence supports the idiosyncratic rather than the rivet hypothesis. Considerable effort has therefore been invested in developing experimental designs that distinguish the effects of species diversity from those of individual influential species – so called 'functional diversity' (e.g. see Tilman 1997; Leps *et al.* 2001; Spaekova and Leps 2001).

The other main arena of investigation has been laboratory-based, in mesocosms. The Ecotron, for example, yielded some influential findings showing relationships between ecosystem processes and diversity of plants, herbivores and soil fauna (Naeem *et al.* 1994). Mesocosms are very attractive as a tool for studying these processes – a particular strength being the opportunity to make accurate measurements of ecosystem functions and to fully control the species composition. Drawbacks, however, centre around the obvious artifacts in terms of loss of natural physical processes affecting ecosystem processes – e.g. variation in nutrient availability, climatic variation, etc. – and limits to the number and size of species that can be included (Lamont 1995). Because assemblages are compiled, rather than species deleted progressively from complete assemblages, diversity is generally lower in laboratory than in field experiments and laboratory experiments are less likely to detect unexpected roles of rare species. Laboratory studies also create an artificial medium for behavioural interactions and do not permit natural shifts in abundances of other species (e.g. compensation for loss of one species by immigration of others).

More field experiments are sorely needed to complement the progress being made in mesocosms by reducing those artifacts, while of course suffering drawbacks of their own, particularly relating to the difficulty of accurately measuring ecosystem processes (see below). The mixture of field and laboratory approaches used can make it difficult to synthesise a cohesive overview, but most authors agree that an integrated approach is most likely to lead to rapid progress (e.g. Schläpfer and Schmid 1999; Díaz and Cabido 2001).

The bulk of the research to date has concentrated on the effect of diversity within a trophic level on functions of that level (e.g. manipulating diversity of plants to test effects on primary productivity). Schläpfer and Schmid (1999) noted a particular lack of information about the effects of herbivore diversity on herbivory. Hence there have been calls for research into effects of diversity at one trophic level on function of another (Naeem *et al.* 1999).

THE NEED FOR TESTS IN MARINE SYSTEMS

Responses of marine ecosystems to loss of biodiversity have not been extensively studied. In 1999, keyword combinations of the terms biodiversity, biological diversity, species diversity, species richness, stability, ecosystem stability, ecosystem function, productivity, yield and food web produced no relevant papers from the marine literature (Schläpfer and Schmid 1999), despite an already large body of work in other habitats. This is unfortunate for two main reasons. The first is that marine ecosystems are fundamentally different from their terrestrial counterparts (Steele 1985, 1991) and therefore models derived from terrestrial research may not apply to marine systems. For example, nutrient availability depends on oceanographic processes, and dramatic variation can occur over relatively short time scales via upwelling events (c.f. Vasquez *et al.* 1998). Unlike on land, where organisms are generally decomposed where they die, materials in marine systems are often transported away from where they were produced and decomposed elsewhere. Given such differences, marine environments will probably require tailor-made models to predict effects of loss of species on ecosystem function. Such models will need to be developed and tested in marine environments.

Secondly, marine diversity is very different from that on land. In particular, the marine fauna is diverse at higher taxonomic levels than the terrestrial fauna (May 1994; Vincent and Clarke 1995; Ormond 1996). Twenty-eight phyla are found in the marine environment, of which thirteen are endemic (Grassle *et al.* 1991). This compares to eleven terrestrial phyla, of which only one is endemic (Grassle *et al.* 1991). It therefore seems likely that marine systems have scope for greater functional diversity than terrestrial systems and may therefore be extremely valuable in settling the debate over the roles of species diversity versus functional diversity.

THE ROLE OF INTERTIDAL SYSTEMS

Intertidal systems, particularly rocky shores, are among the classic experimental model systems in ecology, with an extraordinary track record of influential research, including Kitching and co-workers' research in Lough Ine, Co. Cork (e.g. Kitching *et al.* 1959), Connell's (1961) pioneering experiments on competition on Cumbrae and Paine's (1974) keystone predator removal on the west coast of the USA. Intertidal systems have a high degree of functional diversity, they are accessible and experimentally tractable (Connell 1974; Paine 1977, 1994 and see McGrath, this volume) and, due to a long history of research, a considerable degree of essential background knowledge is available. They are also particularly pertinent in this context, as they are among the marine systems most threatened by man's activities and are therefore quite likely to suffer increased rates of local extinction in the coming years (Crowe *et al.* 2000; Thompson *et al.* 2002). It is therefore appropriate for research into effects of loss of biodiversity on marine ecosystem function to focus on intertidal systems.

EVIDENCE TO DATE FROM INTERTIDAL SYSTEMS

Although there has been a considerable body of potentially relevant research in intertidal systems, surprisingly little research has been done to tackle these questions directly. There has, of course, been a wealth of research testing hypotheses about the roles of individual species in affecting community structure – the experiments on predation and competition mentioned above being classic examples. I will not deal with work on removals of individual species here because their relevance in the current context is not as great as multi-species removals – without knowledge of how the system responds to loss of >1 species, it is not easy to differentiate among the redundancy, rivet and idiosyncratic hypotheses. Nevertheless, reviewing extensive bodies of separate single-species removals in the same system can yield considerable insight, as discussed below (next section).

In this section, then, I will briefly review studies involving removals of two or more species at a time. Given the theme of the symposium, I have generally restricted the review to intertidal studies. However, some studies on shallow subtidal systems (seagrass beds) are included because the work specifically addressed the relevant hypotheses and the species involved have intertidal analogues.

Some of these studies were not originally conceived to test hypotheses about the relationship between biodiversity and ecosystem function. However, in measuring response variables such as cover or biomass of algae, the authors made it possible to infer likely impacts on primary productivity. In fact, very little of the experimental work actually measured rates of primary production directly (by measuring rates of accumulation of biomass and losses to grazing and other causes). This would be extremely difficult in intertidal systems, particularly exposed rocky shores, given the rapid advection of broken material and the difficulties of estimating consumption by grazers, particularly of microalgae (but see Epstein 1997; Thompson *et al.* 1997; Middelburg *et al.* 2000). The use of tractable surrogates is widespread in this context (Hector 1998; Waide *et al.* 1999) and it can certainly be argued that impacts on the cover or biomass of macroalgae will undoubtedly alter the mechanism and magnitude of primary production. It should be noted, however, that in doing this we are extrapolating the link between the roles of species in affecting community structure to include the link between community structure and ecosystem function. This distinction is important and the latter link has rarely been tested in intertidal systems (Allison *et al.* 1996).

In contrast to much of the research in other systems, a significant proportion of the relevant work in intertidal systems has been done on inter-trophic effects. The findings clearly indicate that the diversity of one trophic level (e.g. primary consumers) can affect the diversity and function of other trophic levels (e.g. primary producers).

The majority of effects were idiosyncratic (Table 1, e.g. Scheibling 1994; Jernakoff and Nielsen 1997 and see Paine 2002). Perhaps this is not surprising, given the high incidence of strongly interacting 'keystone' species (and the inevitable bias of researchers towards manipulations of those species thought likely to have marked effects). Typically, the loss of strongly interacting species has dramatic effects and the effects of loss of other species are different and/or less dramatic (Table 1, and see Allison *et al.* 1996). Thus, the identity of the species lost is of key importance. Given the predominance of high level, high functional diversity in marine systems, this may well be a characteristic feature of them. It is striking, however, that idiosyncratic effects were also found after removal of different species from within a functional group – grazing limpets: Beovich and Quinn (1992) found that only loss of *Siphonaria diemenensis* would lead to major effects on foliose algae (e.g. *Scytosiphon lomentaria*); removal of *Cellana tramoserica* had little effect. This difference was partly attributed to differences in radula morphology and feeding biology, such that only *Siphonaria* could graze mature foliose algae.

Functional groups are not always defined by trophic considerations. Ecosystem engineering (*sensu* Jones *et al.* 1994) can provide another basis for classification and the importance of different ecosystem engineers also varies depending on the identity of the engineer. Emmerson and Raffaelli (2000) used microcosm experiments to test effects of diversity *per se* and functional diversity of bioturbators (allogenic ecosystem engineers) on flux of ammonia from sediments into the water column. They found that different species had markedly different effects and also showed that complementarity could act in soft sediment marine systems as it does in terrestrial plant communities (see Hector 1998).

One of the main insights to emerge from manipulations of two or more species in orthogonal designs is that not only is the identity of the species lost important, but also the identity of the combinations of species lost. Differences in the effect of losing species *a* depending on the presence or absence of species *b* give rise to statistical interactions in analyses of response variables – hence the category *idiosyncratically interactive* in Table 1. This is an issue that has rarely been considered in other systems (see Lamont 1995). As an example, ephemeral algae grew on a north Cornwall shore only if limpets (keystone grazers) were absent or if mussels (autogenic ecosystem engineers) were present to provide a refuge from limpet grazing; where limpets were present and mussels absent, no ephemerals grew (Crowe *et al.* unpubl data). Similar effects have been reported by Geller (1991) and Table 1 includes details from Scheibling (1994) and Navarrete and Menge (1996).

Not only is the identity of the species lost important, but also the structure of the community from which they are lost. Where studies were done at more than one site, results of experimental removals tended to differ from site to site. For example, the growth of ephemeral algae at a different Cornish shore from the one described above depended only on the presence of mussels, probably because the dominant ephemeral alga there was

Table 1. Summary of models relating biodiversity to ecosystem function from intertidal/shallow subtidal systems in which loss of >1 species was simulated experimentally. Studies marked '†' were not done specifically to test hypotheses about effects of loss of biodiversity. Variables sampled serve as surrogates for ecosystem functions (e.g. changes in algal cover or biomass indicate changes in primary productivity). In these cases, conclusions in relation to loss of biodiversity were not drawn by the authors of the original papers, but have been added by the current author.

System	**Approach**	**Level/ group & N° taxa manipulated**	**Trophic level sampled**	**Response variables**	**Effects / *model supported***	**Citations**
Saltmarsh, southern California	Field & greenhouse experiments–selective plantings	Primary producers (saltmarsh macrophytes) • 8 taxa	Primary producers	• recruitment • canopy architecture • biomass and N accumulation	Different species important for different functions– *rivet / idiosyncratic*	Zedler *et al.* 2001 Sullivan & Zedler 1999
Rocky shore, Western Australia†	Field experiment–manual removals	Herbivores (grazing gastropods) • 2 taxa	Primary producers (macroalgae)	• algal cover and biomass	Removal of limpets & chitons had strong effects, removal of abalone only effective in absence of limpets & chitons– *idiosyncratically interactive*	Scheibling 1994
Rocky shore, SE Australia†	Field experiment–cage enclosures	Herbivores (limpets) • 2 taxa	Primary producers (foliose, encrusting algae)	• cover of foliose and encrusting algae	Only one species of limpet affected growth of macroalgae – *idiosyncratic*	Beovich & Quinn 1992
Rocky shore, SW UK	Field experiment–manual removal	Herbivores (limpet) & ecosystem engineers (mussel) • 2 taxa	Primary producers (macroalgae)	• cover of macroalgae	Spatially variable interactive effects– *idiosyncratically interactive*	Crowe *et al.* (unpubl.)

Seagrass, eastern US (shallow subtidal)†	Outdoor mesocosms	Mesograzers (amphipods) • 2 taxa	Primary producers	• epiphyte biomass • seagrass biomass	Different effects of different grazers–*idiosyncratic*	Duffy & Harvillicz 2001
Seagrass, Western Australia (shallow subtidal)†	Field exclosures (some artifacts identified, effects still detectable)	Mesograzers (amphipods and gastropod) • 2 taxa	Primary producers	• periphyton biomass • epiphyte diversity & biomass • seagrass mortality	Mixed effects on periphyton; gastropods affected epiphyte biomass but not diversity, amphipods vice versa; seagrass mortality reduced by gastropods only–*idiosyncratic*	Jernakoff & Nielsen 1997
Rocky shore, NW USA	Manual removals • 2 taxa	Predators (starfish, dogwhelks)	Filter feeders (mussels, barnacles)	• survival of filter feeders	Whelks only become important in absence of starfish, i.e. partially compensate for loss of keystone–*idiosyncratically interactive*	Navarrete & Menge 1996

Porphyra spp., which was strongly associated with mussels. Barnacles did not provide an effective refuge for algae from grazing limpets on the Isle of Man (Johnson *et al.* unpubl), but did in California, where they were ineffective as a refuge from grazing by littorinids (Geller 1991). In this case, the value of barnacles as a refuge depended on the sizes of the grazing gastropods.

Environmental conditions can also alter the effects of losing species. For example, Zedler *et al.* (2001) found different effects of manipulating diversity of saltmarsh plants under different conditions of drought and nutrient availability. These findings indicate that effects of loss of biodiversity are 'context dependent', much like many other ecological phenomena (see also Allison *et al.* 1996; Jonsson and Malmqvist 2000).

Very few studies (in any system) have considered more than one ecosystem function at a time. Zedler *et al.* (2001) included recruitment and canopy architecture as 'ecosystem functions' (along the lines suggested by Martinez 1996) as well as accumulation of biomass and nitrogen. They found that different species were more important for different functions and indicated that biodiversity was therefore of key importance as the loss of any species could reduce efficiency of at least one ecosystem function.

EVIDENCE FROM PAST RESEARCH – A NEW SYNTHESIS

In the rush of research to test these new ideas in the current context, we must not forget the volume of research done on intertidal systems in the past. There have been large numbers of experimental removals of single species, geared largely to testing hypotheses about their roles in affecting community structure. Allison *et al.* (1996) reviewed a section of the literature that related to the effects of secondary consumers on their prey as a basis for predicting effects of loss of biodiversity in coastal habitats. They proposed a predictive framework to help categorise the effects of loss of biodiversity, which I will outline here.

Their categories depended on the type of system from which species are lost. They differentiated among systems involving strong keystone predatory effects, strong diffuse predatory effects and weak effects (see also Menge *et al.* 1994). Strong keystone effects occur when a single predatory species exerts an overwhelming influence on prey species.

The classic example is the exclusion of mussels from low tidal levels on rocky shores in northwest USA by *Pisaster ochraceus* (Paine 1972). Strong diffuse effects occur where several predatory species are each capable of influencing prey species, such as on the tropical rocky shores of Panama (Menge *et al.* 1986). In systems where predators exert only weak effects, there may be other processes that override their influence. For example, on a sheltered shore that is repeatedly inundated by sand, predators are only a minor source of prey mortality (Menge *et al.* 1994).

Where predators exert only weak effects, the loss of one or more species has little effect, because there was little combined effect of all the species and/or compensation is possible (Figure 2). Where diffuse effects occur, the loss of one or more predators can usually (but not always) be compensated for by the other strongly interacting predators present, either via a functional response or by an increase in abundance (Figure 2). Such

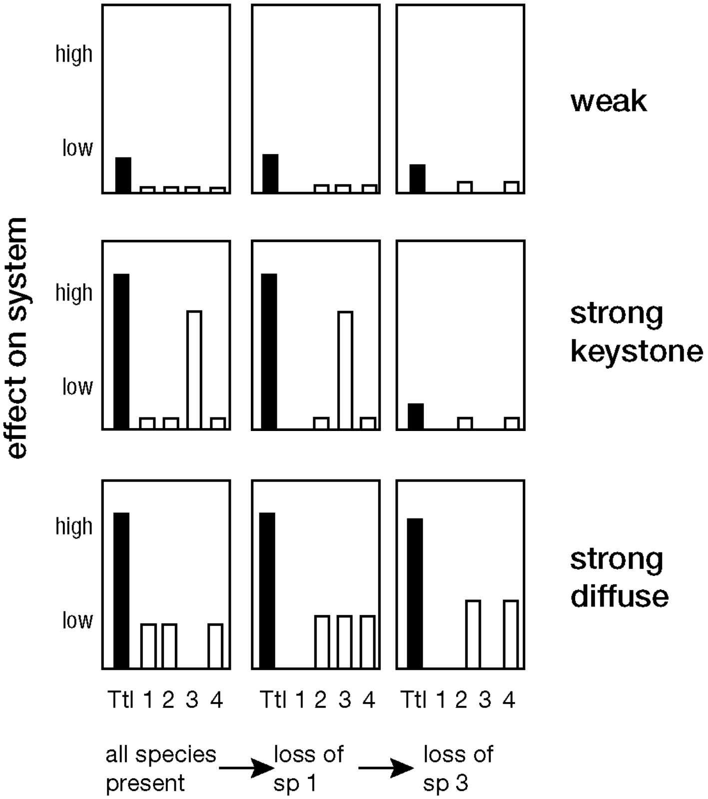

Figure 2. Overall influence of a functional group and the effects of species loss. Solid bars represent the total effect of the group on the system; open bars represent the relative effects of individual species within the group. Panels on the left represent the system with all species within the group present, the middle panels represent the system with one species removed, the panels on the right represent the system with two species (species 1 and 3) removed. The three types of system are represented – weak effects, strong keystone effects (species 3 is the keystone) and strong diffuse effects. Figure from Allison *et al.*(1996), used with permission from SCOPE 55, *Functional Roles of Biodiversity: A Global Perspective*, edited by Mooney, H.A., J. Hall Cushman, Ernesto Medina, Osvaldo e. Sala, and Ernst-Detlef Schulze, 1996, John Wiley & Sons Ltd, Chichester, UK.

systems contain a degree of redundancy, or biological insurance (Walker 1992; Allison *et al.* 1996; Yachi and Loreau 1999). Idiosyncratic effects are most likely to occur in systems containing a keystone species (Figure 2) – or perhaps only two to three influential predators with markedly different functional roles and little scope for compensation.

General predictions in ecology inevitably carry a high degree of uncertainty. For example, in this context, compensation for loss of a species may not occur if compensating populations are strongly recruit-limited (see Gaines and Roughgarden 1985) or if the species lost was very specialised. These basic categories (i.e. systems involving either strong keystone, strong diffuse or weak influences of consumers) do, however, provide a helpful starting point for predicting effects of loss of species from ecosystems. It also remains, of course, to determine which category any given system fits into. For a number of well studied localities, this information is already available (e.g. see Allison *et al.* 1996). However, for many others a targeted body of experimental research is required. Given the potentially significant consequences of losing as yet unidentified strong interactors, Allison *et al.*(1996) recommend a conservative approach to management where there is uncertainty.

DIRECTIONS FOR FUTURE RESEARCH

Vitousek and Hooper (1993) have suggested that systems with relatively few species (<10) may offer the best opportunity to explore relationships between biodiversity and ecosystem function, because in those systems it should be possible to characterise the roles of each species in some detail. This was part of the rationale underlying the research of Zedler *et al.* (2001) , which is among the most comprehensive studies to date. It seems likely, however, that systems of differing diversity may exhibit different patterns of response to species loss. For example, Schläpfer and Schmid (1999) suggested that low diversity systems might be more likely to exhibit idiosyncratic effects and high diversity systems were more likely to contain redundant species. It should be possible to find intertidal systems with a range of degrees of diversity to test these ideas. Some specific hypotheses that require further work, and for which intertidal systems could be particularly amenable, include:

1. Functional diversity is more important to ecosystem function than species diversity *per se*.
2. Loss of diversity at one trophic level affects the functioning of other trophic levels.
3. Loss of diversity will decrease stability.
4. There is a negative relationship between invasibility of ecosystems and species diversity (and/or functional diversity).

Tests of hypotheses 1 and 2 require experimental investigation, ideally using both mesocosms and field research. Such tests could benefit from the potentially high level of functional diversity available in marine systems. For example, manipulations of herbivores could include amphipods, gastropods, echinoderms and fish, all of which graze in different ways on a diverse and productive assemblages of marine plants.

Examinations of the role of functional diversity are hampered, however, by the lack of a universal system for classifying functional groups (Sullivan and Zedler 1999; Díaz and Cabido 2001). There is essentially a two-tiered hierarchy of functionality. On the first tier, species can be grossly divided on the basis of trophic levels (primary producer, primary consumer, decomposer, etc.) or other broad roles, such as autogenic or allogenic ecosystem engineers (Jones *et al.* 1994). Within each broad category, species can be further subdivided into functional groups on the basis of morphological, dietary or other characteristics. For example, intertidal primary producers can be divided into microalgae, crustose algae, foliose algae, articulated calcareous algae, etc. (e.g. see Steneck and Dethier

1994) and primary consumers include microalgal grazers, macroalgal grazers, epiphytic grazers, etc. Such classifications are extremely difficult to develop, however. This is partly because species group differently depending on the criteria used for classification (e.g. a classification based on trophic roles will differ from a classification based on engineering activities). Species perform many different functions and may often vary their function under different circumstances (e.g. the abalone *Haliotis roei* sometimes feeds on drift algae and sometimes grazes (Scheibling 1994)).

In general, investigations of different ecosystem functions are served best by different classifications of functionality. Sullivan and Zedler (1999) found that a classification of saltmarsh plants based on morphological and metabolic criteria did not predict a classification subsequently derived from experimental evidence of a range of ecosystem functions of the species. Although the loss of any given species may not have an effect on any one ecosystem function (e.g. productivity), this does not necessarily imply that it is not critical for other functions (e.g. nutrient retention). Ideally, therefore, it would be of value to measure more than one function at a time, an approach currently lacking in much of the relevant research (but see Naeem *et al.* 1994, Zedler *et al.* 2001).

The challenges involved in testing hypotheses 1 and 2 also include making more explicit tests of the link between changes in community structure (e.g. cover of macroalgae) and ecosystem functions (e.g. productivity) – see Allison *et al.* (1996). This will require the development of elegant and effective methods for measuring ecosystem functions (e.g. productivity) in the field.

Incorporating treatments to simulate different environmental contexts (e.g. changes in temperature or disturbance regime) would make it possible to evaluate the biological insurance hypothesis, which proposes that different species may become important under different circumstances (Yachi and Loreau 1999). An alternative, although less equivocal approach to testing this hypothesis would be to run experiments for long enough periods to enable natural shifts in environmental context, or to find several geographically remote sites with similar assemblages under different natural regimes. For this, and for tests of hypotheses 3 and 4, concerted long-term research at large networks of sites is necessary. The European Union is supportive of such networks and BIOMARE (*www.biomareweb.org*) is among several currently being established.

CONCLUDING REMARKS

Perhaps unsurprisingly then, given the high degree of functional diversity in the marine fauna and flora, a considerable proportion of the research to date has provided evidence in support of the idiosyncratic hypothesis. Importantly, the use of spatially replicated factorial experiments has also indicated that effects of losing species can depend on the identities of combinations of species lost ('idiosyncratic interactions') and are context-dependent – varying from place to place, perhaps due to the composition of the communities from which they are lost. This supports the theoretical findings of Cardinale *et al.* (2000). Loreau (2000) and Díaz and Cabido (2001) have also suggested that variation in environmental conditions among sites is likely to mask effects of diversity, for example where environmental conditions play a stronger role in determining ecosystem functions than species diversity (e.g. rates of productivity may primarily be affected by nutrient availability rather than diversity). In fact, environmental conditions strongly influence both diversity and function, such that relationships between ecosystem function and diversity may be correlative rather than causal (e.g. see Rosenzweig and Abramsky 1993; Huston 1997).

One would also expect to see temporal variations in environmental conditions and community composition, which might also influence the effects of loss of species on ecosystem function (see also Cardinale *et al.* 2000; Allison *et al.* 1996). The influence of such temporal variation has rarely been tested in this context, particularly over long periods of time. This is an important omission and such data will be needed to determine the value of the biological insurance provided by so-called redundant species (Hector *et al.* 2001).

It is also important to recognise that, with few exceptions (e.g. Zedler *et al.* 2001), each experiment tends to focus on one ecosystem function. No amount of experimental research would be able to provide a basis to predict changes in all ecosystem functions as a consequence of loss of particular species. This again provides an important rationale for conserving species regardless of the degree of redundancy found in any given system in relation to any given function (Hector *et al.* 2001). In pursuing this debate, it is worth noting that conservation of species can also be justified by their intrinsic and aesthetic worth; their functional roles simply build on this argument (Ghilarov 2000; Hector *et al.* 2001). Nevertheless, tests of hypotheses about the role of biodiversity in ecosystem function provide an excellent opportunity to pursue basic research about fundamental ecological questions, while providing results which have valuable implications for conservation and management.

ACKNOWLEDGEMENTS

I would like to thank the Academy, particularly Jim Wilson, for the invitation to prepare this review. Thanks also to the Natural Environment Research Council and Enterprise Ireland for funding my research in this field, to colleagues for discussions and to Bret Danilowicz and Tom Bolger for commenting on an earlier draft.

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In: James G. Wilson (ed.) *The Intertidal Ecosystem: The Value of Ireland's Shores*, 134–146. Dublin: Royal Irish Academy.

PROJECTIONS FROM POPULATION AND COMMUNITY MODELS OF ROCKY SHORES

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ABSTRACT

Environmental concerns motivated by issues such as climate change, harvesting or the loss of biodiversity often focus on the rates of change or ecological stability. These issues of population and community dynamics can be analysed in a number of ways. A modelling approach complements time series and experimental studies and can be applied to a wider range of contexts. Complex models can be difficult to parameterise, hence a simpler approach often provides more useful insights about population and community dynamics. One such approach is to use transition (Markov) matrix models specified from repeated observations. Projections from transition matrix models are used to describe rates of change, composition and stability. Examples from rocky shores demonstrate the importance of recruitment variability in population dynamics and may predict community responses to loss of biodiversity. A particular advantage of the transition matrix approach is that the models are relatively easy to formulate from field surveys.

INTRODUCTION

Populations and communities are generally in a state of flux. Change may be driven by the internal dynamics of a system or may reflect responses to external factors. The patterns and causes of change become particularly relevant in areas such as conservation and sustainable resource exploitation. This paper introduces a set of modelling tools that may be particularly useful in analysing the population and community dynamics of rocky intertidal systems.

There are a number of approaches that can be used to understand and predict environmental change. In the rare cases where long-term data sets exist, time series analysis can be used to characterise the system. This characterisation can include estimates of long-term trends (Southward 1991; Allen *et al.* 1998), return times of extreme events such as large waves (Gaines and Denny 1993) and the presence of cyclic fluctuations (Jassby and Powell 1990; Kendall *et al.* 1998). Commonly applied techniques include spectral analysis and autocorrelation (Chatfield 1996). More recent advances include phase plots and other techniques for identifying patterns in population time series (Sugihara and May 1990). Such techniques relate the current state of a system to a historical context and indicate the patterns that are likely to reoccur. As time series techniques characterise pattern, they cannot unambiguously identify the processes associated with the pattern (Jassby and Powell 1990). It is difficult to predict how a system will respond to novel situations such as the loss or introduction of a species. More formally, time series analysis cannot generally be used to discriminate between alternative hypotheses concerning the mechanisms of ecosystem function. In contrast, experimental manipulations are an unambiguous method of characterising ecosystem process (Underwood 1997). Unfortunately, due to restrictions on the timescale of grants and PhDs, experiments may only run for a relatively short period. Hence experimental studies have tended to provide a snapshot of slow-moving or abundant species and may underestimate important population and community processes occurring at longer timescales (Underwood 2000).

In an ideal situation, time series and experimental approaches would be combined into a single investigation of population and community dynamics. However, the availability of resources and the pressing nature of many environmental problems often mean that combined investigations are rare. In such circumstances a modelling approach can bridge the gap between time series and experimental studies and can be applied to a wider range of contexts. Numerical models can aid in hypothesis construction, focus on what is actually known or testable (Speirs *et al.* 2000) and allow a fuller description of possible system behaviour. Of course mathematical models have their own limitations. Some of these problems, such as hidden or unwarranted assumptions, are also found in verbal models of ecological communities. It is, however, difficult for mathematical models to deal with the complexity of natural systems while remaining mathematically tractable. Hence models often simplify ecological interactions. This is not necessarily a problem, as tests of predictions examine whether a limited set of processes in the model is sufficient to describe the natural world (Kareiva 1990). However, models may be reduced to generic descriptions of phenomena such that they can make only the broadest predictions for particular systems (Tilman and Kareiva 1997). When constructing tractable mathematical models, a further issue arises over choice of parameter values. Parameter values (e.g., population intrinsic growth rate) affect model behaviour, but they are often estimated or imported from separate studies. The errors associated with different parameters may be unknown, limiting the use of complex or realistic models (Johnson 1998).

A potential solution to some of the problems of model construction is to use a framework where parameters are estimated in a single field study. By basing a model directly on observations, the parameters are estimated from the same source and predictions can be made for a specific system. Markov transition matrix models are a class of models suited to this observation-based approach. The techniques can be applied to communities or populations. Wootton (2001) emphasised that Markov models are probably the easiest community models to parameterise from field data. A comprehensive review of transition matrix models for populations is given by Caswell (2001). This paper will describe the application of a Markov transition matrix approach to rocky intertidal communities. For more detailed examples of intertidal population modelling see Åberg (1992a,b), Engel *et al.* (2001) and Hyder *et al.* (2001). Developments and limitations of the models are discussed under the heading of 'projection or prediction in the intertidal?' and in the concluding remarks.

CONSTRUCTION AND ANALYSIS OF MARKOV MODELS

Markov models are based on estimating the probability of transition between different states. For a community these states are different species, aggregated groups of species or functional groups. A population model describes transitions between age or size classes. Transition probabilities are derived from repeated observations of marked individuals or areas. Hence p_{jk}, the probability of transition from state k to state j, is defined by the number of transitions from k to j over the defined time period divided by the number of cases of state k at the start of the time period. A set of field observations are summarised in a transition matrix (**A**) of the form:

$$\mathbf{A} = \begin{vmatrix} p_{11} & p_{12} & p_{13} & \cdots & p_{1n} \\ p_{21} & p_{22} & p_{23} & \cdots & p_{2n} \\ p_{31} & p_{32} & p_{33} & \cdots & p_{3n} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{n1} & p_{n2} & p_{n3} & \cdots & p_{nn} \end{vmatrix} \tag{1}$$

Transition probabilities can be zero. For example there can be no transitions to younger age classes, so an age-structured model contains zeros in the top right corner. A restriction on community models is that columns in the matrix sum to one, as sites are usually not destroyed or created. The matrix is a summary of transitions occurring between two dates. The gap between the two dates (the time step) gives the model an explicit timescale. A null hypothesis can be proposed: all the transitions are random. If this is the case a Markov model is not applicable. The null hypothesis is tested using a likelihood ratio test (Usher 1979) where the quantity –21nλ is calculated as:

$$-2 \ln \lambda = 2 \sum_{j=1}^{m} \sum_{k=1}^{m} \mathrm{n}_{jk} \ln \left(\frac{p_{jk}}{p_j} \right) \tag{2}$$

where

$$p_j = \sum_{k=1}^{m} \frac{n_{jk}}{\sum_{j=1}^{m} \sum_{k=1}^{m} \mathrm{n}_{jk}} \tag{3}$$

and n_{jk} is the number of transitions from state k to j in the original data matrix, p_j is the sum of transition probabilities to state j and m is the order of the transition matrix (number of rows). The test statistic ($-2\ln\lambda$) is compared to χ^2 with $(m-1)^2$ degrees of freedom. Rejection of the null hypothesis suggests that a Markov approach can be followed.

Accepting a Markov model implies that the state of a system can be predicted from the state of the system one time step previously. In mathematical notation:

$$\mathbf{x}_{(t+1)} = \mathbf{A}\mathbf{x}_{(t)} \tag{4}$$

where $\mathbf{x}_{(t)}$ is a vector describing the frequencies of separate states in the population or community at time t (e.g., four size classes of barnacle, Hyder *et al.* 2001). It is therefore possible to simulate the dynamics of a system through several time steps by repeatedly multiplying a column vector. Simulations of this type are straightforward to lay out using a spreadsheet programme on a personal computer. Most transition matrices will reach a stable steady state, defined by the right hand eigenvector of the transition matrix (Tanner *et al.* 1994). Other mathematical properties can be used to summarise elements of the system described by a transition matrix. For example, the rate of convergence to a steady state is given by the 'damping ratio' (Tanner *et al.* 1994; Caswell 2001):

$$\rho = \lambda_1 / | \lambda_2 | \tag{5}$$

where ρ is the damping ratio and λ_n is an eigenvalue of the transition matrix. λ_1 is the largest eigenvalue. Convergence to a steady state will generally be smooth unless the larger eigenvalues are complex numbers, in which case damped oscillations are possible. The damping ratio can be referenced to the time step in the Markov model using a convergence ratio, t_x (Caswell 2001):

$$t_x = \ln(x)/\ln(\rho) \tag{6}$$

Typically x equals ten, giving the time taken for influence of the first eigenvalue on matrix dynamics to be ten times larger than the contributions from the second eigenvalue (Caswell 2001).

ROCKY SHORE COMMUNITY TRANSITION MATRICES

Field data are not generally collected in a form that can be used for transition matrices. Often the locations of quadrats or measurements are not recorded as investigators are generally not interested in going back to exactly the same location. The justification for this is that measurements need to be independent in order to meet the assumptions of many statistical tests (e.g. ANOVA). In contrast, a matrix model summarises the dependence between measurements at the same location on different occasions. Repeated measurements are, however, relatively easy to incorporate into most field studies. Rocky shores are particularly tractable as many of the organisms are sessile and it is easy to mark locations with paint or screws put in holes drilled into the rock.

Repeated measurements at the same location are available for three of the maps used in a study on the spatial structure of intertidal communities in the Isle of Man (Johnson *et al.* 1997). This study involved surveys of 5 × 5 m quadrats, with the corners of each quadrat marked using screws in the rock. A 0.25 m^2 quadrat, divided into 0.01 m^2 squares ('cells'), was moved methodically across the larger quadrat to produce a map of the community. The community in each cell was recorded as dominated by mature fucoid algae (over 0.1 m long), containing juvenile *Fucus* algae only, dominated by barnacles, dominated by coralline red algae or dominated by bare rock. Cells were also classified as empty or containing limpets, the most important grazers in the community (Hawkins *et al.* 1992). The mapping was repeated after one year for three of the 5 × 5 m quadrat locations (Port St. Mary a, Port St. Mary b and Gansey). This allowed matrix models to be derived from a total of 2500 observed transitions for each location. An example transition matrix is shown in Table 1.

Observed transitions relate to some of the community dynamics proposed for moderately exposed shores by Hartnoll and Hawkins (1985). For example, juvenile *Fucus* are more likely to appear in areas of coralline algae, bare rock or barnacles when limpets are locally absent. The derived matrices represented non-random transitions at all three locations (likelihood ratio test, $p < 0.001$ in each case). The equilibrium communities at each location differed. Mature algae dominated at Port St. Mary a (79% of the predicted community as m+ or m−). The most common community state at Gansey was also mature algae, but community composition was more even (39% of the predicted community was m+ or m−). The pattern was quite different at Port St. Mary b. The most common states at equilibrium for this location were bare rock, juvenile algae and barnacles, all in the absence of limpets (Figure 1). This may reflect that Port St. Mary b was higher on the

Table 1. Example transition matrix for an intertidal site surveyed at Gansey in the Isle of Man. Cell states are classified as barnacle dominated (b), juvenile *Fucus* present with no larger algae (j), mature *Fucus* dominant (m), coralline red algae dominant (cr) and bare rock (r). The presence (or absence) of limpets is indicated by + or – modifiers to the states based on the presence of sessile organisms. Column headings represent the original state with rows as the state after one time step

	b+	b–	j+	j–	m+	m–	cr+	cr–	r+	r–
b+	0.038	0.015	0.000	0.014	0.072	0.034	0.000	0.037	0.086	0.022
b–	0.423	0.351	0.600	0.359	0.299	0.332	0.000	0.279	0.241	0.324
j+	0.000	0.010	0.000	0.007	0.021	0.006	0.000	0.000	0.000	0.002
j–	0.269	0.309	0.400	0.310	0.134	0.100	0.000	0.167	0.121	0.233
m+	0.000	0.002	0.000	0.007	0.031	0.037	0.000	0.005	0.034	0.002
m–	0.038	0.015	0.000	0.049	0.041	0.057	0.000	0.028	0.034	0.016
cr+	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000
cr–	0.000	0.010	0.000	0.014	0.000	0.011	0.000	0.219	0.069	0.014
r+	0.038	0.015	0.000	0.000	0.021	0.037	0.500	0.019	0.052	0.017
r–	0.192	0.274	0.000	0.239	0.381	0.384	0.500	0.237	0.362	0.370

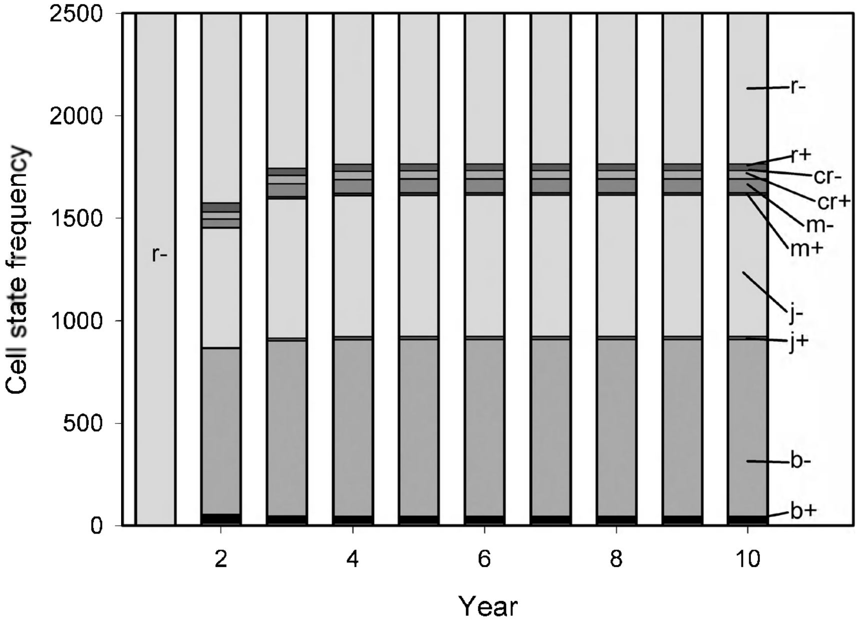

Figure 1. Projected cell state frequencies for a Markov transition matrix model of Port St. Mary location b. States are classified as barnacle occupied (b), juvenile *Fucus* (j), mature *Fucus* (m) coralline red algae (cr) and bare rock (r). The presence or absence of limpets in the cells is indicated by ± modifiers. Community composition is simulated from an initial condition of 2500 cells containing bare rock without limpets.

shore than the other two locations. Simulated community dynamics also indicate how a shore might recover from a disturbance. For example Port St. Mary b is predicted to recover to a steady state within a few years of a perturbation that reduces the shore to bare rock (e.g. an oil spill and clean up, Southward and Southward 1978).

Recovery rates from a perturbation vary between locations, with t_{10} values of 4.17, 1.51 and 1.23 years for Port St. Mary a, Port St. Mary b and Gansey respectively. These convergence times are illustrated by the relative speeds of approach to equilibrium in frequencies of mature algae and limpets at the different locations (Figure 2). It is not yet clear why Port St. Mary a appears to be the least resilient location. One possibility under investigation is that community stability can be related to the complexity of the rock surface.

PROJECTION OR PREDICTION IN THE INTERTIDAL?

Although the Markov matrix approach makes a minimum of assumptions in deriving a model from observations, there are three important conditions (Caswell 2001):

1) The classification of individuals into ages and sizes or of communities into states is appropriate.
2) Dynamics within and age/size/state classification are not important
3) The system is linear and transition rate processes do not vary over time.

The first condition is not overly restrictive, but it does emphasise that the most appropriate stage classifications will vary between models. Age may not always be a good predictor of the growth and mortality of individuals (Caswell 2001). For example, predation of sessile organisms may be size-dependent (Hughes and Burrows 1993). The classification of communities into states is a novel area of research. The division of states in the quadrats on the Isle of Man was based on the most conspicuous species. More sophisticated algorithms could include multivariate definitions of states. The second condition affects the temporal and spatial scales of the transition matrix. Dynamics should be homogeneous in the area where the transitions are defined. Hence a transition matrix that combines data from the high and low intertidal may be meaningless. A more robust approach is to construct matrices for different areas and compare predictions and transition probabilities (Usher 1979; Tanner *et al.* 1994) before combining data. Dynamics should also be homogeneous for all individuals or patches within a particular state. This issue is reflected in the development of algorithms to choose category widths in population models (Vandermeer 1978). Åberg (1990) applied the category selection method to size class selection in a model for *Ascophyllum nodosum* (L.) However, these category selection methods may not always work (Hyder *et al.* 2001). An analysis by Tanner *et al.* (1996) found that community states in their model of coral reefs should include subdivision of states by age, although the dynamics of more complex second order models were not greatly different from their original age-averaged models.

The third condition seems to be the most restrictive. One would surely expect rates to change as one state or another becomes more common. For example, dominance by a state could lead to increases the local reproductive output or some density-dependent response such as higher levels of predation. 'Supply side' ecology emphasises variation

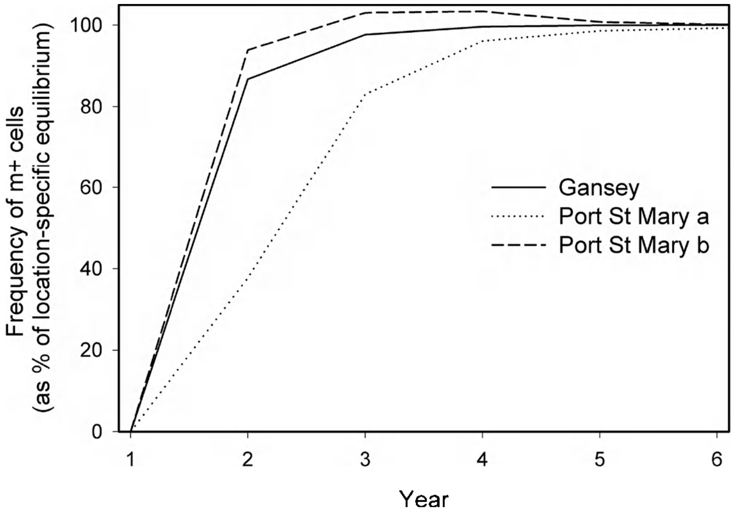

Figure 2. Comparison of rate of return to equilibrium between Markov models for Port St. Mary a, Port St. Mary b and Gansey. Simulations start with all sites as cr– (comparisons could not be made on the basis of bare rock as this state was not recorded at Port St. Mary a).

in recruitment to marine populations and communities, so variation in transition rates between years can be expected. Caswell (2001) and other demographers have addressed this problem by emphasising the difference between projection and prediction. Variable rates would be needed to make a prediction of what will happen to a particular population or community. In contrast a projection emphasises 'what would happen if the present state of the community were to be maintained indefinitely?' Caswell (2001) uses the analogy that a speedometer reading of 60 miles per hour is a poor prediction of where the car will be in one hour. Additional information on traffic and road layout is the minimum that would be needed to predict where the car will be. The information on speed is, however, a projection giving relevant information on the current state of the car and how it might respond to external events (such as an emergency stop). Hence projection is used to emphasise that useful information is still possible in the absence of exact predictions.

Despite the conditions associated with matrix modelling, comparisons with field data are often favourable. Steady state projections for the three locations in the Isle of Man explained between 45% and 95% (r^2) of the variation in observed frequencies (e.g. Figure 3).

Projections were always closer to observations than randomly assembled communities (G tests, *p* fit better than random < 0.05). However, significant G tests between observed

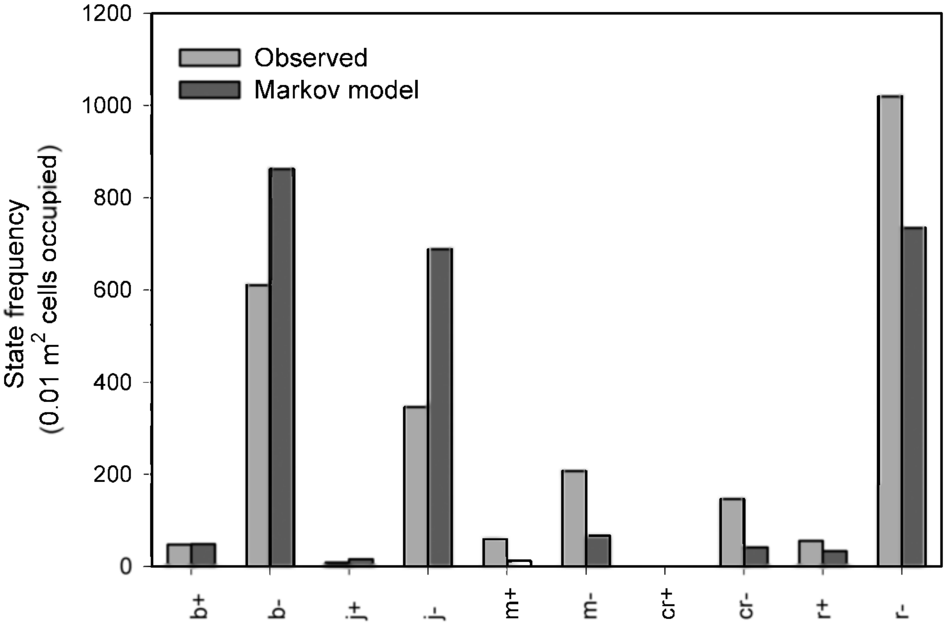

Figure 3. Comparison of observed and projected Markov model state frequencies for Port St. Mary b. States are classified by the same codes as in Figure 1. The projected cell state frequencies are equilibrium values from a transition matrix model. Model predictions are significantly better than random (G tests, p < 0.05) and explain a majority of the variance in observed frequencies (r^2 = 75%).

and projected frequencies suggested that the models could be improved (G tests, *p* projected and observed frequencies equal < 0.05). There is a danger of circularity in that these comparisons are between observed data and models derived from the same data. Wootton (2001), however, reported good fits to data collected independently from that used to derive transition matrices.

CONCLUSIONS AND FUTURE DIRECTIONS

Applications of matrix modelling to intertidal populations include studies of barnacles and macroalgae. Model analyses suggested that *Chthamalus montagui* populations in the mid to upper shore were intrinsically stable with a high adult survivorship (Hyder *et al.* 2001). These results were consistent across a number of European shores, with some differences in timing of events between the Mediterranean and Atlantic. The stability of populations means that population fluctuations can be interpreted in terms of environmental influences on recruitment or mortality (Hyder *et al.* 2001). Models of *Ascophyllum nodosum* also emphasise high adult survivorship (Åberg 1992a). The models applied to rocky shores have included competition for space (Hyder *et al.* 2001) and stochastic variation in environmental conditions (Åberg 1992b). More generally, the methodology of population models has been expanded to address density dependence in transition rates and stochastic variability in transitions (Nakaoka 1997; Tuljapurkar 1997; Caswell 2001). Such modifications may improve models to the extent that they are considered robust enough to make predictions about population persistence (Fieberg and Ellner 2001).

Markov models of rocky shore communities are less common than population models. Wootton (2001) has modelled mussel assemblages on the Pacific coast of North America. Comparison of model output and field data suggested that the transition matrix approach could have predictive power: Wootton's (2001) model described the changes in community composition between horizontal and vertical surfaces associated with changes in mussel recruitment and predation by birds. The quadrat maps from the Isle of Man could be used to make similar predictions about phenomena such as loss of species from the community. Limpets have a clumped spatial distribution (Johnson *et al.* 1997), so it is possible to derive a 'no limpets' matrix of transitions from areas where limpets were locally absent. Transitions were recorded in cells where there were no limpets in any of the adjacent cells (square neighbourhood consisting of 9 cells). Applying the 'no limpets' condition left 943 transitions to derive a matrix model from (for Port St. Mary a: results from other locations were similar). In this instance, the projected dynamics can be referred to as a prediction for the shore community in the absence of limpets. The predicted dynamics for a limpet-free shore, starting from all sites occupied by barnacles, are shown in Figure 4. Predictions of community dynamics qualitatively match those seen in experiments where limpets are excluded from areas of the shore (Hawkins *et al.* 1992). Juvenile algal abundance peaks and then falls away as the community becomes dominated by mature fucoid algae. Barnacle abundance declines under the canopy of fucoids (Lewis 1964). The predicted abundance of coralline algae is three times higher than the level observed

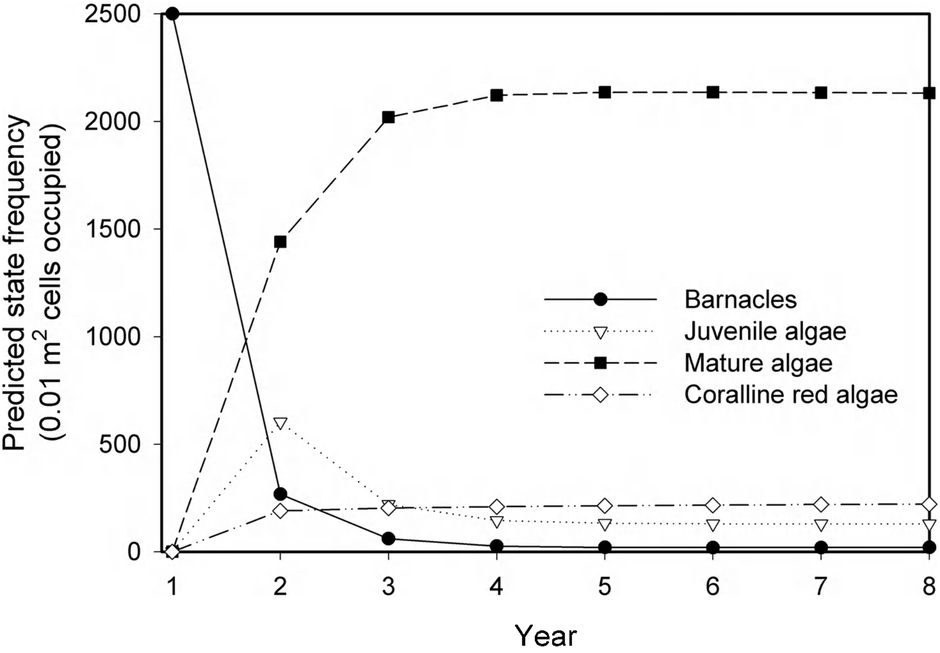

Figure 4. Predicted dynamics in the absence of limpets for Port St. Mary a. The transition matrix model used was derived from areas of the shore where limpets were absent. All cells were initially specified as barnacle occupied.

in the presence of limpets. This may reflect the processes that lead to facilitation of 'red algal turfs' by fucoid canopies (Jenkins *et al.* 1999). Although the simulated community patterns following limpet removal qualitatively resemble those seen in grazer exclusion experiments, the predictions could be confounded by other factors that may have been different in areas where limpet densities were low (for example these may also have been slightly drier or wetter areas). Experimental tests of transition matrix predictions are needed to define the limits of where predictions can be made.

As mentioned previously, rocky shores may be an ideal system in which to apply Markov transition matrix models. Many individuals are sessile and locations can be fixed. The utility of Markov models may be enhanced where populations and communities are 'open'. When new recruits to the community arrive from external sources, parameters such as transition or recruitment rates are unaffected by local densities (e.g. Hyder *et al.* 2001). Hence the assumption that rates do not change with state frequencies may not be too inaccurate. The projected community dynamics have real timescales and provide reasonable approximations to patterns seen in the field. Convergence ratios could potentially be used to classify the sensitivities of different communities to disturbances. Further work is needed on the choice of states, appropriate spatial scales and cell sizes in community models. Tests to identify 'keystone' species have been developed (Tanner *et al.* 1994; Wootton 2001), but these tests need refining due to problems in dealing with covariance of different transition rates. Applied developments of the models could be to study sustainable harvesting of intertidal species (c.f. Frisk *et al.* 2002). A key advantage of Markov models is that they can be parameterised from repeated field surveys. Observed transitions are easy to define in comparison to more traditional model parameters such as carrying capacities. As Markov models can complement survey and experimental work for little extra effort, future studies are likely to benefit from integrating such observation-based models into the research framework.

ACKNOWLEDGEMENTS

I thank the Royal Irish Academy for the invitation to participate in the intertidal seminar. Fieldwork on the Isle of Man was supported by a grant from the Natural Environment Research Council. Prof. S.J. Hawkins and Dr M.T. Burrows provided useful discussion on the early stages of this work.

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CHLOROPHYLL *A* PRODUCTION MODELLING OF INSHORE WATERS

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ABSTRACT

Increased anthropogenic activity in many coastal regions is placing significant pressures on inshore waters. Many of the estuaries and bays accepting the discharges from large conurbations are heavily polluted preventing their use for recreational activities. The relatively poor water quality in parts of Dublin Bay and Cork Harbour are examples of adversely impacted waters. Discharges of nutrients, in particular, through outfalls and rivers can lead to the occurrence of algal blooms with the associated environmental problems. Computer-based models have been developed to investigate the relationships between nutrient inputs and chlorophyll *a* production in inshore waters. These models have been applied to Cork Harbour and used to perform scenario modelling. Two scenarios are simulated using the models: the first considers the effects of discharging significant nutrient loads into Cork Harbour, and the second scenario considers the water quality when there are no discharges from domestic and industrial outfalls. Good agreement was obtained between model predicted chlorophyll *a* and measured data. There is significant reduction in chlorophyll *a* production during the latter simulation, primarily due to the reduced phosphorus loads. The application of the model to Cork Harbour illustrates how spatially and temporally refined models can be used to assist total water quality management of inshore waters.

INTRODUCTION

Traditionally, the collection and analysis of physical, chemical and biological field data were the main techniques used to quantify the movement and quality of coastal waters. Since about the mid-1980's computer models have been applied with increasing frequency to coastal water quality issues (Townend 1994). Currently, it is common practice to combine field measurements and modelling studies to achieve the best results in estuarine and coastal water quality management. One of the main stimuli leading to research into the development of water quality models has been the significant amount of legislation that was enacted pertaining to water quality. National legislation and EU directives, such as the European Parliament Water Framework Directive (WFD) 2000/60/EC, prescribe limits on various water quality parameters. Integrated modelling and field measurement studies have proven to be amongst the best approaches to ensure compliance with these legal instruments. The central role of water modelling in implementing the WFD has been widely accepted throughout the European Union. The European network EurAqua recently published a review of the modelling as a tool in implementing the Directive (Euraqua 2001). Fourteen EU countries present papers in this review underpinning modelling requirements in water management.

The research community at large have demonstrated their commitment to long-term modelling activities through various international collaborative activities. Large-scale networks such the EU supported European Land-Ocean Interaction Studies (ELOISE) and its global counterpart Land Ocean Interface in the Coastal Zone (LOIZC) demonstrate the significant role that modelling now plays in helping scientist and engineers understand coastal processes and manage this sensitive environment (Mathy 2001).

The trophic status of estuaries is currently a major worldwide environmental issue and is the subject of considerable research. Many Irish estuaries are considered to be eutrophic due to diverse anthropogenic activities which interact with the coastal zone (EPA 2001). Coupled physical/chemical/biological models are required to understand complex marine processes and are used to investigate the effects of anthropogenic activities through scenario modelling. Such models are also useful tools in establishing trophic indices for water bodies.

In the following sections, details are provided of a water quality model and its application to Cork Harbour. In applying the model to Cork Harbour, the author investigated the water quality impacts of current discharge regimes into the Harbour and the likely improvements in water quality if all domestic and industrial discharges were switched off. By comparing the results from these two scenarios it is possible to attempt to ascertain some of the impacts of urbanisation on the water quality of Cork Harbour. This study also illustrates how water quality scenario modelling may be utilised to guide effluent treatment in order to achieve acceptable quality of the receiving waters.

WATER QUALITY MODELLING

The model, DIVAST, used in this research is a two-dimensional model which solves for various parameters on a horizontal plane, assuming homogeneity in the vertical plane. This assumption is generally found to hold well in shallow coastal waters, (Falconer 1986). The model contains three main sub-modules: hydrodynamic, solute transport and water quality. Each of these sub-modules is briefly outlined below.

Hydrodynamic module

The governing differential equations used in the numerical model to determine the water elevation and depth-averaged velocity fields in a horizontal plane are based on integrating the three-dimensional Navier-Stokes equations over the water column depth. This results in a two-dimensional model which resolves variables in two mutually perpendicular horizontal directions (x and y). It is assumed that the vertical accelerations are negligible compared with gravity, i.e. the existence of a quasi-hydrostatic pressure distribution, and that the Reynolds stresses in the vertical plane can be represented by a Boussinesq approximation. The depth-integrated continuity and x-direction momentum equations can be shown (Falconer 1977) to be given by equations (1) and (2) respectively:

$$\frac{\partial \zeta}{\partial t} + \frac{\partial q_x}{\partial x} + \frac{\partial q_y}{\partial y} = 0 \qquad (1)$$

$$\frac{\partial q_x}{\partial t} + \beta \left[\frac{\partial U q_x}{\partial x} + \frac{\partial V q_y}{\partial y} \right] = \qquad (2)$$

$$f q_y - gH \frac{\partial \zeta}{\partial x} + \frac{\tau_{xw}}{\rho} + \frac{\tau_{xb}}{\rho} + 2\frac{\partial q_x}{\partial t} \left[\epsilon H \frac{\partial U q_x}{\partial x} \right] + \frac{\partial}{\partial y} \left[\epsilon H \left[\frac{\partial U}{\partial y} + \frac{\partial V}{\partial x} \right] \right]$$

where

ζ = water surface elevation above mean water level

t = time

q_x, q_y = depth integrated velocity flux components in the x,y directions

β = momentum correction factor

U, V = depth integrated velocity components in the x,y directions

f = Coriolis parameter

g = gravitational acceleration

H = total depth of water column

τ_{xw} = surface wind shear stress component in the x direction

τ_{xb} = bed shear stress component in the x direction

ρ = fluid density

A depth-integrated momentum equation analogous to equation (2) is also developed for the y-direction.

Solute transport module

Solute transport refers to the mechanics of the movement of solutes in water due to the above hydrodynamics and turbulence within the water. These transport effects are incorporated into the model through the well-established advection-diffusion equation (Falconer and Liu 1988). This equation in two-dimensions is:

$$\frac{\partial \phi H}{\partial t} + \left[\frac{\partial \phi Uh}{\partial x} + \frac{\partial \phi Vh}{\partial y}\right] - \frac{\partial}{\partial x}\left[HDxx\frac{\partial \phi}{\partial x} + HDxy\frac{\partial \phi}{\partial y}\right]$$
$$- \frac{\partial}{\partial y}\left[HDyx\frac{\partial \phi}{\partial y} + HDyy\frac{\partial \phi}{\partial y}\right] - H\left[S_o + S_d + S_k\right] = 0 \qquad (3)$$

where

ϕ = solute concentration

Dxx, Dxy, Dyx, Dyy = depth averaged longitudinal dispersion and turbulent diffusion coefficients in the x,y directions

S_o = source or sink input

S_d = first order decay rate or growth rate of the solute

S_k = total kinetic transportation rate

Water Quality Module

The water quality module simulates the nitrogen, phosphorus, oxygen and chlorophyll *a* cycles and some of their main interactions. Figure 1 presents a schematic representation of the model used; by inspection, it is clear that the chlorophyll *a* cycle is at the centre of the system. This module includes interactions between the following variables:

salinity
temperature
BOD
dissolved oxygen
organic nitrogen
ammoniacal nitrogen
nitrate nitrogen
organic phosphorus
orthophosphate
chlorophyll *a*

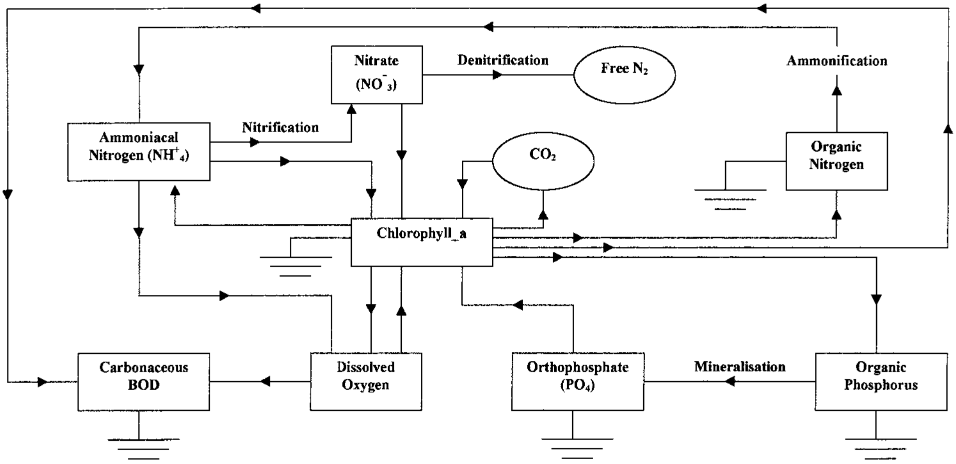

Figure 1. Schematic of system interactions.

These constituents get transported about an estuary through the mechanisms of advection and diffusion as outlined above and, at the same time, also undergo various biochemical reactions. These reactions are represented in the model by partial differential equations. The equations describe the rate at which each constituent changes over time due to various processes (Chapra 1997). All of these reactions and processes are not be presented here in detail; but some aspects of the chlorophyll *a* and nitrogen cycles are presented to give an insight into process modelling.

Chlorophyll *a* cycle

The primary influences on chlorophyll *a* production in the marine environment are nutrients, dissolved oxygen, light and temperature. The model represents these influences through the following partial differential equation describing the growth rate of chlorophyll *a*:

$$\frac{\partial C_p}{\partial t} = \left(G_{PI} - D_{PI} - \frac{V_{S4}}{H} \right) C_p \tag{4}$$

where

C_P = chlorophyll *a* concentration (mgl^{-1})
G_{PI} = specific growth rate constant (d^{-1})
D_{PI} = death plus respiration rate constant
V_{S4} = settling velocity (md^{-1})
H = depth (m)

The growth rate for phytoplankton in a natural environment is a complicated function of species present, solar radiation, temperature, transport processes and nutrient availability (Chapra 1997). In most models the population of phytoplankton is estimated by considering the total phytoplankton biomass. In practice the commonest way of measuring phytoplankton biomass is to measure chlorophyll *a*. The principle advantage of this approach is that the measurement is direct, it integrates all cell types and ages and accounts for cell viability. Thus chlorophyll *a* was modelled to represent phytoplankton.

It is known that the specific growth rate for chlorophyll *a* in equation (4) is related to temperature, light and nutrients; this relationship is expressed as

$$G_{PI} = \acute{G}_{PI} \bullet G_{RTS} \bullet G_{RNU} \bullet G_L \tag{5}$$

where

$\acute{G}_{PI}$ = maximum growth rate given optimum light and nutrients at 20°C
G_{RTS} = temperature correction when water temperature is other than 20°C
G_{RNU} = nutrient limitation factor.
G_L = light limitation factor.

The manner in which the above factors are incorporated within the model is presented below.

Temperature correction

G_{RTS} can be obtained from the Arrhenius equation

$$G_{RTS} = \theta^{(T-20)} \tag{6}$$

where

θ = temperature coefficient = 1.068

T = temperature of water

Nutrient limitation factor

The effect of nutrient concentrations on phytoplankton growth rates is complex but acceptable results can be obtained by representing phytoplankton production as a function

$$G_{RNU} = \mathrm{Min}\left[\frac{DN}{K_{MN} + DN}, \frac{DP}{K_{MP} + DP}\right] \tag{7}$$

of the relevant nutrients using the following Monod type growth kinetics (Chapra 1997).

where

DN = concentration of total inorganic nitrogen

DP = concentration of total inorganic phosphorus

K_{MN}, K_{MP} = half-saturation constants for DN and DP respectively and

Light limitation factor

Obviously light is required to generate green chlorophyll. The relationship between the chlorophyll *a* growth rate and light is complicated due to diurnal surface light variations and light attenuation with depth. Brown and Barnwell (1985) developed a relationship for the limiting effects of light on chlorophyll *a* growth. This relationship relates the limiting effect to surface light intensity, photoperiod, water depth and a light extinction coefficient. This general formulation was used in the model during this research.

Phytoplankton take-up of DN has a preference for NH_4^+ over NO_3^-, is incorporated into the model as outlined below in the next section.

The value for D_{PI} , death plus respiration rate, in equation (4) is calculated from: where

$$D_{PI} = k_r + k_d + k_z \tag{8}$$

k_r = endogenous respiration rate

k_d = death rate due to parasitisation, infection and toxic materials

k_z = death rate due to grazing organisms.

The endogenous respiration rate of phytoplankton is the rate at which the phytoplankton oxidises their organic carbon to carbon dioxide per unit weight of organic carbon. Once again the value is temperature dependent and is described by the Arrhenius equation at any temperature T

$$k_r = k_r(20)\,\theta^{(T-20)} \tag{9}$$

where

$k_r(20)$ = endogenous respiration rate at 20°C

$\theta = 1.045$.

Finally, sedimentation is an important contributor to phytoplankton removal from the water column, particularly in lakes and coastal waters. The actual value of settling velocity, V_{S4}, can be calculated using Stokes Law. However, in practice phytoplankton tend to behave as a flocculent, Class 2 suspension, and this together with vertical turbulence, density gradient and whether or not the phytoplankton are flagellated greatly influence the settling velocity. A settling velocity of $0.2 m.d^{-1}$ was chosen from Bowie *et al.* (1978).

NITROGEN CYCLE MODELLING

The nitrogen cycle normally employed to represent the important interactions in modelling studies is shown schematically within Figure 1. This model considers the following five different forms of nitrogen: phytoplankton nitrogen, organic nitrogen (ON), ammoniacal nitrogen (NH_4^+), nitrate nitrogen (NO_3^-) and free nitrogen (N_2). The governing equations for these processes, and their interactions, are described by Brown and Barnwell (1985).

Phytoplankton Nitrogen

It is assumed that the amount of nitrogen in a given concentration of phytoplankton is given by ($C_p \times A_{NC}$), where A_{NC} is the fraction per unit mass of phytoplankton. Thus, from equation (4), the temporal rate of change in phytoplankton is given by:

$$\frac{\partial}{\partial t}(C_p A_{nc}) = \left(G_{PI} - D_{PI} - \frac{V_{S4}}{D}\right) C_p \bullet A_{nc} \tag{10}$$

Organic Nitrogen (C_{ON})

When phytoplankton decays the phytoplankton nitrogen will be recycled and hence contribute to the pools of organic nitrogen and ammoniacal nitrogen. The amount recycled to organic nitrogen is in proportion to a preference factor, f_{ON}. Some of the organic nitrogen will be converted to ammoniacal nitrogen and some will settle. Thus the net temporal rate of change of organic nitrogen is represented as:

$$\frac{\partial}{\partial t}(C_{ON}) = D_{PI} C_P A_{NC} f_{ON} - k_{71} \theta_{71}^{(T-20)} C_{ON} - \frac{V_{S3}}{D} C_{ON} \tag{11}$$

where

k_{71} = decay rate for hydrolysis of organic nitrogen at 20°C

$\theta_{71}^{(T-20)}$ = temperature correction for hydrolysis of organic nitrogen

V_{S3} = settling velocity of organic nitrogen ($m.d^{-1}$)

Ammoniacal Nitrogen (C_{NH3})

The source terms for NH_4^+ are from nitrification of organic nitrogen and conversion of phytoplankton nitrogen. The sink terms for NH_4^+ are due to phytoplankton take-up and denitrification to NO_3^-. The take-up of NH_4^+ by phytoplankton depends on the preference that the phytoplankton has for NH_4^+ over NO_3^-. This preference is represented in the model by the factor $P_{HN4}^{\ +}$. The net temporal rate of change of ammoniacal nitrogen is represented as: NH_4^+ NO_3^-

$$\frac{\partial}{\partial t}(C_{NH4}^{\ +}) = k_{71}\theta_{71}^{(T-20)} C_{ON} - G_{PI}P_{NH3}C_PA_{NC} - k_{12}\theta_{12}^{(T-20)}\left(\frac{C_{DO}}{k_{DO}+C_{DO}}\right)C_{NH4}^{\ +} + D_{PI}C_PA_{NC}(1-f_{ON}) \qquad (12)$$

where

k_{12} = rate oxidation of NH_4^+ to NO_3^- at 20°C

$\theta_{71}^{(T-20)}$ = temperature correction for oxidation of NH_4^+ to NO_3^-

C_{DO} = concentration of dissolved oxygen

k_{DO} = half saturation concentration of dissolved oxygen

Nitrate Nitrogen ($C_{NO3}^{\ -}$)

The source term for NO_3^- is from denitrification of NH_4^+. The sink terms for NO_3^- are due to phytoplankton take-up and denitrification to NO_2^- and N_2. The preference for phytoplankton to take-up of NO_3^- is represented in the model by the factor (1-$P_{HN3}^{\ -}$). The net temporal rate of change of nitrate nitrogen is represented as:

$$\frac{\partial}{\partial t}(C_{NO3}^{\ -}) = k_{12}\theta_{12}^{(T-20)}\left(\frac{C_{DO}}{k_{DO}+C_{DO}}\right)C_{NH4}^{\ -} - G_{PI}(1-P_{NH4}^{\ -})C_PA_{NC} \qquad (13)$$

Similar sets of partial differential equations are used to describe the oxygen and phosphorus cycles in the model. The partial differential equations describing the water quality parameters and their interactions are approximated by finite difference expressions and solved for using the computer program DIVAST. Details of the numerical aspects of the model can be found in Falconer and Liu (1999).

CHLOROPHYLL *A* PRODUCTION MODELLING OF CORK HARBOUR

Cork Harbour is located on the south-west coast of Ireland and is one of the most important sea inlets in Ireland. It is a busy seaport, a significant receiver of domestic and industrial waste and a popular recreational resource.

The study area extends from the lower exits of the River Lee in the northwest to the open sea below Roches Point in the south. The River Lee flows into Lough Mahon, which, in turn, enters the main harbour through Passage West and Passage East, located to the west and east of Cobh or Great Island. Passage West and Passage East are deep steep-sided channels running from north to south, with rock and shingle beaches exposed between tides. The main harbour is connected to the open sea through a deep channel to the south.

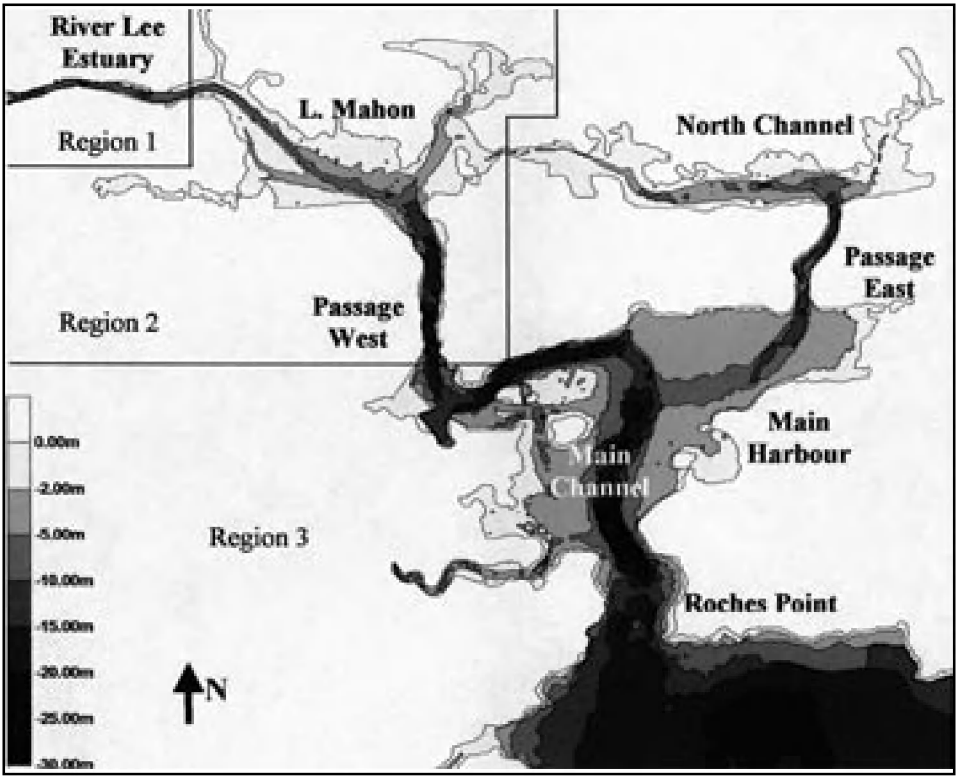

Figure 2. Plan of Cork Harbour model showing water depths.

The model study area measures approximately 354 km^2 (Figure 2). A finite difference grid composed of 565 × 697 (393,805) cells at a 30 m grid resolution was used in the model to represent the study area and provides a high spatial resolution. The finite difference grid was used to construct a detailed bathymetric model of the domain. All hydrodynamic and water quality parameters were resolved at each grid point.

The rise and fall of the tide in Cork Harbour is typical of many Irish coastal locations. The mean tidal range is 3.7m on spring tides and 2.0m on neap tides. Extensive areas of mudflats become exposed within the study area at low water, particularly in Lough Mahon and the North Channel. In Lough Mahon the plan area of the water at low water is *c.* 70% of the high water plan area. Similarly, in the North Channel, the plan area at low water is *c.* 56% of the high water plan area. These areas of mudflats give rise to odours because of decaying organic material deposited there at high water. The four main freshwater inflows to Cork Harbour (Figure 2), are the Rivers Lee, Glashaboy, Owenacurra and Owenabuidhe.

The generic model DIVAST was applied to Cork Harbour to simulate water circulation and water quality processes. The hydrodynamic module required detailed information on the tidal regimes of the study area. These data included tidal ranges and periods for the spring / neap tidal cycle.

The hydrodynamic module was calibrated, in the generally accepted manner, by 'tuning' empirical parameters until good measured current data set was attained. The

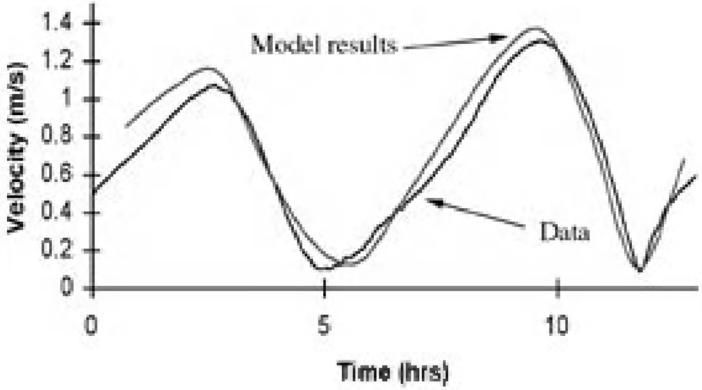

Figure 3. Hydrodynamic model validation.

main tuning parameters were time step, bed friction and coefficient of eddy viscosity. During calibration the model is run for boundary conditions (principally tide, wind and river inflows) that correspond to conditions that prevailed during survey conditions. The above parameters were tuned until good correlation was achieved between predicted and measured water elevations and current speeds and directions. Different data sets were then used for validation to ensure that the model was accurately predicting the hydrodynamic regime in the study area. Figure 3 shows one of the model validation comparisons between measured and predicted current speeds at a point near Roches Point. Validation was carried out at over 10 different sites with similar close agreements between predicted and observed current speeds (Costello *et al.* 2001).

The solute transport module was calibrated using salinity as a tracer; the EPA provided salinity data to the project for this purpose. The water within the model domain was specified as having completely freshwater initially and the water at the sea boundary to the south was specified as having a salinity of 35psu. The solute transport module was then run until steady state conditions were attained with respect to salinity. After steady state was reached strong salinity gradients were observed from south to north throughout the domain. The predicted salinity concentrations were compared against measured salinity data for both summer and winter conditions separately. Figure 4 shows a comparison for summer conditions between measured and predicted salinity at two points in the model, one near Roches Point and at the northern end of Passage West. In Figure 4 the curve represents the model predictions and the two horizontal lines represent minimum and maximum measured salinity. It is seen that the model predicts salinity values close to the minimum and maximum measured data. In all, ten stations were used to compare summer and winter model predictions with salinity data throughout Cork Harbour. Comparisons similar to the above showed that the model accurately predicts the spatial variations in salinity throughout the study area and temporal variations in salinity due to tidal dynamics.

Salinity modelling is important not only with regards to validating the solute transport module but also directly in assessing trophic status. In a recent report (EPA

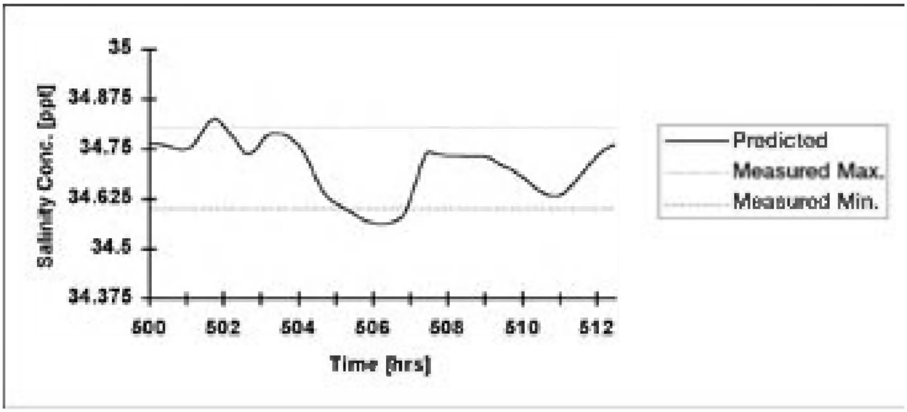

Figure 4. Salinity model validation.

2001) trophic assessment criteria are explicitly related to salinity. It is therefore extremely important that models developed can accurately predict salinity.

The chlorophyll *a* production model was then developed by specifying all the major relevant discharges into Cork Harbour. Concentrations of nutrients, oxygen, BOD and chlorophyll *a* associated with all riverine, domestic and industrial discharges were defined. Further, fluxes of these parameters across the sea boundary were estimated based on fieldwork data collection. The locations of the existing domestic and industrial discharges are shown in Figure 2. The daily loads of organic nitrogen (ON), total ammoniacal nitrogen (TAN), total oxidised nitrogen (TON), organic phosporous (OP) and orthophossphate (MRP) into Cork Harbour during typical summer conditions are presented in Table 1.

Estimates were also made of the influxes of nutrients into Cork Harbour across the sea boundary based on Costello *et al.* 2001 and are presented in Table 2.

Table 1. Daily discharge of nutrients (summer conditions)

Source	ON (kgd^{-1})	TAN (kgd^{-1})	TON (kgd^{-1})	OP (kgd^{-1})	MRP (kgd^{-1})
Domestic & industrial discharges	1218	16063	2217	508	3099
Riverine discharges	1575	97	3434	30	53
Total	2793	16160	5651	538	3152

Table 2. Nutrient loads during the flooding portion of a mean tidal cycle (summer conditions)

ON (kg/d)	TAN (kgd^{-1})	TON (kgd^{-1})	OP (kgd^{-1})	MRP (kgd^{-1})
84564	4374	17010	3159	1701

The loads presented in Table 2 represent the masses of nutrients transported into Cork Harbour from the open sea during the flood half of a mean tidal cycle, approximately 6 h. Much of this will get transported back across the sea boundary into the open sea on the ebb tide. Although it is often difficult to obtain good data for sea boundary water parameters, it is necessary to specify these data as accurately as possible in order to fully describe nutrient budgets of the domain.

Ignoring nutrient fluxes across the sea boundary, Table 1 shows the relative contributions to nutrient loadings from the two main sources. In particular, it is seen from this table that the domestic and industrial discharges contribute substantially more to the total phosphorus load than for the riverine discharges. This is very significant for water quality since the Irish EPA has concluded that phosphorus is the limiting nutrient in the upper reaches of Cork Harbour (EPA 2001).

RESULTS

The DIVAST model was used to simulate chlorophyll *a* dynamics throughout Cork Harbour at each model grid point every 40 seconds throughout model simulations. Two discharge scenarios were modelled to investigate the system response of chlorophyll *a* production to nutrient inputs:

Scenario I – all discharges shown in Table 1

Scenario I – all domestic and industrial discharges in Table 1 set to zero

The main emphasis during the analysis of the model results is on the Lough Mahon region since it is known to suffer from adverse water quality and, in particular, from the occurrence of algal blooms. In order to consider the impacts of switching off the domestic and industrial discharges it was decided to compartmentalise Cork Harbour into 3 regions as shown in Figure 2. These regions are:

Region 1	River Lee Estuary
Region 2	River Lee Estuary, Lough Mahon and Passage West
Region 3	Entire model domain

There were a number of reasons for subdividing the study area in this manner. Firstly, most of the nutrient inputs are discharged along the estuary of the River Lee; thus it was considered necessary to analyse this area of the model in detail. Secondly, it is known that there is relatively little water exchange between Lough Mahon and the Main Cork Harbour area and so it is instructive to look at Region 2 in isolation from the greater Cork Harbour. Thirdly, the EPA has defined Region 2 as a distinct water region for water quality monitoring and analysis. In order to compare model predictions with EPA measurements it was necessary to consider similar water regions. Finally, it was considered best to assess the differences between Scenarios I and II over a regional basis, rather than at individual locations, to obtain a more complete understanding of the marine response to the two loading conditions.

The model was used to determine average concentrations of nutrients and chlorophyll *a* over each of the three regions at each computational timestep. This was achieved using the following expression

$$C = \frac{\sum_{i=1}^{N} C_i V_i}{\sum_{i=1}^{N} V_i} \tag{14}$$

where

C = average concentration of parameter over the region

C_i = concentration of parameter in the i^{th} cell of the model

V_i = the volume of the i^{th} cell of the model

N = is the total number of cells in the region

The results from Scenario I were firstly compared with measurements of water quality parameters produced by the Irish EPA for the Lough Mahon region. The EPA had a number of measurement stations in the Lough Mahon region where they sampled water for levels of % dissolved oxygen saturation (DO), chlorophyll *a* (CHL), orthophosphate (MRP) and dissolved inorganic nitrogen (DIN). From these data the EPA deduced average concentration levels for the four water quality parameters throughout Region 2 for summer and winter conditions. Results from Scenario I modelling were averaged and compared with the EPA values for the more critical summer period. Table 3 presents this comparison for the four water quality parameters chosen by Irish EPA.

Model MRP values appear to be under-predicted, but there is very close agreement between the EPA and model values for chlorophyll *a* and the other parameters. There are a number of reasons for the discrepancies between the EPA data and model results. The locations of the EPA data collection stations in Region 2 were biased towards the estuary of the River Lee close to the major sources of phosphorus loading. The averaging technique used to obtain both sets of results in Table 3 were different. The EPA data were simply averaged arithmetically over all the six sampling stations, whereas the model averages were computed over the entire area of Region 2 using equation (14). However, in general, the above comparison provides good confidence in the ability of the model to predict chlorophyll *a* production in the region.

This good agreement may be attributed to:

- Good calibration and validation of the hydrodynamic model
- Good calibration and validation of the solute transport model
- Access to extensive data sets of nutrient inputs into the harbour

Figures 5–7 show comparisons of predicted chlorophyll *a* concentrations between the model results for Simulation I and II for the 3 regions. During a mean tidal cycle, amplitude 1.5m, the volume of water contained within Cork Harbour at high water is approximately $8.12 \times 10^8 m^3$ and at low water the volume is approximately $5.69 \times 10^8 m^3$, giving a per tidal exchange volume of approximately $2.43 \times 10^8 m^3$. Thus the model results as presented exhibit diurnal variations due to tidal dilutions.

Figure 5 shows that throughout the Lee Estuary there is a significant reduction in the production of chlorophyll *a* when the outfalls are switched off. Scenario I predicts maximum chlorophyll *a* concentration levels in the order of $18 mg.m^{-3}$ and still increasing after 500 hours of simulation, whereas Scenario II predicts maximum chlorophyll *a*

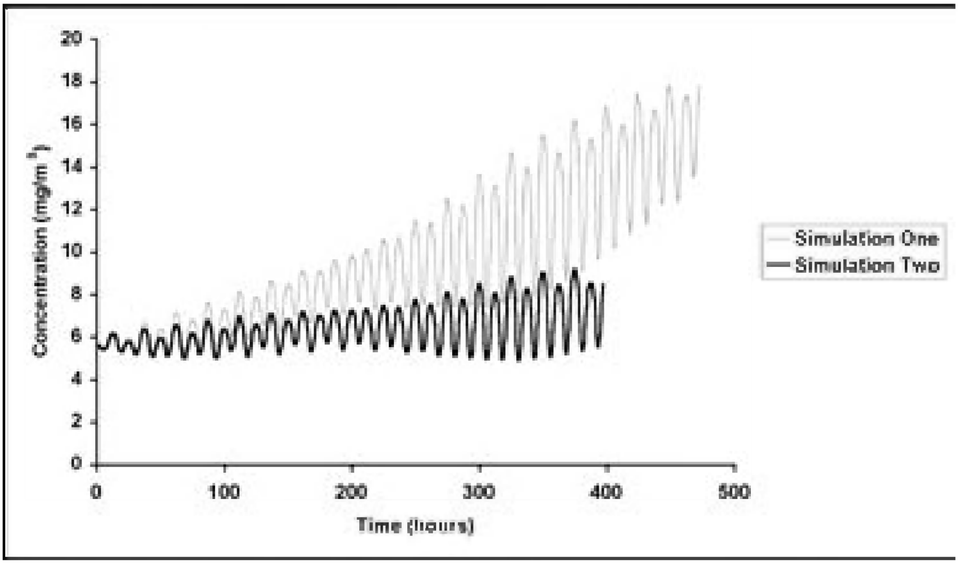

Figure 5. Chlorophyll *a* comparisons–Region 1.

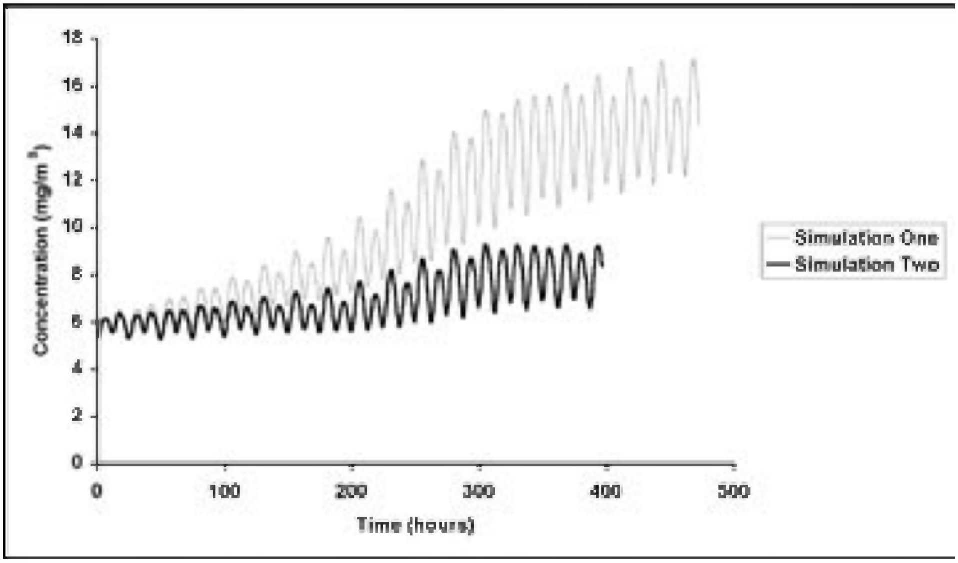

Figure 6. Chlorophyll *a* comparisons–Region 2.

Table 3 Comparison between model and EPA results (see text for abbreviations)

Parameter	EPA Data	Model
DO (% saturation)	80.6	84.3
CHL (mg m^{-3})	12.9	12.8
MRP (mg m^{-3})	76.3	56.2
DIN (mg l^{-1})	1.2	1.4

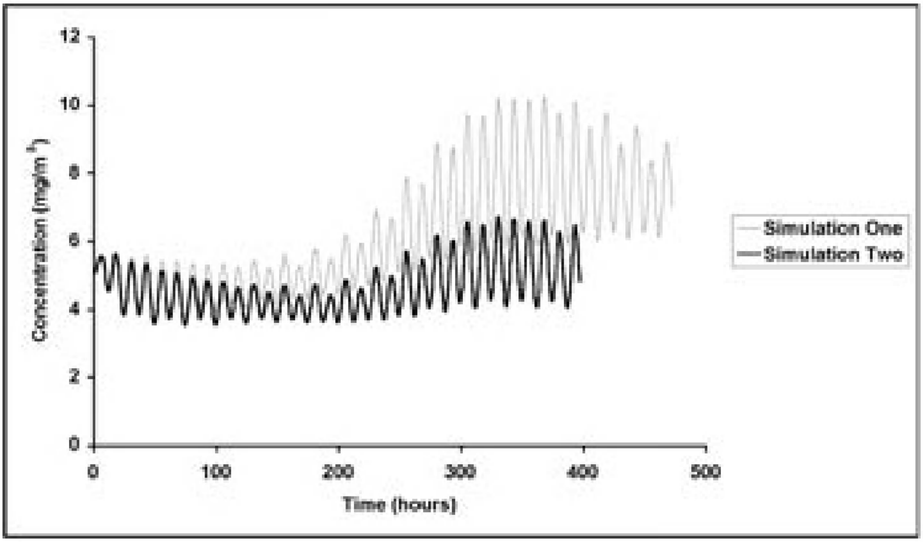

Figure 7. Chlorophyll *a* comparisons–Region 3.

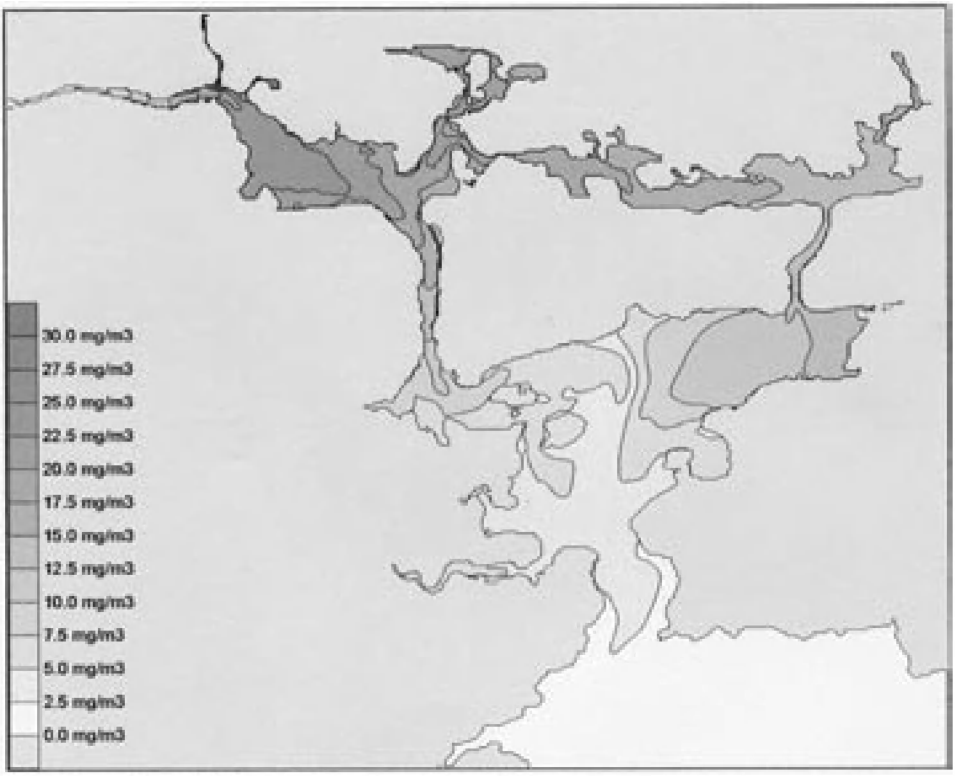

Figure 8. Chlorophyll *a* concentrations at low water, Scenario 1.

concentration levels in the order of 8mg m^{-3} and steady state conditions appear to have been reached. Figure 6 illustrates that a similar situation prevails in Region 2, but the chlorophyll *a* levels appear to have reached steady state during Scenario I also. Again, in Region 3 steady state appears to have been reached for both simulations with a noticeable decrease in concentrations during Scenario II. Although Scenario I results have not yet reached steady state, 500h simulation times for both scenarios is adequate to indicate the significant differences between the two model simulations.

Figure 8 shows a snapshot of chlorophyll *a* concentrations at low water throughout the entire domain for Scenario I. This figure illustrates that much higher chlorophyll *a* concentration levels are predicted in the Lee Estuary and Lough Mahon regions than the rest of Cork Harbour. This is because the major nutrient discharges from the outfalls are in this region and because there is limited water exchange between Lough Mahon and the greater Cork Harbour area due to the restriction of Passage West. This mechanism has previously been studied and is well documented during various water quality investigations (Costello *et al.* 2001).

CONCLUSIONS AND DISCUSSION

The model of Cork Harbour detailed above is highly resolved both spatially and temporally and well defines the main nutrient discharges into Cork Harbour. The collation of the physical and discharge information to develop and run the model was undertake through an EPA funded research project entitled ‘Investigation of nutrient inputs, fluxes and productivity in selected brackish water bodies’ and was quite time consuming. The project integrated conventional data collection, remote sensing and modelling to provide a detailed analysis of the nutrient budget in the River Lee Estuary and Cork Harbour. The model developed resolves the main components of chlorophyll *a* production and decay (Figure 1) and hence is quite complex to solve. Because of the large number of model cells and small timestep, the model simulation time is only twice as fast as real time and hence computationally very expensive. Currently there are developments at National University of Ireland, Galway to parallelise the computer code to allow it to run on high performance computers with parallel processors and allow web access to perform simulations. Preliminary developments improve computational efficiency by a factor of three.

The above model results show that by eliminating domestic and industrial discharges a significant reduction in chlorophyll *a* levels could be expected throughout Cork Harbour. When compared with other nutrient sources, particularly riverine sources, domestic and industrial discharges provide significant percentages of the overall MRP budget. Domestic and industrial inputs of MRP represent approximately 98% of the freshwater inputs (Table 1) and approximately 64% of all MRP inputs (Table 1, Table 2). The predicted reductions in chlorophyll *a* by eliminating these sources concurs with EPA (2001) that chlorophyll *a* production in Lough Mahon is phosphorus limited.

While complete elimination of domestic and industrial discharges into Cork Harbour is not realistic, the model results illustrate how scenario modelling could be used to comply with water quality standards. Such scenario modelling could also be used to assess the likely effects on water quality of reduced nutrient runoff from agricultural activities.

A GIS based tool, MarGIS has been developed by the modelling company MarCon to store all relevant environmental data pertaining to water bodies and to interface with the DIVAST model of specific water bodies. DIVAST can be run easily through MarGIS and displayed in the ArcGIS environment. Through MarGIS all data and model results are integrated in one management tool. Often monitoring programmes for water bodies are devised before models have been developed and it is recommended that water quality models be developed at the planning stages for two fundamental reasons. Firstly, model results from tools like MarGIS will provide useful information on the strategic deployment of instruments programmes so that the data from these programmes can then be applied with more confidence in assessing the trophic status of water bodies. Secondly, the results of the monitoring programmes can subsequently be used for further model validation. A final recommendation is that, in general, more long-term data acquisition is required to aid model calibration and validation. The close agreement between model predictions and data obtained in this work was possible only because good data sets were available for model boundary conditions. In this recommendation, the author agrees with one of the primary conclusions of Jones *et al.* (2002) on their appraisal of the role of decision support systems in estuarine management.

It is possible that the current EPA sampling stations in the estuary of the River Lee overestimate average MRP concentrations and underestimate average DO. Thus the EPA water quality figures are probably quite conservative.

ACKNOWLEDGEMENTS

The author wishes to acknowledge the following who contributed to aspects of the research presented: EPA, EcoServe Ltd., MarCon Computations International Ltd., Stephen Nash and Alan Berry.

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sedimentary shores were later and fewer than those on rocky shores and lacked an overall synthesis of ecosystem functioning.

Work on interactions between organisms on the rocky shore has in fact provided two major ecological paradigms. The first, chronologically speaking was Connell's (1961) work on the barnacles *Balanus* (now *Semibalanus*) *balanoides* and *Chthamalus stellatus* while the second was Paine's (1974) experiments with the mussels *Mytilus californianus* and the starfish *Pisaster ochraceus*. The first (Connell 1961) demonstrated that the upper limit of distribution on the shore was set by physical tolerance limits, while the lower limit was a function of biological factors, in this case competition. The second (Paine 1974) advanced the concept of 'keystone' species, in which the structuring of the community, both physical and biological, is determined by the control (usually top-down) of species which might be numerically insignificant, but whose interactions (in this case predation of the mussels by the starfish) determine the current status. Other work has yielded valuable insights into the functioning of the wider marine system, ranging from the mechanisms of habitat selection by larvae (e.g. Crisp, 1961) to the pressures of and responses to evolutionary driving forces (e.g. McMahon, 2001), and a useful review of community function is given in this volume by Crowe.

In contrast, work on sedimentary shores has tended to be dominated by the habitat itself, in that many of the factors which apply directly on the rocky shore are buffered or mediated by the sediments. One aspect of the buffering is that sedimentary environments display a spatial homogeneity (Wilson 1977, Thrush *et al.* 1989) and this in turn has made it a lot easier to put together budgets and derive metrics for the system (e.g. Baird and Milne 1981).

There have been many studies since Baird and Milne's (1981) first energy budget, but the majority have tended to focus on estuaries and other, mainly sedimentary, locations (e.g. Brown and McLachlan 1990, Wilson 2002). These investigations have been extended into consideration of the systems' reaction to anthropogenic and other pressures such as resource exploitation or pollution (Baird *et al.* 1991, Wilson and Parkes 1999). However, the number of systems for which sufficient information exists for ecological modelling is still extremely limited (e.g. Soetart and Herman 1995). Energy budgets have also been used to investigate system properties through network analysis (Baird and Ulanowicz 1993, Wilson and Parkes 1999), from which metrics can be derived quantifying properties such as system throughput, capacity and stability (Wulff *et al.* 1989).

McArthur (1955) was one of the first to articulate the view that system stability was linked to diversity through the provision of parallel, often redundant, functions. Sanders (1968) 'stability-time' hypothesis developed this and thus would predict low stability for littoral systems. This view has also been supported by other studies, for example those of Roth and Wilson (1998) who calculated system metrics signifying low stability in the littoral communities of Dublin Bay. Nevertheless, palaeontological records and archaeological records show some constancy in the general species' associations at particular coastal locations (e.g. Wilson 1993b), while workers such as May (1973), McNaughton (1977) and Tilman (1996) have teased out the diversity/stability relationship and emphasised the distinction between the responses at population and at community level.

In: James G. Wilson (ed.) *The Intertidal Ecosystem: The Value of Ireland's Shores*, 165–178. Dublin: Royal Irish Academy.

THE INTERTIDAL SYSTEM: SUSTAINABILITY AND LONG-TERM INDICATORS OF SYSTEM STATUS

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ABSTRACT

The intertidal system provides the classic control paradigm of physical control at the landward extreme to biological control at the seaward. Consequently, stability is an unlikely property, yet many intertidal systems display remarkable consistency in character and community type or biotope, if not in individual species' abundances or biomass.

There are several barriers to sustainability, as outlined by the OECD. Principal among these are sea level rise under climate change, habitat loss, habitat degradation (including over-exploitation) and pollution.

Selection of long-term indicators of intertidal system status is limited both by the characteristics of the system, and in particular its susceptibility to physical disturbance, and by the lack of long-term data by which the noise of natural variation can be distinguished from that of anthopogenically-induced change. Community measures such as H' or SAB curves, which again have reference conditions, can be used to assess status, although they operate under the restrictions of both species' impoverishment and variability in community structure. However these approaches can yield false positives, in that departures from reference condition are the norm rather than the exception.

The final approach is long-term monitoring of selected 'key' species such as *Tellina tenuis, Cerastoderma edule* or *Macoma balthica*. Results suggest that several species are needed for an overall picture.

INTRODUCTION

Accessibility has been a major factor in our knowledge of the intertidal ecosystem. Mathieson and Nienhuis (1991) acknowledged this influence, in terms both of the geographical coverage and of the type of shore, where they pointed out that studies on sedimentary shores were later and fewer than those on rocky shores and lacked an overall synthesis of ecosystem functioning.

Work on interactions between organisms on the rocky shore has in fact provided two major ecological paradigms. The first, chronologically speaking was Connell's (1961) work on the barnacles *Balanus* (now *Semibalanus*) *balanoides* and *Chthamalus stellatus* while the second was Paine's (1974) experiments with the mussels *Mytilus californianus* and the starfish *Pisaster ochraceus*. The first (Connell 1961) demonstrated that the upper limit of distribution on the shore was set by physical tolerance limits, while the lower limit was a function of biological factors, in this case competition. The second (Paine 1974) advanced the concept of 'keystone' species, in which the structuring of the community, both physical and biological, is determined by the control (usually top-down) of species which might be numerically insignificant, but whose interactions (in this case predation of the mussels by the starfish) determine the current status. Other work has yielded valuable insights into the functioning of the wider marine system, ranging from the mechanisms of habitat selection by larvae (e.g. Crisp, 1961) to the pressures of and responses to evolutionary driving forces (e.g. McMahon, 2001), and a useful review of community function is given in this volume by Crowe.

In contrast, work on sedimentary shores has tended to be dominated by the habitat itself, in that many of the factors which apply directly on the rocky shore are buffered or mediated by the sediments. One aspect of the buffering is that sedimentary environments display a spatial homogeneity (Wilson 1977, Thrush *et al.* 1989) and this in turn has made it a lot easier to put together budgets and derive metrics for the system (e.g. Baird and Milne 1981).

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The OECD provide regular updates on the current international development goals (e.g. OECD 2002), but these are seriously deficient as regards the marine environment even if 'marine quality' is listed as one of the localised environmental issues under consideration by the DAC Working Party on Environment and Development. The Bruntland Commission in 1987 defined a sustainable society as one that meets the needs of the present without compromising the ability of future generations to meet their own needs and this is generally accepted as the starting point for most discussions. However, Meadows *et al.* (1992) drew a sharp distinction between growth and development. Quantitative growth must inevitably reach its limit in a finite system, while qualitative development, which they argued follows different laws, should result in something better or at least different (Meadows *et al.* 1992). Other workers such as Goodland (1995) have distinguished environmental sustainability from social and economic stability and pointed out that the environment has now become a major constraint on human progress.

In the littoral zone, there a number of barriers to sustainability. These include climate change, habitat loss and degradation and pollution. Climate change incorporates a range of possible impacts, including wholesale and fundamental alterations of physical, chemical and biological characteristics, but arguably the most important and certainly the most predictable is that of sea level rise (Wilson 2002). The IPCC Second Assessment Report in 1997 estimated a rise of between 15–95 cm in mean sea level by 2100 (IPCC 2001). The immediate consequence will be accelerated erosion of unprotected coastlines, along with an increased risk of flooding of the hinterland. It is entirely possible that the intertidal systems could adjust, as they have in the past, to the new regime, but there will be difficulties where managed retreat is not possible. In these circumstances, the intertidal area may be further squeezed between reclaimed land and the rising sea level.

Loss of intertidal habitat is fortunately becoming rarer, partly as a result of increased awareness of the many vital functions performed by these zones and partly also because a lot of the more accessible intertidal land has already been reclaimed. On the other hand, habitat degradation is increasing as a result particularly of population pressure, and the loss of mangroves is one of the few 'marine quality' issues specifically cited by the OECD (OECD 2002). GESAMP's (1990) report on the *State of the Marine Environment,* differentiated strongly between the threats in the open sea and those inshore. For the latter, the report that considered habitat loss, along with fishery pressures, were at least as important as pollution.

Many shores, particularly estuaries, in the industrialised nations still suffer from high levels of contamination, but it would be fair to say that the past thirty years has seen a considerable effort on the part of many nations to remove the worst of the persistent contaminants from the system. A growing body of international legislation now limits what may and may not be discharged and under what conditions and this, coupled with the decline of much of the heavy industry in Europe and the USA has resulted in at least partial recovery. TBT, which first came to prominence in the 1970's for its commercial impacts on intertidal oyster culture and for its environmental impacts on intertidal gastropod populations, was reviewed over ten years ago by Bryan and Gibbs (1991), and provides an excellent example of how the focus of pollution concerns have changed. In 1967 the wreck of the *Torrey Canyon* provided a spectacular example of impacts on the shore some of which may still be detected tens of years later (Hawkins and Southward 1992). Now, although it is fair to say that the capacity for spectacular oil spills is still with us, the focus has shifted from the acute to the more subtle sub-lethal effects, such as shown by the TBT imposex response, itself paralleled by the impacts of oestrogen mimics, and to more subtle ecosystem disruptions like eutrophication and harmful algal blooms (HABs). The latter are now being tackled under a regulatory framework which covers all inputs, including diffuse sources from river catchments (e.g the co-called Framework Directive 60/2000/EC dealt with in detail in this seminar) and mandatory treatment standards for point sources (e.g. Wastewater Treatment Directive 96/1995/EC). However, there still remain considerable difficulties in extrapolating measurable changes even up to population level to community impacts *in situ*, even for the best-studied substances (Hawkins *et al.* 1994).

Investigation of ecosystem disruption of necessity entails consideration of long-term changes and this calls into consideration the natural cycles and variability of the system, and the partitioning of impacts between natural variation, anthropogenic variation and inevitably now, climate change variation.

In this study it is proposed to set out the controls on the sedimentary intertidal ecosystem, to examine what properties of the system may be used to quantify the stability of the system, and to look at long-term changes in the system and in some of its more prominent components.

MATERIALS AND METHODS

Details of the physico-chemical characteristics of the selected sites in Dublin Bay have been published in Desprez *et al.* (1991) and Ducrotoy *et al.* (1991), while the mapping of the topography of the South Bull (Figure 1) is set out in Wilson (1993b).

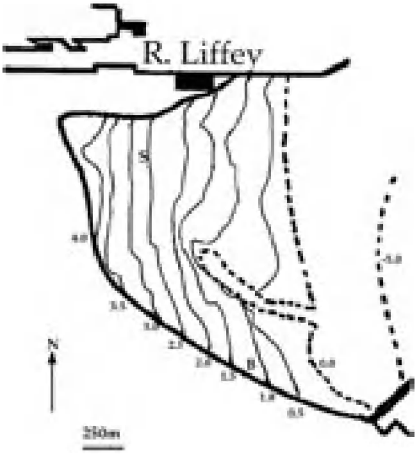

Figure 1. South Bull, Dublin Bay showing shore heights relative to Chart datum (CD) along with position of long-term sample sites Blackrock (B) and Sandymount (S): dotted lines indicate low water mark (0.0 m CD) and the five metre contour (–5.0 m CD).

Unless otherwise specified, the calculations of parameters including density (individuals m^{-2}) and biomass (g wet flesh weight^{-2}) related to height on shore are based on samples of 0.25 m^2 (Wilson 1982). Those for the long-term monitoring (after 1985) are based on multiple cores of 0.03 m^2 (Wilson 1993b, 1997, Wilson and Emblow, 2002). Productivity was calculated using Schwinghamer *et al.*s (1986) relationship for macrofauna

$P:B = 0.525*W^{-0.304}$

where W = individual body size (kcal).

RESULTS

Figure 1 shows the map of Dublin Bay with height contours and sample sites/transect across the South Bull (Sandymount strand). The height contours indicate a fairly gentle and consistent slope toward low water mark, but also emphasise how the upper margins of the shore have been truncated and squeezed by urbanisation. Within these contours, there are also smaller features which vary in size from irregular small channels and runnels to patterned ripples.

Figure 2 shows the metrics for a transect from the landward edge of Sandymount Strand down to the low water mark. Densities (individuals m^{-2}) increase from low to high shore, but the peak of biomass is clearly around mid-shore (Figure 2a: note the log scale on the y-axis). The Shannon-Weiner index (H') and evenness ($J = H'/H_{max}$) were both highest at low shore, reasonably consistent over the bulk of the mid shore, but declined precipitously at the topmost sites (Figure 2b). The different pattern of response in abundance and biomass up the shore is clearly demonstrated in Figure 2c, not only simply in terms of the individual body size (biomass) but also in terms of the Shannon-Weiner Evenness Proportion ($SEP = H'_{biomass}/H'_{abundance}$, M^{c}Manus and Pauly, 1990). The latter indicates clearly that partitioning of biomass among the species at high shore is much more equitable than the partitioning of abundance. Productivity (Figure 2d) is low at both high and low shore, but the overall pattern seems to suggest that it is the higher levels (> +2m) which contribute most to littoral productivity.

The Species Abundance Biomass (SAB) curves (Warwick 1986, Warwick and Clarke 1994) suggest that the greatest difference is between the low shore (Figure 3a), where the curve for biomass is well above that of numbers, and the mid shore (Figure 3b) with high shore (Figure 3c) somewhat in-between. This ranking implies a gradient of stability low>high>mid shore.

Clarke (1990) has recommended using partial dominance curves, in which the dominance of each species is calculated successively. This avoids the problem, particularly prevalent where there are random fluctuations of small, numerically dominant species, that the shape of the curve is essentially decided by the characteristics of the first-ranked species. The partial dominance curves, shown also in Figure 3 essentially confirm the patterns and the rankings of the full ABC curves and support the hypothesis that the influence of shore height pervades the whole community and is not simply being expressed through a single dominant species.

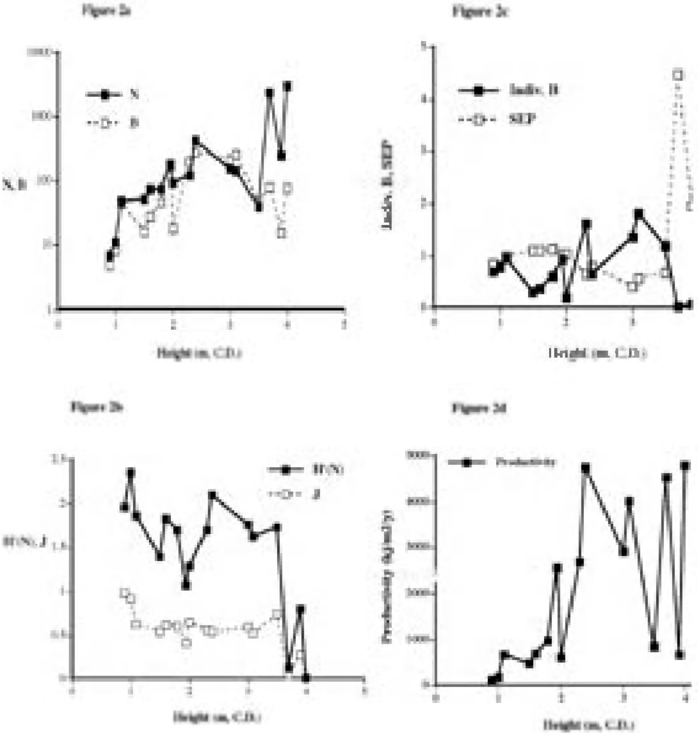

Figure 2. Upshore transect showing community metrics with height (m CD) on shore: a) numbers of individuals (N, 0.25m^{-2}) and biomass (B, 0.25m^{-2}); b) Shannon-Weiner Index (H') and evenness (J); c) individual biomass (B, g) and Shannon-Weiner Evenness Proportion (SEP); and d) productivity (kj.m^{-2}.y^{-1}).

Figure 4 shows the long-term changes in numbers of species (Figure 4a) and in H' (Figure 4b) at the Sandymount site (mid shore) and the Blackrock site (low shore) in Dublin Bay. The two measures of diversity show radically different patterns. The numbers of species at the two sites has essentially remained unchanged over the sampling period, albeit with considerable inter-annual variation. There is perhaps some slight suggestion of higher numbers of species at the mid shore (Sandymount) site in the last five years or so, but this period also contains very high and very low numbers (Figure 4a).

A marked contrast is shown in the pattern of diversity, H' (Figure 4b). Although both sites follow much the same trends, until recently anyway, there seems very much more variability in H' at mid shore, which can change from extremely low values (<1.0) to relatively respectable values (>2.0) within the same year. For most of the period of monitoring, the inter-annual trends followed the same pattern suggesting that perhaps the controlling factors were operating at the level of the Bay, whereas the recent divergence may imply a much more localised influence. Note that the influence can cover also the removal of a restriction, such that a species' numbers may suddenly increase not because of the sudden increase in one parameter, but a decrease in another, perhaps limiting or controlling factor. This is discussed further in relation to the numbers of *T. tenuis*.

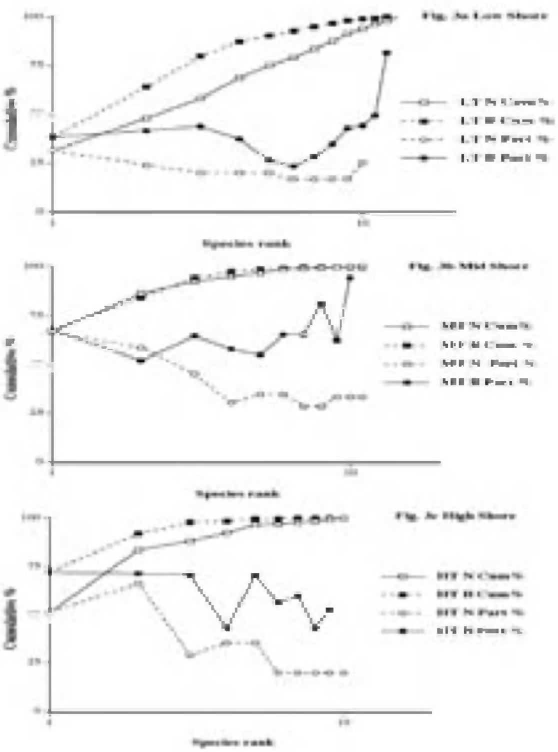

Figure 3. Abundance Biomass Comparison (ABC) curves (squares) and partial dominance curves (circles) showing ranked species' contribution to numbers (N, open symbols) and biomass (B, filled symbols) for a) Low shore (LT); b) Mid shore (MT); and c) High shore (HT).

The decline in H' at low shore (Figure 4b) coincides with the remarkable increase in the numbers of one species, the bivalve *Tellina tenuis* (Figure 5a) whose density increased almost ten-fold from 1996 to 1998. In contrast, cockle (*Cerastoderma edule*) densities (Figure 5b) have declined from a peak in the mid 1980s, with a slight resurgence after 1995, to the levels recorded by West *et al.* (1978) in the early 1970s. In addition, the cockle densities show much greater variability, both between years and within years, than do those of *Tellina*. The decline in the cockle populations is mirrored in the decline of *Macoma balthica* (Figure 5c), again at mid-shore, to the extent that the population has almost disappeared. As with *C. edule*, there was considerable variability in the *M. balthica* density from one sampling interval to the next.

There were few indications that the benthic populations in Dublin Bay are responding directly to climatic or other large scale variables. Figure 6 shows the winter average NAO Index and the annual first year's growth in *C. edule* and the two were significantly correlated ($r = 0.49$, $0.05 > p > 0.01$). A similar, though slightly less strong correlation was obtained for the annual average NAO index and *C. edule* first year's growth ($r = 0.45$, $0.05 > p > 0.01$). However, neither growth in subsequent *C. edule* age-classes nor in any age-class of *T. tenuis* (Figure 6) was correlated with the NAO index.

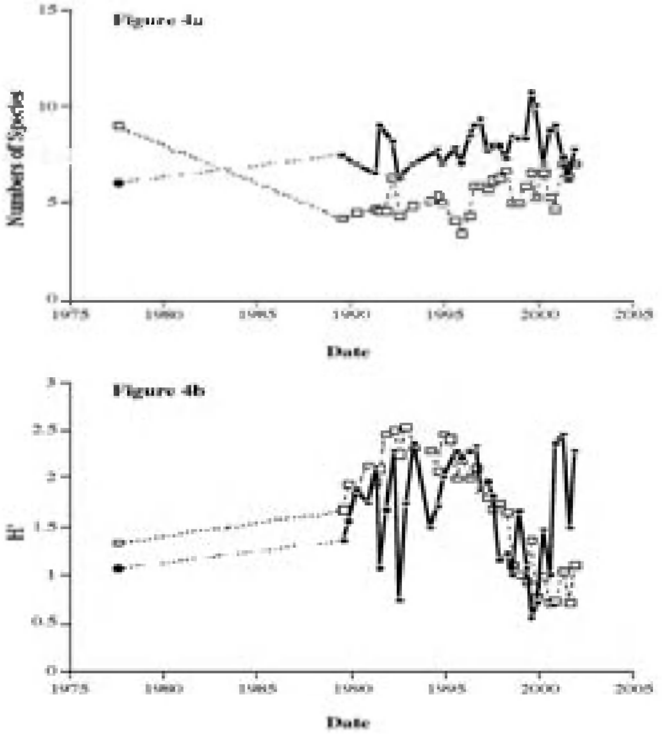

Figure 4. Long-term monitoring of Blackrock (squares) and Sandymount (circles), showing a) Numbers of species; and b) Shannon-Weiner Index (H'): 1977 data from Wilson (1982)

DISCUSSION

The sustainability of the Dublin Bay littoral system will depend on the system's responses to external forcing factors such as sea level rise, climate change or increase in mean temperatures and on the varying pattern of response of the component species.

Sea level rise will be a major factor in the future of the Bay, since the landward extension of the intertidal zone is curtailed by development and hard defences. Wilson (1993b) modelled a scenario in which the sole consequence was loss of area, but there are complications. High, mid, and low shore communities display differing properties and any change in their proportions may result in a disproportionate change in the Bay system. The various metrics presented here suggest that mid and high shore communities may be less stable and resilient than those of low shore, yet these contributed most to the benthic productivity, which in turn provides food for the overwintering waders in Dublin Bay. The results presented here support some, but not all of the concepts embedded in Sanders (1958) 'stability-time' hypothesis and developed by others such as Odum (1969) and McCann (2000). Currently, the disturbance-diversity-productivity model incorporates the intermediate disturbance and other hypotheses, and while evidence broadly supports this theory, there is still considerable debate as to the nature of the relationship(s) (e.g. Liebold 1999).

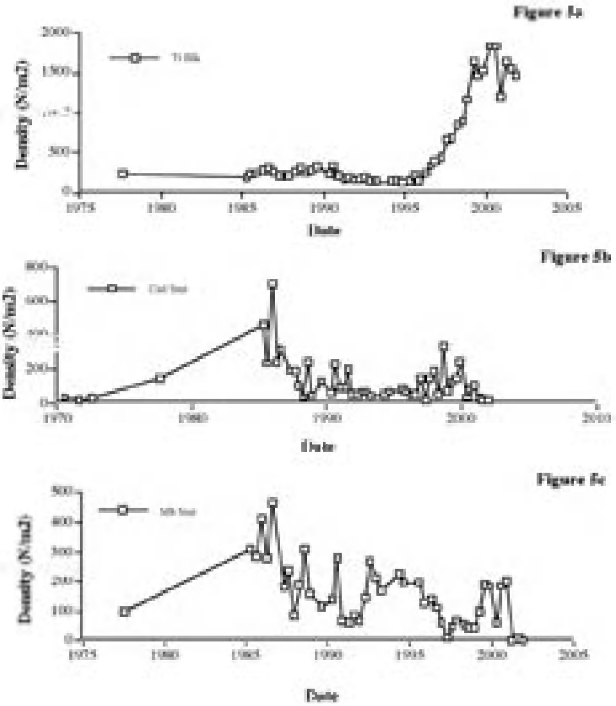

Figure 5. Long-term monitoring of selected bivalve species: a) *T. tenuis*, Blackrock; b) *C. edule*, Sandymount (1971–1973 data from West *et al.* 1978); c) *M. balthica*, Sandymount.

Firstly, the gradients of change in system properties down the shore are not linear. As the physical gradient, in terms of shore height, does change in a fairly regular fashion, then the conclusion must be either that there are processes operating at a smaller spatial scale than mapped here or that change proceeds on a version of punctuated equilibria.

Thrush *et al.* (1989) have identified patterns and patches of heterogeneity of the distribution of species on sandflats at a variety of scales from some tens to some thousands of m^2. Aronson (1994) has even suggested that scale independence is a property only of large, interactive systems, clearly implying that some effect of scale should not be expected in the organisation of intertidal systems. However, both Thrush *et al.* (1989) and Aronson (1994) emphasised the random nature of the majority of species' distributions.

As the gradient of physical control increases up the shore, then clearly the probability of disturbance increases. Does the shore then confirm to the 'intermediate disturbance' model? The answer would appear to be, yes, to some extent, in that the zone of potentially highest disturbance (high shore) was consistently lowest in terms of species numbers and diversity (H', J), but not SEP. However, the low shore/mid shore transition was less clear and it was the mid-shore sites which showed the least stable ABC pattern.

The long-term results also point to radical differences in interpretation according to which of the metrics are examined. The numbers of species has remained fairly constant, even perhaps increasing over time, yet the Shannon-Weiner diversity (H') showed a clear and consistent decline over much of the same period. To what extent the decline, which

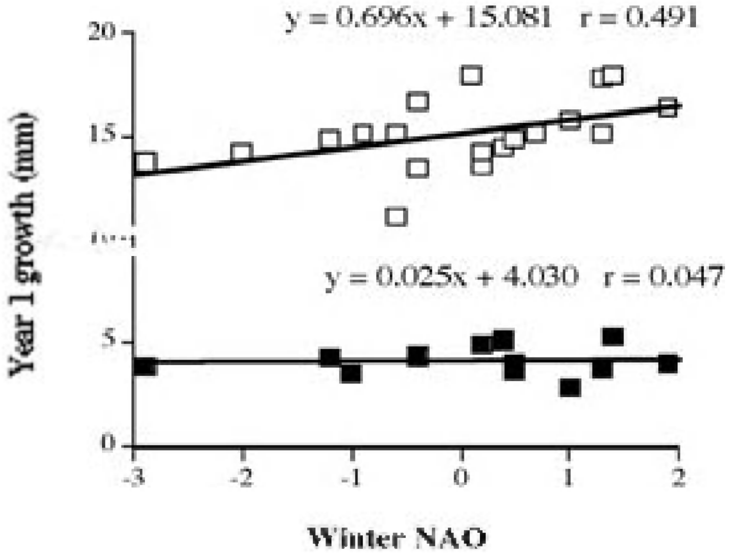

Figure 6. First year's growth (shell length (mm) at 1-y-o) of *C. edule* (open symbols) and *T. tenuis* (closed symbols) with average winter NAO Index 1981–1999.

was mirrored at both low and mid shore, was symptomatic of larger changes in the Bay as a whole, is still questionable, especially as the two zones dramatically diverged following the recruitment success of a single species (*T. tenuis*) at low shore.

In terms of sustainability, the results present certain contradictions. The metrics for low, mid and high shore zones suggest that while the low shore presented the most consistently stable values, there was nevertheless a long-term decline in H' over the middle ten years or so of the monitoring period. However, since low shore showed low biomass and low productivity, perhaps changes here are less important in terms of system function than changes at mid or high shore. Wilson (1993b, 2001) has demonstrated that species such as *C. edule* and *M. balthica* have declined on the whole in Dublin Bay, but reported that these changes showed no correlation with changes in bird numbers, even with those species for whom they are a primary food source. In fact the evidence that bird numbers have been high, indeed with densities as high as anywhere in Europe, for many years seems to imply that the system overall is extremely resilient and has shown considerable resilience in the face of the many natural and anthropogenic stressors to which it has been subjected. It has even been suggested that the essential character of the Bay, and its prominent species have remained largely unaltered over the centuries (Wilson 1993b, 1997).

Ducrotoy *et al.* (1989) proposed *C. edule* as a 'key' species, whose fluctuations reflect short term changes in environmental variables or pollution, whereas *M. balthica* should be considered more of a 'target' species for large-scale (temporal or spatial) monitoring. While this suggestion is somewhat borne out by Beukema's long-term data from the Wadden Sea (Beukema 1988; Dekker and Beukema 1999) and by a pan-European comparison of the two species (Desprez *et al.* 1991, Ducrotoy *et al.* 1991), the driving forces on the continent were climate extremes, which, moderated by Ireland's Atlantic influence, are much dampened down in the Dublin Bay populations. This point was further considered by Wilson (Wilson 1993a, Wilson and Elkaim 1992) who noted moreover that many estuarine species, including the supposedly stable *M. balthica* did in fact display the characteristics of opportunist or r-strategist species associated with disturbed environments. There was however support for the suggestion of *M. balthica* as a candidate for long-term monitoring, but with the eurytolerant *M. edulis* as a stress indicator (Wilson 1993a, Wilson and Elkaim 1992). Overall, it is probably worth persevering with the larger shore bivalves as indicator species, partly on the grounds of ease of collection and identification, but mostly because they are major contributors to biomass and productivity especially in Dublin Bay (Wilson 1982).

Prediction of future changes to the system is still largely guesswork, although the extent of changes to the driving forces (sea level rise, climate (temperature) change, sewage input) are well documented. Thus, the sustainability of current usages is also uncertain. As shown here, there are already forces which are shaping the Dublin Bay system and there have been speculations, discussed above, as to the nature and causes of these changes. It may be therefore that present incompatibilities within the system usages (e.g. sewage disposal and bathing water) may be replaced by other causes of conflict (less organic input leading to fewer birds) and that an essential component of sustainable management is an understanding of how the ecological system operates.

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THE ECOLOGY OF ESTUARINE INTERTIDAL FLATS – THE EXAMPLE OF THE WESTERSCHELDE

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ABSTRACT

The ecology of estuarine intertidal flats is characterised by low species diversity and high productivity. The consequences of these two main characteristics have been investigated in detail on an intertidal flat in the Schelde estuary in the Netherlands. The existence of a species minimum in the oligohaline section of the estuary, as postulated by Remane, could not be confirmed for nematodes and macrofauna for the Schelde, nor for several other European estuaries. Rather, a linear decrease in species richness from the sea to the freshwater was observed.

The productivity of estuarine tidal flats depends on an *in situ* source of primary produced material, the microphytobenthos, as well as on the capacity of the macrofauna to transfer material from the water column to the sediments. A very rapid transfer of ^{13}C labelled carbon from primary production to the higher trophic levels was observed.

INTRODUCTION

Tidal flats, like other intertidal habitats, are on the border between the marine and terrestrial biosphere. During the tidal cycle they are exposed either to the atmosphere or to the overlying water, and the substrate gradually transforms from sediment to soil as one approaches the upper tidal levels. In contrast to rocky shores and sandy beaches, estuarine tidal flats can completely drown and lose their connection to the land at high water. The resident biota therefore must be able to cope with this change from an aquatic to a semi-terrestrial environment twice a day, and to resist the pressure from both aquatic and terrestrial predators and competitors. Because of that, tidal flats are unique in the biosphere, and, although quite limited in surface, they are of great importance to fish and

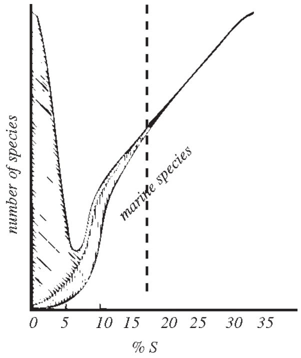

Figure 1. The Remane diagram showing the hypothetical distribution of benthic invertebrate diversity along a marine–freshwater salinity gradient, with a species minimum in brackish waters. Vertical hashed area corresponds to brackish water species, slanted hashed area freshwater species. (from Remane and Schlieper 1971).

birds as feeding areas. Moreover, they have high commercial value as areas of shellfish exploitation and eco-tourism.

Ecological wisdom has it that, at least in temperate areas of the world, estuarine tidal flats are characterised by few species and high productivity. Brackish waters in general are assumed to show a species minimum in the oligohaline zone (Remane and Schlieper 1971) (Figure 1). This implies that system functioning can be understood from the knowledge of resident species, that ecosystem models can be built based largely on population characteristics, and that management of these systems can be based at least partially on knowledge of population biology. Moreover, if we are able to predict the number of species and their distribution, then we may explore the direct link between biodiversity and ecosystem functioning and use this information in operational ecological models. Such comparative and experimental studies are now increasingly being reported (e.g. Emmerson *et al.* 2001), but the full potential of the estuarine soft-bottom system to serve as a model case for the link between biodiversity and ecosystem functioning is not yet exploited. Many studies in the rocky intertidal have significantly contributed to ecological theory (see e.g. recent review by Robles and Desharnais 2002), but although comparisons with soft-sediment systems have been analysed (Seitz 1998), it is clear that more progress could be made, especially in a better understanding of trophic and biogeochemical interactions in soft sediments.

Predictability is also an important aspect of ecosystem monitoring. The use of biological indicators for water quality and ecosystem health has gained support in the last two decades. Within this ecological indicator system approach, many studies have investigated macrobenthic communities in relation to the abiotic environment and how human activities affect them. Examples include the ABC method (Warwick 1986) where dominance patterns are investigated, and studies on functional life-history characteristics (trophic structure) (Pearson and Rosenberg 1978; Boesch and Rosenberg 1981; Gaston *et al.* 1998). As these indicators are weak in demonstrating cause-effect relationships and in general suffer from poor predictability and low explanatory power, the demands for more reliable and quantitative predictive tools have become more and more pronounced (Constable 1999; Thrush *et al.* 1999) On the one hand, such tools are required for *post-hoc* interpretation of changes that have been observed in the estuarine environment. On the other hand, they are needed to predict the future response of the system to planned or anticipated changes in environmental conditions (Ysebaert *et al.* 2002).

The other part of the estuarine ecology paradigm is that estuarine intertidal flats are areas of high biological production. Here one usually refers to the yield in biomass that benefits humans and other vertebrate and invertebrate predators. This term can be estimated in a straightforward way, but to estimate total production (primary, secondary, tertiary. . .) and system mineralisation, or to evaluate whether estuarine intertidal systems are net exporters or importers of organic matter, is more complex. Indeed, although estuarine tidal flats are simple biological systems, they are quite complex biogeochemically and hydrographically, and the evaluation of autotrophic and heterotrophic processes in such a complex framework is very difficult (Heip *et al.* 1995). For instance, primary production occurs by microphytobenthos and macrophytobenthos on top of the sediments, but organic matter on the flats may or may not be derived from higher plants in salt marshes (Nixon 1980), or derived from import of primary produced organic matter from the river and often from the seas as well (Soetaert and Herman 1994). All these processes vary in space and time depending on the conditions in the estuaries.

These primary sources of organic matter serve as food for microbial, microbenthic, meiobenthic and macrobenthic life forms, which often attain considerable biomass on intertidal flats (Heip *et al.* 1995) and are directly responsible for a substantial fraction of the whole system energy flow in these estuarine systems (Herman *et al.* 1999). Part of the biomass of these secondary producers on intertidal flats is consumed by highly mobile organisms (crabs, fish, birds and mammals) that may export the production very rapidly. The main part of organic matter is, however, not exported but ultimately mineralised (respired) locally in the intertidal sediments (Middelburg *et al.* 1996). This process is mainly attributed to microbes, although the benthic fauna is an important player as well, both directly and indirectly (D'Andrea *et al.* 2002).

MATERIAL AND METHODS

In what follows, we will elucidate some of these important paradigms, using research performed in a well-known estuary, the Westerschelde and especially from a small intertidal flat in that estuary, the Molenplaat (Figure 2). The Westerschelde is a temperate, macrotidal, turbid, nutrient-rich and heterotrophic estuary in the Netherlands. The Molenplaat (51° 26' N, 3° 57' E) (Figure 2) is located in a region where salinity varies around 20–25. Most of the intertidal flat is located between-1 m and +1 m relative to mean tidal level. Mean tidal range is approximately 5 m. The average period of emersion varies between 4.5 h (site 1), 7 h (sites 2, 3, 4) and 8 h (site 5) per tidal cycle. Other areas in the Dutch delta in which our studies have taken place are the Oosterschelde, Veerse Meer and Grevelingen. Description of those areas can be found in Heip (1989) and Nienhuis and Smaal (1994).

The diversity of several groups of benthic and pelagic biota was examined during the EC-supported JEEP project (Major Biological Processes in European Tidal Estuaries), the results of which have been summarised by Heip (1995) and partly in Herman and Heip (1999). During this project the species composition of phytoplankton (Muylaert and Sabbe, 1999), zooplankton (Soetaert and Van Rijswijk 1993), hyperbenthos (Mees *et al.* 1995), microphytobenthos and metazoan meiofauna (nematodes) (Soetaert *et al.* 1995) was compared along the estuarine gradient between several European estuaries. We will discuss only those studies dealing with tidal flats.

Much of our discussion will deal with the macrofauna, of which an extensive data set exists for the Schelde estuary. To evaluate the impacts of the dredging activities, the macrobenthos has been monitored extensively since 1990, resulting in a database containing over 5000 macrobenthos samples at present. Parts of this large dataset on macrobenthic species and community composition in the Schelde estuary have been analysed very recently (Ysebaert *et al.* 2002; Ysebaert and Herman 2002).

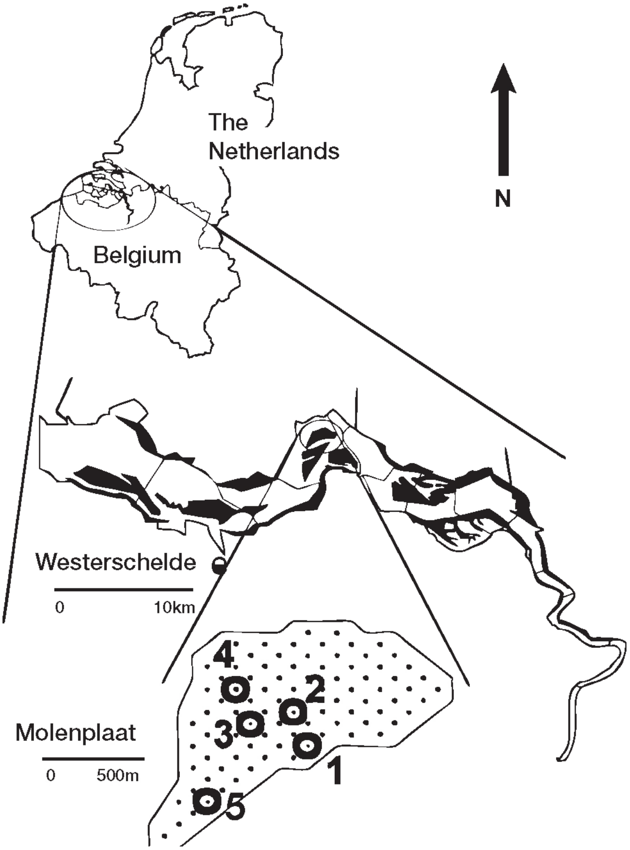

Figure 2. Map of the Westerschelde estuary (The Netherlands) showing the intertidal flat Molenplaat with the five sampling sites

RESULTS AND DISCUSSION

Species richness

Soetaert *et al.* (1995) made a detailed study of meiofauna and especially nematode communities in six European estuaries. Total meiofauna densities showed an idiosyncratic picture, with nematodes dominating the meiofauna everywhere. However, the groups ranking second in importance were quite different between the estuaries, but the cause of this was unclear. For instance, the Ems had the lowest dominance of nematodes in the mesohaline reach, and soft-shelled foraminiferans and copepods were more abundant relative to other estuaries. For nematodes Soetaert *et al.* (1995) observed a general increase of nematode genus diversity from freshwater to the sea and remarkably similar values in six estuaries (including literature data from the Tamar) of α-diversity (number of genera per sample) but no sign of an estuarine species minimum (Figure 3). This similarity is even more striking when one realises that the identity of these species is very different, that most species only occur in one estuary and that only three species out of 220 were found in all six estuaries. Meso-scale variation (in the order of kilometres) due to salinity changes or grain size differences along the estuarine axis is more important than regional variation (hundreds of kilometres) among estuaries and micro-scale variation (centimetres).

Based on a very large dataset for macrobenthos, Ysebaert *et al.* (2003) demonstrated the role of both salinity and depth in explaining large-scale patterns in diversity, abundance

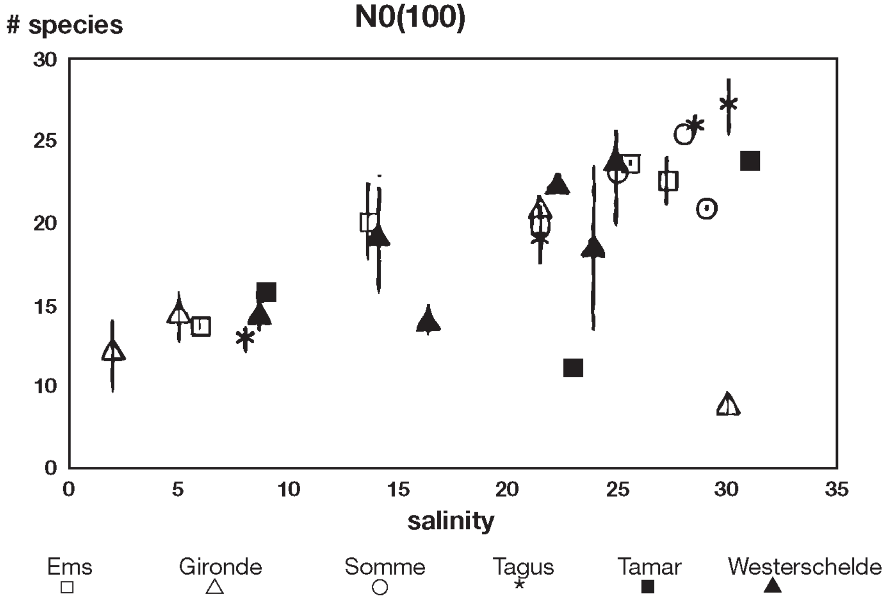

Figure 3. Expected number of nematode genera per 100 individuals in six European estuaries (from Soetaert *et al.* 1995)

and biomass of the macrobenthos in the Schelde estuary. Overall, the subtidal zone had a relatively higher number of species (γ-diversity) as compared to the intertidal zone, but α-diversity (mean number of species per sample) was higher in the intertidal zone (Ysebaert *et al.* 2000; Ysebaert *et al.* 2003). Not only α-diversity but also total number of species found decreased with decreasing salinity. Based on an analysis of the intertidal zone for the period 1990–2001 with a yearly effort of 30 samples, a total of 93 taxa were observed in the polyhaline zone of the Westerschelde, 86 in the poly-mesohaline transition zone and 59 taxa in the mesohaline zone.

Multivariate analyses indicated that the structural complexity of the macrobenthic assemblages decreased from the polyhaline zone towards the meso-oligohaline zone. In the meso-oligohaline transition zone, where salinity shows large seasonal fluctuations, benthic communities change frequently (with sudden dramatic events linked to peak river discharges), resulting in communities that seldom progress beyond early succession stages. Similar patterns were observed in the Loire estuary (Marchand and Gascuel 1988).

In the freshwater tidal zone of the Schelde estuary, no increase in the number of species was observed, probably due to a high degree of pollution in this part of the estuary. Only an impoverished benthic fauna, consisting solely of a few Oligochaeta species, was observed here (Ysebaert *et al.* 1993; Seys *et al.* 1999).

Heip *et al.* (1995) summarise data from many estuaries on biomass and productivity of macrofauna. In many cases, in particular estuaries with a well-developed maximum turbidity zone in the oligohaline zone, biomass increases dramatically from the freshwater upper part to the downstream part of the estuary. Exceptions to the rule are lake-like estuaries where the downstream shallow part is an area of fine sediment deposition unsuitable for suspension feeders, or intermittent estuaries where occasional freshwater runoff is the main source of nutrients.

Productivity

Estuarine intertidal systems are reputedly highly productive systems. The net yield of organic matter from the system is probably the best measure for productivity but is difficult to calculate. We will restrict our discussion to the benthos, as it is the main intermediate between primary production and biomass export from the system and, is responsible for an important part of the total consumption of the primary produced material. Heip *et al.* (1995), extending previous data compilations by Nixon (1980), Dollar *et al.* (1991) and Kemp *et al.* (1992), presented a general relation between system-averaged water depth and the fraction of total estuarine primary production mineralised in the sediment.

The relation is given by the equation

$$\log_{10}(F) = 1.6 - 0.0146\ H$$

where F is the percentage of the system mineralisation in the sediment, and H denotes water depth (m). The factor–0.0146 has the dimension m^{-1} and was interpreted by Heip *et al.* (1995) as representing the multiplicative effect of two factors: a degradability constant ($time^{-1}$) and an effective sinking speed ($m.time^{-1}$).

Drawing upon this equation, an order-of-magnitude estimate for sediment mineralisation in shallow estuaries can be made. The fraction mineralised in shallow

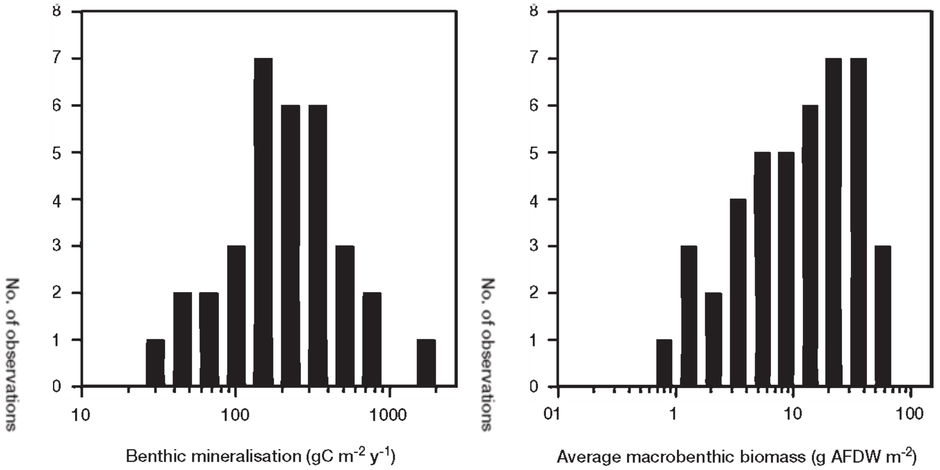

Figure 4. Frequency distribution of observations of (A) total sediment mineralisation (measured as either total inorganic carbon production or oxygen consumption) and (B) system-averaged benthic biomass. Most observations are listed in tables 23 and 29 of Heip *et al.* (1995); for Figure 4A additional data (Herman *et al.* 1999) have been taken into account.

systems (~10m) is around 60% of the total primary production. Taking an estimate for yearly primary production of ~200g C m^{-2} yr^{-1}, one would arrive at ~120g C m^{-2} yr^{-1} for sediment mineralisation, coinciding with the mean value obtained by Heip *et al.* (1995) from (highly variable) measurements in 13 estuarine systems. These values were later complemented by Herman *et al.* (1999) to a total of 33 sites, with several Westerschelde sites included. The frequency distribution shown in Figure 4A was obtained. The median value for this data set, which however is probably biased by intertidal Westerschelde sediments, is 181g C m^{-2} yr^{-1}.

Benthic microalgae can contribute significantly to total system primary production of estuarine systems (Colijn and de Jonge 1984) and can present a primary food source for intertidal food webs. Cahoon (1999) made an extensive compilation of benthic primary production by microalgae and reported a mean (±SD) of 111±99g C m^{-2} yr^{-1} for temperate intertidal sediments. This estimate is about 50% of typical coastal and estuarine pelagic primary production (Heip and Herman 1995; Cahoon 1999) and remarkably similar to estimates of mineralisation in estuarine sediments (about 120g C m^{-2} yr^{-1} (Heip and Herman 1995). This indicates that all benthic primary production could be mineralised in the sediments, consistent with reports for sandy sediments by Middelburg *et al.* (2000) and D'Andrea *et al.* (2002). It is also consistent with rapid and efficient transfer of microalgal-derived carbon within intertidal food webs (see below) and the lack of stable isotope evidence for significant burial of microalgal-derived carbon in intertidal sediments (Herman *et al.* 2000).

It is difficult to establish which fraction of the carbon mineralised in estuarine sediments is directly attributable to the metabolism of the macrobenthic animals. At a system scale, one would need concurrent estimates of sediment respiration and of benthic production or respiration from a representative sampling of the different strata in the system. From the median figures on macrobenthic biomass and benthic mineralisation from the database discussed by Herman *et al.* (1999) it can, however, be qualitatively deduced that this fraction is significant. Taking a median ash-free dry weight (AFDW) biomass of 15g AFDW m^{-2} (Figure 4B), a carbon: AFDW ratio of 0.5, a P/B of 2 yr^{-1} (Heip *et al.* 1995) and a respiration/production ratio of 1.8 (Banse and Mosher, 1980), one would estimate a typical macrobenthic respiration rate in estuaries of the order of 25g C m^{-2} yr^{-1}, which constitutes around 15–20% of the median total respiration of the sediment. The general conclusion, as repeated from the recent review by Herman *et al.* (1999), is that a substantial fraction of the carbon flow in estuarine systems passes through macrobenthic populations.

Conversely, macrobenthic populations at a system level may be limited by food fluxes to the sediments. This is confirmed by several studies. Beukema and Cadee (1997) provided direct observational evidence for limitation of system-averaged benthic biomass by estuarine productivity. They showed that in the Balgzand area (Dutch section of the Wadden Sea) a substantial increase of pelagic primary production between the 1970s and the 1980s (nearly a doubling), was followed by a nearly proportional increase of system-averaged benthic biomass. The proportional increase was equally large for suspension feeders and deposit feeders.

Field evidence for a direct coupling between benthic biomass and pelagic primary production was also produced by Josefson *et al.* (1993) who showed an increase in biomass and a change in community structure in the Skagerrak-Kattegat area between the 1970s and 1980s. The increase in biomass correlated (with a time lag of 1–2 years) with runoff variables known to be directly related to phytoplankton primary production. Austen *et al.* (1991) described similar long-term changes correlated to (indirectly determined) increases in primary production for two widely spaced sites, one in the Western North Sea and one in the Skagerrak.

In Figure 5 the relationship between benthic biomass and system productivity is given for a series of estuarine systems (see Herman *et al.* (1999) for more details). The resulting relation suggests that for these shallow estuarine systems between 5% and 25% of the annual primary production is consumed by macrobenthos and shows up as macrobenthic respiration. On a system-averaged basis, suspension feeders are often the dominant component (with respect to biomass) of estuarine benthic assemblages. They typically occur in much higher local biomass than deposit feeders, which are much more equally spread over (generally lower) biomass classes. In the Oosterschelde, over 75% of the total biomass of suspension feeders was found at local biomass values of more than 100g AFDW m^{-2} (Figure 6), whereas 53% of the samples contained less than 1g AFDW m^{-2} of suspension feeders and 28% of the samples contained no suspension feeders at all (Herman *et al.* 1999). For deposit feeders, only 15% of the system biomass was found at local biomass values of more than 100g AFDW m^{-2} (Figure 6) but only 20% of the samples contained less than 1g AFDW m^{-2} of deposit feeders and there were virtually no samples without deposit feeders (Figure 6). Similar patterns were observed for the Westerschelde (Ysebaert *et al.* 2003).

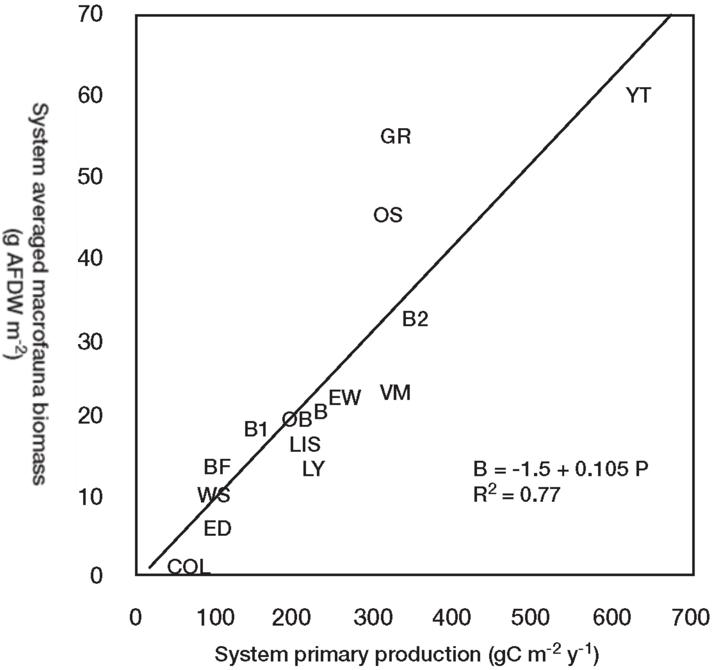

Figure 5. Relation between system-averaged macrobenthic biomass and primary productivity of shallow well-mixed estuarine systems. Data points are indicated by the abbreviation of the name of the system. The regression line is a predictive linear least squares line. System abbreviations (for sources see Herman *et al.* 1999) are: YT: Ythan estuary; GR: Grevelingen; OS: Oosterschelde; B1: Balgzand (Dutch Wadden Sea) in the 1970s; B2: Balgzand (Dutch Wadden Sea) in the 1980s; VM: Veerse Meer; EW: Ems Estuary near the Wadden Sea; ED: Ems Estuary, inner part ('Dollard'); SFB: San Francisco Bay; LY: Lynher estuary; WS: Westerschelde; BF: Bay of Fundy; COL: Columbia River estuary; LIS: Long Island Sound; CB: Chesapeake Bay. (from Herman *et al.* 1999).

Heip *et al.* (1995) showed a dependence of total system biomass of commercial benthic suspension feeders on residence time of the water in the system. This pattern was modelled assuming that residence time was an inverse measure of food exchange with the coastal sea, and that system productivity was the basic limiting factor for the suspension feeder biomass (as in the relation between system productivity and benthic biomass presented above). Dame and Prins (1998) and Dame (1996) tested the model proposed by Heip and Herman (1995) for a number of systems. They concluded that commercial bivalve filter-feeder populations are mostly found in systems with short residence times and high relative rates of primary production.

The benthic food web

As argued above, an important part of the primary production in the estuary is captured on the intertidal flats by the benthic fauna and transferred into the benthic food web. This transfer has been studied in detail at the Molenplaat stations 2 (muddy) and 4 (sandy) using natural stable isotope ratios in different components of the food web, and using stable isotope labelling experiments (Middelburg *et al.* 2000; Herman *et al.* 2000; Moens *et al.* 2002).

Herman *et al.* (2000) compared three different approaches to estimate the relative importance of planktonic microalgae, benthic microalgae and bulk detritus in the sediment as a food source for macrofauna: natural stable isotope ratios in the animals, an *in situ* labelling experiment reported by Middelburg *et al.* (2000) and a dual labelling flume experiment where planktonic and benthic microalgae were labelled with ^{15}N and ^{13}C, respectively. They showed that macrobenthic species differed in their relative dependence on benthic and pelagic microalgae. Suspension feeders (*Cerastoderma edule, Mya arenaria*) were directly dependent on pelagic microalgae and had little traces of uptake of benthic microalgae. Surface grazers (e.g. *Hydrobia ulvae*) had a pure signature of benthic microalgae. Deposit feeders (e.g. *Macoma balthica, Arenicola marina*) were intermediate in their signature, but benthic microalgae were an important fraction of their food. The biomass of (surface) deposit feeders correlated significantly with the primary production by benthic microalgae.

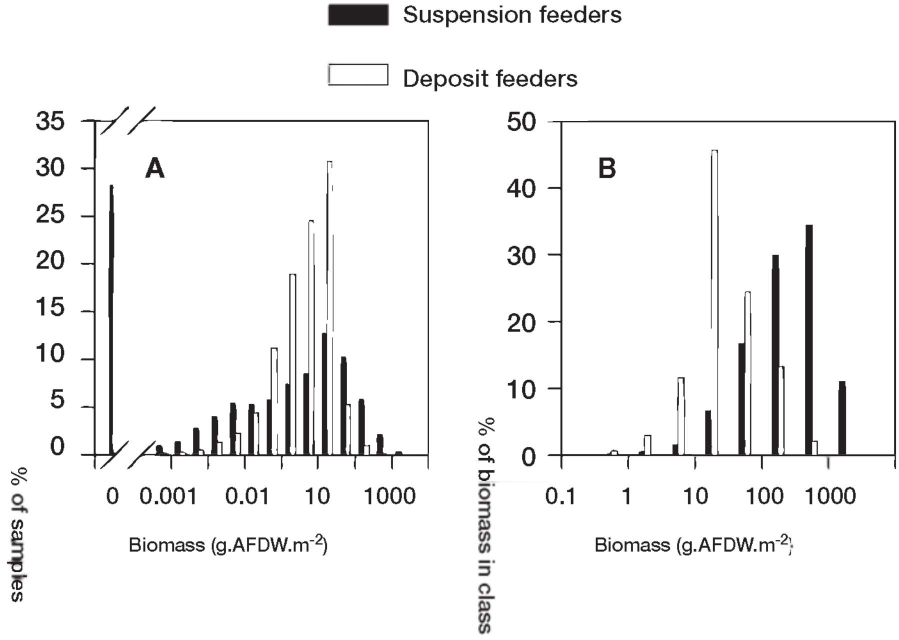

Figure 6. (A) Frequency distribution of suspension and deposit feeder biomass in the Oosterschelde (n = 2368, data collected between 1990 and 1998) over logarithmic biomass classes. Suspension feeders are absent from a large number of samples, and occur more frequently in very high local biomass classes. (B) Percentage of the total recorded biomass found at local biomass values in logarithmic classes. Over 75% of the recorded suspension feeder biomass is found at a local suspension feeder biomass of over 100 g.AFDW.m^{-2}, whereas the largest fraction of deposit feeder biomass is within the 10–100 g.AFDW.m^{-2} class. (from Herman *et al.* 1999).

Stable carbon isotope signatures of nematodes from a salt marsh and 4 tidal flat stations in the Westerschelde were determined in spring and winter situations, and compared to isotope ratios of organic matter sources within the estuary by Moens *et al.* (2002). Nematodes collected from a fine sandy tidal flat sediment in late spring and during mild and sunny late winter weather had ^{13}C values consistent with microphytobenthos being their prime carbon source. Nematodes from a silty station and individuals sampled under cold and dark winter conditions had ^{13}C values intermediate between those of microalgae and particulate organic matter. In combination with experimental results, this suggests that tidal flat nematodes preferentially utilise labile organic carbon derived from microphytobenthos or settling phytoplankton; organic matter from terrestrial or riverine origin does not contribute significantly to the diet of nematodes at the sites studied (Moens *et al.* 2002).

Whereas the above-mentioned studies elucidated the *nature* of the food of benthic animals, other studies have explored the *rate* at which food cascades into the trophic web.

Moodley *et al.* (2000) used ^{13}C-labelled *Chlorella* to study the utilisation of phytodetritus by bacteria, foraminifera and other meiofauna in intertidal estuarine sediments. The response of the community was rapid: about 5% of the added carbon was respired to CO_2 within 6h and bacteria assimilated 2% to 4% of the added carbon within 12h. Among the foraminifera, the dominant genus *Ammonia* exhibited rapid uptake and

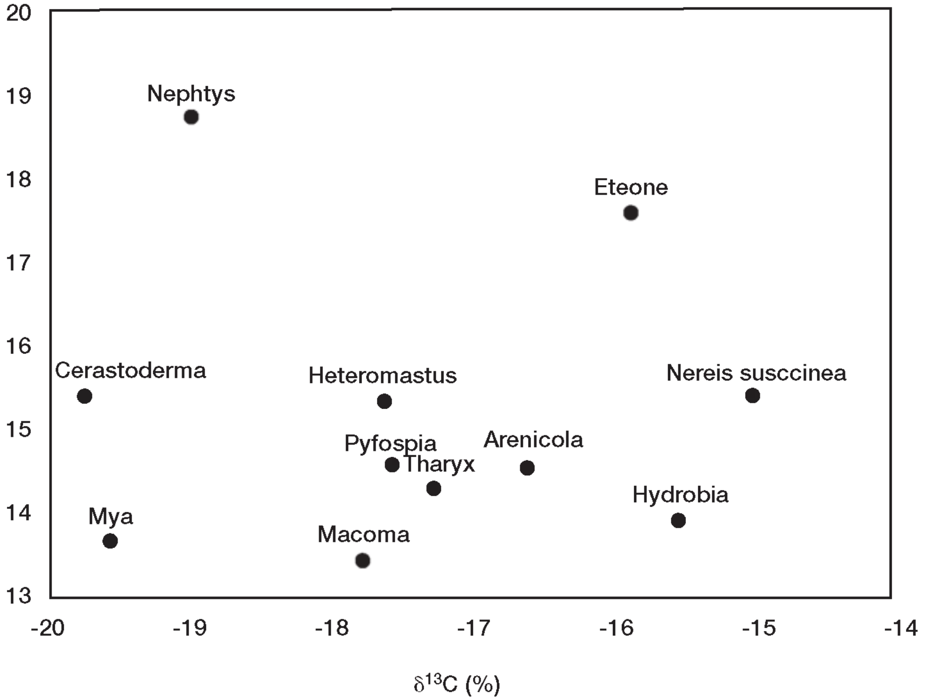

Figure 7. Natural stable-isotope signatures of macrobenthic species sampled at sample site 2 in June 1997 on the Molenplaat tidal flat (see Figure 2). (from Herman *et al.* 2000).

it is estimated that 1–7% of the added carbon was ingested within 3h to 53h. Limited ^{13}C enrichment was recorded for two other genera. This suggests a preference for other carbon sources and implies resource partitioning among the foraminifera. The rapid uptake and significant contribution of *Ammonia* to meiobenthic abundance and biomass indicates that this genus plays an important role in moderating the carbon flow within intertidal food webs.

Middelburg *et al.* (2000) sprayed inorganic $NaH^{13}CO_3$ onto the sediment surface at the beginning of low tide, and followed the fate of the ^{13}C label through the benthic food web during the consecutive days. They showed a linear uptake of the label by the benthic microalgae with time during the first ebb period. The label was transferred quickly to bacteria, presumably to a large extent *via* extracellular excretions. Bacterial labelling peaked after one day, and decreased afterwards. Nematodes were significantly labelled within a period of a few hours; their specific labelling increased during the following days. This corroborated the importance of microphytobenthos as a carbon source for nematodes, yet at the same time contradicted the hypothesis that direct grazing would be the main pathway of microalgal carbon to nematode consumers (Moens *et al.* 2002). Mixing of the label into deeper sediment layers was fast at the sandy station. After 3–4 days, the major groups in the benthic food web that were measured (bacteria, meiofauna, macrofauna) had attained similar specific labelling levels and the amounts of label incorporated were proportional to their biomass.

These studies demonstrate that organic matter produced *in situ* by benthic microalgae is transferred very rapidly and efficiently into the benthic food chain. At the sandy station, there was loss due to resuspension, but this loss was not extremely high (about 34% after 3 days). No major loss due to resuspension could be demonstrated for the muddy station. This study also demonstrated that the turnover of the benthic microalgae was much faster at the sandy than at the muddy station: primary production levels were similar, although the microalgal biomass at the sandy station was almost an order of magnitude lower than at the muddy station.

Benthic organisms as system engineers

Disciplinary studies during the last few decades have resulted in detailed knowledge on tidal flat microbial ecology (e.g. degradation pathways), trophic interactions within the macrobenthos domain (e.g. predator-prey, competition) and sedimentology, but our understanding of interactions between different size classes of benthic organisms and between the sediments and benthic organisms is rather limited. Heip (1976), Jones *et al.* (1994) and Jones *et al.* (1997) advanced the concept of organisms as ecosystem engineers in which they provide structure or modify their physical or chemical environment and thus affect the availability of resources to other organisms. This may generate organism-organism interactions via the environment. Tidal flats provide numerous examples (e.g. Van De Koppel *et al.* 2001; Reise 2002) including stabilisation of sediments by microalgae, destabilisation of sediments by moving fauna, deposition of (pseudo)faecal pellets by suspension feeders, mixing of sediments by animals (bioturbation) and the construction of tubes and burrows by macrofauna. The construction of burrows has dramatic effect on the biogeochemical processes (e.g. Aller 1983; Herman *et al.* 1999), the bacterial community structure (Marinelli *et al.* 2002) and meiofauna communities (Levin *et al.* 2001). Macrofauna-induced structures and processes may generate (via coupled positive and negative feedbacks) a diversity of microhabitats that can host a diverse community of bacteria and micro and meiofauna.

GENERAL CONCLUSIONS

Conventional ecological wisdom has it that species diversity is lowest in the brackish water regions of estuaries. The 'brackwasserminimum' as described by Remane and Schlieper (1971) from the Baltic Sea is usually ascribed to the low tolerance of most species to the salinity fluctuations existing in those areas. In the data series we investigated there is indeed a reduction in α-diversity going from marine to freshwater reaches of the estuary, but this reduction is gradual and often linear and there is no indication of a real species minimum in the oligohaline brackish water region of Western European estuaries in several groups of animals that were studied in more detail. Unfortunately, most detailed studies from tidal areas in Western Europe fail to include the freshwater tidal areas or freshwater biotopes adjacent to the main channel of the estuary, which may serve as refuges for many species. It is therefore still unclear how the total species richness of an estuary and its intertidal flats is distributed. This is mainly a problem of sampling methodology and spatial scale. Spatial scale has been discussed by Ysebaert and Herman (2002) who showed that at meso-scale (>100m–10 km) a considerable fraction of the variation in occurrence, density and biomass of eleven dominant macrobenthic species correlated very well with physical factors (depth, tidal current velocity, sediment composition). At larger scales within the estuary salinity changes these relations significantly (Ysebaert *et al.* 2003). One important conclusion from the analysis of spatio-temporal variance components (Ysebaert and Herman 2002) was that a significant amount of variation occurs in the 'station*year' interaction factor. Stations (characterised by replicate samples within 1 m^2) varied significantly from year to year in their macrobenthic species composition, and this variation was not part of a general trend at larger scales, nor could it be correlated to fluctuating physical factors. It shows that patchiness at relatively small scales (10–100 m) is an important feature of these communities.

The other general perception, that estuarine intertidal flats are highly productive ecosystems, is supported when one considers the biomass of higher trophic levels, including the benthos. An important part of total system production is mineralised in the sediments and much of this can be attributed by benthic animal activity. Moreover, our food web studies have demonstrated that the transfer of organic matter in the benthos is very rapid.

Often one assumes that high productivity is associated with silty sediments. Sandy sediments have traditionally been neglected by biogeochemists and microbial ecologists because stocks of carbon (food for benthos) were low. However, recent studies presented convincing evidence that mineralisation rates of sandy sediments are not necessarily lower than those of organic-carbon-rich silty or muddy sediments (Boudreau *et al.*

2001; D'Andrea *et al.* 2002). Organic matter mineralisation in sandy sediments can be significant because of the high quality (i.e. degradability) of the organic carbon (Dauwe *et al.* 1999). The consequent high rates of turnover are maintained by steady resupply of fresh carbon derived from microphytobenthos production (Middelburg *et al.* 2000) and benthic filtration of water column phytoplankton (Huettel and Rusch, 2000). This high-quality microalgal-derived organic matter provides the base resource for the complex and diverse micro and meiobenthos food webs characteristic of sandy tidal flat sediments.

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THE USE OF INTERTIDAL SALT MARSH CREEKS AS FISH NURSERY AREAS: A SEASONAL SURVEY OF THE FISHES IN NORTH BULL ISLAND, DUBLIN BAY

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ABSTRACT

The presence of juveniles of 10 fish species in two salt marsh intertidal creeks in Bull Island, Dublin Bay supports the premise that they serve as nursery areas.

The creeks were sampled from June 2000 till September 2001 to determine the seasonal composition, abundance and distribution of fish species. A 1 m × 1 m trawl net with a 1 cm mesh was used almost every month and the samplings included both ebb and flood phases, so as to reduce sampling bias to a minimum. Water temperature and salinity were measured *in situ* with an ST probe. Water samples were also taken for SPM and Chlorophyll *a* determination.

All fish caught were counted and weighed and their total length was determined. The resident gobies dominated the catches, but also juveniles of exploited and threatened species such as the bass, *Dicentrarchus labrax* and the catadromous *Anguilla anguilla* were hosted. Only one species was taken in October 2000 and the highest number of species at any one time (6) in September 2001.

Four indices were calculated. The Shannon-Wiener species diversity index (H'), the Shannon-Wiener Evenness Proportion (SEP), the "species richness" component (D), and the "Evenness" index of Pielou (J') were used to assess differences between the sampling sites and between seasons. All index values indicated low heterogeneity and diversity within the fish community.

The estuarine fish using the intertidal marsh creeks have rarely been studied in Europe and the role these habitats play for them remains largely uninvestigated. The need for similar research is stressed.

TIDAL, DIEL AND LUNAR CHANGES IN ESTUARINE MARSH NEKTON

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ABSTRACT

The utilisation of a brackish estuarine marsh by nekton was investigated over a lunar cycle in August 1994. The nekton migrating in and out of the intertidal creeks of the marsh 'Het Verdronken Land van Saeftinghe' in the Westerschelde estuary, SW Netherlands, was sampled passively during 7 complete tidal cycles. Sampling one tidal cycle yielded three consecutive flood samples and four consecutive ebb samples. Sampling occasions, occurring every two to three days, covering all diel and lunar situations, allowed comparing tidal, diel and lunar influences on the composition of the intertidal nekton fauna.

Two different tidal migration modes were observed. The mysid shrimp *Mesopodopsis slabberi* showed maximum abundance around high tide. For the remaining common nekton species: the mysid *Neomysis integer;* the shrimps *Palaemonetes varians;* the amphipod *Corophium volutator;* the crab *Carcinus maenas* and the goby *Pomatoschistus microps;* highest densities were recorded during lower water heights. The fauna assemblage shifts clearly between the different tidal stages. The total amount of detritus was found to be the most important parameter structuring the assemblages.

On two occasions consecutive day and night samples were taken. Total densities were clearly higher during night samples. During full moon a clear difference in community composition was noticed between the night and the day samples. During neap tide, differences between day and night were less clear.

No clear correlation was found between water height and total nekton densities except for the two most abundant species *Mesopodopsis slabberi* and *Neomysis integer*, of which recorded averages were higher during spring tide and lower during neap tide. A clear shift in community composition was observed between the spring tide and the neap tide, with water height as the main environmental factor.

THE USE OF SEDIMENTARY INTERTIDAL SYSTEM AS RECREATIONAL HAND FISHING AREA AND ITS IMPACTS ON EELGRASS BEDS (*ZOSTERA MARINA*) IN WEST BRITTANY (FRANCE)

Christian Hily, Maryvonnne Le Hir and Maud Milliet

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ABSTRACT

Hand fishing on intertidal soft sediments for bivalves on the low-water period of spring tides induces strong perturbations of sediments and associated fauna and flora. This activity has been increasing these last years and the tools used are becoming more and more destructive for the biotope. Many of the sediments sheltering rich populations of Veneridae and other bivalves are often colonised by *Zostera marina* beds. *Zostera* beds are recognised as habitats of high value in term of patrimonial, ecological and economic interests. A study aimed at understanding the consequences of the the hand fishing perturbations on habitat and on community of the *Zostera* beds is carried out in West Brittany in the bay of Brest. The first results show that the impacts on the habitat are both on the the *Zostera* population and on the sediment characteristics. The impacts on the associated community result in a drastic decrease of specific and functional biodiversity, abundance and biomass. Small opportunistic polychaetes became dominant and, according the frequency of the perturbation, the *Zostera* beds community is progressively replaced by a heterogeneous muddy sand community. This human activity can be considered as contributing to the uniformisation and standardization of the soft sediment intertidal system by decreasing the diversity of habitats, ecosystem functions and species. From these results, we suggest that management proposals should be developed to decrease the impacts, while taking in account the sensitivity of the users of the intertidal area towards their traditional fishing activity.

MACROFAUNA ORGANISATION AND VARIABILITY IN INTERTIDAL BOULDER FIELDS

Maryvonne Le Hir and Christian Hily

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ABSTRACT

Boulder fields are between hard and soft sediments, and are consequently very heterogeneous habitats. Yet they have received little attention, and the ecology of their associated communities remains largely unknown. Although boulder fields are one of the most diversified habitats of the intertidal area, they are heavily exploited by amateur and tourist hand-fishing activities in western Europe.

Macrofaunal assemblages living in intertidal boulder fields were studied at different spatial scales in western Brittany in terms of distribution, abundance, biomass, species and functional diversities. Five different spatial scales were considered during the study: regional scale (western Brittany), island scale (1 km^2), transect scale (500m^2), sample scale (m^2) and boulder scale (dm^2). More than 300 macrobenthic species were identified. Results showed different patterns of spatial variability in the macrofaunal assemblages, that could be explained in part by the study at the finer scale. This latter allowed identification of three distinct biotopes in the boulder field, corresponding to i) an open rock community, ii) a sheltered rock community and iii) an infaunal sediment community. These three communities were, at a smaller scale, composed of different groups of species, each associated with a specific habitat that we termed microbiotopes.

The complex combination of these microbiotopes in the field, depending on the habitat structure (boulders/rock/sediment combinations), defines the observed faunal assemblages at higher spatial scales. Moreover, patterns of unvariability of communities parameters along the scale gradient were also observed, that could be useful in a conservation context of this habitat, for monitoring or assessment of disturbance.

A CHECKLIST, ATLAS AND BIBLIOGRAPHY FOR THE MARINE MOLLUSCA OF IRELAND

Julia D. Nunn[1], Shelagh M. Smith[2], Bernard E. Picton[1] and David McGrath[3]

[1]*Ulster Museum, Botanic Gardens, Belfast BT9 5AB, Northern Ireland*
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Publication date: summer 2005
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Content: text & distribution map for each species; photographs of marine biotopes in Ireland; photographs for 200+ species; historical background; ecology & description of the coast/sublittoral where relevant to Mollusca etc.

TRUNCATELLA SUBCYLINDRICA (LINNAEUS, 1767) IN IRELAND

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ABSTRACT

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A project was undertaken in 2001, supported by a grant from the Praeger fund of the Royal Irish Academy, to study the ecology and associated fauna and flora of *Truncatella subcylindrica*, and to search for further colonies. A total of 50 site visits was made in August and November to Counties Galway, Clare, Mayo, Kerry and Wexford, with more detailed work undertaken at the two known colonies at Rincarna and Carrowmore.

The presence of *Truncatella subcylindrica* at Rincarna and Carrowmore was confirmed, and the extent of the colonies elucidated. Three shells of *Truncatella subcylindrica* were also found in shell sand from Rine Point, Co. Clare. A search at 47 other sites in the counties listed failed to find new colonies with live shells.

In many invertebrates there is a tendency for habitat preferences to become narrower close to the northern range limits. At Rincarna and Carrowmore, *Truncatella subcylindrica* is confined to muddy gravel near the top of the shore, on shingle spits impounding brackish lagoons, often in gravel under large boulders. The gravelly habitat is probably inundated only at spring tides but is kept constantly moist by the impoundment of the lagoon which leaches through the spit back into the sea. It has been observed on or in *Vaucheria* inside an inundated lagoon, and can stand immersion in fully saline water for some days although it is primarily amphibian or terrestrial. Densities of up to 500 animals.m^{-2} were recorded on the *Vaucheria*. From observations, it is clear that that *T. subcylindrica* requires constant moisture, high (near fully marine) salinity, and gravelly or bare rock surfaces which serve to absorb the sun's heat.

The Rincarna and Carrowmore sites are possibly unique in Ireland, although there is a slight chance that similar sites may exist in Co. Kerry. Both lagoons are small, and very vulnerable to disturbance. There has already been some dumping of rubbish at the western end of Rincarna Lagoon. It is suggested that these two sites be considered for maximum protection under available conservation legislation in Ireland.

A COMPARISON OF THE MACRO-INVERTEBRATE FAUNA OF MUD FLATS VEGETATED BY *SPARTINA ANGLICA* AND *SALICORNIA* SPP. AT NORTH BULL ISLAND, DUBLIN BAY

Mark J. McCorry and Marinus L. Otte

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ABSTRACT

A *Salicornia* flat, with substantial numbers of *S. anglica* clumps scattered across it, is present at North Bull Island. This study compared the macro-invertebrate fauna and some physical parameters of sediments beneath clumps of *S. anglica* and the surrounding *Salicornia* spp.

The study found that overall, the species assemblage beneath *S. anglica* and *Salicornia* spp was quite similar. The fauna beneath *S. anglica* usually had a greater mean abundance of individuals and a greater mean diversity of species except in a number of cases where samples from *Salicornia* had greater mean abundances and diversity, though there were few statistically significant differences. The sediment beneath *S. anglica* clumps had a much greater root density than beneath *Salicornia*, though the amount of organic detritus collected from the samples of both *S. anglica* and *Salicornia* were quite similar. There were few differences in water content and organic matter content of the sediment (%LOI) between *S. anglica* and *Salicornia*, though bulk density was significantly greater in the sediment samples from *Salicornia*.

It was concluded that even though *S. anglica* forms tussocks with dense stem densities and much greater biomass (reflected by the root density) relative to *Salicornia* spp., it has not substantially affected the macro-invertebrate fauna of the sediments in this area.

FUNGI OF THE BULL ISLAND SALT MARSH SYSTEM: CULTURAL AND MOLECULAR DIVERSITY

Niamh Ní Bhroin, Eleanor Landy and Nicholas Clipson

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ABSTRACT

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The salt marsh studied was situated at the north lagoon of Bull Island, Co. Dublin. This marsh is divided into three vegetational zones, termed the upper, middle and lower marshes. Each zone possesses a characteristic flora, and is influenced to a different extent by tidal inundation. The lower marsh (mud flats) typically supports *Salicornia* spp., together with *Spartina anglica*, and is most affected by tidal inundation and low soil redox potentials. On the middle marsh *Puccinellia maritima, Halimione portulacoides, Limonium* spp., *Spartina anglica,* and *Salicornia* spp. dominate, with grasses and *Juncus* spp becoming more frequent on the upper marsh. The marsh also becomes progressively drier, being flooded more infrequently by the tide.

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