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Biodiversity of Coastal Marine Ecosystems
Functional Aspects

Carlo H.R. Heip, Herman Hummel, Pim H. van Avesaath, Richard Warwick

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Biodiversity of Coastal Marine Ecosystems

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Contents

Introduction

Carlo Heip
Richard Warwick

The coastal marine environment is under heavy human pressure. For several decades discussions on the effects of pollution and physical disturbance have been ongoing and the role of the oceans in mitigating the effects of global climate change has been intensively studied during the IGBP.

These changes involve species, the interactions between species and therefore the composition of biological communities and the behaviour of ecosystems. At the present time we are almost completely ignorant of the ecosystem consequences of changes in biodiversity in marine systems. We urgently need to summarise the state of the art: what theory exists specifically for marine populations and ecosystems, what observations do we have, what do we need in terms of new technologies (molecular biology, remote sensing, probes, continuous observation platforms etc.) in order to assess change and what can we do about it (marine reserves: how large must they be, where must they be etc.; what limits can be set for exploitation of marine resources).

We also want to create a community of marine scientists that will remain involved with this important problem for a period of time that is sufficient to significantly enhance our knowledge on the effects of biodiversity changes for the behaviour of coastal marine ecosystems.

Marine biodiversity research has borrowed its concepts and paradigms from terrestrial biodiversity studies. The realisation that this is inappropriate is slowly dawning. Processes governing the origin, maintenance and change of marine biodiversity in the sea are very different from those on land. Life originated in the sea and although overall species diversity is much lower in the sea than on land, higher taxon level and therefore probably genetic diversity is much higher: out of 33 animal phyla presently known, 13 occur exclusively in the sea against only one which is restricted to land. Marine biodiversity is poorly known and estimates on the number of undescribed species vary from hundreds of thousands to tens of millions. The taxonomic expertise available in the world to deal with even a fraction of this is totally inadequate and a rigorous scientific approach to deal with functional marine biodiversity without involving knowledge of the exact identity of the species present is a necessity.

The importance of biodiversity in the flows of energy and matter through marine systems is only now starting to be explored. Pelagic systems have characteristic length scales varying orders of magnitude, from small-scale turbulence to oceanic gyres, and life is greatly determined by the physics of the system. Benthic systems are completely different again, with far greater species richness locally and globally. They resemble terrestrial soils but dispersal of many benthic species is by means of pelagic larvae travelling hundreds of kilometres from their place of birth. We have to develop theory for systems with a totally different trophic structure and a totally different physical and chemical environment than on land. We have to develop the appropriate technology to study these systems at different scales and at different levels of biological organisation.

The different structure of the marine food web and its implications for energy and matter flow through the system have been considered in programmes such as JGOFS when evaluating human influence through e.g. the production of CO_2 which is taken up in enormous quantities by the oceanic phytoplankton. Such programmes have more or less neglected some of the basic biological facts: that species have a genetic lay-out and a history, that they have complex non-linear interactions, that they adapt physiologically and through evolution to a changing environment, that they change their environment themselves etc. This link between basic biological facts and the global cycles of energy and matter may well prove to be basic in our understanding of a changing planet. Marine systems offer good practical possibilities to study the relationship between biodiversity and function.

The conference was the second of a series of two Marine Biodiversity Conferences that together aimed at bringing together the separated marine biodiversity research projects that are now being carried out in many countries as a consequence of the Rio Convention on Biodiversity ratified by a large number of countries.

The first conference focussed on patterns and processes, while the emphasis of the second conference was on functional studies that try to understand the role of biodiversity in biogeochemical cycles, ecosystem productivity and food web structure.

Generation of Biodiversity

Chaired by
John Gray

Seascape biodiversity patterns along the Mediterranean and the Black Sea: lessons from the biogeography of benthic polychaetes

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The purpose of this study is to investigate seascape biodiversity patterns along the Mediterranean and the Black Sea through the study of the benthic polychaete biogeography of the region. A series of non-parametric multivariate analyses and recently developed sample-size, sample-effort free diversity indices were performed on the benthic polychaete inventories of the main areas of the region. Both the numbers of species and the pattern deriving from the multivariate analyses demonstrate a west-east zoogeocline, which is shown by the decreasing number of species and by the multivariate similarity pattern of the areas taken into account. Application of the "second-stage" multi-dimensional scaling (MDS) shows, when species information is aggregated to genera, results practically into the same similarity pattern, independent of the similarity coefficients utilized. The same similarity pattern is derived when species information is aggregated to the zoogeographical categories of amphi-atlantic, atlanto-mediterranean, cosmopolitan and endemic species. BIOENV analysis reveals a large number of geographic, climatic and trophic variables to be highly correlated with the similarity pattern derived from the various taxonomic/zoogeographical categories. The synergistic effect, however, of the environmental variables is best reflected in the case of the endemic Mediterranean species. The latter category is considered as the critical zoogeographic category with respect to providing information on the evolutionary history of the taxon in the region. Application of the taxonomic distinctness indices results in a diversity ranking of the areas, which appears to be independent of the number of species hosted in each area. However, this is not the case for the phylogenetic diversity (PD) index. In addition, the results from the former 2 indices signify that the benthic polychaete species-pool, hosted in the Mediterranean and the Black Sea areas, may well serve as a useful basis for future comparisons in environmental assessment and in rapid biodiversity assessment studies. The main result from the application of the area-diversity formula is that the equilibrium model can be applicable for the endemic benthic polychaetes of the region: the number of endemic species can be considered as a function of the degree of isolation of the area from the source region against the degree of within-area isolated habitats.

Arvanitidis C, Bellan G, Drakopoulos P, Valavanis V, Dounas C, Koukouras A, Eleftheriou A (2002) Seascape biodiversity patterns along the Mediterranean and the Black Sea: lessons from the biogeography of benthic polychaetes. Marine Ecology Progress Series 244:139-152

Diversity and divergence in the North Atlantic

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Understanding the population dynamics of marine organisms in the North Atlantic over the past 3 My is of interest because it provides a window through which we can witness how biodiversity has been generated and continues to be generated. During the last glacial maximum (18-10,000 y BP), most of the North Atlantic was covered by ice and sea-surface isotherms were pushed south towards the equator. These climatic oscillations caused species (both marine and terrestrial) to shift into refugia or become extinct. Thus, virtually the entire shallow-water marine biota of the North Atlantic has been recolonized within this short time. Some species reentered from the Pacific—cascading down through the Davis Strait and Greenland Sea; others have spread northward from refugia in more southerly latitudes—mostly on the European side because of suitability of substrate. This natural experiment provides a unique opportunity to explore geographic genetic variation and the underlying processes that have caused it.

Before continuing with the results from our recent work on the seaweed *Fucus serratus* and the seagrass *Zostera marina*, I would like to take the first few minutes to dissect the title of the symposium *(the generation of biodiversity and phylogenetic constraints on function*) for I suspect that it has different meanings for different investigators and the links between *species* and *population* level studies are not always clear.
What processes generate biodiversity? At the most fundamental level, it is genetic variation, which is itself affected by mutation, drift and the sculpting effects of selection. At the population-species interface, it is speciation itself. Measurement of biodiversity at the species level relies on species richness and other classic diversity indices of evenness, which can be compared over various gradients ranging from the local landscape to an entire hemisphere. At the population level, we can determine gene diversity and allelic richness—also over various gradients and spatial-temporal scales.
What is meant by (phylo)genetic constraint? In general, a genetic constraint relates to the width of a reaction norm of a genotype, i.e., the parameters within which, a functional response is possible. For example, temperature tolerance is a critical factor in determining the function/performance of virtually all marine organisms. There are, of course, optima and these have been experimentally determined for many species. However, it has also well documented that individuals/species are not necessarily living in their optima—and so their function is also suboptimal. In short, they are not (yet) adapted or, perhaps, cannot adapt depending on the nature of the constraint. In another context, suboptimal "adaptation" is a reflection of changing distributional dynamics—the historical component of any species—in which the *constraint* has become "evolutionary baggage" which may or may not be possible to jettison. Studies in historical ecology provide many examples of species living today in conditions that are suboptimal based on their physiological responses and genetic backgrounds. When genetic constraints extend to several genealogically related species or populations of a single species, they become a phylogenetic constraint—the shared ghosts of "selection past". This does not imply that current selection regimes are not doing their work; it simply means that what we are able to detect with genetic data is what happened in the past (in the same way that the light of a distant star left there light years ago). How long ago depends on many factors—the particular species under study, the genetic markers analyzed and so forth. In general, very deep time (e.g., the metazoan radiation) is difficult; intermediate times (1-50 My) are easier and shallow times (10s to 100s of thousands of years)—well—are becoming easier. In any case, the separation of historical and contemporary processes is increasingly recognized as "critical" to understanding the "biodiversity-function-interplay".
How can we better link population- and species- level patterns and processes? European-wide inventories of species capture the present day pattern of distribution but tell us little about the dynamics that produced and are still producing these patterns. However, choosing a single species of wide distribution can be further dissected at the metapopulation level. Range-wide surveys of geographic genetic variation have been performed on thousands of terrestrial animals and plants, e.g., rodents, grasshoppers, beech and oaks studies recently completed for Europe. Phylogeographic studies show that species ranges are dynamic involving extinction, recolonization and secondary

contact that greatly affect their evolution and divergence. By extension, this also affects their diversity and function although the direct diversity-function link is still elusive. Similar comprehensive studies in marine systems are still limited with the vast majority focused on mammals, fish and shellfish. Only a handful of studies are available for marine plants—algae and seagrasses. Given their importance as structural, functional and engineering species in coastal communities, the lack of attention given to primary producers is all the more surprising.

Returning now to the main subject of today's talk on diversity and divergence in *Fucus* and *Zostera* species, the key objectives are to:

- Use the natural experiment of extinction-recolonziation of the North Atlantic since the last glacial maximum (LGM) to test phylogeographic hypotheses
- Characterize the extent to which populations are subdivided, the spatial scales over which this occurs.
- Link the pattern of geographic genetic variation with the generating processes, i.e., the mating system, hydrographic conditions and historical factors.
- Identify especially diverse populations for potential conservation
- Identify especially vulnerable populations at "edges" or in "isolated" parts of the distribution.
- Develop a basis for linking diversity and function at the population level. This is ultimately the challenge of ecological genomics.

Theory predicts that glacial refugia should harbor higher levels of genetic diversity than recently colonized areas, as a consequence of founder effects or bottlenecks. Predictably, this model is overly simplistic because additional processes such as dispersal into unoccupied areas—both as a function of the reproductive system and of ecological release from initial competition—can greatly affect the rate and complexity of the developing area. If, in addition, formerly separated populations are brought into secondary contact, the possibility for admixture will also exist.

Until recently, most surveys have relied on the classic measures of expected heterozygosity (H_e) and percentage of polymorphic loci (P), neither of which are particularly sensitive to relatively recent changes. In contrast, the addition of allelic richness (α) is very sensitive to effective population size (N_e) and can, therefore, detect natural fluctuations that have occurred during recent recolonization processes, i.e., "shallow time". Allelic richness can be thought of as an analogue to species richness and can be examined over environmental gradients and latitude. Allelic richness is a useful analog to species richness and can be especially useful when applied to a single species that happens to have a wide range as is the case with *Fucus serratus* and *Zostera marina*.

The seagrass *Zostera marina* is found throughout the Northern Hemisphere and is the major seagrass along Atlantic European coastal seas. Individuals are monoecious reproducing sexually by seeds and asexually by clonal spread. Because seagrasses have a modular growth form of genets and many ramets, genetic diversity can be characterized at three levels: gene diversity, clonal diversity and allelic diversity. The species is generally long lived (hundreds of years in some cases) although annual forms are known. The range of diversity so far detected includes ancient monoclonal meadows in the Central Baltic and Black Seas to highly diverse meadows in the Western Baltic and North Seas. Extending the phylogeographic study to the entire Northern Hemisphere has revealed that western Atlantic populations from Rhode Island (US) to St. James Bay (Quebec) are strongly differentiated but clearly linked to *eastern* Atlantic populations. Iceland populations are linked to Norway and not to the US-Canada as might be predicted from the flow of the Gulf Stream. Pacific populations from Northern California and Washington State show strong connections with the Atlantic as compared with Southern Californian populations below Point Conception. An analysis of standardized allelic richness across eight highly polymorphic, microsatellite loci showed no correlation with latitude unless regional histories were separated. The exclusion of the Mediterranean basin from the analysis, then revealed a strong *negative* latitudinal correlation. Edge populations were (predictably) less diverse. The highest allelic richness was found in the Northern Pacific, which suggests the evolutionary origin of the species.

Fucoid seaweeds dominate most rocky intertidal to subtidal shores throughout the North Atlantic. Next to the kelps, fucoids are the largest macrophytes and provide important habitat for invertebrates. *Fucus serratus*, unlike *Z. marina*, is restricted to the Atlantic and mainly European coasts. Representatives in Nova Scotia and Iceland are known introductions, which we are now able to document genetically. The species is monophasic and dioecious. Individuals are thought to live for up to 20 years under favorable conditions. Strong genetic structure is characteristic at small spatial scale (<10 m and up to 1 km). At intermediate scales (1-100 km), isolation by distance follows a stepping stone model. An analysis of standardized allelic richness across seven highly polymorphic, microsatellite loci showed a strongly *positive* correlation with latitude with a clear dominance in the Brittany region. Similar patterns have been found for *Ascophyllum nodosum* (but not for *Zostera marina*). The Brittany peninsula was clearly a glacial refuge and is probably an area of secondary contact (under investigation). This is consist with our model of short-term paleoclimatological oscillations.

Conclusions

One of the goals of biodiversity research is conservation; another goal is prediction of how regional species and population pools will adapt to longer term, global warming. Diversity and divergence have been driven in opposite ways in *Fucus serratus* and *Zostera marina*—mostly because of their separate histories. The metapopulation structures of both species may ultimately be their best insurance as long as they do not become too fragmented and that key populations harboring high diversity are not threatened. Identification of areas harboring particularly rich assemblages is the key — both in terms of Van-Wright's maximization of *species* richness and in terms of Petit's maximization of *allelic* richness.

Temporary and permanent components of zooplankton diversity in the North Sea and English Channel and climate change

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Analyses of data from the Continuous Plankton Recorder Survey from 1958 onwards have shown that species richness of zooplankton is higher in the northern North Sea than in the south and that the number of taxa recorded in the northern areas has increased. In apparent contradiction to this the mean number of species of calanoid copepod per sample ($3m^3$) is higher in the southern North Sea than in the north. This can be explained by the consistent persistence and abundance of several species (permanent components) throughout the year in the south, whereas the northern areas are subject to greater seasonal and interannual variation. The seasonal variation is largely due to inflow of Atlantic water bringing in species assemblages associated with the shelf edge and oceanic waters to the west of Britain where there is a seasonal shift from colder water groups in spring to warmer water assemblages in the autumn and early winter. The increasing diversity in the northern North Sea is due to climate driven changes in the distribution of these assemblages. Species rich warm water groups have extended their range northwards, bringing an increased number of species into the North Sea. Further south, species known from sub-tropical and tropical waters, which were rare in the Bay of Biscay and surrounding continental shelf waters before the late 1980s have become regular and abundant components of the zooplankton of the English Channel. In some cases species that were considered seasonally temporary components of the plankton in the North Sea and English Channel have become permanent residents, present throughout the year.

In addition to the seasonal components of the groups usually considered to be holoplankton, the larval meroplankton contribute to the temporary zooplankton. In the North Sea, the meroplankton is much more species rich than the holoplanktonic groups. There is great seasonal variability both in the number of species occurring in the plankton and the species composition of the assemblage present. In the CPR samples there is a peak of 30 species of decapod larvae in August and each month being clearly separated in MDS analysis of species composition. In the English Channel, which has higher temperatures and a longer productive season, there is a period of 3 summer months when about 35 species are present and the seasonal distinctions are less clear cut. The mean duration of records of a species in the samples is <5 months in the North Sea but nearly a month more in the Channel. An increase in the proportion of species that produce multiple broods through the year is a major factor in the differences between the North Sea and Channel. The significance of the meroplankton in shelf areas is indicated by the dominance of the zooplankton counts from CPR samples in areas of the North Sea by echinoderm larvae from the 1980s onwards. The abundance of both echinoderm and decapod larvae has been increasing and the timing of their occurrence in the plankton has been becoming earlier, trends most highly correlated with the NAO for echinoderms and with winter temperatures for decapods.

A example of the function effects of changes in the North Sea is the replacement of the cold water *Calanus finmarchicus* by its temperate congener, *C. hegolandicus* as the dominant calanid of the North Sea. The two species are of similar size and nutritional value. However the former reaches its maximum abundance in late spring to early summer, when it can be exploited by the planktotrophic larvae of cod but the latter is most abundant in autumn when the juvenile cod are feeding on larger prey. Another consequence of the changes has been a reduction in mean size of calanoid copepods in the North Sea, which has implications for rates of turnover and residence times of particles in the water column.

The results of the CPR survey have demonstrated changes in biodiversity of the zooplankton, that these changes are climate driven and that there are significant ecological and economic consequences.

The generation of biodiversity and phylogenetic constraints on function

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Life is monophyletic, it began with a single species with a double role: primary production and decomposition. This suggests that ecosystems can function at very low diversity. During the history of life, biodiversity increased continuously, with some crises known as mass extinctions. The causes of the increase in diversity are linked to speciation. Ecosystems worked since the very first occurrence of life, then the biota became increasingly complicate, the number of species started to increase, and bio*diversification* began, probably due to Red Queen processes, arms races, and escalation. These three basic and ultimate causes of speciation (but there are more) suggest that biodiversity is a chain reaction and that once the diversification of living matter has started, it cannot be stopped.

The course of evolution is caused by contingency: improbable episodic events led to the present state of life. Life, however, obeys a set of rules and both functional and structural constraints pose a limit to its "freedom of expression". Both views can be reconciled into chaos theory. Contingencies are the unpredictable side of chaos. Constraints are the attractors of chaotic systems, causing the regularity of their main features over the long term. It is increasingly evident that important genes are more or less conserved throughout the animal kingdom. HOX genes are being found in all Metazoa, and the genes coding for some structures of insects are found, with the same structure but with presumably different functions, in the Cnidaria. These similarities at a genetic level induce the hypothesis that the language of life is not so modified during evolution and that the same sequences might remain more or less unaltered while sometimes producing different results. Genetic constraints are then confronted with ecological constraints: when the brachiopods dominated the bottom of the seas, for example, the molluscs were negligible actors of the ecological play. Once the brachiopods were wiped out the stage, bivalve molluscs took their role in dominating marine soft bottoms. Being bivalve and a ciliary filter feeder seems to be a state that is rarely outcompeted by other body architectures, so that if a contingency leads a group with these features to the edge of extinction, an ecological constraint will induce another group with the very same features to take its place. Biodiversity, thus, is the result of historical events due to both contingencies and constraints.

After the Cambrian biodiversity explosion, body plans did not increase in number: life, therefore, is very conservative. A representative of a body plan (a phylum) might evolve a different body plan, but this will not lead to the loss of the original body architecture, conserved in other species: the origin of further diversity adds new organisations but it seldom erases the preceding ones. Species, of course, become extinct, and genera, families, orders and classes, but it is more difficult to have extinct phyla or kingdoms. Mutations are the mechanisms that allow a species to become something else. Not all mutations are the same, however. If a mutation occurs at an early stage of development, it will affect the whole rest of development, leading to a descendant that is very different from the ancestor. The probability that such a mutation might be successful is very small, though. Such a mutation might lead to a new phylum, or a new class, in other words to a new body plan. Mutations acting later in development cause smaller and smaller changes.

At a functional level, life is mostly a matter of physics and chemistry. At a structural level, however, life is inextricably complex and the unity of functions is overwhelmed by the diversity of structures. Life is a baroque accomplishment of nature and obeys a few general rules blurred by a host of differences in organisation. The world is as it is because this is the way it is. If it were different, as it was in the past (and will be in the future), it would be so for no apparent reason, if not its history. Extinction is a normal event in the history of life and all species, eventually, die. The most dangerous threat that we are inflicting to biodiversity is habitat destruction. Since ecosystems can work (and actually worked) with very low diversity in structure, this might induce the concept that all this diversity is "useless" and that, consequently, most of it is expendable. The same concept stems from the assignment of "important" roles for some species, implying that other species are less important, but we do not know even the simple list of the species inhabiting the planet, so we cannot know their roles. And the roles change with time...

Biodiversity and Ecosystem Function

Chaired by
Jeanine Olsen
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Anthony Hawkins

Xenodiversity versus biodiversity: non-indigenous species in coastal marine ecosystems

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Evolutionary separation and specialisation of coastal marine life over millions of years created much of the biogeographical peculiarities of Europe. These peculiarities, in great extent, have been lost during the last five hundred years because of different human activities. Humans have started a revolution in the structure of marine and other aquatic ecosystems through the worldwide introduction in ecological time of non-native species that had been isolated for millions of years over evolutionary time (Carlton 2000). Often beginning of marine bioinvasions is attributed to the 19th century; however the scale of invasions that must have occurred prior to appearance of first inventories of world flora and fauna is practically unknown. Since the time of early overseas voyages, ships were transporting organisms on and in their hulls as well as in rock and sand ballast. That process inevitably had to result in establishment of hundreds of coastal species that are now regarded as "naturally cosmopolitan", in fact being early introductions of the 16th – 18th centuries. In the beginning of the 3rd millennium, due to globalisation of human activities, the number and variety of available invasion corridors (high volume overseas shipping, inland waterways, frequent air or surface transportation of species for stocking, etc) is rapidly growing.

Results of this global exchange of species are evident in most coastal and inland aquatic areas of Europe (Leppäkoski et al 2002). Much of its present structural and functional diversity is of foreign origin. This human-mediated addition of non-native species was termed "xenodiversity" (Gr. *xenos* - strange) to indicate the diversity caused by nonindigenous (alien, exotic, introduced) species (Leppäkoski & Olenin 2000). The xenodiversity might be traced at different hierarchical levels: genetic (hybridization and addition of genetically modified organisms); species (addition of alien species, elimination of native species); functional/community (emergence of novel or unusual functions, changes in community structure, alterations of food webs and ecosystem functioning) and, even habitat/landscape (habitat engineering, encrusting of solid objects, and changes in bottom micro-topography).

The study of invasions in coastal marine systems, now being a rapidly growing ecological discipline only really began a little more than two decades ago (Carlton 2000; Grosholz 2002). Not only theoretical aspects of marine bioinvasions are studied. Presently, the scientific interest is in great deal driven by practical needs due to serious ecological and economical consequences of bioinvasions. In fact, the problem of "biological pollution" (Boudouresque & Verlaque 2002; Elliott 2003), became multidisciplinary, involving not only biological/ecological (genetics, ecophysiology, biogeography, etc) but also technical and socio-economic aspects. The marine bioinvasion problem should be better covered in the European marine biodiversity research agenda.

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Marine benthic biodiversity and ecosystem functioning: approaches and extensions

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Several conceptual models have been developed of the relationship between the number of species in a system and the rates of ecosystem processes: positive linear (often termed the "rivet" model), positive curvilinear (often termed the "redundancy" model) and the random model, where there is no formal relationship, but where different species have different effects on process rates. Field and laboratory-based experiments involving assembled communities of terrestrial plants with differing species richness have provided some evidence for the curvilinear model, although the results remain contentious (Loreau et al. 2001).

A variety of complimentary approaches have been adopted for addressing biodiversity and ecosystem functioning issues in the marine sediment benthos. These include *in situ* (field) experiments (Bolam et al. 2002), tank or mesocosm experiments (Raffaelli et al. 2003) and data-mining of the existing benthic literature (Emmerson & Huxham 2002).

***In situ* field experiments**, where natural assemblages are manipulated to provide different richness treatments, have the advantage of greater environmental realism than mesocosm experiments, in particular they experience a natural hydrodynamic regime (see below). However, the manipulation responsible for the different richness levels can be a confounding factor in the analyses as it is possible to attribute any between-treatment effects either to differences in richness or to the manipulation. Fortunately, this is very unlikely to be the case for Bolam et al's (2002) work on sandy beach assemblages and their results are convincing in this respect. They examined a number of relevant sediment properties under different richness treatments, but could find no consistent effect of richness *per se*, concluding that functional groups may be more important for ecosystem functioning.

Tank or mesocosm experiments have been carried out at a number of sites in the UK, in Sweden and Australia (Emmerson et al. 2001, Raffaelli et al. 2003). In this approach, relatively small tanks of azoic sediment have been dosed with different biomasses of single species and species in combination, from intertidal sand and mudflats, and nutrient release recorded after c. 20 days. The advantage of this approach is the tight experimental control and the unambiguous experimental design, but the experimental set-up can never be considered entirely natural. However, it has been possible to explore the effects of flow regime in these experiments through the use of flow chambers and there have been extensions to the field (Biles 2003, Biles et al 2003). As with the *in situ* field experiments described above, these experiments indicate that functional group richness is more important than species richness. The effect of flow on biodiversity-ecosystem functioning can be marked and seems to be through flow-induced changes in species behaviour rather than direct effects on sediment processes.

Data-mining of the existing literature (Emmerson & Huxham 2002) has revealed much information on relevant ecosystem processes which can be matched to biodiversity data for individual study sites or for comparison of areas differing in their biodiversity. Several of the relationships that emerge are compelling but must be viewed with caution as they are necessarily correlative and likely to include confounding variables. Nevertheless, they may provide confirmatory or supporting evidence for relationships derived from controlled experiments, and they have the advantage that they often relate to much larger spatial and longer temporal scales than can be tackled in experiments. In particular, such relationships will be useful for identifying the kinds of experiments that need to be done under more controlled conditions.

All three approaches described above should be seen as complimentary and when used together are likely to provide insights into the nature of and mechanisms underpinning marine biodiversity-ecosystem functioning relationships. However, the research community also needs to ensure that it delivers science which is relevant to the needs of policy makers and managers. This will mean finding ways of extending our understanding of biodiversity-ecosystem functioning to larger spatial and temporal scales, exploring the effects of simultaneous but differential biodiversity loss at several trophic levels as occurs in real loss scenarios, and ensuring that the ecological processes examined are those which are pertinent to the ecological goods and services in which society has a stake.

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PICODIV: Monitoring the diversity of photosynthetic picoplankton in marine waters (2001-2003), an FP5 European project

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Picoplankton (defined operationally as cells that pass through a 3 micron filter) dominate the photosynthetic biomass in many marine ecosystems, not only in the very oligotrophic regions of the world oceans, such as the Eastern Mediterranean Sea, but also in mesotrophic areas. However, to date, fewer than 50 species of picophytoplankton have been described. A clear proof of our poor knowledge of picophytoplankton diversity is revealed by the discovery of novel algal classes in the last ten years described from picophytoplanktonic taxa (Andersen et al. 1993, Guillou et al. 1999). Because so little is known about the taxonomy and systematics of picophytoplankton we have very little data to estimate the levels of its diversity under natural conditions and how picophytoplankton are affected by environmental variability linked to either anthropogenic influence or to larger scale phenomena such as those linked to climate change or global warming.

The major objective of this project is to develop, test and validate probing methods based on molecular biology techniques that allow for routine and extensive assessment of picophytoplankton diversity (species composition and relative contribution of taxa to total community) in the marine environment.

Our strategy to meet our objectives is encapsulated in the following four steps:

1. Obtain SSU rDNA sequences for as many as possible picophytoplankton taxa from both cultures and natural samples. Novel taxa will be assessed using a combination of methods including in particular pigment analysis and electron microscopy.
2. Using this sequence database, develop hierarchical probes recognizing each taxonomic group having picophytoplanktonic representatives
3. Develop fast and efficient techniques to quantify the fraction of the picophytoplankton recognized by the probes in natural samples.
4. Test and validate these probes on time series of picophytoplankton biodiversity in three coastal ecosystems.

During the PICODIV project, a large number of strains from the Roscoff Culture Collection (RCC, http://www.sb-roscoff.fr/Phyto/collect.html) have been isolated and characterized and several new picoplankton species are being described. In parallel, we obtained more than 1,300 partial and complete SSU rDNA sequences from 46 environmental clone libraries that have been merged for phylogenetic analyses into a large database of more than 30,000 prokaryotic and eukaryotic rDNA sequences running under ARB. Using this database, oligonucleotide probes recognizing specific taxonomic groups have been designed and applied to seasonal time series from coastal waters with techniques such as FISH coupled with epifluorescence microscopy.

The data obtained during the PICODIV project suggest that picoeukaryotes are extremely diversified (Diez et al. 2001, Moon-van der Staay et al. 2001), especially, heterotrophic ones (Vaulot et al. 2002) We focused our effort on several groups of interest: the cyanobacteria *Synechoccoccus* and *Prochlorococcus* (Scanlan & West 2002), the Prasinophyceae (Guillou et al. submitted), and different novel eukaryotic lineages belonging to the alveolates (A. Groisillier, unpublished) and the stramenopiles (Massana et al. 2002). We also discovered a novel algal group closely related to the red algae (Valentin, unpublished).

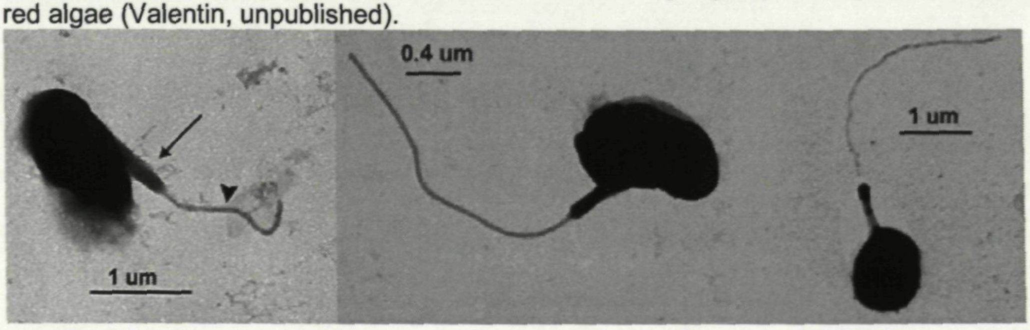

Figure 1
Micromonas spp. (Prasinophyceae) An important picophytoplankton group in coastal waters.

The use of oligonucleotide probes demonstrated that the genus *Micromonas* spp. (Fig. 1) is the most abundant picoeukaryote detected throughout the year in English Channel and Mediterranean Sea coastal waters (F. Not, unpublished). Phylogenetic analyses demonstrated that this genus is complex and composed of three independent lineages that cannot be distinguished based upon morphological features or swimming behavior (Guillou et al. submitted)

Despite very significant advances in the past three years, an important effort is still necessary to describe the picoplankton diversity and many species remain to be discovered and described. The ecological role of the new eukaryotic alveolate and stramenopile lineages needs to be understood. Finally the dynamics and physiological responses of these populations under different environmental conditions will have to examine in detail in order to be able to predict carbon flow within the oceanic microbial food web.

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Biodiversity and ecosystem function - case study of two contrasting arctic regions

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The food and foraging strategy of fifteen species of seabirds and sea mammals from two high arctic regions were analysed. Kongsfjorden region (79°N) is influenced strongly by Atlantic warm waters, while Hornsund region (77°N) is of more Arctic character. The set of 97 prey species that are essential for the diet of top predators were divided for those of Atlantic and of arctic origin. Prey species in the Atlantic area were more diverse (87 species and 11 functional groups), compared to 70 Arctic prey species. The consumption of top predators from Hornsund in July (peak season) was estimated for 2.86 MJ, while such in Kongsfjorden ranged 1.35 MJ. For the function of ecosystem (transfer of energy to top trophic levels) the specific size and nutritional value of individuals of prey species is of key importance and not the diversity, abundance or biomass per se. The areas of the lowest diversity and biomass – glacial basins, were of great importance for the feeding of top predators – because the prey species were accessible and concentrated in small area. The arctic prey species grow slow in low temperature, attain large body size and their life span use to be of 3-4 years, compared to the smaller, faster growing atlantic counterparts of 1 year life span (e.g. *Themisto libellula* versus *T. abyssorum*). The larger size of average prey, permits top predators in the Arctic waters feed on the lower trophic levels, compared to those of Atlantic waters. We suggest that since the primary production is light controlled in the Arctic, the increased temperature will have minor effect on the production of the system. However the low temperature results in prolonged life span and large size of marine poikilotherms. The presence of separate annual cohorts reduces the species diversity in plankton. In contrary, warmer Atlantic waters have the more diverse food web that may be less favorable for top predators, because energy and resources are spread among large number of smaller items.

Biodiversity and ecosystem function: A multi-disciplinary approach at an island marine station

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The objective is to understand, assess and forecast marine biodiversity on the species, genetic and community level in an ecosystem context. Complementary to research on sedimentary shores, the characteristic species richness of the rocky littoral and surrounding shelf-waters at Helgoland is studied. This work is underpinned by long-term observations of the biota. We investigate the function of biodiversity and in turn the functional diversity of species, particularly to elucidate the adaptive diversity in key-species which determines the performance and persistence of theses species in the ecosystem. Accordingly, research on the causes and consequences of changes in biodiversity is in the foreground. Effects of such changes on marine ecosystem stability and functioning and on the ability of a rich ecosystem to provide goods and services to humans are considered.

Particularly, life-history strategies and physiological performance in model- or indicator-organisms are determined in response to environmental changes such as temperature, eutrophication or UV-radiation. Process studies in the field are combined with controlled experiments in the laboratory. Here, the long term observation series on the abiotic and biotic environment have a second function: they serve as a constant reference in experimental studies. In this way the current situation in the field is constantly assessed and allows the direct iteration between laboratory and field measurements. Appropriate parameterisation for predictive modelling and generation of future environmental scenarios is a further objective.

Based on a viral culture bank, the diversity of naturally occurring virioplankton is studied. Furthermore, abundance and seasonal variation of both virio- and bacterioplankton are determined by molecular tools.

The functions and uses of symbiotic relationships between bacteria and invertebrates are studied in a combination of basic and applied research. Firstly, symbiotic partners are identified and localised and their specific roles and activities are determined. Mediators are often secondary metabolites which can then be further used in pharmacological and agrochemical research.

The identification of key species in pelagic foodweb interactions is a primary objective. Species interactions and chemical communication within associations and consortia of organisms are a major point of focus. In the seasonal succession of bacteria, phytoplankton and zooplankton the biotic interactions are still not understood and therefore studied. The spatio-temporal dynamics in the pelagic communities are analysed with respect to major driving factors such as the seasonal temperature and light regime, as well as currents and nutrient concentrations. Case studies in benthic-pelagic coupling, e.g. in mero-plankton, complement the truly pelagic aspects,

Shallow-water coastal ecosystems on rocky shores are structured by seaweeds, which form dense submarine forests. These rich benthic communities serve as habitat, nursery and feeding grounds for various invertebrate taxa, some of them with high economic relevance. Seaweeds themselves are utilised in industry for production of food and phycocolloids. Multi-culture techniques will be applied in future windfarm-fields off Helgoland.

Besides classical biotope mapping procedures airborne remote sensing techniques for macroalgal dominated hard bottom communities will be applied for the long-term survey of biotope complexes. Digital geo-referenced airphotos with high resolution shall enable the generation of a digital elevation model of the littoral zone. The latter shall be used to simulate exposure duration to air during low tides and its implications for specific communities, seen under the scope of elevated flood tide levels. GIS tools help to visualize and quantify change in biotope areas.

Detailed studies are carried out on the physiology, life history strategies and species competition of typical pelagic and benthic invertebrates, particularly crustaceans, being also compared in various climatic zones in other shelf-seas. Applications relate to mariculture-techniques in shrimp and lobster. The response of individual key species will be studied from the molecular, cellular and organ level. Chemical communication is a relevant theme in this respect. The interaction between seaweeds and their associated fauna will also be studied and quantified through a combination of field and laboratory based experiments.

Biodiversity and Ecosystem Function

The research is coordinated with all national marine research institutes in Germany and also bears a strong European component. In the latter respect, comparative studies of functional diversity along latitudinal and longitudinal gradients of climate, salinity or pollution is envisaged, based on cooperations with a multitude of European marine stations.

New findings are disseminated in numerous university-courses held at the especially equipped station, including accommodation of international guest-researchers. Furthermore, ecological advice is offered to political bodies as well as stakeholders aimed at establishing an integrated shelf seas management.

I thank my BAH-colleagues for contributing ideas and text.

Aspects of biodiversity and ecosystem functioning of marine microbes

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More than a century ago it was suggested that for microorganisms it applies that "everything is everywhere" meaning that a given microbial species will occur anywhere on the globe, provided that its habitat requirements are met. Recently this has been studied in detail especially with respect to eukaryotic microbes (protists). It was attempted to identify all eukaryotic species within a 2 ha area in a marine shallow-water area. Among them – altogether about 700 species – 80 % measure <1mm and about 65% are unicellular. In contrast – on a global scale organisms measuring <1mm constitute only about 15% of all described marine organisms and only about 10% are unicellular.

The fraction of locally recorded species with a demonstrated cosmopolitan distribution increases with decreasing size, so that among species measuring 1 mm about 50% are cosmopolitan and most of the identified protists (<1 mm) are cosmopolites. Due to under-sampling of small species (protists and meiofauna) in many parts of the globe, the fraction of species with cosmopolitan distribution is probably an underestimate.

The reason for this pattern is attributed to the huge absolute population densities of microbes. This means that dispersal is very effective whereas local extinction of populations is a very rare event. In accordance with different versions of "neutral community models" this predicts ubiquitous distribution and a flat species-area curve.

It was also demonstrated that for any particular habitat that – in addition to numerous thriving species populations that are readily recorded – there is always a large pool of rare species that will increase in numbers whenever habitat properties are changed, e.g., the availability of other types of food particles, changes in salinity, temperature, oxygen tension, etc.

The findings were discussed in terms of species concepts for microbes. Evidence was presented to show that for sexual out-breeders, isolates of nominal species from different continents are interfertile. In the case of asexual (clonal) forms a biological species concept does not apply and substantial genetic distances may be expected within nominal species. However, there is so far no evidence to suggest that different genotypes show any biogeographical patterns, but this is not yet fully established.

Some nominal species of protists appear to have a wide tolerance range (e.g., they occur in hyperhaline, marine, as well as limnic habitats). Experimental studies on isolates from different habitats and continents indicate that in such cases, individual isolates also display a wide tolerance. Thus an isolate of the ciliate *Cyclidium glaucoma* from the Sound grows equally well in salinities ranging from freshwater to 90 ppt. An isolate of the ubiquitous ciliate *Uronema marinum* from Greenland could grow at temperatures ranging between about –1°C and 38°C.

Together these findings have profound implications for microbial community ecology. It is a central tenet that the composition of biotic communities is contingent on a variety of factors (historical, stochastic local extinctions, size of the regional species pool, etc) – and that this may affect ecosystem functioning. In the case of microbial communities this may not apply: their composition is solely determined by the properties of the habitat - and ecosystem functioning is in principle predictable on the physical and chemical environmental properties.

Scaling up: the role of species and habitat patches in ecosystem functioning

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Complex scientific questions are often addressed through simplifications. This has certainly been the case in the debate about biodiversity and ecosystem functioning. Often some attribute of ecosystem functioning is plotted against biodiversity (usually number of species) (e.g. Emmerson et al. 2001; Tilman et al. 2001; Wardle 2001). Where theory and conjecture has moved into empirical studies this simplified bivariate approach has been followed. Unfortunately, in most instances a surrogate of an ecosystem process has been used; most often biomass as an index of productivity. A lively debate has ensued on the validity of this approach and the designs used. In essence, one structural attribute has been regressed against another – rather than the rate of an ecosystem process such as primary or secondary production (productivity), detrital decomposition, nutrient recycling or the balance of respiration and photosynthesis being considered as a response variable to a measure of biodiversity. This approach may be justifiable in terrestrial ecosystems such as grasslands, where material flow is largely local (e.g. leaves to soil locally).

Such an approach may not apply in many coastal and marine ecosystems. They are largely open and fuelled by import and export of material and exchange between populations via propagule dispersal. Little primary production is consumed at the place of origin, especially on rocky coasts, and the nature of coastal and nearshore ecosystems is driven by a multiplicity of environmental factors such as currents, upwelling, waves and coastline complexity. There are often sharp physical gradients affecting ecosystem processes and strong biological interactions with a few species or functional groups have disproportionate effects.

Rather than a simplistic solely reductionist approach a more holistic systems-based philosophy to the biodiversity-ecosystem functioning debate should be adopted. It is important to see where biodiversity fits in with the multiplicity of other factors (see fig.1) that are known to determine ecosystem functioning in coastal and nearshore systems. Oceanographic and biogeographic context, physical environmental gradients, propagule supply plus post-settlement biotic interactions all determine biodiversity in a location. This biodiversity further interacts with the physical environment and material imported (phytoplankton, detritus) and exported (dissolved and particulate matter). Thus, the biota in a defined place interacts with environment to shape functioning of the ecosystem and its emergent properties.

For open systems, species diversity may be too fine a scale of resolution to investigate the importance of biodiversity on ecosystem functioning. In particular, higher levels of biodiversity implicit in the Rio Convention, such as habitat patch diversity, warrant more attention. Interestingly, the importance of landscape (seascape) units of diversity have long been appreciated by conservation agencies leading to vegetation and biotope classifications. In open systems physical transport integrates ecosystem processes over broad scales. The challenge is to scale up resolution of biodiversity to encompass the appropriate broad scales over which ecosystems operate in open coastal and nearshore systems.

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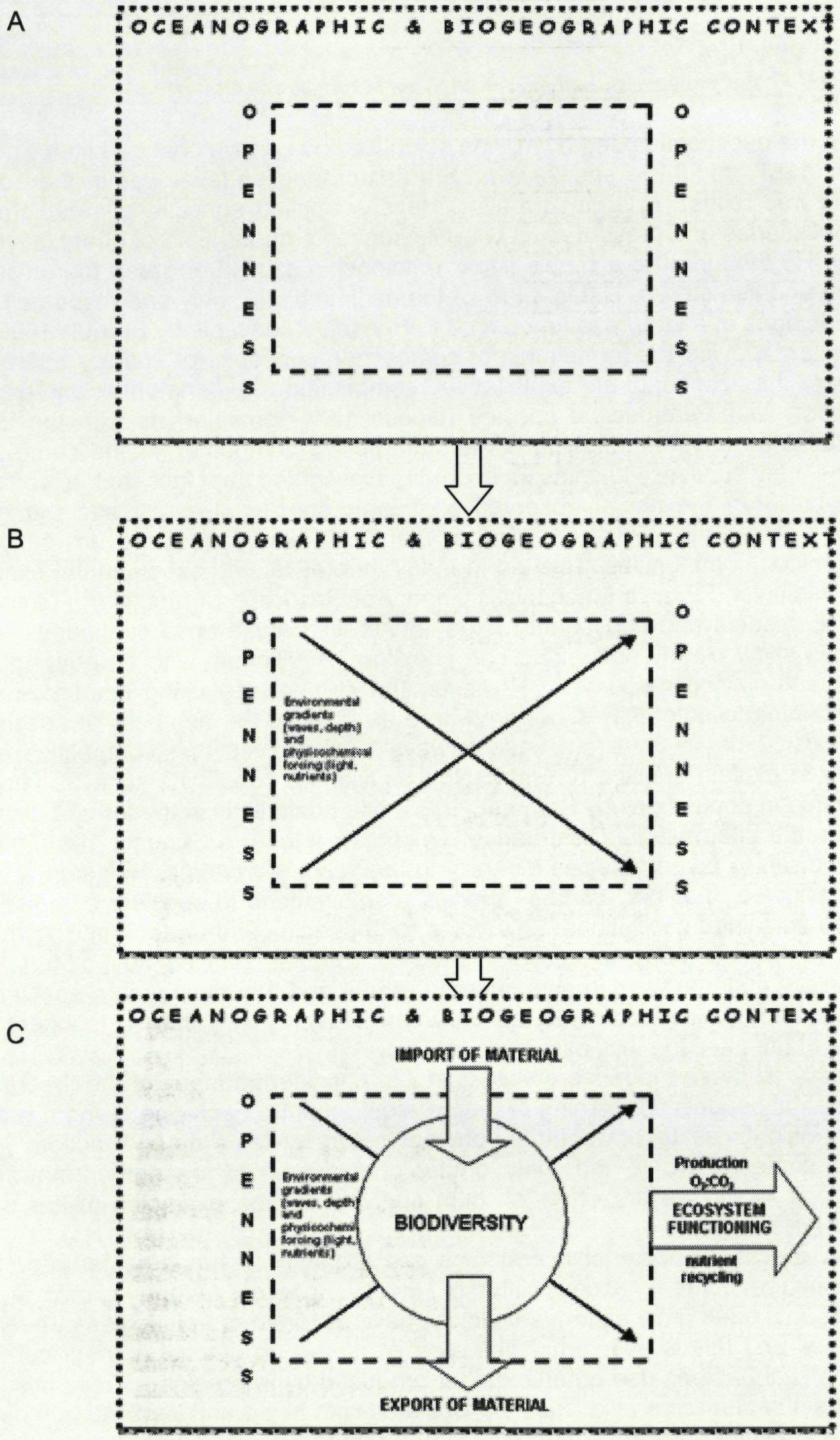

Figure 1
Stages in considering the role of biodiversity in ecosystem functioning in coastal and nearshore ecosystems: oceanographic and biogeographic context (a), interact with local and environmental gradients and physico-*chemical forcing* factors (b) to determine the biodiversity of the system (c). This is turn interacts with the physical environment to determine ecosystem functioning. Rates of flow of material in and out of the system can be crucial.

Nutrients and phytoplankton biodiversity

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Some of the questions posed by marine scientists today have changed little since Victor Hensen, 1887, sought to answer what the fish production level was in the ocean and how this was related to organic matter. Hensen applied agricultural paradigms to the study of fisheries and presented us with his concepts on the field of quantitative marine ecology. He thought that a simple linear relationship existed between the environment, plankton and fish stocks. Liebig´s law of the minimum, i.e., only one resource limits the growth of algae at a time, was introduced to Hensen´s concepts by Brandt (1899).

Liebig´s law allowed the formulation of competition concepts for species interactions in particular the concept of exploitative competition. Experiments on exploitative competition with *Paramecium* species (Gause 1934) provided us with the Exclusion Principle: in an environment with numerous species competing for the same resource only one can survive. Hutchinson in 1961, highlighted the fact that a contradiction existed between the actual observed planktonic species diversity and the exclusion principle. Thus, the "Paradox of the Plankton" was introduced to our view of phytoplankton communities. This led to many theoretical and experimental experiments and in particular Tilman's Mechanistic Theory of Resource Competition (Tilman 1982). Tilman´s models and subsequent experiments with algae on a continuous supply of resources show clearly how algae can coexist at equilibrium with an equal number of species and limiting resources. However, the number of limiting resources available (from vitamins to nutrients) is not anywhere as high as the numbers of species which can coexist. Indeed, there are several ways to circumvent the competitive exclusion principle to explain species diversity. Non equilibrium conditions such as imposed on phytoplankton populations by Sommer (1985) and particularly in the form of disturbance; based on the Intermediate Disturbance Hypothesis (Floder & Sommer 1999) have been clearly shown to favour species diversity in macrocosm systems. Huisman & Weissing (1999) showed that for certain species combinations 3-species competition can generate sustained oscillations. This holds for 9 species and up to 4 limiting resources. With 5 resources many simulations showed irregular species fluctuations. Species replacement patterns were shown never to repeat and that each time a species tried to dominate another invaded. This led Huisman & Weissing (1999) to suggest that the paradox of the plankton was essentially solved.

Undeniably all these models are very useful in considering many of the theoretical and experimental aspects concerning resource requirements. Each one of them will provide us with insights as to how nutrient-phytoplankton systems could function. However, when it comes down to the "nitty gritties"of explanations on nutrient-phytoplankton interactions *in situ* we are often left high and dry. Some examples of this some are outlined here.

The fact that algal bacterial interactions are probably of fundamental importance to phytoplankton nutrient accessibility is mostly ignored. Algae grown in axenic environments often grow either very slowly, have distorted morphologies or even will not grow at all and this is even when the alga is offered an optimal nutrient combination. We know that bacteria use organic matter produced by living algae. Thus, it is plausible that certain bacteria are also closely associated with algae and involved in their nutrient uptake and availability.

Zooplankton algal interactions are also linked in an intricate manner. The obvious is of course the classic view of zooplankton grazing on algae and thus, effecting the release of nutrients from attacked and digested cells. However, algae also can pass the gut of their predators unharmed (Aberle and Wiltshire in prep) and this might be seen as a means to picking up nutrients. Indeed, similar to K. Porter (1976) we have shown (Wiltshire & Boersma in prep.) that phosphorus limited algae can pick up phosphorus on their passage through zooplankton after ingestion. Another aspect to be considered is the fact that the presence of zooplankton can cause changes in algal morphology, making the algae almost unrecognisable in the classical sense (see fig 1) . This has been particularly well documented for *Scenedesmus-Daphnia* interactions and been attributed to the excretion of urea by the *Daphnia*. (Wiltshire & Lampert 1999). Recently we have found that copepods can have a similar effect on marine diatoms (see fig 2), whether this is a result of excretory nutrients remains to be seen. Regardless of the mechanism involved, these interactions result in an increase in cell size and potentially a higher sinking rate and thus, a quicker loss of these algae and carbon from the pelagic

Biodiversity and Ecosystem Function

zone. This could have implications for our views on nutrient cycling and budgets in pelagic systems.

Perhaps the most important aspect when trying to understand nutrient- phytoplankton interactions is the question of scale (see Smetacek & Pollehne 1986). This should not only be considered in terms of organism- organism interactions in food webs but also time. Are we interested in hourly changes such as the production of mucous by algae as a result of excess photosynthesis and depletion of nutrients, or are we interested in days-weeks which are the time scales for grazing effects? In terms of regional global considerations, e.g., in the recycling of bottom sediments or input from terrestrial sources we are dealing with years- thousands of years.

There is a need to carefully consider the scales we are interested in when examining phytoplankton-nutrient interactions. Food web and ecosystem interactions of organisms, as well as phytoplankton succession often cannot be simply explained by existing models because their scales (organism and time) do not fit. It is time rethink some of our modelling concepts on nutrient-phytoplankton interactions and break away from of the classical views of nutrient cycling.

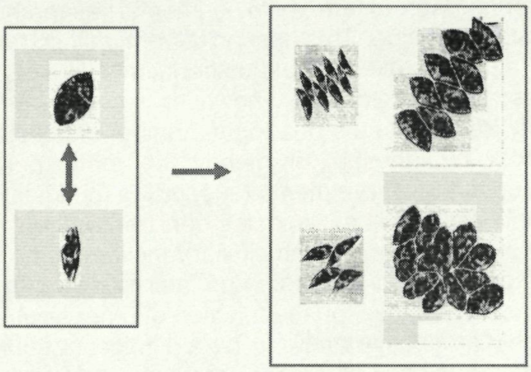

Figure 1
Induction of *Scenedesmus* morphs by *Daphnia*

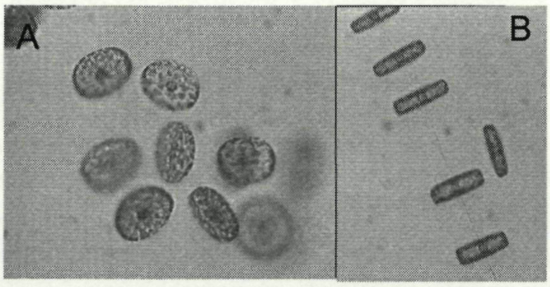

Figure 2
Induction of *Thalassiosira* morphs (B) by copepods

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Biodiversity and ecosystem function: distinguishing between effects of the number of species and their identities

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Given high rates of extinction and potential loss of ecosystem 'goods and services', there is a clear need to understand the consequences of loss of biodiversity for the functioning of ecosystems. Although documented global extinctions are rare in the marine environment, local extinctions and dramatic changes in abundance are widespread. To maximise the practical value of research into effects of loss of species, it should be targeted, where possible, towards species that are threatened by such local extinctions and whose loss may affect provision of important ecosystem goods and services. Tests of theories predicting consequences of loss of diversity require complex experiments, however, and can only be done in tractable systems. Ideally, research should be done on systems that are both relevant and tractable.

In recent years, there has been extensive experimental research into effects of loss of biodiversity on ecosystem function. This has included highly controlled manipulations in mesocosms and, to a lesser extent, field experiments in less controlled but more realistic circumstances. It is not yet clear, however, whether reductions in ecosystem function in low diversity treatments are due to the number of species present (supporting the rivet or redundancy hypotheses) or merely the reduced likelihood of including particular ('key') species in those treatments (supporting the idiosyncratic hypothesis). It has been proposed that loss of some species can be compensated for by increased abundance or activity of other species with similar functions – the insurance hypothesis. There have also been calls for more research on inter-trophic effects – testing effects of losing species from one trophic level on the function of other trophic levels.

Rocky shores are highly productive and can be a significant source of detrital material underpinning coastal food webs. The primary productivity of rocky shores comprises a microalgal and a macroalgal component. Much of the microalgal component passes directly into an often diverse assemblage of local primary consumers, whereas macroalgae are more likely to be dislodged and supply detritus to coastal food webs. Changes in cover of macroalgae are therefore likely to affect significantly the flow of energy from rocky shores to the coastal ecosystem as a whole. Grazing gastropods have been shown to affect cover of macroalgae on many shores and are convenient for experimental manipulation. Furthermore, several species are exploited or known to be sensitive to pollution and are therefore likely to suffer dramatic local reductions in abundance.

We have set up a field experiment to test whether loss of diversity of grazers will affect the diversity and cover of macroalgal communities at a shore on the west coast of Ireland. The experiment is designed to distinguish between the effects of reducing numbers of species and the effects of losing particular species. Treatments were also incorporated to enable a test of the insurance hypothesis. These treatments involved the replacement of lost species with an equivalent biomass of the other experimental species. From an assemblage comprising gastropods, chitons, mesograzers, urchins and perhaps also fish, we simulated loss of combinations of three species of gastropod: *Patella ulyssiponensis*, *Littorina littorea* and *Gibbula umbilicalis*. *Littorina* are widely harvested for food on Irish shores; patellid limpets are exploited in other countries and are known to be sensitive to oil pollution. Experimental assemblages of differing diversity, biomass and/or identity of grazers were maintained in cages. The cages excluded urchins and fish, but smaller gastropods, chitons and mesograzers remained part of the assemblage. Comparisons of two treatments with corresponding uncaged controls showed that there were no artifacts of cages on algal diversity and cover.

Preliminary results collected four months after the start of the experiment suggest that it is the identity rather than the number of species present that most strongly affects ecosystem function in this case. The limpet *Patella* has a particularly strong effect on algal communities and its loss, alone or in combination with other species, affects total cover of algae. This result supports the idiosyncratic hypothesis. It is also apparent, however, that the function of *Patella* could potentially be fulfilled by increased densities of *Littorina* and *Gibbula*, as predicted under the redundancy or insurance hypotheses. Different outcomes may emerge as the experiment progresses, however. At this stage, the only significant difference in structure of algal communities is between plots with all grazers present and those with all three gastropods removed. Where the three species have been removed, ephemeral algae (*Ulva*, *Enteromorpha*) have become more abundant and cover of some perennial algae (*Fucus spiralis*, *Ceramium rubrum*) has been somewhat reduced.Given differences in radular morphology and feeding preferences of the grazers, it is anticipated that such effects may become more apparent with algal settlement and growth and increased grazing during the spring and summer. A final destructive sample will be taken one year after the start of the experiment to test differences in biomass of algae.

At this stage, the experiment leads us to conclude that it is the loss of key species that matter in this system rather than reductions in diversity *per se*, but that the function, even of key species, can potentially be taken up by other species if they increase in density. It should be noted, however, that this experiment is tackling effects of variations at only one trophic level on only one ecosystem function at one place during a discreet period of time. Clearly, it does not enable prediction of effects on other functions or under the full range of environmental conditions that may arise over time. Modelling approaches are undoubtedly needed to make predictions involving multiple trophic levels, large-scale ecosystem functions and changes in environmental circumstances (both physical and biological). However, experimentalists must be guided by such models to test key assumptions and predictions and to clarify the mechanistic links that must underly them. An integrated approach is needed for such experimentation, harnessing both the convenience and control afforded by mesocosms and the relative realism of field studies. Longer term manipulations are also needed to assess ecological responses over long periods of variable circumstances and to test effects of diversity on other aspects of ecosystems, such as stability and invasibility.

Note: details of the other experiment referred to can be found in the proceedings of the first conference in this series, held in Corinth in May 20

Biodiversity and Ecosystem Function

Function of cold-water *Lophelia* coral reefs as fish habitat in coastal and deep-seas

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Lophelia pertusa.

(Photograph by Andre Freiwald)

Lophelia as a habitat

The cold-water coral, *Lophelia pertusa*, is colonial, predatory, grows at a few millimetres per year, and can form reefs kilometres long and tens of metres high. Since the mid-1990's underwater video surveys have been discovering *Lophelia* reefs off the coasts of Norway, Scotland, Ireland, Gibraltar Straits, off west Africa, and in the North-western Atlantic. It is recorded from the southern Atlantic, Pacific and Indian oceans (Figure 1), so it is likely that further video surveys will discover more reefs. In the north-east Atlantic, Lophelia is recorded from 40 to over 1,000m depths. Especially in deeper waters there is little other three-dimensional habitat. Therefore Lophelia pertusa is an important habitat because it is widespread, forms reefs, and occurs in areas where alternative habitats are very limited or absent.

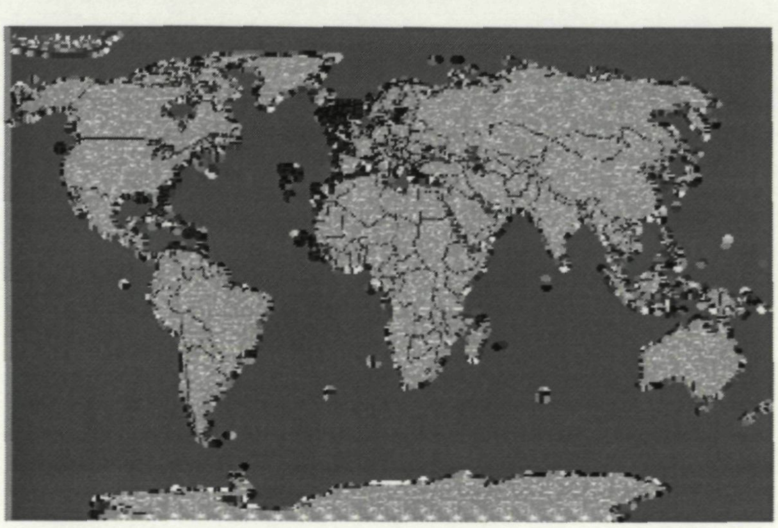

Figure 1
The distribution of *Lophelia pertusa* plotted from literature reviewed by Rogers (1999).

We studied fish associated with *Lophelia* in the North-east Atlantic, at 11 study sites at 8 locations; namely the Trondheimsfjord and Sula Reef in Norway, Kosterfjord in Sweden, Darwin Mounds west of Scotland, Rockall Bank, Rockall Trough and Porcupine Seabight off Ireland, and associated with a shipwreck west of Shetland.

Biodiversity and Ecosystem Function

Video (80 hours) and still (15 reels) photographs were collected from six different sampling platforms: (1) the manned submersible JAGO; (2) Remotely Operated Vehicles (ROV); (3) the "Hoppercamera" suspended below the survey ship as it drifts; (4) the Wide Angle Survey Photography (WASP) platform suspended below the survey ship and towed at ca. 0.5 knots; (5) the Seabed High Resolution Imaging Platform (SHRIMP) suspended below the survey ship as it drifts; (6) the "Bathysnap" platform deployed on the seabed from the survey ship using a freefall method and left in situ for a period. Sampling effort was standardised by duration of observation.

These methods were very effective in the identification of fish to species level; 90% of fish were identified to species level and 6.6% to genus or family level. Only 3.6% of the fish were not identifiable. A guide to the fish is given at www.ecoserve.ie/projects/aces/.

Twenty-five species of fish from 17 families were recorded over all the sites (Table 1), of which 17 were of commercial importance and comprised 82% of fish individuals observed. These commercial fish species contribute 90% of commercial fish tonnage in the North Atlantic.

Table 1
The families, species and numbers of fish recorded in this study.

Scyliorhinidae
Scyliorhinidae indet. 2
Scyliorhinus stellaris 3
Rajidae
Raja sp. 1
Raja fyllae 1
Chimaeridae
Chimaera monstrosa 52
Noatocanthidae
Notocanthus sp. 28
Synaphobranchidae
Synaphobranchus kaupii 402
Macrouridae
Macrouridae 17
Coryphaenoides rupestris 10
Moridae
Moridae 227
Lepidion eques 21
Gadidae
Gadus morhua 81
Melanogrammus aeglefinus 2
Pollachius virens 925
Trisopterus luscus 10
Trisopterus minutus 27
Lotidae
Brosme brosme 49
Molva molva 266
Phycidae
Phycis/Urophycis 1
Lophiidae
Lophius piscatorius 9
Oreosomatidae
Neocyttus helgae 5
Sebastidae
Helicolenus dactylopterus 2
Sebastes viviparus 1317
Cottidae
Icelus bicornis 1
Micrenophrys lilljeborgi 1
Zoarcidae
Lycodes vahli 3
Anarhichadidae
Anarhichas lupus 3
Pleuronectidae
Hippoglossus hippoglossus 1
Microstomus kitt 7

Multivariate analyses divided the fish into distinct deep (> 600m depth) and shallow (< 400m) water assemblages at both the species and family level. In both assemblages, fish were associated with particular habitats. Overall, 69% of the fish species and 79% of individuals were associated with the reefs; either as the reef or its immediate coral debris and transitional zones. Few fish were observed over the adjacent seabed although most video was from this habitat.

Like other three-dimensional habitats, *Lophelia* reefs provide a feeding ground, refuge from predators, and breeding ground for fish. This study thus shows that *Lophelia* provides a very important fish habitat at both local and regional scales, and perhaps ocean scales. Its importance was previously overlooked because of the lack of appropriate sampling in deeper continental shelf and slope waters.

Acknowledgements

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Conservation and Restoration of Biodiversity

Chaired by
Anthony Hawkins

Restoration of estuarine biodiversity and function

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Estuaries are geologically young and dynamic. At most developed coasts they have been significantly altered by human impacts. Overriding changes have been the embankment of estuarine marshes and the deepening for shipping with cascading effects on estuarine hydrodynamics, morphology and the biota. The gradual transition between marine, limnic and terrestrial biota became steeper, truncated and squeezed. Habitats changed and became fragmented. The ecological retention and filtering capacities between the land and the sea declined.

These developed estuaries cannot adapt to ongoing or accelerating sea level rise, and thus are not sustainable. Attempts to preserve remnant habitats under these circumstances are difficult. It is more promising to develop an integrated plan for habitat restoration at the scale of entire estuaries. A first step to let estuaries adapt to a rising sea level is to relocate ports from the head of estuaries into offshore positions in order to keep out large vessels which require unnatural depths. Sedimentation at the bed of the estuary should be allowed to keep pace with the rising level of the sea.

The second step is to provide more space for tidal waters as well as storm tides. This can only be partially fulfilled in a populated landscape, and should concentrate on the lower parts of the embanked marshes. These are to be flooded in a through-flow system, while sea walls and storm surge barriers are maintained to protect other parts from flooding. The loss of arable land may be compensated for by attractive waterside housing and recreation along these created side arms of the estuary.

A third step mitigating the effects of sea level rise at a fixed coastline, may be feeding the shore with sediment from offshore areas. In front of sea walls, a physical buffer of sand bars, islets, sandy hooks and beaches serve as soft analogues to the hard and inflexible groynes and other shoreline petrifications. These soft structures have the advantage to directly feed the sediment hunger caused by sea level rise.

The combination of such measures may keep the costs of flood defences low, help to maintain a competitive economy, and recreate an attractive estuarine environment with a diversity of dynamic habitats. The overall aim is to foster natural processes which enable an estuary to adapt to sea level rise and to regain its brackish water biodiversity and its ecological retention and filtering function between the land and the sea.

Marine protected areas and biodiversity of temperate reef fish communities - A case study

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The structuring patterns of fish communities associated with coral reefs have been intensively studied in the past years. The development of accurate quantitative census techniques applied to long-term studies opened the door to studies of stability, resilience and the impact of disturbances in coastal reef fish communities. Regular monitoring of recruitment processes, combined with that of adults, is helping to assess the importance of stochastic and deterministic control mechanisms in different habitats and geographical locations. It is also helping to detect which life stages are most susceptible to the controlling factors limiting the populations of each species. Quantitative data on fish populations and new forms of habitat characterization, often combined with experimental manipulations, are helping to clarify the relationship between biodiversity and habitat complexity. Finally, these new monitoring methods are allowing the study of the impact of human activities, both fishing and habitat degradation, and are essential in the building of predictive models of drastic environmental changes, such as those likely to be caused by global warming, as well as in the planning, design and management of marine protected areas.

There are however few studies dealing with biodiversity, composition and dynamics of temperate reef fish, largely owing to the harsh environment of these habitats. Information on subtidal fish communities is available for only a limited number of sites, despite the fact that almost all important questions raised by coral-reef fish ecology are fully applicable to temperate habitats. On European shores, many of these studies have been carried out in the Mediterranean and more studies in the Atlantic and at higher latitudes are clearly needed. This applies especially to long-term studies with adequately standardized procedures. Such information is fundamental for comparative analysis between geographical locations and to distinguish between inter-annual fluctuations and long-term trends, such as those predicted by global warming. This applies in particular to ecosystems that are changing rapidly, because of either climatic change (in its broad sense) or habitat degradation.

The role of marine protected areas in preserving intact marine habitats, where these comparative studies can be performed in a meaningful way, is fundamental for evaluation and comparison with other areas where human activities are affecting the marine communities.

Our study area is a 30 Km stretch of coast on the west Portuguese shore that has recently been assigned as a Marine Park (Marine Park of the Arrábida Nature Park). From a biogeographical perspective, mainland Portugal is located in a transitional zone where many cold and warm water fish species reach their southern and northern distribution limits, respectively. This situation contributes strongly to the maintenance of a high level of biodiversity in the Lusitanian province, and also makes it very sensitive to climatic oscillations such as those predicted by Global Warming. In this study, we analysed the fish community composition in the marine reserve and ascribed a hierarchical importance for the coastal sectors and the different habitats present. A set of management measures is suggested. The aim of this research is to build a long-term database of the fish communities present in this area, assessing the main factors influencing its structure and distribution patterns and to monitor the reserve effects in a long-term basis.

A fuller understanding of the nature of reef fish assemblages and the processes responsible for their structuring and dynamics will be of direct benefit to managers, both those who manage reef fisheries and those who manage coastal rocky areas for conservation, tourism or other purposes.

Biodiversity and recolonisation of coastal systems

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Since the early 1970s, a functional group approach has been used by several authors to detect possible changes in algal communities. This study used such an approach, based on algae morphology, applied to the recovery of an intertidal rocky shore, following a major disturbance. In 1993, a landslide was followed by intensive engineering work on a wave cut platform at Scarborough (Yorkshire, England). Recolonisation was assessed by determining changes in the spatial heterogeneity of algal communities through changes in species functional group levels. A gridding interpolation method helped synthesising spatial and temporal processes that took place over the four-year study period. Use of the functional group approach was robust enough to recognise stages in the recolonisation processes and to determine the importance of seasonal climatic disturbances such as winter storms. Further work will be needed to better define the various groups and also to understand the role of invertebrate grazers on ecosystem recovery.

Modelling and Experimental Design

Chaired by
Karsten Reise

Diversity in different dimensions

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Current research on biodiversity focuses almost entirely on species numbers and on the consequences of changes in species numbers on ecosystems functioning. A number of recent studies emphasize the importance of spatial diversity in terms of self-organized spatial structuring on ecosystem functioning. Insights on the importance of spatial structures have primarily been obtained from ecosystems with regular patterning. These patterns are found, for example, in arid grasslands, peat lands and intertidal mudflats. A unifying principle may explain these patterns across different ecosystems: scale-related differences in facilitating and competitive interactions between organisms. Theoretical models suggest that spatial interactions that form the basis of these patterns increase the resilience against disturbances and increase the productivity of ecosystems. These studies emphasize the importance of aspects of biodiversity other than species numbers, such as spatial structuring, in the conservation and restoration of natural systems.

Linking biodiversity and ecosystem models

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Ecosystems are large and complex entities within which biodiversity exists. Biodiversity is not generally a clearly defined concept in practical terms and its role in ecosystems, and therefore its importance to man, is often assumed rather than understood. The 'goods and services' that ecosystems supply to mankind such as the sequestration and cycling of carbon and nutrients, the provision of which biodiversity is often assumed to influence and sustain, are generally large-scale processes. There is no framework for arriving at sensible decisions concerning biodiversity and ecosystem functioning at the appropriate scales.

Much of the rationale used to justify studies of biodiversity and ecosystem function focuses on providing information to assist decision making in practical applications. In order to understand complex problems systems analysis is a useful framework of thought, primarily aimed at helping decision makers choose appropriate courses of action. Systems analysis is the orderly and logical organisation of data and information into models, which represent formal expressions of essential elements of selected problems in physical or mathematical terms. This is followed by the rigorous testing and exploration of these models to validate and improve them. Model outputs may then be used to evaluate alternative courses of action, leading to the implementation of the results. Central to the process are models, and in a systems analysis context experiments are embedded in a conscious effort to model the system in question.

There is a huge variety of types of models appropriate to studies aspects of the relationship between biodiversity and ecosystem functioning. Among them are complex dynamic models, such as biomass functional-group ecosystem models. Such a model may be considered as a series of interacting physical, chemical and biological processes represented mathematically, chosen to include all those processes which may significantly influence ecosystem dynamics, that together exhibit a coherent system behaviour. State variables are chosen to keep the model relatively simple without omitting any component that has a significant influence on the energy balance of the system. The biotic components are aggregated groups representing basic functional roles (production, consumption and decomposition), divided into size classes to form a food web. Physiological processes and population dynamics are described by fluxes of carbon or nutrients between functional groups. Much effort has been put into the development of such models, and coupling them to complex physical models, over recent decades. The latest generation of such coupled models accurately reproduce large-scale dynamic ecosystem processes, and pilot forecasting systems for ecosystem processes at large spatial scales are under development.

So where does biodiversity come into the picture? The short answer is that it does not. Functional group models assume that whatever compositional changes occur within each functional pool over time they are not large enough to cause substantial and persistent errors in the prediction of pool scale rate processes. Another way of putting this is that biodiversity simply represents noise in the system. The models have been extensively validated using many data. Sensitivity analysis has been applied to search for high-leverage variables which significantly influence system behaviour. Neither activity has identified biodiversity (except in the broadest context of relative biomass in functional groups, physiological and size divisions) as being important. This implies that in the real world biodiversity is of little consequence to gross ecosystem functioning in coastal and oceanic marine ecosystems. Ecosystem modellers do, however, accept that large-scale functional group models do not reproduce accurately the behaviour of higher organisms (large zooplankton > motile epibenthos > fish), especially where active migration and functional switches during life occur. This implies that biodiversity research should focus on the ecology of higher organisms (matching societal perceptions of what biodiversity means to them) rather than lower organisms whose contribution to ecosystem processes, for which they are almost entirely responsible, can adequately be modelled.

Large-scale models, however, offer many advantages to researchers interested in large-scale long-term changes such as alterations in fishing pressures or climate modification, which may be expected to impact biodiversity but which cannot adequately be addressed by reductionist experiments. For biodiversity to be explicitly and accurately included in such models we would need to be able to represent relationships between biodiversity and ecosystem processes mathematically. At present we do not even know that such relationships exist with any degree of certainty. Strategies for linking the outputs of complex ecosystem models to biodiversity data (at the species and community levels) collected in the real world are described which may offer an indirect but powerful route to coupling large-scale and/or long-term data to models in order to examine the possible consequences of change. The approach also offers the potential of exploring the influences of processes which may be modelled but which are difficult to measure at appropriate spatial scales, such as fluxes of detritus and nutrients at the seabed, on the development of marine benthic communities.

Modeling ecosystem consequences of species diversity and distribution: a case study addressing multi-species aquaculture in China

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Areas of intensive multi-species aquaculture represent excellent experimental opportunities for the development and validation of models that simulate effects of species composition and distribution on ecosystem functions. Asia in particular has a long history of combining different species in polyculture, which embraces principles of ecological engineering within integrated farming systems, enhancing both productivity and sustainability through the utilisation of waste products from one species by another. A large-scale ecological simulation from recent project funded within the European Commission's fifth framework programme has been undertaken for one such site at Sanggou Bay in Northern China. The simulation integrates separate hydrodynamic, biogeochemical and biological models in a common two-dimensional grid to predict and compare the ecosystem consequences of different scenarios for combined long line cultivation of the Chinese scallop *Chlamys farreri*, the Pacific oyster *Crassostrea gigas* and the kelp *Laminaria japonica*.

Outputs confirm that we are able to simulate the general behaviour of key ecosystem variables, both in space and time. They also illustrate how very sensitive total production can be to changes in the composition, densities and/or distributions of dominant cultured species. For example, the highest total combined yield for oysters and scallops is predicted upon avoiding inter-specific competition between different shellfish species through the combined culture of scallops with kelp. Changes in the local densities of separate cultured species may also have effects at the bay scale. In this, it has been important to consider degrees of spatial and temporal resolution, adjusting each according to different modelling requirements. Increased spatial resolution did not necessarily improve overall accuracy. Alternatively, spatial variations in shellfish growth that we modelled using our detailed 2D description of small-scale hydrodynamics would otherwise have been masked using a whole-system approach.

Accounting for complex temporal and spatial interrelations, integrated simulations of this type offer great potential for helping to predict and understand how species assemblage and distribution affect ecosystem functioning and productivity. Certainly, they have helped to synthesize knowledge of ecology in Sanggou Bay. Given the object-orientated architecture of these models, they may easily be adapted to include different species or functional groups. In addition, where including stake holder's societal and economic interests as further objects, such integration is unquestionably facilitating more sustainable management of our natural resources.

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The experimental analysis of biodiversity: the importance of identifying tractable questions

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There is an increasing demand to ecologists to anticipate the consequences of loss of biodiversity and to provide remedial actions for its conservation. This requires a better understanding of the extent to which biodiversity is causally related to productivity, stability and other aggregate properties of natural systems. Manipulative experiments are increasingly used to unravel these causal links in terrestrial and aquatic habitats. Although most studies have succeeded in identifying a relationship between biodiversity and some functional property of the manipulated system, experiments often fail to provide a mechanistic explanation of this relationship. In this paper I discuss previously recognized shortcomings of experimental analyses of biodiversity and less appreciated pitfalls in design and logical structure. Possible solutions are offered, but logistical constraints pose severe limits to the amount of realism that can be added to experimental manipulations of biodiversity.

The basic design of an experiment on biodiversity involves comparison of a response variable across treatments of increasing number of species or groups of species. The prediction is that the value of the response variable increases as diversity increases. The results of these experiments are generally criticised on the ground that apparent effects of biodiversity may occur due to 'sampling/selection effects'. These effects are likely if only few species in the assemblage can have a large effect on the response variable of interest. In this case the high-diversity treatment has a greater chance to include one or more important species compared to the other treatments. This is a realistic scenario when the morphological, physiological or life-history traits that contribute most to the response variable are unevenly distributed across species and only few species possess these traits. The effect of diversity of species is confounded with that of identity of species in these circumstances. Hierarchical designs have been proposed as a possible solution to this problem, with replicate assemblages nested within each level of diversity. Replicate assemblages are generated by choosing species randomly from a common pool for each level of diversity. However, there is always a larger number of possible selections in the high-diversity treatment compared to the low-diversity ones in balanced designs. Thus, sampling/selection effects may still occur when there are replicate assemblages within each level of diversity. In order to explore this possibility, I used a Monte Carlo procedure to simulate the effects of experimental manipulations of biodiversity (number of species) on primary productivity, with species drawn randomly either from a log-normal distribution (to simulate the uneven distribution of relevant traits) or from a uniform distribution (to remove the possibility of sampling/selection effects). The probability of Type I errors under the null hypothesis of no effect of diversity was determined from sets of 1000 simulations for each distribution of traits. Simulations were repeated for different numbers of replicate assemblages within each level of diversity for simple (2, 4 and 8 species) and complex (6, 12 and 24 species) assemblages. Having no replicate assemblages resulted in rates of Type I errors between 0.795 (simple assemblage) and 0.972 (complex assemblages), when traits followed a log-normal distributions. In contrast, Type I error was very close to the nominal value of 0.05 for traits that were distributed uniformly across species. Having two replicate assemblages greatly reduced the problem for unevenly distributed traits, but the probability of rejecting a true null hypothesis was still larger than the nominal value of 0.05. Surprisingly, increasing the number of replicate assemblages (from 2 to 8) within each level of diversity further increased the rate of Type I errors (from 0.08 to 0.15). In contrast, the probability of rejecting a true null hypothesis of no effect of diversity was always close to the nominal value of 0.05 for traits that followed a uniform distribution. Therefore, having several replicate assemblages nested within each level of diversity did not solve the problem of sampling/selection effects in the simulated experiments. In real experiments, in contrast, having a large number of replicate assemblages is desirable to increase the statistical power for the main effect of diversity.

A second problem with the experimental analysis of biodiversity is the possibility of confounding the effect of number of species (or higher taxa) with that due to differences in relative density of species (taxa) across treatments. This occurs because the relative abundance of each species must be reduced as diversity increases to maintain overall abundance constant across treatments. Consider a simple experiment consisting of treatments with one or two species. If treatments with one species are maintained at densities of 1 unit of A and 1 unit of B, then the treatment with two species includes 0.5 units of A and 0.5 units of B. This is common practice in experiments on biodiversity. This design confounds number of species and relative density across treatments, whereas overall abundance is controlled properly. Suppose that species A affects the response variable negatively when maintained at the density of 1 unit (e.g. through indirect interactions), whereas it has no effect at the density of 0.5 units. In this scenario an apparent effect of biodiversity would be detected when, in fact, the effect would be driven by changes in relative density of species. To accomplish this, the experimental design must explicitly include initial density (or biomass) as an crossed factor to diversity. That is, the effect of increasing diversity must be assessed under different levels of relative abundance of species. Thus, the relevant test to unconfound the effect of biodiversity from that due to changes in density of manipulated organisms, is the interaction between density and diversity. The null hypothesis of no effect of diversity is rejected if the effect of adding new individuals/biomass to a pre-existing pool of organisms is more pronounced when a change in density is also accompanied by an increase in diversity.

To be reliable, experiments on biodiversity must deal with the problem of sampling/selection effects and with the problem of confounding diversity with density simultaneously. This requires multifactorial experiments with diversity and density as fixed, crossed factors and assemblage as a random effect nested within levels of diversity and crossed to density. In order to achieve this, it is necessary to use a constrained random selection of assemblages. That is, once the species that made up the assemblages in the low-diversity treatment have been selected, these must also occur in the high-diversity treatments. Simulations based on this design showed that the rate of Type I errors for the density x diversity interaction was not inflated under the null hypothesis of no effect of diversity, even when effects due to changes in relative density of species where imposed to the data. These simulations also showed that the design was robust to sampling/selection effects, at least in the specific case being simulated, consisting of 4 replicate assemblages for each level of diversity. This is likely to be a consequence of the constrained random selection of species.

Although problems such as the sampling/selection effect and the issue of confounding diversity with density are explicitly recognized in the literature, it seems that most of the experimental designs that have been used to study biodiversity cannot cope with both problems simultaneously. Those experiments that incorporated replicated assemblages within levels of diversity did not provide a context to test for a diversity x density interaction and vice versa.

In conclusion, there is clearly a scope for improving experiments in which biodiversity is a predictor variable. This, however, requires articulated experimental designs that may be logistically difficult to do. For example, manipulating the relative abundance of species (or event that of morphologically similar species) would be problematic in assemblages of turf-forming algae or other assemblages with similarly complex spatial organizations. More tractable questions must be identified to understand biodiversity in these systems. Furthermore, there is also the need to provide better tests of hypotheses about the processes that affect patterns of distribution and abundance of species. Apparently, studies in which biodiversity is a response rather than a predictor variable are becoming old-fashioned. I argue that both approaches are necessary in order to make progress in this hot area of ecology, provided they focus on tractable questions.

General Issues

Chaired by
Mark Costello
Steve Hawkins

Socio-economic aspects of marine biodiversity

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Until recently the economy was considered to be an open system with infinite environmental resources available and indefinite economic growth was assumed. As environmental resources were not considered to be limiting they were not included in the economic accounts, and this 'free' availability has led to their over-exploitation. In recent years, however, the dependency of the economy on the environment has become increasingly apparent, and a closed system with finite resources, as depicted in Figure 1, is now thought to be a more accurate view of the global economy. It is now recognised that continued economic growth is dependent upon the sustainable use of environmental goods and services. This can be achieved only by incorporating the environmental system into economic decision making, and this, in part, is the aim of environmental economics.

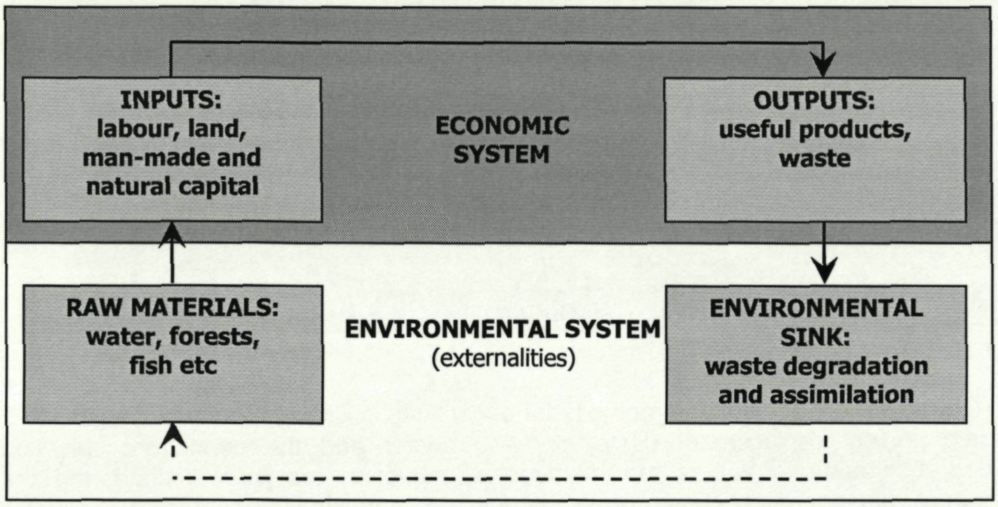

Figure 1
The Finite Environmental - Economic System (adapted from Milner - Gulland 1999)

The marine environment provides many goods and services of use to mankind through natural ecosystem functioning e.g. provision of food, regulation of waste and climate. The importance of different marine ecosystems and of the species, functional group and habitat diversity within them, for providing these goods and services varies between the systems. Provision of different goods and services is vulnerable to large, medium and small scale threats and again vulnerability varies between ecosystems e.g. estuaries and coastal shelf face more threats than deep sea ecosystems.

In the same way that marine biodiversity studies are integrated with other disciplines such as chemical and physical oceanography we now need to integrate with socio-and environmental economics to help strategic decision making and to communicate the importance of marine biodiversity to the public community. There are increasing funding opportunities for such interdisciplinary research and it is intellectually stimulating. In this presentation we will provide a very brief overview of some of the approaches which are employed by environmental economists, including monetary valuation, stakeholder analysis, multi criteria analysis and decision support systems.

Monetary valuation is a familiar and commonly used method. Valuing the environment in monetary terms allows the transfer of ecosystem functions and properties into the economic system and hence encourages inclusion of ecosystem properties and functions in policy and management decisions. Prior to undertaking a valuation study it is important to determine all the valued components of that environment, i.e. The Total Economic Value of an environmental resource which can be divided into its use value and non-use value, as depicted in Figure 2. A use value arises from humans actually using the environment, for example the coast for recreation, or a forest for timber. There are generally considered to be three types of use value:

Direct Use Values arise from the direct exploitation of the environment. The environmental functions listed under direct use are generally demand driven goods.

Indirect Use Values are benefits which are derived from the environment, without the intervention of man, for example climate regulation and waste degradation.

Option Use Value is the value associated with an individual's willingness to pay to safeguard a natural resource weighted by the probability that the asset will be used in the future

Non use values are representative of the value which humans bestow upon an environmental resource, despite the fact they may never use or even see it. Non use values are generally divided into two categories:
Bequest Value is the value the current generation places on ensuring the availability of a natural resource to future generations.
Existence Value is the value placed on simply knowing that a natural resource is there, even if it is never experienced. An example of this is the fact that many individuals would be willing to pay some amount to ensure the continued survival of polar bears, and other charismatic species, which they will never see, but they derive value simply from the knowledge of their existence.

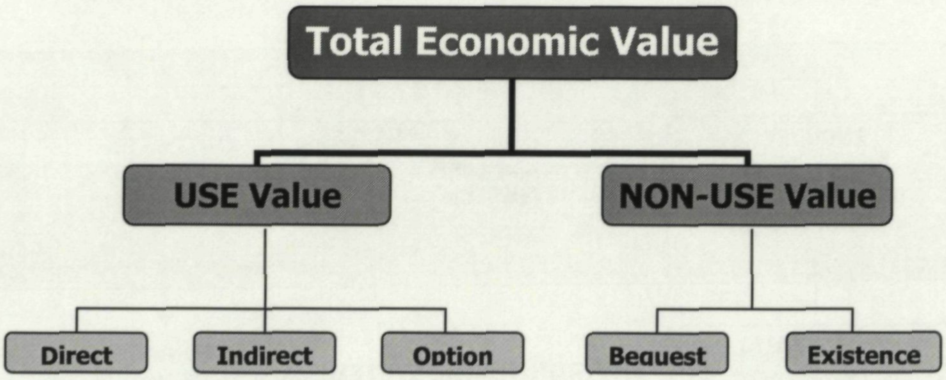

Figure 2
The Total Economic Value of Environmental Resource (adapted from Bateman & Langford 1997)

There are a variety of valuation methods for use values including the travel cost method, hedonic pricing, replacement costs, benefit transfer and the contingent valuation method. For non-use values the methods of valuation are more limited and the contingent valuation method is currently the only regularly applied approach.
Stakeholder Analysis identifies individuals or groups with an interest in an issue; they may be controllers, winners or losers, local, national or international. The aim of stakeholder analysis is to include all views in the management or valuation decision, to identify and resolve conflict and hence encourage acceptance of decisions made. Stakeholder input is achieved through structured interviews, focus groups and questionnaires.
Multi-criteria analysis is a management tool used to appraise different development options, and evaluate trade-offs between social, economic and environmental costs and benefits. It converts large amounts of information, often with a variety of different units, into consistent numerical values. There are a variety of models used but it is important to avoid those where the criteria used are not explicit and obvious.
Decision support systems are a synthesis of results from monetary valuation, stakeholder analysis and multi-criteria analysis. Correctly applied, they aid informed, transparent decision making by considering all resources and equity of all stakeholders. They have a variable format ranging from complex bio-economic models to simple cost-benefit analysis tables.
The EU Framework 5 project Cost-Impact: Costing the impact of demersal fishing on marine ecosystem processes and biodiversity (www.cost-impact.org), which we are currently working on, provides a good example of interdisciplinary research. The aim of this project is to provide advice to decision makers on how demersal fishing impacts the biodiversity of marine benthos and how this in turn influences other marine ecosystem processes and consequently the associated goods and services provided by the benthos, and what the likely values of marine ecosystem goods and services are and how these values are affected by fishing.

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The impact of biodiversity changes on structure and function of coastal marine benthic ecosystems (BIOCOMBE)

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The consequences of changes in biodiversity, natural and anthropogenic, for the functioning of coastal ecosystems are not known. To address this problem, two phenomena with regard to the (changes of) benthic biodiversity, occurring along the Mediterranean, Atlantic and Baltic coast, are further unravelled. Firstly, for some dominant benthic species a strong northeastward shift in distribution along the European coast has been noticed.

Global change and pollution could be probable causes. However, due to changes in species composition the stability in coastal benthic systems might be disrupted leading to unstable unproductive systems. Secondly, in the Baltic an on average low diversity of life is noticed. Despite the low diversity, the structure and productivity of the food web in the Baltic is reported to be similar to that of the Atlantic. This would indicate that biodiversity is not essential for ecosystem functioning, and biodiversity loss is not an issue (except for ethical reasons).

To address the problems, the strong northeastward shift in distribution of several ecotypes (subspecies, races) along the European coast of two dominant benthic species (the economically important blue edible mussel *Mytilus sp.* and the clam *Macoma balthica*) is assessed, together with the consequences for the function and structure of coastal benthic communities. Moreover, the impact of low species numbers (Baltic), in comparison to a high diversity (Mediterranean, Atlantic), on the stability and production of coastal ecosystems will be studied.

Therefore, the objectives of this project are:

1. to assess the degree and impact of changes in diversity of dominant marine benthic species on coastal ecosystems, by describing the (changes in) distribution of the clam *Macoma balthica* and the blue edible mussel *Mytilus edulis*, and the consequences for ecosystem functioning.
2. to understand the functional aspects of a high level of biodiversity in benthic systems of coastal areas by comparing three systems (Mediterranean, Atlantic, Baltic) with a very different biodiversity but apparently similar productivity.

In a series of surveys and experiments the objectives are studied in parallel. At organism and population level the (variation and changes in) genetic and ecophysiological diversity along the European coast is indicated for the two dominant key-species. At community and system level the relation between the degree of (changes in) species/ecotype diversity and the functioning (community structure) and production (energy flow) of Mediterranean, Atlantic and Baltic benthic systems in coastal areas will be compared.

The differences in the degree of genetic (intraspecific) diversity of key species, and thereby the present distribution areas of different ecotypes, will be assessed for populations from Italy to the northern Bothnian Gulf, by means of electrophoretic isoenzyme and (nuclear, mitochondrial) DNA analysis. The major differences in the performance of the observed ecotypes under different environmental conditions will be assessed in exposure experiments and field translocations. From this the major influencing factors causing the shifts in distribution (or disappearance) of ecotypes can be deduced. The importance of differences in the (level of) species diversity (Mediterranean versus Atlantic and Baltic) on the benthic communities and on the production in coastal benthic ecosystems (WP4), will be assessed in laboratory and field enclosures by artificially changing the number of species, and measuring changes in species diversity or stable isotope composition. The results, obtained at different organisational level, will be integrated in a database and mathematically analysed (WP5).

The concomitant determination of diversity at different organisational levels will indicate how the function and structure of coastal and estuarine systems will be endangered and destabilised by a changing biodiversity. This provides support to the development, identification and selection of indicators that discriminate between natural and human-induced effects on biodiversity and (its relation with) the functioning of coastal marine benthic ecosystems.

Marine biodiversity research in the European perspective

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Research on marine biodiversity in Europe has gone through a slow implementation process. In the beginning of the 90's biodiversity was identified as one of the grand challenges for European marine research and a Euroconference as well as a workshop to develop a Science Plan were organized that did unfortunately not have any follow-up after 1994.

The subject was again taken up by the European Commission at the occasion of the MAST-EUROMAR days in September 1995 in Sorrento. A large meeting of over one hundred marine scientists debated whether marine biodiversity should be a priority issue for the coming years and agreed that this was indeed the case. From here on the CE funded a series of workshops, starting with a catalogue of research and, later joined by the ESF and MARS (The Network of European Marine Research Stations), to the production of a Science Plan and an Implementation Plan.

The IP was submitted to the CE under the 5th Framework Programme as the Concerted Action BIOMARE that had two main objectives: establishment of a series of research or flagship sites that would support long-term and large-scale research into marine biodiversity and a list of indicators for marine biodiversity. At the Renesse meeting the first results of BIOMARE were presented, including the system of sites adopted. This system distinguishes between reference (pristine) and focal (impacted) sites on the one hand and between ATBI (All taxa biodiversity Inventory) and LTBR (Long Term Biodiversity Research) sites on the other. A catalogue of these sites is being printed.

A further step in the development of marine biodiversity research in Europe is the establishment of networks. At the Renesse meeting the infrastructure measure MARBENA was demonstrated. In MARBENA electronic conferences are organized to cover subjects of interest to the European Platform of Biodiversity Research and Strategy. Besides these conferences also workshops will be organized to involve scientists and laboratories from Eastern Europe and the Southern Mediterranean.

Finally, in the 6th framework programme an expression of interest was launched to establish a Network of Excellence in Marine Biodiversity and Ecosystem Functioning. This network was approved in July 2003 and will start its activities early 2004.

Young Scientist Session

Chaired by
Joan Roughgarden

Drifting algae as a means of re-colonising defaunated sediments in the Baltic Sea. A microcosm study

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In the northern Baltic Sea drifting algal mats (conglomerates of several species of filamentous annual brown, green and red algae), have become an increasing problem due to eutrophication. Though extensive amounts of these algae have been found to stress the benthic communities, mainly by inducing hypoxia or even anoxia in the underlying sediments, patchy occurrences of drift algae may be beneficial to the benthic community by increasing habitat complexity and/or providing alternative habitats to bottom fauna. Some animals may even use them as an escape-way in cases of severe disturbance of the underlying sediments. The drifting algae may then provide a means of transport and a “mobile” corridor connecting different areas (i.e. disturbed and undisturbed) within and between habitats. This is likely to enhance re-colonization of previously disturbed patches or the colonization of new areas (thereby decreasing recovery time from disturbance events impacting a certain zone) and dispersal of benthic fauna over wider regions. These processes may have major implications in the community structure and the diversity of fauna inhabiting these areas.

A microcosm experiment was conducted in order to evaluate the capability of fauna inhabiting or being transported by drifting algae to colonize defaunated sediment. Naturally drifting algae were collected from the field and placed on 1 litre aquaria with 5 cm of defaunated sediment. After 3 and 6 days, one core sample (5 cm deep) was taken from each aquarium. The first 2 cm were sliced into 2 mm layers, and the remaining fraction into 1 cm layers to assess the distribution of recolonising meiofauna within the sediment column. Afterwards, the sediment remaining in the aquaria was sieved through a 0.5 mm sieve and the recolonising macrofauna retrieved. Both macro- and meiofauna were included in this study, though analyses at species level within the meiofauna were only performed for harpacticoids and nematodes.

Both macro and meiofaunal taxa were found associated with the drifting algae. The dominant macrofaunal taxa inhabiting the algae were juvenile bivalves and gastropods, with *Cerastoderma* sp. accounting for the majority of the bivalves and *Hydrobia* sp. for most of the gastropods. Both of these species were also represented in adult form. Other representative species were the isopods *Idotea viridis* and *Jaera albifrons*, the bivalve *Mytilus edulis* the gastropods *Theodoxus fluviatilis* and *Monoporeia affinis*, the nemertine *Prostoma obscurum* and gammarid amphipods. After 3 and 6 days, the most abundant macrofaunal taxa colonizing the sediment were *Cerastoderma* sp. individuals and gammarids, though individuals from all the other taxa present in the algae were also found. Higher abundances were registered after 6 days than after 3, though these were not significant for any of the major taxa.

Meiofaunal taxa inhabiting the algae were dominated by rotifers (46% and 40% after 3 and 6 days respectively), nematodes (14% and 11%), ostracods (11% and 14%), chironomid larvae (9% and 10%) and harpacticoid copepods (8% and 9%). Mites and cladocerans were also present but in lower proportions, while ciliates were registered only on the second experimental time, that is, after 6 days.

Analysis at higher taxonomic level indicated that most meiofaunal taxa present in the algae had also successfully re-colonized the defaunated sediment. Dominant taxa present in the sediment after 3 and 6 days were nematodes, rotifers and harpacticoid copepods. Other relevant taxa were copepod nauplii, ostracods and chironomid larvae. Most animals concentrated on the upper layers of the sediment, but some (especially nematodes, harpactiocoids and ostracods) appeared also evenly distributed in the lower layers.

However, when harpacticoid copepods were identified at species level, it became apparent that a methodological mistake occurred and these results could no longer be relied upon. While the algal community consisted almost exclusively of the species *Mesochra rapiens*, *Onychocamptus mohamed* and *Nitocra spinipes*, the species inhabiting the sediment were *Paraleptatascus spinicauda*, *Huntemania jadensis* and *Tachidius discipes*, with only punctual appearances of the “algal” species. The most plausible explanation is that these animals had survived the defaunation by freezing and thrived in the sediment during the whole experimental time. This may be true for other meiofaunal taxa and hence results from this group must be interpreted with caution.

Nevertheless, it seems apparent that the harpacticoid species inhabiting the drifting algae were not driven to sediment re-colonization and rather remained in the algae.

Our results indicate that drifting filamentous algae seem to provide an alternative habitat to both macrofaunal and meiofaunal animals and a means of transport and re-colonization at least for some macrofaunal species. Prolongation of the experimental times may however disclose new information concerning the suitability of the new habitat under the drifting algae and the distribution of animals within the sediment column.

Biodiversity-function relationships in the photoautotrophic communities of intertidal sediments

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Estuaries are among the most valuable ecosystems in the world, when scaled in terms of total ecosystem services to humanity per unit area (Costanza et al. 1997). Many ecosystem services within estuaries are enhanced or modified by the presence of algae or aquatic plants. Examples of such ecosystem functions are processing of excess nutrients from the water column, and stabilisation of otherwise mobile sediments. Primary production of benthic algae (including microphytes, macrophytes and seagrasses) may greatly exceed that of the overlying water column in many shallow coastal areas. Photoautotrophic biofilms, consisting of diatoms, cyanobacteria and euglenoids, are encountered on intertidal or subtidal soft sediment surfaces, and contribute a large fraction of primary production in turbid estuaries. In order to understand the response of estuaries to climate change or biodiversity loss, the role of the many diverse species of algae that form the microphytobenthos must be better understood. Microalgal cells range in size from < 5 μm to > 500 μm and display a range of adaptations that enable survival in the sediment habitat. These include the ability to orientate and move towards the photic zone, the utilisation of extracellular organic compounds, and a strong resistance to environmental stressors such as temperature or UV radiation. Although some data is available on the habitat requirements of individual species with respect to nutrient and salinity conditions, the niches of most species remain undefined.

To address these issues, the interaction between microalgal diversity, and net ecosystem processes such as primary production, is being studied by means of mesocosm experiments and field observations. Regular sampling along the natural salinity gradient of the Westerschelde estuary is used to detect locations with low and high diversities of microphytobenthos, with both traditional and molecular methods employed for quantification of biodiversity. Coupled measurements of physiological responses of the sediment algal community then allow selected ecosystem functions to be related algal diversity.

Recent methods to evaluate structural and functional biodiversity: What can harpacticoid copepods teach us?

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Biodiversity or the variability of life within biological communities, is an important feature in the regulation of ecosystem functioning (Tilman & Downing 1994, Chapin et al. 1997, Yacchi & Loreau 1999). Interestingly, the most prominent biodiversity research has examined how community diversity might regulate other functional properties, like productivity or stability (Tilman & Downing 1994, Drobner et al. 1998, Yacchi & Loreau 1999).

On the other hand the opposite question, or 'What regulates diversity in communities?' has been extensive examined (Connell 1978, Sommer 1984, 1993, 1995, Reynolds et al. 1993) but has not been subjected recently to the same synthetic treatment. In this context, the resource-competition theory of (Tilman 1982) is a major paradigm for both aquatic and terrestrial ecologists although the relative importance of resource competition in regulating the structure of ecological communities is an endless matter of debate (Reynolds 1997). Despite this controversy, the theory is useful because it makes distinct predictions about community structure, which can be tested in a number of ways (Tilman et al. 1982, Carney et al. 1988, Interlandi et al. 1999). This theory predicts that diversity should be directly proportional to the number of resources at limiting levels within a system. Species richness is directly predicted by the theory, and should exactly equal the number of limiting resources when equilibrium conditions are met (Interlandi & Kilham 2001). Most biodiversity studies discuss one single trophic level and only recently the consequences of diversity changes on different trophic levels in food webs are studied in detail (a.o. Duffy 2002, Fox & McGrady-Steed 2002). It seems that especially changes in distribution of interaction-power are of major influence on functional processes. In general, biodiversity of communities is due to niche diversification of co-occuring species and such diversification will lead to larger productivity as a result of more effective resource exploitation (McNaughton 1993).

In this context, harpacticoid copepods (Crustacea, Copepoda, Harpacticoida) are interesting organisms for case-studies as they are known for their habitat selectivity and high level of morphological adaptation. Especially in epiphytic communities i.e. collected from algae and seagrasses in the coastal zone, this high level of habitat selectivity is closely related to the maintenance of a high species diversity and offers possibilities to address some key questions.

Detailed ecological study on epiphytic and benthic communities showed a remarkable species-specific niche segregation of harpacticoid copepods (De Troch 2001, De Troch et al. 2003). In order to evaluate the role of the source-competition for this niche diversification a study on the feeding selectivity of harpacticoid copepods by means of diatoms enriched with stable isotopes, in addition to observations on prey selection and food uptake was started.

Four common phytal harpacticoid species (*Paramphiascella fulvofasciata*, *Tigriopus brevicornis*, *Nitocra spinipes*, *Amphiascoides debilis*) were offered pelagic (*Phaeodactylum tricornutum*) and/or benthic (*Navicula* sp.) diatoms species as food in a laboratory experiment. The pelagic diatoms were enriched in the stable carbon ^{13}C isotope to facilitate tracing of the diet in the harpacticoids. We tested the hypothesis that choice in the harpacticoids is dependent on available resources and will increase with increasing resources.

A clear uptake of labelled diatoms was measurable after 3 hours. In a control experiment, copepods were starved for 18 hours after feeding in order to evaluate if the effective assimilation of ^{13}C rather than the gut content was measured. From this, it was clear that copepods assimilated the ^{13}C of the diatoms as the signal was equal or even higher after starvation.

Evidence for resource partitioning was illustrated by means of experimental series containing 4 times as many copepods and resulting in a lower uptake of enriched diatoms. The presence of faecal pellets on the other hand resulted in an increase of uptake. Yet, a clear explanation for this positive effect of faecal pellets is lacking.

Overall, there was a clear species specific uptake of the labelled material among the harpacticoids. Two of the harpacticoid species (*P. fulvofasciata*, *A. debilis*) showed rapid uptake of the pelagic diatom when offered solely in low quantities, while the other two showed only a marginal uptake. All of the harpacticoid species showed a clear preference for the benthic diatom *Navicula* sp. when resources were limited and *T. brevicornis* and *N. spinipes* even when resources were plentiful. The results indicate that food preference is species specific in harpacticoids associated with macroalgae (*Fucus* sp.).

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On the impact of cultural practices on marine genetic resources: evolution of the genetic composition of wild stocks of pearl oyster (*Pinctada margaritifera cumingii*) in French Polynesia after ten years of spat translocation

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We studied the genetic impact of the cultural practice of junevile ("spat") collection and translocation between genetically distinct stocks of the black-lipped pearl oyster, *Pinctada margaritifera cumingii*, a heavily exploited resource in French Polynesia. In common with most bivalve aquaculture production, stocks are cultivated in "open-water", i.e. in lagoons, and most farms rely on the collection of wild spat. From the beginning of the 20th century, when exploitation started in French Polynesia, the farm stocks were essentially made up of mature oysters collected in the wild until the 1960's, after which stocks started to be supplemented with locally collected spat. The development of pearl-culture accelerated in the 1980s and, since the early 1990s, due to the great spatial and temporal variability of spat collection (Friedman & Bell 1999), the demand for spat from the increasing number of farms in Tuamotu-Gambier could not always be satisfied by local spat collection. Subsequently, some spat started to be collected from the Society archipelago for export to farms of Northern Tuamotu. The first of these transfers concerned limited exportations (about 40,000 individuals) in 1992 from the Society Islands to four atolls of the Tuamotu archipelago. Then in 1994 400,000 juveniles collected in the Society islands were transferred to Tuamotu, and in 1995 500,000 from the same two Society Islands were sent to the same four atolls plus an additional two. We used anonymous nuclear markers presenting length polymorphism (Arnaud-Haond et al. 2002) to study the potential genetic impact of this cultural practice through the following questions:

1. Does effective reproduction happen on farms? (By answering the question "Did spat transfer between atolls and between archipelagoes affect the pattern of genetic differentiation?")
2. Does spat collection induce a significant decrease in genetic variability (i.e. adaptative potential)?
3. Would the use of broodstocks present a real risk for genetic resources?

We compared samples collected in 1980's (Arnaud-Haond et al. 2003a) and 2000's from seven atolls. Seven additional contemporary samples from Tuamotu-Gambier were analysed to try to estimate the number of dynamically independent populations in this area. Both the evolution of the estimated level of genetic differentiation and the estimated population admixture showed that the genetic composition of some of the wild stocks of Tuamotu-Gambier has strongly been affected by translocations. These results highlight a surprisingly high success of translocated animals (about 30 to 50% of the actual wild stock would be offspring of translocated individuals), which can be partly explained by higher fertilization success in farms due to the very high density of cultivated pearl oysters, but might also be attributable to a heterosis effect in hybrids. However, our results do not allow us to estimate to what point this apparent short-term advantage could be accompanied by the assimilation or the loss of adaptations in the long term. Then the answer to the first question is yes, reproduction occurs in farms and seems to be very efficient.

No significant loss of genetic variability (heterozygosity) was observed while comparing samples from farmed and adjacent wild stocks, so that the methods used to collect spat to stock farms seem to be sufficient. However, a systematic decrease in the number of alleles (known to be more sensitive to loss of variability than heterozygosity) was observed, and the use of hypervariable markers might be useful to give a more precise and accurate picture (Arnaud-Haond et al. 2003b).

The use of broodstocks may be a good solution to allow the regular stocking of farms, despite the spatio-temporal variability of spat collection. However, the results obtained in this study led to the conclusion that, given the efficiency of reproductive events in farms and the known high variance in reproductive success suspected to occur in most bivalve species (Hedgecock 1994, Li & Hedgecock 1998, Boudry et al. 2002) the potential future use of broodstocks should be genetically monitored in order to avoid a massive loss of genetic variability available in the wild laying beds.

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The role of biodiversity on ecosystem functioning: seston-suspension feeder interactions

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Resolving the relationship between biodiversity and ecosystem functioning is one of the prime imperatives of current marine and terrestrial ecological research (Schulze & Mooney 1993). Alterations and losses in biodiversity composition and distribution presently occurring worldwide due to human activities are believed to lead to the loss of ecosystem-functions and the many services they provide to society (Daily 1997). Obvious candidate functions to determine the effects of biodiversity on ecosystem functioning are primary and secondary production rates. The former has been the main focus of terrestrial studies (Petchey et al. 2001).

Because life evolved in the sea, there is a much higher level of phyletic diversity compared to land prompting doubts about the applicability of paradigms from terrestrial studies which have been largely limited to manipulations of numbers of species within the same major groupings (i.e. angiosperms). Sessile marine invertebrates however, enable comparisons of the effects of both species and phylum diversity on ecosystem functioning. Suspension-feeding is a major feeding mode in the sea which occurs in nearly every marine animal phylum (Okamura 1989). The rate at which suspension-feeders remove particles from the water is a process determining much of secondary production in coastal waters. Suspension-feeding communities capture large quantities of particles and provide valuable ecosystem services (Dame et al. 1989). However although much work has been done on pelagic-benthic fluxes, relatively little work has been done on the potential impacts of mixed suspension-feeder communities on ecosystem functioning. Still less has considered the role of suspension-feeders in interactions between trophic levels.

The overall aim of this project is to determine the effects of suspension-feeder biodiversity on ecosystem functioning, particularly interactions between trophic levels, and the effect of non-native suspension-feeder species using fouling assemblages as tractable systems. It will address the question of whether increased suspension-feeder diversity results in a more efficient use of the resource pool. More diverse suspension-feeding communities will recycle the same food particles through several species before becoming detritus, compared to communities consisting of one or few species (Mook 1981). If resource partitioning and niche differentiation occurs this would result in greater utilisation of resources and a corresponding increase in secondary productivity (Gili & Coma 1998). A contrasting view is, however, that in hard-substratum communities where space is a main limiting resource, suspension-feeders with high clearance rates may exclude smaller species during their settlement, thus reducing species richness (Paine 1966) and may result in decreased productivity. Furthermore, since suspension-feeders exhibit a huge diversity in body-plan and food-capture and rejection methods, at both species and phylum level, they provide a unique opportunity of experimental evaluation of the role and potential redundancy of biodiversity at species and higher-level taxonomic divisions within suspension-feeders rather than across widely different feeding methods.

Another question is determining whether species within the same phyla perform a similar role on the ecosystems (for example ascidian A ≡ ascidian B), due to the fact that that they employ a similar capture and feeding method, and whether it is phyletic representation in communities that is important in ecosystem functioning because different phyla perform different roles (ascidian ≠ sponge). Ascidians and bryozoans for example are both suspension-feeders, but differ in their capture and feeding method, the former using mucus nets and the latter lophophore based feeding. This in turn affects both secondary production (the capture and processing method) and detrital matter available (the rejection process) and thus ecosystem functioning.

The effect of non-native species is also another key issue, since community composition and ecosystem functioning may be considerably altered as a result of biological invasions (Wilcove et al. 1998). Different ecosystems and communities appear to vary in their susceptibility to invasion and theory predicts that species-rich communities, which have a more complete utilization of resources should be less susceptible to invasion. However, there have been few rigorous tests of this prediction so experimental tests of diversity are needed to assess directly the effect of diversity on invasions (Stachowicz et al. 2002).

The rea in and around Plymouth provides the opportunity to carry out manipulative experiments on the effects of non-native species on ecosystem functioning in suspension-feeding invertebrates, since a large number of non-native species can be found. One example of a potentially important non-native species is the large stalked ascidian Styela clava. It may displace native species, is a fouling pest on ships' hulls and oyster beds, and if the population becomes large enough, serious competition for food between individuals and with other species can result. However owing to its large size and abundance it may actually increase secondary production and filtration rates in a community, and might even aid localised increases in biodiversity as it provides additional settlement space for many epibionts.

Experimental manipulation of native and non-native suspension-feeder diversity will be carried out, at both species and phyletic level, and species examined will include bivalves, barnacles, sponges, ascidians and bryozoans. Both naturally settled fouling assemblages and artificially assembled communities will be used to study subtidal communities. These assemblages will be "gardened" to contain different species and phyla diversities, and including or excluding non-native species.

Secondary production and particle clearance rates will be used as measures of ecosystem functioning. Biomass will be used as a measure of secondary production, where dry weight of settlement tiles will be measured at monthly intervals, whilst percentage cover will be used as a surrogate for biomass on remaining manipulated tiles. Differences in fine scale resource partitioning on the differential utilisation of particulate matter between species will also be determined by comparing seston composition of inhalent, exhalent and overlying water. The complex size overlap in natural seston previously limited the possibility of carrying out such studies, however by using flow cytometry it is now possible to discriminate particle type based on cell size and relative chlorophyll content very accurately (Cucci et al. 1985).

Expected outcomes

The expected outcomes of this project are that

Phyletic identity is more important than species identity, but identity more important than diversity.

1. Increased diversity in suspension feeding communities will lead to enhanced particle processing and hence secondary production.
2. There is some potential redundancy / biological insurance within each phyla
3. Non-native species may have a negative effect on biodiversity but a positive effect on ecosystem functioning.

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Linking biodiversity to behaviour: bioturbation potential

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Benthic macrofauna have been the subject of many surveys and biodiversity studies linked with monitoring anthropogenic disturbance of the soft seafloor. It has been widely demonstrated that it is sufficient to monitor at taxonomic levels higher than species to detect deleterious change in benthic communities. Well-established paradigms exist describing macrofaunal succession in fine sediments following disturbance events. Central to these paradigms is the notion that well developed communities cause a great deal of biogenic sediment mixing and exchange across the sediment water interface or "bioturbation". This process strongly influences diagenetic processes in the seafloor and is an essential ecosystem function in maintaining habitat quality on the soft seafloor. Here we describe a comprehensive study that attempts to link biodiversity to bioturbation. A pseudo taxonomic level of functional type was devised, incorporating bioturbation mode, burrowing depth and size. This was compared to other taxonomic levels. Functional type was strongly correlated to species but not in a way similar to the link between species and other taxonomic levels. A univariate index of bioturbation potential (BP) was also devised incorporating bioturbation mode, size and abundance of the constituent species. This index appears to be sensitive to disturbance effects. Multivariate correlation of macrofaunal and sediment profile imagery (SPI) data has shown that faunal distributions are closely linked to structures in the sediment profile. *In situ* time-lapse SPI observations have shown not only the presence of structures in the sediment profile, but also the rate of structure formation is dependent on biodiversity. Direct observation has revealed novel burrowing behaviour and that the activities of some dominant species may mask those of others. A non-local, behaviourally driven model of particle bioturbation is being devised. The results of early tracer work indicate that the model is an improvement on the traditional biodiffusive analogy. An expected outcome of this work is evidence of the link between biodiversity and the maintenance of habitat quality on the soft seafloor.

Synthesis

Richard Warwick
Chair of the conference

The conference provided the opportunity to assess the degree to which Europe had begun to address the widely accepted research agenda established in 1991 (From Genes to Ecosystems: a Research Agenda for Biodiversity, ed O T Solbrig, IUBS/SCOPE /UNESCO) with respect to the marine environment. This was the product of an international workshop that specifically addressed the question "What is the importance of biodiversity for the proper functioning of biological systems, from populations to ecosystems". More than in many other sciences, marine studies require European co-operation. A network of scientists in this field has higher chances of successfully competing for both national and European funds, and fulfilling the obligations of the European states under the Rio Convention to survey and monitor biodiversity. This conference was a further step towards the establishment of a dedicated group of excellent marine scientists that together want to discover and summarise the general features of marine biodiversity and what their implications are for management, conservation and restoration of marine ecosystems. Within the European Union and its associated countries clear progress has been made in the networking of marine biodiversity research activities, catalysed by the ESF (EmaPS board) and the MAST programme of the CEC, and the activities of MARS, BIOMARE, MARBENA etc. It was clear that there had been a dramatic increase in research activity in the two years since the first conference in this series (Corinth, Greece, May 2001), particularly concerning functional aspects of marine biodiversity. One senior participant from the USA commented on the "stunning degree of collaboration within Europe", which is clearly the result of the variety of structured coordinating mechanisms noted above. Marine scientists are also becoming more environmentally responsible, with greater attention to management, conservation and economic aspects of biodiversity.

More attention is now being paid to the appropriate spatial and temporal scales, and scales of biological organisation (genes to ecosystems), that are relevant to the management of biodiversity, and to scaling up from small-scale reductionist experiments to the wider field situation. From the range of oral and poster presentations it is clear that marine systems are superbly tractable for linking biodiversity (at all levels) with ecosystem processes due to short life-spans, high turnover, microbially-driven primary production and decomposition processes, high phyletic diversity and a strong tradition of systems ecology (coastal), biological oceanography (offshore) and field experimental ecology. It is much easier to conduct experiments linking biodiversity with ecosystem processes than in terrestrial systems. Rates of processes can be measured better and interacting biological systems can realistically be maintained in laboratory systems (microcosms) where they can be manipulated. Although still the subject of some controversy, the marine realm is estimated to comprise around 200,000 species, less than 2% of the total number of species on earth, but these are rather equitably divided among 34 higher groups or phyla, none of which is strongly predominant. The more recently evolved terrestrial biota, on the other hand, comprises around 12 million species which belong to only 15 phyla, with more than 90% of the species belonging to the phylum Arthropoda. High phyletic diversity may result in stronger species identity effects, especially in low diversity assemblages (estuaries, shores). The functional roles of many if not most species are not well understood, and there is a requirement for more "old-fashioned" natural history.

Unlike terrestrial systems that are essentially 2-dimensional, marine systems are more 3-dimensional and organisms living in the water column and on the seabed must be integrated because of life history linkages (many species living on the seabed are transported from place to place in the water column as planktonic larvae, for example) and the openness of the system. It is dangerous to consider the biodiversity of one of these ecosystem components in isolation. In marine science there has been a tradition of reductionist approaches, for example experiments on small artificially assembled subsets of species, and there are problems associated with scaling up to the relevance of such experiments for real field situations. We do not know to what extent and over what timescales ecosystem function is impaired by the loss of species. This is not the same question as how functional processes are affected by an increase in the number of species in artificially assembled communities, because we can't deal with long time scales in such experiments. In order to understand functioning of these open marine ecosystems biodiversity needs to be viewed at a higher level in addition to the more traditional approaches of species in assemblages/communities. Thus, habitat patch diversity (biotope) or assemblage mosaic diversity is an appropriate level to investigate influences on ecosystem functioning (with species in assemblages nested within habitat patches). Although habitat fragmentation is an important threat to biodiversity on land, habitat homogenisation may be a more important factor in open marine systems. Mathematical modelling is the best way to integrate small scale experiments undertaken either in the laboratory or the field into a systems approach. There is also a need for speculative theoretical mathematical modelling; marine ecologists could and should play a greater role in the development of more general theory.

New molecular tools have resulted in the discovery and characterisation of new microbial diversity, especially photosynthetic picoplankton that can functionally contribute up to 30% production, especially in winter. These organisms have considerable functional significance. Molecular markers with different degrees of resolution and conservedness can show the phylogeographic mechanisms generating biodiversity but also can detect changes in within species diversity due to human activities (e.g.accidental introductions of non-indigenous species, transplantation, aquaculture, habitat loss).

Abstracts of the poster presentations

Recolonization genetics: The development of genetic diversity during colonization of the seagrass *Cymodocea nodosa*

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Seagrass colonization proceeds from the initiation of patches, from seed, followed by clonal growth. It is as yet unclear how genetic diversity evolves during the colonization process. We examined the development of genetic diversity during seagrass colonization by examining genetic diversity varies across a gradient of patch age and size of *Cymodocea nodosa* growing in Alfacs Bay (Ebro Delta, NE Spain). The *Cymodocea nodosa* there is arrested in a permanent recolonization state due to patch extinction-recolonization derived from disturbance by sand waves. We used 12 recently developed microsatellite markers to unambiguously determine clonal identity within and among patches. Reconstruction techniques were used to characterize patch demography, estimating age and the reproductive output at the patches. The relation between patch genet richness (number of genotypes) and age or size was analyzed and compared with expectations from vegetative growth and dispersion models. Relatedness analysis was performed using the microsatellite genotype data from individuals inside the patches and surrounding seedlings, in order to verify the species dispersion hypothesis.

Monothalamous soft-shelled foraminifera in Sevastopol bay (Crimea, the Black Sea)

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Introduction

Foraminifera are a meiobenthos group that can be very important in the organization of bottom communities. Total biomass can be very high, even comparable to that of macrobenthos. On basis of the shell morphology, foraminifera can be divided into 3 groups: calcareous, arenaceous and protein (soft-shelled).

The Black sea benthic foraminifera have been studied extensively. Yanko and Troitskaya (1987) described 46 calcareous and arenaceous species from the Black Sea. From the Bosporus region 79 calcareous and arenaceous species have been recorded (Yanko and Vorobyeva, 1991). Recent studies also recorded soft shelled Foraminifera in the Black Sea, belonging to the families Allogromiidae and Saccamminidae (Sergeyeva, Kolesnikova, 1996). These families have been described for the Atlantic and Indian Ocean (Nyholm and Gertz, 1973; Loeblich and Tappan, 1988; Gooday et al., 2001). Preliminary research found 7 soft-shelled Foraminifera in the Black Sea.

Results and discussion

This paper presents work that was part of a hydrobiologic survey in the Sevastopol bay (32 stations; depth range: 3–18 m) in July, 2001. The bay is the largest in SW Crimea (7.5 km long, about 1 km wide). Calcareous Foraminifera were found at 22 stations, while at 16 stations also soft-shelled forams were found (Table 1).

Most dominant species was *Psammophaga simplora* (Arnold, 1982). This species has not yet been recorded in the Black Sea. It occurred at 10 stations, ranging from 10 to 17 m deep (Table 2). No relation was found between depth range and spatial distribution.

P. simplora from the Black Sea does not differ from the type species on principal features. It is a monothalamous small foraminifera (wheat grain till water drop in form) with an organic elongated shell (test). The test's wall is slightly agglutinated by fine sand. The length of the test varies from 250 - 430 µm, with an average width of 125–220 µm. The wall is translucent (thickness: 3 – 6 µm). Coefficient **c** (ratio between length and width of the test) is about 2.

The test's length of the type species varies from 250 to 350 µm (there are almost no differences in the shell's width in comparison with the Black sea species). The wall thickness varies from 6 till 10 µm. Coefficient **c** of the type species is 1.5.

At the sharpest end of the test there is an aperture (a simple round opening on the short 'neck') with a diameter ranging from 14 to 28 µm. The protoplasm (situated near the aperture) contains many stercomata (used cell material) and mineral particles. Because of the mineral particles conglomeration in the protoplasm, the nucleus was difficult to recognize: from 11 analysed animals we managed to measure it in only 4. The diameter of the nucleus varies from 30-60 µm. Within the protoplasm of some animals diatom fragments were found. The average individual weight is 9 µg.

Biomass of *P. simplora* in the Sevastopol bay ranges from 6 - 90 mg/ m^2.
One of the controlling factors of the distribution of Foraminifera could be grain size distribution of the sediment. In the Sevastopol bay *P. simplora* prefers fine silt and fine sand with a size fraction < 0,1–0,25 mm. They rarely inhabit larger sand fractions. Choice of such fine sediments by these animals can be explained by the presence of the delicate protein test, which they could damage among more coarse particles of the bottom sediments.

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Table 1. Number of calcareous, arenaceous (C) and soft–shelled (B) foraminifera in the Sevastopol bay (ind. per m^2)

Station №	Depth, м	Foraminifera		Station, №	Depth, м	Foraminifera	
		C	B			C	B
1	3,5	11000	0	14	16,5	0	3000
2	6,5	25000	0	15	17	2000	0
3	9	52000	1000	17	8	28000	0
4	9	79000	5000	18	16	390000	0
5	4	3000	1000	20	17	12000	0
6	10	5000	17000	21	15	2000	0
7	7	1000	0	22	12	2000	17000
8	16	34000	5000	23	16	6000	4000
9	11	1000	26000	24	4,5	2000	2000
10	10	0	18000	27	14	500	4000
11	13	1000	500	28	4	4000	0
12	15	0	500	30	12	2000	9000
13	6	0	1000	32	16	5000	0

Table 2. Part of the *P.simplora* (n) in general number of soft-shelled foraminifera (N) in the Sevastopol bay (the Black Sea), (ind. per m^2; %)

№ stations	Depth, m	N, ind. per m^2	n, ind. per m^2	%
6	10	11600	2200	19
8	16	4400	2700	61
9	11	22600	8800	39
10	10	19900	9900	50
14	16,5	3300	1100	33
20	17	600	600	100
22	12	1100	1100	100
23	16	1600	600	38
27	14	3300	3300	100
30	12	7200	4400	61

Genetic variability and population stability in *Posidonia Oceanica* (Delile) meadows

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The seagrass *Posidonia oceanica* is a clonal angiosperm endemic of the Mediterranean Sea. The large and widespread meadows of *P. oceanica* range on the littoral zone where they strongly influence the shallow water benthic biotopes. They are characterized by a high biodiversity and productivity, making them key-species of the coastal ecosystems of the Mediterranean Sea. The recently described pattern of widespread local regression of *Posidonia* meadows in the Mediterranean Sea can be attributable either to the long-term global climate change, or to short-term modifications linked to anthropic activities that have resulted in increased turbidity, bed erosion and biomasses losses.

The widespread regression of *Posidonia oceanica* was also assigned to the low level of genetic variability believed to be present within the populations of this species. However, use of new microsatellite markers have shown that the P. oceanica meadows contain far more genetic diversity that hitherto believed. A number of meadows, spanning from Cyprus to SE. Spain, ranging from expanding to declining populations, have been sampled and the population dynamics of the species assessed in parallel to its genetic diversity to test whether there is a link between the stability of the populations and the extent of genetic diversity therein. Among seven meadows analysed so far, the pattern of clonal variability (number of genotypes versus number of samples analysed), and of spatial clonal distribution, is highly variable among meadows, ranging from 0.4 in Port Lligat (Northern Spain) to 0.88 in Les Rotes (Central Spain). Variation is also observed between very close meadows: in Formentera (Spain, Balearic islands), clonal diversity was found to vary between 0.48 and 0.64 among meadows separated by less than 10 km. The preliminary data on four meadows for which both genetic diversity and demographic data are available suggest a correlation between the density and the clonal diversity in a meadow.

Benthic macrofauna as an index to biodiversity, biomass and productivity in Mediterranean coastal lagoons

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In Mediterranean coastal lagoons, pollution and other human activities are not the only agents which influence environmental quality conceived in terms of biodiversity, biomass and productivity. Natural factors such as temperature salinity oxygen turbidity and water circulation, because of their high variability in these ecosystems, can also generate negative conditions. The field method proposed below serves to assess the state of the environment as determined principally by these natural factors.

The following are the prerequisites for environmental quality in a coastal lagoon:

- salinity values that keep within the range of 20 - 40 ‰,
- oxygen levels never under 4 ppm,
- temperatures that stay above 6°C in winter and below 30°C in summer,
- strong light reaching the substrate,
- an open channel to the sea, especially during spring.

To monitor these conditions directly is very labour intensive. Instead, we propose an easier and faster method using the benthic macrofauna as indicator organisms.

A recurrent pattern is recognised in the bionomics of Mediterranean coastal lagoons. Following the gradient determined by the influence of the sea penetrating into the basin, six possible benthic assemblages of macrofauna, or Zones, can be recognised (Frisoni *et al.*, 1984). Biodiversity diminishes gradually as the distance from the sea mouth increases: highest in Zone 1 most subject to marine influence, and lowest in landlocked Zone 6. Biomass and productivity increase proceeding from Zone 1 to Zone 4 but then drop from 5 to 6. The best lagoons are those mostly comprised of Zones 3 and 4.

In order to evaluate a particular lagoon a sample of the benthic macrofauna is taken so that the zonation, the extent of each Zone, and the biomass and number of species found in each can be defined. The Λ Index expresses the environmental quality according to a scale of increasing value from 1 to 10.

$$\ln\left(\sum_{i=1}^{6}\frac{n_i}{N}\bullet b_i\bullet S_i\right)=\Lambda$$

Where i = index which denotes the Zone (I - VI)

n_i = number of sampling units falling within Zone i.

N = total number of sampling units in the sample.

b_i = mean biomass (g wet weight/m^2) of Zone i

S_i = number of species of benthic macrofauna within Zone i

Λ = value of the environmental quality of the lagoon (1-10).

Is the role of an invasion different in "rich" and "poor" benthic communities? - a study on solute transport across the sediment-water interface

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Invasion of the burrowing polychaete *Marenzelleria* cf. *viridis* into the European waters was reported in the mid eighties (Essink and Kleef, 1988).

In a relatively diverse ("rich") benthic communities of the south-eastern Baltic Sea (10±4 species, 55±35 g m^{-2}, Van-Veen grab samples), the species contributes about 8±5 % of the total benthic biomass. On the other hand, in low diversity ("poor") soft bottoms of estuarine environments (*e.g.* Curonian lagoon), dominated by oligochaets and chironomids (3±1 species, 5±4 g m^{-2}, core samples) the species after its invasion accounts for approx. 90% of the total macrofauna biomass.

Before polychaete invasion oligochaets and chironomids occupied sediment down to 15 cm depth. In the deposits below this depth no macrofauna activity was found. After the invasion, relatively few individuals of *M.* cf. *viridis* (300 ind m^{-2}) increased the sediment surface area up to three times. Approximately one quarter of this contact zone was located beneath the depth of sediment reworked by oligochaets and chironomids before invasion.

The results from experimental incubations of sediment with natural benthic community show that addition of the new species *M.* cf. *viridis* had no statistically significant effects either on tracer (bromide) or nutrient (ammonia and phosphate) fluxes. However simulated species invasion to the defaunated sediments resulted in significantly enhanced net tracer fluxes. Addition of single polychaete specimen facilitated the penetration of the tracer to sediment depths of 10 cm exceeding two times limits faced by molecular diffusion. Transport of tracer was enhanced by factor 1.6 relative to molecular diffusion on average and single specimen of *M. viridis* generated about one fifth of solute exchange when compared to the average of relatively diverse soft sediment community. This effect is also similar to that reported for meiofauna communities by Aller and Aller (1992).

Experimental results support the hypothesis that species' contribution to exchange of solutes is dampened in a habitat with already high rates of sediment-water interaction. In "azoic" sediment or impoverished macrofauna communities, however, colonisation/extinction of benthic species may have much more pronounced effects in exchange rates of solutes.

Population structure of the dwarf eelgrass *Zostera noltii* along the Iberian Peninsula: data from microsatellite analyses

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The dwarf eelgrass *Zostera noltii* can be found from Northern Europe throughout the Mediterranean, Black Sea, Azov Sea and Mauritania. Several marine species associated with the Portuguese coast display disjunct distribution because of the Tagus River and/or the Nazaré Canyon. Our objective is to define patterns of population structure of *Z. noltii* along the Portuguese coast in order to determine the possible effects of these geographic barriers to gene flow.

Eight populations of *Zostera noltii* were sampled along the Iberian Peninsula coast and their genotype determined based 9 microsatellite loci. Clonality in populations was highly variable ranging from almost maximum clonality where every individual has a unique genotype to highly clonal populations with some clones consisted of multiple ramets. Strong population differentiation among all populations was found and there was small but significant isolation by distance. A neighbor joining analysis based on Reynold's distances revealed two significant clusters separating the northern from southern *Z. noltii* populations. This split between northern and southern populations is the result of the presence of two probable geographic barriers to gene flow in the area, i.e. the Tagus River and the Nazaré Canyon.

In the future more focused sampling along the Portuguese coast is planned, especially around these probable geographic barriers to study their contribution to gene flow limitation. This in combination with field studies to investigate the dispersal potential of *Zostera noltii*.

Determination of phytoplankton community with HPLC pigment analyses from fish farms area

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Photosynthetic pigments have proven to be useful biomarkers of the abundance, composition and physiological status of phytoplankton biomass in the marine environment. Phytoplankton pigments were investigated using High Performance Liquid Chromatography (HPLC) analysis as well as selected physical and chemical parameters in areas near fish farms as well as at a control site in June 2000 and in July, August, September and November 2001 were performed. Among the pigments in average zeaxanthin was the most abundant at the fish farm location, followed by 19'-hexsanoyloxyfucoxanthin and fucoxanthin. This shows the dominance of cyanobacteria (29.3±14.1%), followed by Prymnesiophyceae (23.1±10.4%) and diatoms (22.2±10.1%). The phytoplankton composition at the control site was almost the same (28.7±13.3% of cyanobacteria, 23.1±9.2% of Prymnesiophyceae and 22.4±9.0% of diatoms). But there was evident difference between different samplings. Season was found to be the factor mostly influencing the phytoplankton composition, while there was no obvious difference between the fish farms area and the control site. Higher concentrations of nitrate, total nitrogen and silicate were measured near the fish farms.

Introduction

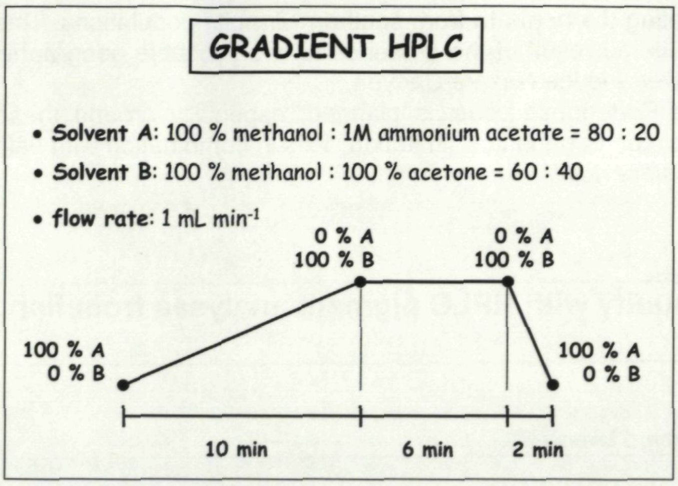
Photosynthetic organisms contain one or more photosynthetic pigments that absorb visible spectra and take part in photosynthesis. Photosynthetic pigments have proven to be useful biomarkers of the abundance, composition and physiological status of phytoplankton biomass in the marine environment. Chlorophyll *a* concentration is a good parameter for the estimation of phytoplanktonic biomass while pheopigments act as an indicator of the physiological state of phytoplankton. In addition to chlorophyll *a*, all phytoplanktonic organisms contain many carotenoid pigments among which are several biomarkers for chemotaxonomic determination of the phytoplankton community (Table 1).

Table 1. Photosynthetic pigments useful as biomarkers of algal groups.

PIGMENT	ALGAL GROUP
CHLOROPHYLLS	
Chlorophyll *a*	All photosynthetic microalgae (except prochlorophytes)
Chlorophyll *b*	Green algae
CAROTENOIDS	
Alloxanthin	Cryptophyceae
19'-Butanoyloxyfucoxanthin	Silicoflagellates
Fucoxanthin	Diatoms
19'-Hexanoyloxyfucoxanthin	Prymnesiophyceae
Lutein+Zeaxanthin	Cyanophyceae
Peridinin	Dinoflagellates

Methods

Phytoplankton pigments were investigated using High Performance Liquid Chromatography (HPLC) analysis (Fig. 1) as well as selected physical and chemical parameters in areas near fish farms as well as at a control site in June 2000 and in July, August, September and November 2001 were performed.



- **Solvent A**: 100 % methanol : 1M ammonium acetate = 80 : 20
- **Solvent B**: 100 % methanol : 100 % acetone = 60 : 40
- **flow rate**: 1 mL min^{-1}

Figure 1. Gradient HPLC method

Results

In contrast to the normal decrease of biomass during the summer, at the fish farm area we measured chlorophyll *a* concentrations similar to other seasons (in September 2001 in average 980±420 ng L^{-1}) due to higher nutrient inputs. Among the pigments in average zeaxanthin was the most abundant at the fish farm location, followed by 19'-hexanoyloxyfucoxanthin and fucoxanthin. This shows the dominance of cyanobacteria (1.5-60.1 %; 29.3±14.1 %), followed by Prymnesiophyceae (0.0-43.0 %; 23.1±10.4 %) and diatoms (9.3-57.0 %; 22.2±10.1 %). The phytoplankton composition at the control site was almost the same (28.7±13.3 % of cyanobacteria, 23.1±9.2 % of Prymnesiophyceae and 22.4±9.0 % of diatoms). But there was evident difference between different samplings (Fig. 2). Season was found to be the factor mostly influencing the phytoplankton composition, while there was no obvious difference between the fish farms area and the control site. Higher concentrations of nitrate, total nitrogen and silicate were measured near the fish farms

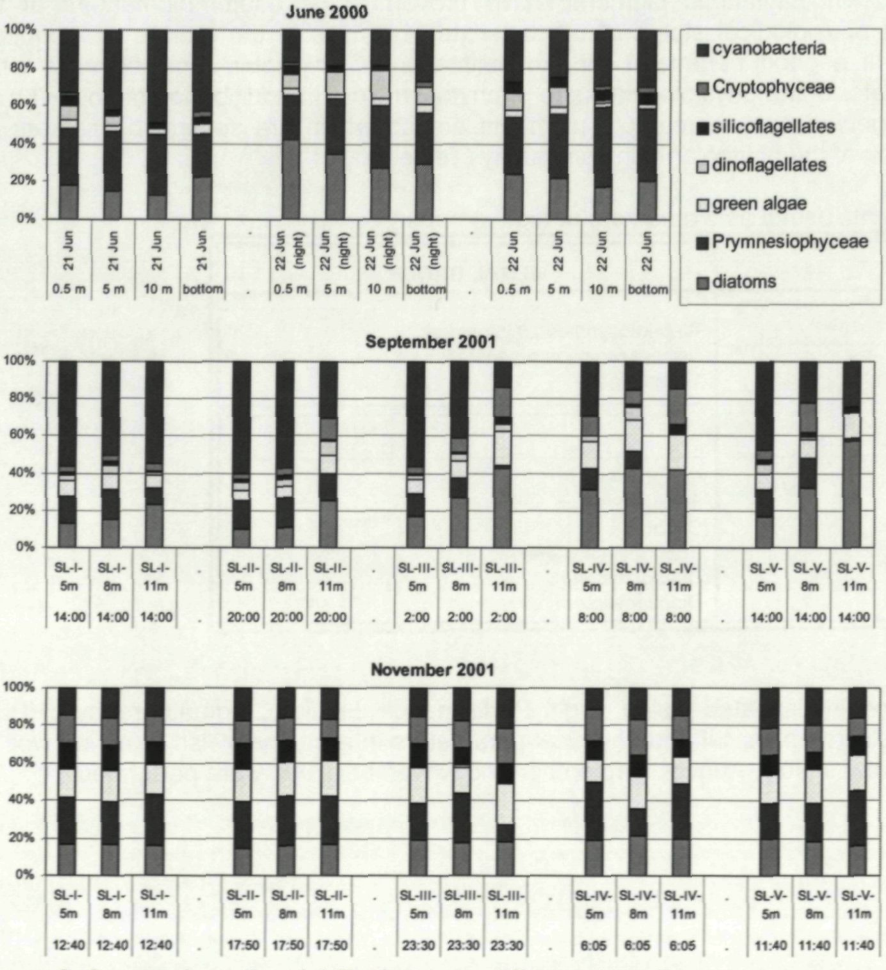


Figure 2. Season based variability between different samplings

Testing the relationship between biodiversity and invasibility of marine communities

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Concern over the impacts of biodiversity loss on the functioning of ecosystems has stimulated renewed interest in the importance of species diversity to community stability. Resistance to invasion is a common measure of stability and it is a commonly held belief that more diverse systems are less likely to be invaded.

The current work will investigate the relationship between biodiversity and invisibility in marine systems using the invasive seaweed *Sargassum muticum* on British shores. Observational studies of *Sargassum* at its distribution range edge will measure the process of colonisation of new habitats and the relationship with community diversity. An experimental approach will also be used to test this relationship by constructing communities of seaweeds with different levels of diversity and measuring their resistance to invasion by *Sargassum*.

The structure and role of the macrofauna community in seaweed disintegration in the supralittoral zone of the Polish sandy coastal system

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The overall functioning and character of sandy beach ecosystems is shaped by a small number of key species that exert a major impact on community metabolic processes such as primary and secondary production, remineralisation, vertical export and bioturbation, and predation. The impact of these species can be disproportionate to their abundance or biomass. Sandy beaches are examples of simple ecosystems, principally driven by the physical forces of waves, tides and sediment movement. Similarly so, the intertidal zones of sandy beaches appear barren when compared with other intertidal habitats. Despite this superficial impression, many beaches support a diverse flora and fauna. A number of sandy littoral localities may be considered highly productive. Marine beaches receive a variety of organic materials from the sea: macrophyte wracks, dead animals and dissolved and particulate organics flushed into the sand by waves. Biota associated with the interstitial system (bacteria, protozoa, meiofauna) and macrofauna process these organic materials and return nutrients to the sea, so on most beaches the interstitial system functions as a biological filter that mineralises organic material and thus cleanses the surf waters.

The coastal zone in general and sandy beaches in particular are strongly subjected to a number of man-induced disturbances including pollution, eutrophication and tourism. Next to their ecological importance as bio-filters, sandy beaches in Europe tend to be of great economic value through tourism. As such, sandy beaches deliver "ecosystem services" with high economic relevance, yet the impact of different forms and degrees of human disturbance of beaches on their sustainable exploitation remains unclear. For instance, it is as yet unclear which biota and what level of biodiversity are indispensable for the above-mentioned bio-filter function, and *mutatis mutandis*, we do not know the carrying capacity of sandy beaches with respect to tourism—the issue is how strong a tourist impact can be tolerated without loosing the beach's cleansing capacity.

The biodiversity of, and the impact of tourism on, sandy beach biodiversity is a subject currently generating great scientific interest in Europe. It sets out to fill important gaps in our knowledge concerning sandy beach biodiversity in Europe, and to link beach biodiversity to touristic impacts, using both a descriptive and an experimental approach. However, beaches are not homogeneous habitats. Next to the typical small-scale patchiness of marine benthos, sandy beaches often show important shifts in community structure as well as biodiversity along their slope. However, information for sandy beaches is extremely scanty. Hence, it is not surprising to find that the links between such diversity patterns and sandy beach functioning remain unknown.

Thus, the current macrofauna species composition and the responses of major macrofaunal taxa to the stranded decaying leaf litter of the seagrass *Zostera marina* were mainly aim to mimic and assess effects of biodiversity and function of beaches. Study was investigated through a field colonisation experiment in a temperate, medium quartz sediment, sandy Hel Great Beach in Poland at the tip of the Hel Peninsula (Gulf of Gdańsk). During field studies over the course of three years (1999-2001), the wrack breakdown was determined, while related faunal assemblages were characterised. To determine the significance of major macrofaunal taxa associated with wrack, with *Talitrus saltator* assemblage in particular, the litterbags of three mesh sizes (12 mm, 0.5 mm, 48 µm) were used. The surface study of the wrack macrofauna was also carried out on the same beach, using Barber's traps specially designed to capture only the active animals on the beach surface.

During three monthly field studies through three years the wrack breakdown was determined and associated faunal assemblages were characterised. 252 replicate litterbags of 12 mm mesh size with fresh wrack were used and retrieved 1, 3, 6, 9, 12, 18 and 27 days post-placement. Barber's samples were taken from 6 traps at the same period, but retrieved 1, 3, 6, 9, 12, 15, 18, 21, 24 and 27 days after start. After a comparison between two methods of sampling (ANOVA tests), both data were examined from a temporal point of view. The aim of present work was to gain information on how, when and where wrack was colonised by invertebrates, keeping in mind cyclical aspects such as diel, monthly and annual phases.

In the litterbags 16 465 macrofaunal arthropods from 30 species or genera were recorded. However, in the Barber's traps 32 082 individuals from 61 species or genera were found. In spite of all differences in sampling, general trends in the composition of the fauna, such as the annual abundance of *Talitrus saltator*, Staphylinidae and Ptiliidae, Diptera, and the virtual absence of some groups during seasonal changes, were confirmed in both litterbags and traps. Coleoptera were the most numerous group, making up 67% of the total of identified invertebrate specimens. Staphylinidae and Ptiliidae were the most abundant, whereas some other coleopterans fluctuated during all the year (Coccinellidae increased in spring, Histeridae dramatically decreased in autumn, as well as Chrysomelidae and Scarabaeidae increased in fall). However, *Talitrus saltator* was common throughout the entire study period, and predominant as a species (approx. 25% annually, with rising up to 40% in summer). Less numerous were Diptera (15-20%), common in the supralittoral zone of the beach, with *Fucellia tergina* as a prevalent species in shallow and lagoon locations. Chilopoda and Hymenoptera made up only 1.91% and 0.75% of the total arthropod material respectively, but in autumn they were more influent. Thus, the macrofaunal species composition of the supralittoral zone varied considerably not only from one sampling method and locality to another but more from season to season.

The wrack was colonised by above mentioned supralittoral fauna in two distinct phases. The macrofauna, including the talitrid amphipod *Talitrus saltator*, adult Diptera and Coleoptera, colonised the wrack within one day, with highest number recorded after three days. Following this, their presence in the samples declined and the meiofauna, which consisted of nematodes, oligochates, turbellarians, and dipteran larvae, became increasingly abundant. After 18 days in the field, the meiofauna dominated the wrack surface. This faunal succession did not relate directly to the degradation of the eelgrass tissue, which proceeded exponentially for the entire study period. Material was lost from the bags at a rapid rate, with only 22-32 percent of the original dry mass remaining after 27 days in the field. Exclusion of the macrofauna from the wrack, using litterbags of finer mesh bags (< 1 mm), had no appreciable effect on the rate of dry matter loss. The major macrofaunal wrack consumers, including *T. saltator* and Coleoptera, therefore, did not affect the rate of seagrass disintegration. The effect of meiofaunal nematodes, oligochaetes, gastrotrichs and turbellarians on wrack breakdown could not be accurately determined. Microbial decay, and abiotic leaching and fragmentation were, thus, likely to be the major causes of seagrass weight loss from the litterbags. The study, however, confirms that the supralittoral macrofauna is usually dominated by talitrid amphipods. *Talitrus saltator* is generally considered to be the primary coloniser of newly stranded wrack in temperate areas and often dominates the supralittoral fauna of beaches with a moderate macrodebris input. Talitrid amphipods, therefore, may contribute greatly to the breakdown of wrack tissue as a result of their own feeding activity and through the spread of microorganisms, and so accelerate and spread the decay. They today occur, however, on isolated localities only along the Polish coast, avoiding the most visited tourist places.

This work has been inspired with the research within the LITUS Project (Interaction of Biodiversity, Productivity and Tourism in European Sandy Beaches) and other international research programmes "Sandy", which involves scientists from 12 European countries.

Bryozoan diversity as tool for determining the environmental conditions

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Former studies place bryozoans as second most diverse (after annelids) component of macrofaunal communities in Svalbard waters. As a main study area Kongsfjorden (79°N, 16°E) was chosen. From 98 stations 282 quantitative samples were taken: 231 by grab, 40 by SCUBA diving and 11 by dredge. Samples were taken along various environmental gradients, including salinity, depth, temperature (water masses), sedimentation and type of substrate. Together with faunistic samples rate of sedimentation, salinity and temperature were measured. Sediment type was determined. All together 144 taxa were determined. Based on multivariate analyses bryozoans candidates indicating the given factor (depth, sedimentation, substrate type, environmental dynamics) were selected. The morphology of bryozoan colony gives important information. Branched, not flexible colony indicates stable conditions (weak current, lack of siltation), while the flexible ones indicate areas with strong currents, sedimentation and biotic interaction (competition). Runner-like colonies indicate the very unstable environment (very small stones, high siltation). On the species level, few species were selected which gives clear description of environment they are coming from. *Alcyonidium disciforme* Smitt indicate soft sediment and siltation above $50g/24/m^2$. *Harmeria scutulata* Busk is an indicator of shallow rocky habitat (down to 15m). *Celleporella haylina* Linneus represent benthic communities with algae dominance. *Hippothoa divaricata var.arctica* Kluge indicate deep, unstable rocky communities. Current Arctic study proved that bryozoans are perfect tool for fast estimation of environmental condition what also was observed in the other areas.

Biodiversity of macrofaunal communities in intertidal boulder fields of Brittany (France): patterns of distribution and hierarchical structure

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The spatial variability of macrofaunal communities in boulder fields was described. The distribution of organisms at small scale (dm²) was first analysed. Results revealed a hierarchical structure in the local community, which was organised in three sub-communities and eight microcommunities.

Vertical variability of the local community was then observed along the hypsometric gradient. The expected intertidal zones of the fauna was partly mixed up, depending on the boulder arrangements, which determined quantity and quality of shelter for organisms. Shelter could extend the intertidal distribution of marine species.

Spatial variability was studied at regional scale (100 km). Three sites were compared, situated in different hydrogeographic areas. Results showed a great variability of the abundance and biomass values. Trophic structures expressed in terms of abundance showed a vertical (hypsometric) and horizontal (inter-sites) variability. They directly depended on environmental variations (microhabitats, trophic resources, etc.). Trophic structures expressed in terms of species richness showed a vertical variability, but were stable between sites at the same hypsometric level. They revealed the existence of a common regional pool of species, structured as a regional metacommunity.

Toxic phytoplankton species on the shellfish farms on the eastern Adriatic coast

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In recent years some phytoplankton species have been found to produce toxic metabolites responsible for shellfish poisoning in the Adriatic Sea. Shellfish toxicity in the Adriatic was first recorded in summer 1989. The presence of dinoflagellatae of genus *Dinophysis* and *Prorocentrum* in the northern Adriatic caused DSP toxicity in mussels (*Diarrethic Shellfish Poisoning*) (Boni *et al.* 1992).

Since then these species have been continuously appearing in the Adriatic periodically resulting in toxic algal blooms (Marasović *et al.*, in preparation).

Because of the regular occurrence of potentially toxic phytoplankton species, and the increased appearance of toxicity in northern Adriatic a monitoring programme on shellfish farms along eastern Adriatic coast was started a few years ago.

For this paper, the samples were taken at four stations within the Monitoring program. The monitoring revealed the continuous presence (but fluctuating abundances) of *Dinophysis* and other suspect toxic phytoplankton species (e.g. *Noctiluca scintilans, Lyngulodinium polyedra, Pseudonitzschia seriata complex)* at all stations along the eastern Adriatic coast from April to November.

The effects of artificial coral reefs on the marine biodiversity: A case study of the Eastern Black Sea

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Black Sea Technical University, Faculty of Marine Sciences, Trabzon, Turkey

A highway construction has been in progress for more than 4 years on the southern Eastern Black sea, Turkey. It has been argued that this construction process would affect the marine ecosystem. Since the onset of the construction therefore, we have been watching the coastal line in question and the ecosystem itself how to react the factors. The results are very interesting.

In this poster presentation therefore, we will provide valuable information concerning artificial coral reefs in the Black Sea in terms of the biodiversity measures.

Current state and long-term changes of seagrass communities in some temperate Euro-Asian Seas

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The study was conducted in the Black, Azov, Caspian and Aral seas. These seas have many common environmental features. The condition and occurrence of seagrasses are presently strongly influenced by anthropogenic factors (river influx, industrial, municipal and agricultural sewage, navigation traffic, sea bottom dredging, dumping, atmospheric events, oil and gas extraction) and the sea level, especially the Caspian and the Aral Seas. Seagrasses play the key role in coastal ecosystems of the seas and occupy vast areas in shallow bays, gulfs and coastal salt lakes. There are two species of *Zostera* and two *Ruppia* represented in these seas. The diversity of algae, invertebrates and fishes is astonishing.

In the middle of the 20th century, seagrass stocks in the Black Sea region was evaluated as 1 million wet tons. The total litter cast ashore was about 100 thousand wet tons. There are many areas of the sea, including those subject to considerable anthropogenic loading, in which biomass yields have increased 1.5 to 3 times. Presumably, this is owing to the reduced influx of industrial sewage and increased recreational load on the coastal areas.

In the Azov Sea, seagrasses are found along all coastlines, including river mouths and flood plains. *Z. noltii* has a distribution larger than *Z. marina*. Vast beds of the two species are situated in the northern part of the sea near sand spits and in the coastal salt lakes. For the recent three decades, the biomass of *Z. noltii* has increased 2 to 3 times, while in *Z. marina* the corresponding estimates are almost unchanged. No drastic changes or degradation events have developed in communities of *Zostera* spp. and other seagrasses in the Azov Sea.

In the Caspian Sea, only *Z. noltii* and two *Ruppia* spp. grow. Extensive *Zostera* beds are concentrated in the northeastern and eastern parts of the sea. In the western part, they are rarely found. These communities also incorporate large amounts of algae, invertebrates and fishes. Total *Zostera* stock was assessed at 700 thousand tons (500 thousand tons on the eastern coast).Exploitation of the shelf and over-regulation of the river inflows disturbed the natural coastline that resulted in the disappearance of many shallow bays which gave shelter to diverse seagrasses. The most recent data regarding Caspian seagrasses were obtained in the mid-eighties. They show that *Z. noltii* occupied vast areas in eastern bays in which this species was never found earlier. Different experts estimated the stock of *Z. noltii* in these bays as from 200 to 440 thousand tons. Seagrasses of the Caspian Sea are of special significance as the favourite food for waterfowl and shelter where many fishes spawn and almost all diadromous and semi-diadromous fish feed, including commercial species.

Scientific evidence regarding seagrasses of the Aral Sea is very scarce. Seagrass species found are *Zostera noltii* and *Ruppia maritima.* The composition and distribution patterns of *Z. noltii* were studied in detail about half a century ago. Almost no data are available about the state of seagrasses after catastrophic events have taken place in the Aral Sea ecosystem. At present, *Z. noltii* may be found in disintegrating coves of the Major (southern end) and the Minor (northern end). It can be presumed that after the coves of the Major Sea disintegrated, communities of *Z. noltii* persisted mostly in the coves of the Minor Sea, because the level of this sea has remained unchanged over the past decade.

Seagrasses of all four seas have been the object of special protection in 19 national and international reserves, which are situated mostly in the Black and the Azov seas.

The role of biodiversity in seston-suspension feeder trophic interactions

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The effect of suspension-feeder biodiversity on ecosystem-functioning, particularly the interactions between trophic levels will be examined through diversity manipulation of benthic marine invertebrate assemblages. The diversity manipulations will be done at species and phyletic level and in both the subtidal and intertidal environment.

The aims of the experiments are to determine:

- how benthic suspension-feeder diversity controls secondary production rates.
- how benthic suspension-feeder diversity affects the potential for resulting primary production by controlling phytoplankton composition and biomass.
- whether phyletic or species diversity is more important in controlling the above.

Benthic habitat quality along a disturbance gradient in Inner Galway Bay: a comparative case study of faunal analyses and sediment profile imagery (SPI)

Ronan O'Reilly
Martin Ryan Marine Science Institute, NUI Galway, Galway, Ireland

Benthic habitat quality was determined along an established disturbance gradient in Inner Galway Bay using both traditional macrofaunal methodologies and sediment profile imagery (SPI). Both methods determined that habitat quality was generally good in the Inner Bay, with strong localised disturbance effects adjacent to the outfall of the Corrib River and sewage outfalls in the vicinity of Galway docks. Disturbed sites were highly variable, whereas undisturbed sites were relatively homogeneous, with a transition from an *Amphiura* community to an *Abra*/*Fabulina* community in shallowing waters. Multivariate correlation analyses revealed that faunal and SPI data were very correlated, and that certain combinations of SPI parameters gave rise to perfect correlation with faunal matrices. This high level of correlation is attributed to the strength of the faunal gradient. SPI is a technique of great utility in monitoring disturbance on the soft seafloor.

In-situ assessment of macroinfaunal activity in an inter-tidal mudflat using time-lapse sediment profile imagery (tSPI)

Adrian Patterson
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Animal sediment relations in an intertidal mudflat were observed for a five-day period by time-lapse photography using a novel scanning sediment profile camera. Dominant macrofauna were Nereid polychaetes, *Corophium* sp. and nematode worms, while foraminiferal activity was also observed. Burrow formation, destruction and abandonment rates were quantified. Both circadian (tidal) and predator prey interactions were observed between the visible macrofauna. The dominant bioturbation type at the sediment-water interface changed rapidly, indicating that ecosystem function is highly dependent on biodiversity on small time scales. An index of bioturbatory activity is described as a method for comparing temporal fluctuation in ecosystem function at sites of varying habitat quality. Direct observation of infaunal activity is of great utility in investigating the relationship between biodiversity and ecosystem function.

The effect of pollution and human impact on the biodiversity in the Eastern Black Sea marine ecosystem

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The Black Sea is a semi closed area surrounded by a number of countries where increase in population, industrialization and urbanization have affected the environment. For example over the last two decades the number of economically important fish species of the Southern part of the Black Sea has dramatically decreased from 25 to 5-6 due to the accidental introduction of the north-western Atlantic ctenophore *Mnemiopsis sp.* as well as over fishing and pollution The decrease was not only in the biodiversity of the fish species but also in the amount of catch by the riparian countries.

Scientific evidence clearly indicates that profound changes have occurred in the Black Sea ecosystem (Mee, 1992). The most dramatic observed on the Northwest shelf being primarily the result of the discharge of the chemicals by polluted rivers, even though the inflows of freshwaters by the major rivers have been reduced by 25-50 % during the same period (Çelikkale, 1991).

The hydrochemical details of these events, however, are still poorly understood (Murray et al., 1993) owing to the difficulty in distinguishing long term changes from short term fluctuations in the hydrochemistry of the upper layer where the major fraction of biogeochemically reactive elements are recycled (Karl and Knauer, 1992). The dramatic changes in the Black Sea ecosystem are also likely to have modified the Marmara ecosystem trough the Bosphorus Strait which connects the Black Sea to the ocean system.

In this presentation, a case study for the Eastern Black Sea Region of Turkey will be summarised in connection with the effect of urbanization, pollution and increase in human impact to the marine ecology as well as from the point of marine biodiversity.

Biodiversity and organic matter processing on a sandy beach: An experimental approach

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Patterns of meiobenthic diversity and phytodetritus decomposition rate were studied across a sandy beach gradient. The meiofaunal community was dominated by Nematoda. Both the meiofaunal densities, number of nematode species and biodiversity changed significantly across the beach gradient. The highest meiofaunal and nematode densities were found near the low water line; a strong increase in species number and biodiversity from high water level towards medium and low water level was observed.

Decomposition rates of organic matter were studied along the same beach gradient by means of litter bags using detritus of the macroalga Fucus sp. as a model. Litter bags with different mesh sizes (10 µm, 125 µm, 125 µm + large openings) were used to assess the contribution of different size classes of biota to the decomposition process. The rates of phytodetritus decomposition changed significantly across the beach gradient, but the link between biodiversity and the observed rates remains to be established.

In addition, a microcosm experiment was performed to study the influence of nematodes and their species diversity on the decomposition process of phytodetritus. In particular, we wanted to assess species redundancy among bacterial-feeding nematodes. The experiment was performed under constant 'environmental' conditions, with either 0, 1, 2 or 4 nematode species and *Fucus* detritus. Nematode diversity had no effects on decomposition rates of *Fucus* in our experiment, but a species-specific stimulatory effect, linked to the presence and activity of *Pellioditis marina*, was observed. It is clear from our results that bacterial-feeding nematodes may influence decomposition processes, but the exact nature of the effect remains to be established. At the same time, while our preliminary results show a significant level of species redundancy, this needs confirmation in open systems under variable environmental conditions.

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