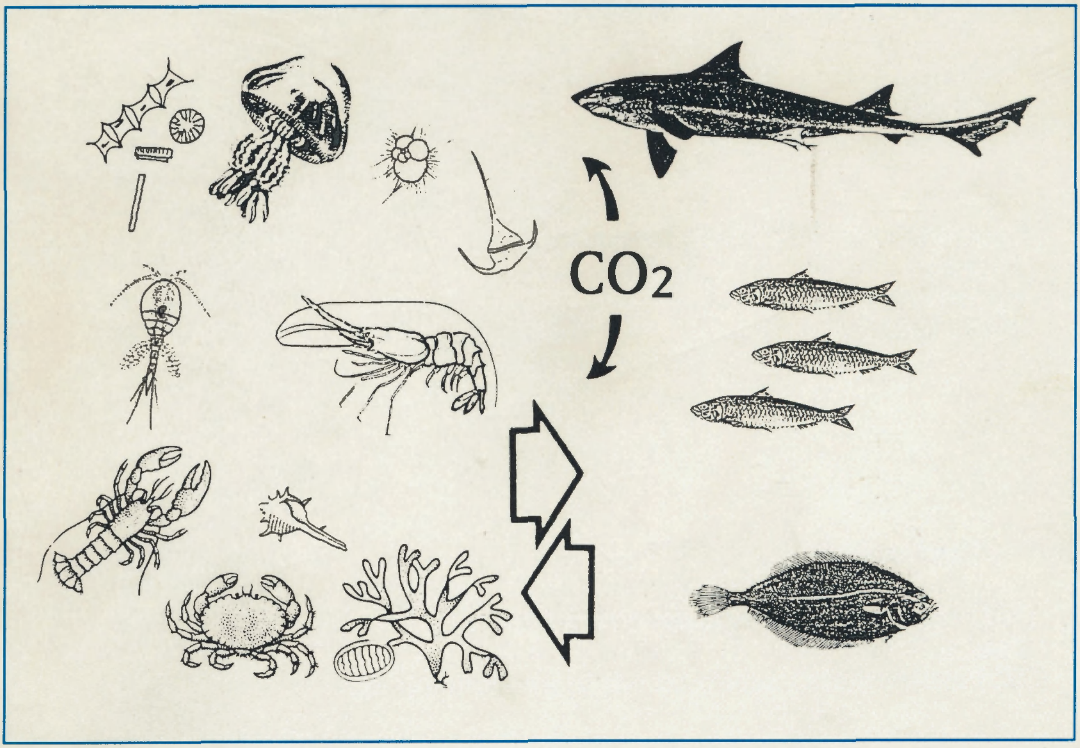
# Biodiversity and Production in the Ocean

A grand challenge for European cooperation in marine science




Outcome of the ECOPS Euroconference

# Biodiversity and Production in the Ocean

**a grand challenge for European cooperation in marine science**

Outcome of the ECOPS Euroconference
held in
San Feliu de Guixols
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# Executive Summary

Biological diversity may not only mean species diversity but also genetic diversity within species and diversity of ecosystems, habitats, and landscapes. Ecological complexity includes diversity of functional pathways and interactions, meaning that varying complexity of the organisation can still lead to the same diversity in different ecosystems. Ecosystem function is the collection of processes in the food web in its chemical and physical setting.
A fourth dimension is time, and changes from natural or anthropogenic causes occur at different rates and scales in the varying functional setting (see Fig. 6, p.21).
The marine environment is rich in the highest systematic taxa of invertebrates. While it contains some 29 phyla (14 of which are endemic) the freshwater and terrestrial environments house 15 and 11 phyla respectively and none of them endemic to these environments. On the species level, however, the terrestrial environment is much richer, mainly because of the fantastic radiation of the insects. The differentiation into specialized niches seem to be higher on land in spite of the vast area and volume of the marine realm. Our understanding of the driving forces behind speciation in the sea is still much poorer than on land. The same accounts for the coupling between species diversity and production - if there is one in the sea. Most scientists seem to believe there is such a coupling, but the scale and nature of this coupling still needs to be revealed.
We know as a fact that major pelagic fish populations undergo vast fluctuations in stock sizes, e.g. herring, sardines, anchovies, but why this is so has not been satisfactorily explained. Variability in the physical and chemical environment certainly accounts for some of this, but also food availability for and predation of the various stages of the fish life stages has to be of major importance. Changes in ecosystem species composition as a result of environmental change (natural or man made) is a factor that needs to be investigated. Understanding biodiversity and its driving forces in relation to production is of fundamental importance for the wise management of the living marine resources. The eight recommendations of this Euroconference - if implemented - will help in this. Joining forces within European marine science will also help to solve some of the problems under discussion within LOICZ (Land-Ocean Interaction in the Coastal Zone; an IGBP programme) and GLOBEC (Global Ocean Ecosystem Dynamics; a SCOR programme and possibly later an IGBP programme). The scientific competence is available within Europe, but most of the scientific questions cannot

be solved single-handedly. Under the aegis of a joint European effort significant contributions can be made. This is indeed a great challenge.

## Recommendations

1. As for the most effective management of marine living and non-living resources, it is essential to understand the nature of any coupling between biodiversity and productivity. Research on this is urgently required. The research will need to accommodate spatial and temporal dimensions and a multivariate approach to estimating biodiversity.

2. Methods for assessing production (particularly at higher trophic levels) and biological diversity have to be improved. Genetic and molecular tools must be incorporated in order to characterize "cryptic" diversity (e.g. sibling species). Such methods are also of great importance for the characterisation of diversity in bacteria, picoplankton and so-called cosmopolitan species, as existing methods are grossly inadequate. New technologies are needed for extracting information relevant to studies of biodiversity over wide ranges of time and space scales.

3. Our ability to understand changes in production and biodiversity of an ecosystem in time and space must be enhanced. The use of multivariate data analysis and the development of simulation models of complex systems, including submodels of species competition, trophic interaction, species life cycles and genetic structure is recommended. The development of theoretical studies of complex systems should be encouraged with the aim of interpreting the variations and maintenance in the biodiversity of marine systems.

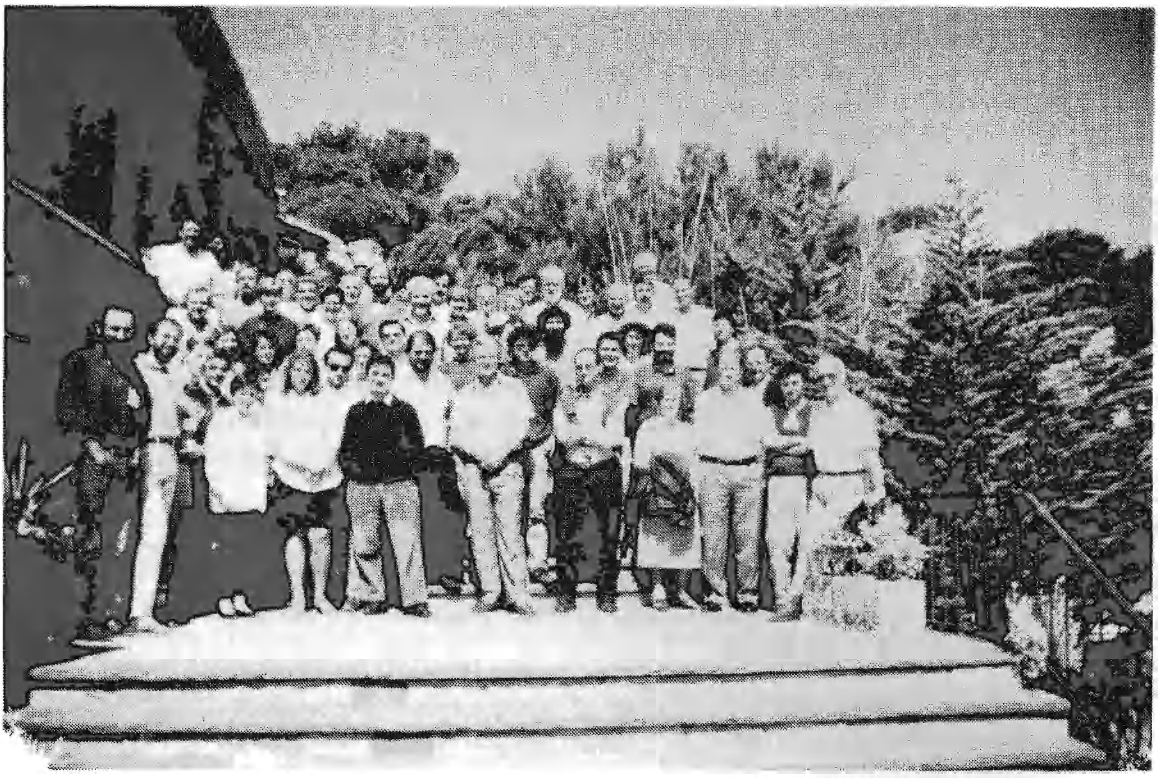
4. We recommend the further development of an integrated information system to store ecological, taxonomical, and functional characteristics of species. This system must be made easily accessible and widely known for an extensive and optimal use.
The flow of matter through an ecosystem as well as its production and its structure depends on the external energy it receives. Nowadays, human activity also adds a significant amount of energy through fishing, mining, or any other use of the marine environment. As a consequence, human impact on the production as well as on the diversity of living organisms must be urgently considered.

5. Taxonomy is absolutely necessary for biodiversity studies. We recommend increasing efforts in taxonomy using the most appropriate of the wide range of techniques available.
Existing taxonomic skills and knowledge as well as the care of taxonomic and ecological collections should be maintained and improved in order to:
- integrate morphological and molecular approaches,
- integrate evolutionary history and recent ecological conditions through phylogenetic studies, and
- study the relationship between genetic characteristics and ecological responses.

6. Marine habitats in coastal, shelf, and deep sea areas should be identified for risk assessment for the purpose of:
- conservation and habitat rehabilitation. These areas should be exposed to a minimum of human impact and used for research in order better to understand community (ecosystem) structure and changes in them. This refers in particular to coastal and shelf seas where human influence is strongest. Time and space scales should be appropriate to the geographical area and scientific problems in question.
- experimental research, in order to improve our knowledge of the resilience of the ecosystem in relation to human induced perturbances (deep-sea mining, dumping, etc.). This involves changes in species composition at all trophic levels, recolonization of disturbed areas, etc.

7. Introduced and transferred species/stocks often proliferate in their new environments to the detriment of native species and the system. Such phenomena should be studied to assess abiotic and biotic controls (competition, predation, diseases, etc.) operating within the respective systems.
Comparative studies with unaffected areas need to be carried out at an early stage to elucidate the impact of introduced species. Such studies would help in assessing the environmental risks associated with transfers and introductions and provide guidance for management to minimize these risks.

8. Pelagic ecosystems, which are of fundamental importance to the generation of global oceanic production, are not amenable to in situ experimentation or manipulation. However, existing monitoring programmes have established a close coupling between changes in planktonic ecosystems, hydrographic regimes, and climatic patterns. We recommend that continued efforts should be made to enhance and extend monitoring programmes to elucidate spatial and temporal patterns in the dynamics of marine ecosystems.



Participants in the Euroconference assembled outside the conference room at Hotel Eden Roc, San Feliu de Guixols.

# Contents

# Introduction

The Euroconference on "Biodiversity and Production in the Ocean" took place in San Feliu de Guixols, Spain, from 4 to 8 May 1994. The objectives of the Euroconference were:

*- to establish our present knowledge of factors and processes regulating biodiversity and production in the ocean and the interconnections between the two,*
*- to evaluate the new techniques for studying biodiversity, and their application to problems in the marine environment,*
*- to assess current and future human impact on biodiversity and production in the ocean, and*
*- to find ways in which the European scientific community may advance the frontiers and then to formulate recommendations to this effect.*

Most of our current knowledge on the relationship between biodiversity (number of species) and production (amount of biomass produced and transferred to higher trophic levels) has been derived from terrestrial investigations and recent experimental studies have shown that, within certain limits, plant production increases with diversity. On the other hand, it is well-known that human impact on natural systems (e.g. clear-cut felling, pollution, overgrazing, eutrophication) leads to over-all reduction in diversity. Indeed, the much publicised, world-wide decline in biodiversity on land has captured public interest to the extent that it is now one of the major global issues. However, much less is known about the relationship between diversity and production in the sea, and, with human impact on marine systems increasing steadily, there is reason for concern that a similar detrimental effect on marine diversity may well be occurring.
The Euroconference was structured according to the aims given above. As most ecological terms are poorly defined and the methods used to measure them often disparate, it was felt necessary to first examine, on successive days, the concepts of diversity and production and their respective methodologies and address some of the following questions:

*- Do we understand the relationship, if there is one, between biodiversity and production in the sea?*
*- Are there equator to pole diversity gradients in the sea as there are on land? - Do we understand, in either case, why?*
*- Which are the important factors driving speciation and also diversification in the sea?*

The third day was devoted to the application of molecular biology methods for assessing and measuring diversity. These represent

powerful new tools that are only now beginning to make an impact on marine ecology.
The final session addressed anthropogenic impacts including some of the following aspects: Are anthropogenic toxins (such as heavy metals, PCBs etc) a coastal problem or does their impact extend to shelf and possibly open ocean areas? What are the effects of fishing on the system in general apart from the target fish stocks themselves. What is the effect of introducing exotic species whether intentionally by aquaculture or inadvertently by various machanisms such as ballast water.

The initiative to the Euroconference was taken by the European Committee on Ocean and Polar Sciences (ECOPS) and a planning committee was organized comprising eight scientists.:

| | |
|---|---|
| Prof. Jarl-Ove Strömberg | (Sweden, chairman) |
| Prof. Victor Smetacek | (Germany, vice-chairman) |
| Prof. Bruno Battaglia | (Italy) |
| Prof. John Beardmore | (United Kingdom) |
| Dr. Vibeke Brock | (Denmark) |
| Dr. Jean-Pierre Feral | (France) |
| Prof. Paul Nival | (France) |
| Dr. Annelies Pierrot-Bults | (Netherlands) |

The present report has been produced by this planning group in cooperation with the rapporteurs of the four sessions and represents the outcome of the Euroconference.

# Report on the session: Biodiversity in the Ocean

Annelies C. Pierrot-Bults (Chairperson)
Instituut voor Taxonomische Zoologie
Amsterdam, The Netherlands

Victor Smetacek (Rapporteur)
Alfred-Wegener-Institute
Bremerhaven, Germany

Biodiversity is a recent and poorly defined term that, nevertheless, is sufficiently well grasped by the public to have become a global issue. The session was opened by Ramon Margalef who approached the issue of diversity and production from a theoretical viewpoint. He argued that, in any system, diversity will decrease with increasing production/ biomass (P/B) ratio. As the human network, manifested in its life-supporting and communication systems, continues its expansion over the globe its P/B ratio increases - hence diversity in the systems impacted by it will perforce decrease. This overall statement was backed by numerous examples from various regions and systems. The next talks by John Beardmore and Siegbrecht van der Spoel addressed the problem of defining and measuring biodiversity. Both pointed out that there are many different ways of defining, and hence also measuring, biodiversity. A single, all-encompassing definition is difficult to formulate and, because of the problems of scaling, will also be difficult to measure. On this score Beardmore was more optimistic than the majority of the participants as became evident during the discussions. The next talks by Paul Nival and Martin Angel dealt respectively with physical and biological factors influencing biodiversity. Nival considered the different physical features of the marine environment that will impact diversity along an hierarchy of scales. Angel, on the other hand, considered distribution patterns of various taxa and indicated trends along which diversification might well occur. Comparative analyses of habitats (e.g. benthos/plankton) and regions (shallow/deep or high/low latitudes) are likely to be a fruitful avenue to increase our knowledge of diversity in the ocean. A general consensus was that our understanding of diversity and its causes in the oceans is at a rudimentary level.

## *Biodiversity, Diversity and Production*

Ramon Margalef
Dept. of Ecology
University of Barcelona, Barcelona, Spain

Diversity may function as a proxy for biodiversity, which is a recently coined term as yet poorly defined. The earlier term diversity, however, retains its importance. Diversity increases when regulation inside the ecosystem operates close to the slowest turnover, or lowest P/B (production/biomass) ratio. Diversity decreases with increasing P/B ratios, as are associated with higher energy flows through the ecosystem. This means that diversity is related to acceleration, a concept very important in physical systems, but which is widely neglected by ecologists, even when purporting to work with physical systems. Not only energy from light and energy associated with chemical bonds play a role, but also energy of evapotranspiration in vascular plants and exosomatic energy utilised by humankind. The latter forces much energy through the present biosphere and the prospects are hence decreasing diversity in anthropogenically impacted areas followed by a general decrease in global biodiversity.

Ecosystems work as if performing experiments in evolution with genetic material taken from the stores of biodiversity and in the frame of diversity dynamics (succession etc.). The modified product is returned to the general store of biodiversity. This store changes in accordance with regimes of local accelerations or decelerations to which the most active part of the biosphere is subjected. The store is the biodiversity but its continuous reconstruction is the job done in the frame of ecosystem diversity.

## *Dimensions of Biodiversity*

John Beardmore
University College of Swansea
Swansea, UK

The term biodiversity is used in a variety of ways and it is necessary to define it clearly. Some definitions exclude some levels of biological variation, others include non-biological elements. It is important to reach agreement and understanding of what constitutes biodiversity within marine environments. The definition needs to include all levels of biological complexity but should not include abiotic factors (though many of these influence biodiversity).

Once there is agreement on what constitutes biodiversity in marine environments it is important to define, as explicitly as possible, the ways in which biodiversity, at each of the component levels, can be estimated and how these estimates may sensibly be combined into a single measure.

The factors affecting genetic variation within a species can be intrinsic (mutation and recombination rates), or extrinsic (population size and structure, habitat heterogeneity and predictability) and related to life history (breeding system, fecundity). The feedback mechanisms involved will be via multiple genotypes (multiple niches) and behavioural changes that will result in shifts in patterns of selection.

Finally, anthropogenic impact will be via harvesting of breeders, excessive harvesting, pollution leading to mutation and competition or introgression with introduced species as well as impact of introduced parasites.

### *Assessment of Biodiversity*

Siegbrecht van der Spoel
ITZ, Zoological Museum
Amsterdam, The Netherlands

The theoretical foundation of biodiversity of the ocean is vague. One should always work with standard surfaces or areas, for example with 1 $m^2$. In the ocean it then is possible to speak of the diversity under 1 $m^2$. When a standard calculation is used for the different groups. all results can be recalculated for 1 $m^2$, or for the biota below 1 $m^2$, and presented as such.

Another standard problem is: which specimens should be considered from one population? It is my opinion that the presence of an adult implies that all developmental states were also present. For this reason one should, as a standard, only consider adult specimens in a diversity calculation. For the pelagic, the meroplankton is thus excluded as the adults are living in the benthos, bringing together the biodiversity of benthos and the pelagic in one value should correct the omission of meroplankton in the pelagic.

We need also need a standard time unit which becomes even more important when one takes the decision to include only adult specimens. I would like to propose to use the term *biodiversity* only for the average condition (over a year) in an area and the term *biomultiformity* for the actual conditions at a given moment.

Biodiversity should thus be plotted in three dimensions of organism, time, environment. All factors related to the species and specimens are dependent on the genetic "print" in the specimens and thus they are all related, they can be multiplied to generate one value. In the formula I proposed on the 1993 meeting (Bijdragen tot de Dierkunde 64(1): 1-31 (1994)) also the organism and the environment are the two components that are multiplied (or to be presented on two crossing axes).

The value "Diversity" has to be based not only on taxonomy, on numbers of species, it should take into account that there are remarkable differences in the representation of families, orders and even classes. The ecological properties of species should be included in biodiversity calculations. The genetic properties of species should be included in biodiversity calculations also. If the genetical properties of a species have to be considered for diversity calculations, it is advisable to incorporate, in numerical analyses, not only the species but also the taxa below species level, probably the populations. The phylogeny should be included in biodiversity calculations. The history of faunas has to be considered when making an assessment of biodiversity as derived faunas are likely to contribute less to future diversity than original faunas will do.

For assessing biodiversity we: 1 - distinguish between the average *biodiversity* (the biological climate) and the actual *biomultiformity* (the biological weather), 2 - standardise the calculations by using fixed area and time limits, 3 - use only reproducing (adult) specimens in calculations, 4 - incorporate in the calculations beside the numerical data on species also those on higher taxa, and on taxa below the species level, 5 - "correct" the number of species for ecologic, genetic, historic and phylogenetic abilities of the specimens, according to the formula (van der Spoel 1993), 6 - need a standard area, or a standard data set, should be selected to relate to all calculations.

It is quite clear that at present we cannot give an exact assessment of biodiversity when we try to incorporate all the factors mentioned and perhaps others as well. But the managers, policy makers, and society are highly interested in information on biodiversity at this moment. This reminds me of the weather forecast: inaccurate as it is, it is produced each hour at hundreds of places over the world. As inaccurate as it may be, one likes to have the information for planning purposes.

Analogously the information on biodiversity and on biomultiformity, inaccurate as it is, should be produced each year or season at hundreds of places over the world because we need this information for planning purposes no matter how inaccurate it may be.

## *Physical Factors Influencing Biodiversity*

Paul Nival
Station Zoologique
Villefranche sur Mer, France

The perception of the biological components of an ecosystem is different for a geochemist and an ecologist. The former is dealing with the results of functions and is mainly interested by groups of species having the same function in the system, that is mainly trophic levels. The ecologist wants to understand the dynamics of each biological entity in the system. He has to consider the different interacting species and consequently the diversity of biological elements.

Most of the work done on marine systems has been oriented towards the effect of physical factors on trophic levels rather than on species assemblages. However, different physical processes have been invoked to explain changes in the qualitative properties of biomass or species succession. Processes leading to mixing and stratification of surface waters are able to shift the pelagic assemblage of species from diatom to flagellate dominance. An important question which needs to be answered is the following: Which physical process or combination of physical and biological processes is able to change the diversity of an assemblage of species?

A particular species can dominate a community if it has a reproductive or a growth advantage over the others. The diversity in the spatial structure and the fragmentation of space into a mosaic of different physical environments, can induce a diversity of assemblages of species. However, the processes which confer an advantage to a species are not the same at the individual and population levels.

At the scale of the individual (mm) the fluid characteristics which are able to change the growth efficiency of a species can be described by non-dimensional numbers. The Reynolds number defines the characteristics of the flow of water around the individual (laminar or turbulent) and the Deborah number indicates the ability of the substrate to affect biological processes. This number is the ratio of deformation time of a biological process to the deformation time of the physical substrate. The instantaneous growth rate of a phytoplankton species will depend on its intrinsic growth rate in relation to the rate of change in nutrient gradients impinging on the cells. The physical processes producing spatial gradients are of great importance in defining the patterns of vertical or horizontal species distribution. Vertical turbulence, upwelling, internal waves, internal tides, which transport phytoplankton cells in the light gradient might decrease or increase the growth of species according to their biological characteristics (photosynthesis and nutrient assimilation).

Strong gradients over short distances can be detected with continuous measurements along a transect. Their spatial scale is related to the spatial extension of populations of different species. Fronts, filaments and all mesoscale structures related to eddies can affect species diversity. For instance the dominant taxonomic groups of phytoplankton depend on the location relative to the center of an eddy. Similarly, spatial distribution of copepod species can be related to mesoscale distribution of shear or velocity gradients in the same type of eddies.

The combination of physical characteristics such as vertical mixing, shear, internal waves, vertical transport with photosynthetic characteristics, nutrient assimilation, nutrient storage and mobility, resulting in different growth ability between species, is the cause of the dominance of some species and of diversity. The increase or decrease of diversity depends on the auxiliary energy introduced into the ecosystem by the meteorological or hydrodynamical forcing.

No physical forcing is permanent. Superimposed on the seasonal variation of heat flux forcing is a high frequency forcing through meteorological variables. Sequential storms introduce perturbations or pulses into the ocean surface layer to which biological processes adapt. The ability of some species to cope with the temporal sequence of such perturbations will give them the capability to dominate the assemblage. Periods of vertical stability following strong mixing allow species succession to proceed and the trend usually is towards an increase in the species diversity. However, the species assemblage is generally in a transient state. Depending on the frequency of the perturbations and on the growth characteristics of the species, different species can grow whereas some of them would disappear in a persistent environment.

Modelling communities with a large number of species and some degree of reality is difficult at the current state of knowledge of parameters responsible for differences in species. In order to explain the diversity changes observed in marine ecosystems, more work is needed on the effect of physical processes or events on species assemblages rather than on biomass.

### *Biological Factors Influencing Biodiversity*

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Deacon Laboratory, Surrey, UK

At all levels of organisation (ecological, functional, species, physiological and genetic) biological diversity as observed has two basic types of causal factors, the historical causes (e.g. evolution of taxa and ocean systems, climatic and vicarious events) and those that serve to maintain it ($O_2$ competition, import/export, extinction etc.). The greater phyletic disparity of marine taxa probably originated in the much greater geological age of metazoans inhabiting the ocean than the land (ca. 150 mio years). It is noteworthy that the phyletic disparity of pelagic faunas is similar to that of terrestrial faunas.

As a result of major changes in ocean basin morphology over the geological past, pelagic ocean faunas retain a memory of gyral circulations in ancient oceans. Vicarious events such as the opening and closing of the Panama Basin and the drying out and reflooding of the Mediterranean have had significant and persistent influence by either breaking down barriers to dispersal or creating isolation. Hence tropical near-surface faunas appear to be circum-global. Speciation may have occurred in isolated deep basins when sea levels have fallen and global cooling events seem to be the cause of major extinctions (followed by speciation which within 10 mio years restored species richness to its former levels).

Ecosystem variability is determined by layer-scale circulation patterns which are also associated with variations in many environmental parameters (e.g. as shown up by maps of the climatology of nutrients such as nitrate and silicate). However, different taxa live in differently scaled worlds, so that bacteria, copepods, and whales are influenced by the very different processes operating at the time/space scales of their environments. So the assemblages we observe and try to understand have components which are influenced by very different factors.

In the north-east Atlantic, satellite imagery has shown that there are considerable latitudinal shifts in surface chlorophyll concentrations and their seasonality. The change from small winter maxima in the tropics and subtropics to a substantial spring and autumn bloom at temperate latitudes occurs at about 40°N. There is at least a doubling of the total annual primary productivity on the pole-ward side of this latitude. Plankton analyses show that the composition of the communities changes substantially. Micronekton standing crop doubles, the ratio between macroplankton and micronekton standing crop decreases, the biomass of migrating macroplankton increases in spring and summer, seasonal migrations to overwinter at depth are more prevalent. However, the logarithmic decrease in biomass with depth remains more or less the same.

Profiles of species richness and H' of a typical planktonic group, the ostracods, show a maximum at all latitudes sampled from 10°N - 60°N at about 1000 m (NB well below the euphotic zone) and the numbers of species inhabiting the deeper water halved to the north of 40°N. As analysis of the numbers of species of four taxa (fish, decapods, euphausiids and ostracods) in the top 2000 m of the water columns show similar trends, peak species richness at 18°N (where an ocean front between south Atlantic and north Atlantic Central Waters happened to be at the time) and a sharp decline at 40°N. The increasing seasonal variation in the production cycle is considered to be the dominant causal factor of this pattern.

Benthic taxa show similar profiles of species richness with maxima at about 1000 m depth. Rex et al. (1993) have published data which suggest that in abyssal Gastropoda and Bivalvia, species richness may also decline polewards across 40°N but no samples south of 40°S were collected. However, this latitudinal trend is absent in some benthic groups and in shallow water soft-bottom communities. This may reflect changes in the seasonal availability of food or the large gap in the spectrum of time/space patterns of disturbance in abyssal benthic habitats.

## Summary of the Discussions

General agreement existed on the necessity of understanding diversity and its driving forces. A central question discussed in this session concerned the definition of biodiversity. Most participants were of the opinion that a single definition yielding a single number was not practical and that a variety of different approaches addressing different spatial and temporal scales would be necessary to adequately describe biodiversity. Thus, diversity can be based on numbers of species and genetic variability within them but it can also be based on functional considerations. This is an important point as it leads to the question of what should be preserved: the species per se, or the system which generates diversity.

The question of whether production and diversity are linked and if so, how, was another important topic. It was pointed out that increasing the number of fish species in aquaculture increased fish production because available niches could be better utilised. However, there will be upper limits to the number of species necessary to increase production rates. Studying the relationship between diversity and production and the responsible mechanisms in the marine realm can be done experimentally, e.g. by using mesocosms. Comparative regional studies in differing environments can be another way. A region recommended for such studies was the transition zone between the North and Baltic Seas. Another recommendation was to acquire more information on individual life cycles as this is a prerequisite to understanding causality, i.e. species occurrence, performance and recruitment, in structuring ecosystems.

The question of speciation also received wide attention: Which factors drive speciation and whether species are also functionally different was discussed at length without reaching consensus. The important practical questions related to this are, e.g. whether increasing eutrophication of the Mediterranean will lead to decreasing diversity; the concept of "redundant species" was rejected in this context. It was also pointed out that 60-year cycles of sardines and anchovies have now been well documented although the driving forces are poorly understood. With the burgeoning human population, competition for space will increase accordingly and hence it is important to assess what is permissible with regard to habitat loss.

The role of stress in speciation and diversity was discussed next. It was maintained that stable systems have high diversity, hence global change, by increasing stress, will lead to decrease in diversity. The discussion swung back to the species concept: A species is a gene pool processing material in space and time. There are fundamental and realised niches and the correspondence between the two is determined by the gene set-up. Hence, it is important to assess genetics of the organisms. The role of mixing of the oceans in influencing speciation was also considered. The impact of stressful environments can be modulated by mixing. If stability, hence predictability breeds diversity so will scarcity. The question of factors driving deep-sea diversity came up frequently during the discussions. Another undecided matter was whether the rate of extinction today is higher than the rate of speciation. However, answers to most of these questions are implicit in Margalef´s generalisations developed in his introductory talk.

# Report on the session: Production in the Ocean

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Richard Warwick (Rapporteur)
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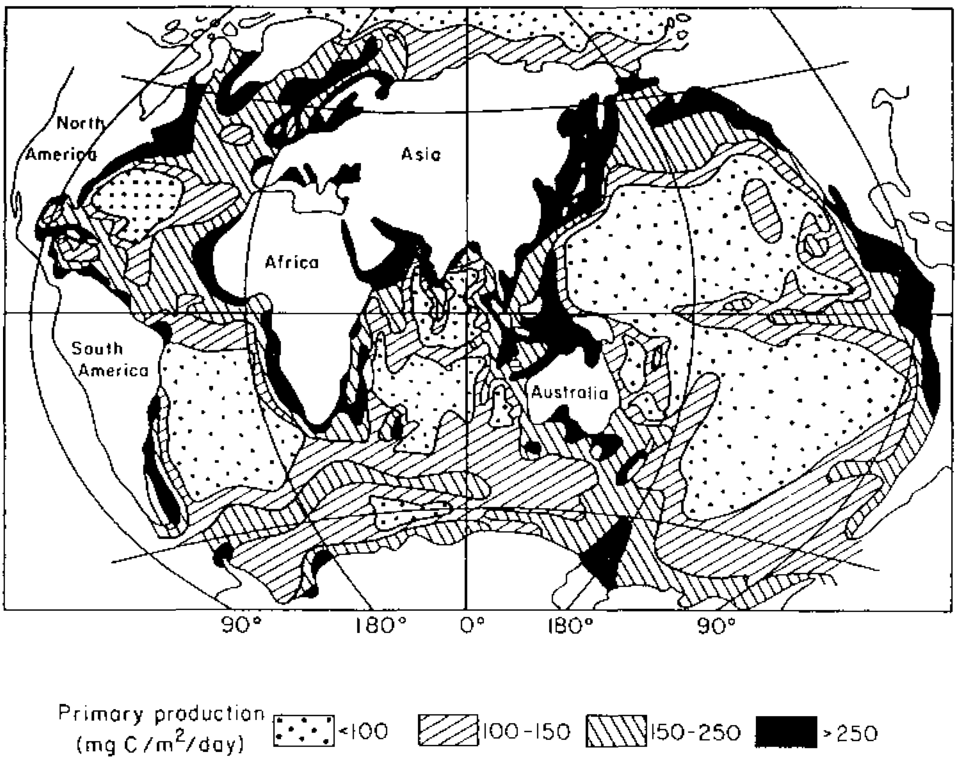


Fig. 1. Distribution of primary production in the oceans (after Koblentz-Mishke *et al.*, 1970).

## *Is There a Link Between Production and Diversity?*

Andrew Clarke
British Antarctic Survey
Cambridge, U.K.

Primary production is distributed patchily over the globe, with areas of high productivity found primarily in coastal or upwelling areas (Fig. 1). There is no apparent latitudinal cline in the intensity of annual primary production, but there is a distinct latitudinal variation in the seasonality of primary production. The importance of size in production is now well recognised, with smaller forms (cyanobacterial picoplankton and nanoflagellates) responsible for significant biomass and very significant production in some waters at some times.

Primary production in the sea has essentially three possible fates. It may be grazed by secondary producers, it may enter the microbial 'loop' through microzooplankton grazing of heterotrophic uptake of exuded dissolved organic material, or may sediment to the sea bed. The vertical flux represents production exported from the zooplankton, and results primarily from blooms of larger cells. Export production links the euphotic zone to the benthos, and in many areas benthic biomass is tightly coupled to the extent of overlying primary production.

We still lack a clear picture of diversity in the sea. Planktonic forms often show a cline with more species in the tropics than in cool or cold water. Many benthic taxa have their highest diversity in the Indo-West Pacific, which also leads to latitudinal (tropics to poles) decline in diversity. Typical examples are gastropods, bivalves and foraminiferans.. Data for other taxa are less convincing and some, such as bryozoans, show no evidence for a cline. Within habitat (a) diversity measures from soft sediments appear to show a latitudinal cline in the northern hemisphere for continental slope samples of macrofauna. Nearshore samples and southern hemisphere samples do not show a convincing cline. Until questions of comparability of sampling protocols have been solved, the question of a latitudinal diversity cline in the sea remains open.

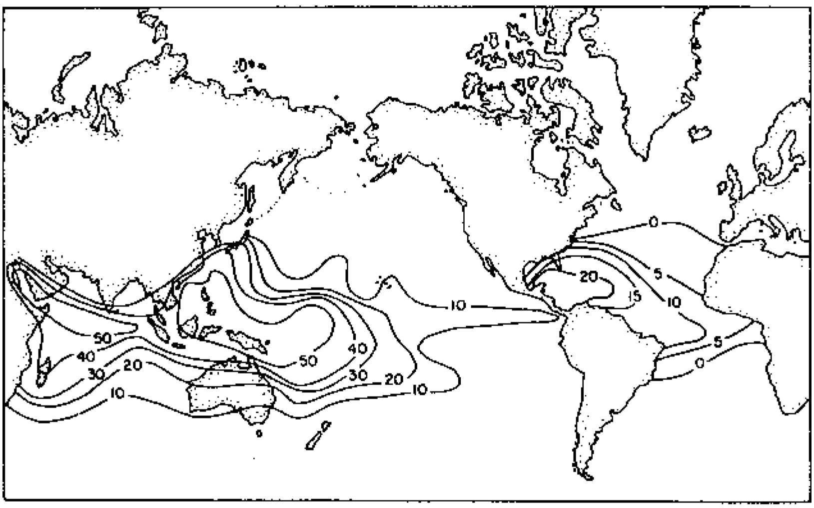


Fig. 2. The global distribution of numbers of reef-coral species.

There is no correlation apparent when global maps of primary production and benthic diversity are compared (e.g. Fig. 2 for coral species). Terrestrial systems suggest that there is a positive correlation between production and diversity in low productivity areas. At very high productivities, for example, where pollution occurs, diversity is also low. At intermediate levels of productivity, characteristic of most marine habitats it would seem that any correlation between production and diversity is obscured by other factors.

### *New Methods for Assessing Marine Primary Productivity*

Frédéric Partensky
CNRS, Roscoff, France

Many different methods are used nowadays for assessing marine primary productivity. They can be classified as: *in vitro* (based on incorporation of stable or radioactive isotopes in phytoplankton cells), bulk property (based on changes in the chemical composition of seawater), optical (based on absorption, fluorescence or light scattering measurements of seawater) and physiological methods (based on growth rate measurements converted into production using conversion factors). Among these, the $C^{14}$ technique is still the method of reference. A recent improvement, involving a deck incubator and artificial light, has recently been proposed by Babin *et al.*

*In vitro* methods always have two unavoidable drawbacks: 1) they are not instantaneous and 2) they do not permit continuous profiles of production to be obtained. However, a new optical method developed by Kolber and Falkowski, "pump and probe" fluorometry, circumvents these limitations. The method uses a submersible fluorometer, which measures the fluorescence of live photosynthetic cells *in situ* before and after excitation of the photosystems by a flash of variable intensity.

Another promising development of production studies, especially with regards to the potential coupling between production and biodiversity, is the estimation of the specific production of phytoplankton species or taxonomically homogeneous groups. An application of this concept has been developed by Vaulot *et al.* who have measured the growth rate and estimated the production of natural populations of the newly discovered prochlorophyte *Prochlorocococcus* in the Equatorial Pacific. This method simply consists of analysing by flow cytometry natural samples of *Prochlorococcus*, harvested at regular intervals during a diel cycle, after adding a DNA stain. From such times series of DNA distributions, the specific growth rate ($\mu$) can be calculated and production can then be derived from the product of depth-integrated values of $\mu$ and cell concentrations (Fig. 3).

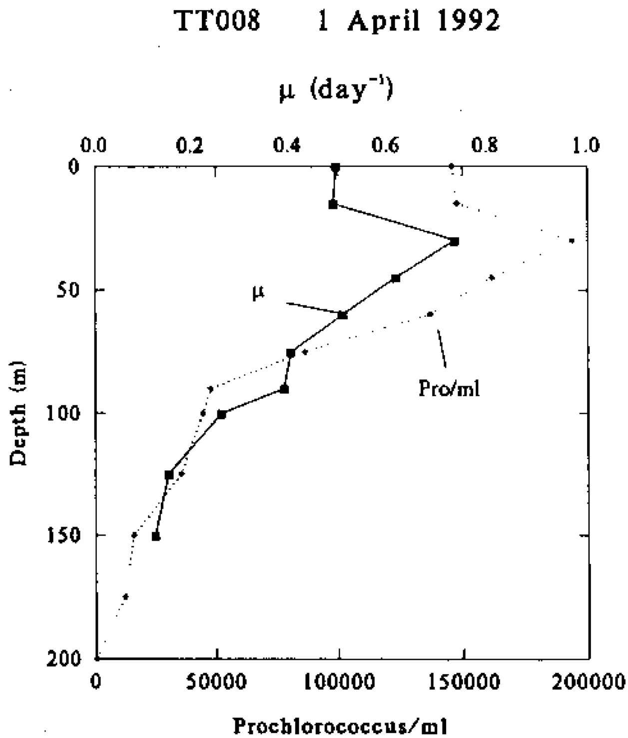


Fig. 3. Vertical profiles of cell concentrations and specific growth rates ($\mu$) of *Prochlorococcus* in the Equatorial Pacific (EqPac cruise). $\mu$ is derived from a function of the length of the terminal phases of the cell cycle integrated over a diel cycle (unpublished data from D. Vaulot and R. Olson).

All the methods described above provide local estimates of primary production, but give no indication of the mesoscale variability of productivity. Satellites are obviously the best means to estimate production at regional or even global scales, an essential requirement to quantify the ocean's role in the carbon cycle. Despite a relatively low sensitivity, the coastal zone colour scanner (CZCS) which was active between October 1978 and June 1986 has provided a huge data bank, from which the first models for assessing marine productivity from ocean colour have been developed. The launching, planned for the end of 1994, of a new satellite (the Seastar) equipped with a very efficient sensor (the SeaWiFS) will provide a new tool for applying and developing such models. Strong intercalibration with field measurements is however still needed to derive reliable values of production from remote sensing measurements. Combining numerous *in situ* estimates of the contribution of the major phytoplankton groups to the total production with global estimates of production by remote sensing could allow us to produce global maps of production for these specific photosynthetic groups, leading to a much better understanding of the functioning of oceanic ecosystems.

### *Physical Factors Controlling Production*

Ulrich Bathmann
Alfred-Wegener-Institute
Bremerhaven, Germany

Annual solar irradiance, in contrast to the map for primary production in Fig. 1, shows distinct geographical trends with rather homogenous daily solar energy flux throughout the year at the equator and a clear seasonal signal at both poles; maximum daily flux in summer reaching the sea surface in all regions is about the same. Primary production in the water column is strongly related to light availability through time, and thus to the degree of vertical mixing. New evaluations of models for critical production depth imply that mixing depths shallower than 40-60 m and water column stabilities lasting longer than 10 days are necessary precursers for phytoplankton bloom development. But also water mixing conditions during winter strongly effect the structure of the pelagic system which in turn determines the mode of production (recycled vs. export).

In polar seas, sea-ice cover impinges on primary production over time scales from days to years. Life cycles of various Antarctic organisms are adapted to sea-ice dynamics. For example, the Antarctic krill (*Euphausia superba*) shows different behaviour throughout the year (Fig. 4). Pelagic copepods (e.g. *Calanus propinguus*) and diatoms (e.g. *Fragelariopsis kerguelensis)* develop their maximum biomass at distinct hydrographical features, i.e. water masses and hydrographical fronts. Stability of the hydrographical entities with time provides the conditions for excessive biomass production (bloom biomass), which may be utilized within the pelagic food web, be exported to top predators (birds, seals, mammals) and/or exported to deeper water layers and to benthic communities.

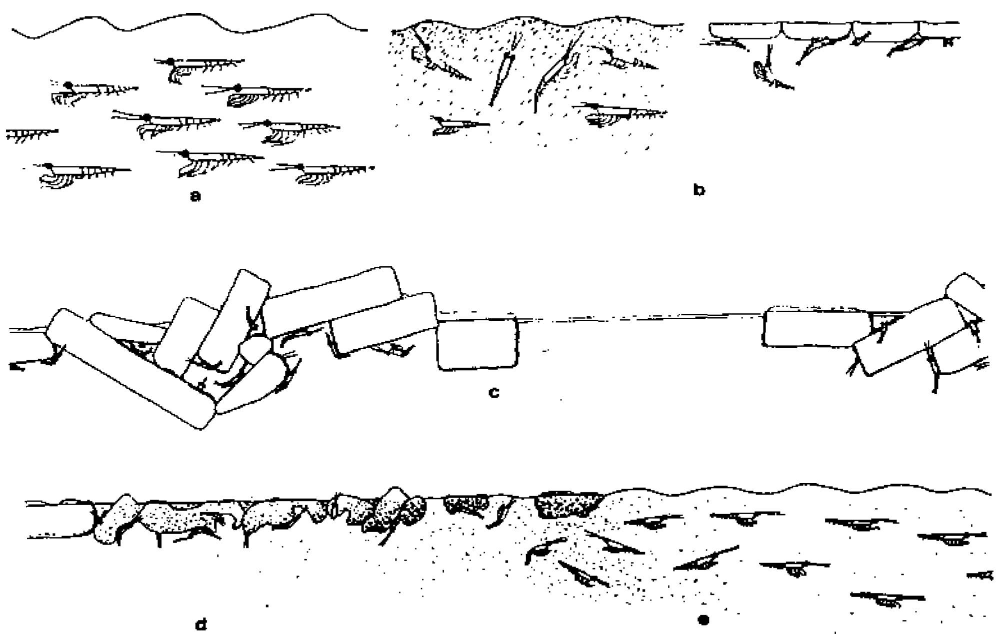


Fig. 4. Schematic diagram of Krill distribution in summer (a), within phytoplankton blooms (b), during sea-ice formation in autumn (c), in winter (d) and during sea-ice melting in spring (e) (after Smetacek *et al.*, 1990).

## *Biological Factors Controlling Production*

Victor Smetacek
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Bremerhaven, Germany

In the course of earth's history, interaction between organisms and their environment has shaped the atmosphere and oceanic ecosystems continue to play a major role in modulating climate. As such, the physico-chemical factors (apart from solar radiation and tides) that control production in today's ocean are themselves largely determined by biological factors operating over longer time scales.

Since oceanic communities have a much longer history of continuous colonisation than the continents, allopatric speciation might well be of lesser importance. Indeed, the structure and dynamics of the pico- and nanoplankton community (the so-called "regenerating communities") that include auto- and heterotrophic phyto- and zooprotists as well as bacteria have probably not changed significantly since the Precambium.

The biomass of this community fluctuates within much the same order of magnitude throughout the world ocean, and hence appears to be independent of nutrient or light supply. Therefore, it appears likely that the abundance of primary producers in nano and pico size classes is controlled by grazing of heterotrophic protists that not only share the same space and time scales but also growth rates. This type of close gearing has been postulated to exist between bacteria and their major grazers, the phagotrophic nanoprotists. Recent surveys suggest that the latter are dominated by comparatively few cosmopolitan species which might be taken as an indication that these organisms have already attained a state of morphological and physiological "perfection" vis-a-vis their food. However, molecular biological methods might well provide new and possibly unexpected insights on protistan diversity.

By and large, biomass peaks in the oceans are due to diatoms which are the most recent arrivals amongst marine primary producers. The very fact that they do give rise to blooms is proof that growth rates can outpace grazing rates. It follows that diatoms as a group are less susceptible to grazer control than the smaller pico and nanoplanktonic cyanobacteria and flagellages. It seems reasonable then to assume that some of the characteristic features of bloom diatoms (chains, protuberances, life history strategies) can also be interpreted in the light of grazer deterrence or avoidance primarily by protistan phagotrophs.

The role of metazooplankton in controlling phytoplankton populations seems to have been over-estimated in the past. The number of species amongst the major groups of metazooplankton is comparatively small as also is the range of morphotypes. Crustaceans have the largest number of species and the various groups such as copepods and euphausiids have basically similar bioplans. However, species differentiation is facilitated by details of appendage morphology or carapace shape. Here again, it is possible that application of molecular biological methods to discrete populations will yield many surprises regarding diversity of marine zooplankton.

## *Global Change and Effects on Biogeographic Patterns*

John Gamble
Plymouth Marine Laboratory
Plymouth, U.K.

It is generally accepted that significant changes are taking place in the marine environment through the effects of fisheries, mineral exploitation, pollution and inorganic nutrient enhancement. In addition, evidence is steadily accumulating on the increased possibility of global climate change induced by the anthropogenic generation of radiatively-active gasses. While increasing trends in appropriate parameters have been shown frequently, the consequences of such changes at the community and ecosystem level in pelagic systems in particular are poorly described and little understood.

With the exception of some large-scale mesocosm experiments, it is very difficult to test hypotheses on the response of planktonic communities to environmental stress and, indeed, the effects of global climate change will be impossible to show experimentally on a biogeographic scale. In this context, the only recourse is to examine changes in populations of plankton which have been monitored consistently over a prolonged period of time starting before the onset of the major environmental perturbations.

The 40-50 year long Continuous Plankton Recorder (CPR) Survey of the mixed layer mesoplankton of the NW European Shelf and North Atlantic Basin fulfils many of the criteria for studying long-term change in planktonic ecosystems in relation to known environmental changes. Sampling and analyses have been carried out consistently and the abundance of almost 400 different phyto- and zooplanktonic entities have been routinely estimated. Long term trends, which are known to be indicative of changes in the planktonic communities of the North Atlantic and North Sea (Fig. 5), have been derived using multivariate techniques on selected groups of the most common taxa.

However, there is now a need to investigate patterns of biodiversity in CPR data using information on all the taxa identified. An investigation of the diversity of plankton in the North Sea has revealed regional differences which can be related to recognised natural and anthropogenic environmental gradients. In particular there was a change in the pattern of dominance of planktonic organisms from holoplanktonic to meroplanktonic taxa in the central region. The question remaims whether such changes were induced by anthropogenic stressors such as persistent fishing activity, or whether by a natural long-term change in the environment. In either case the results argue strongly for a need to investigate changes in the diversity and structure of planktonic communities on appropriate temporal and spatial scales particularly if we require insight into the consequences of global change.

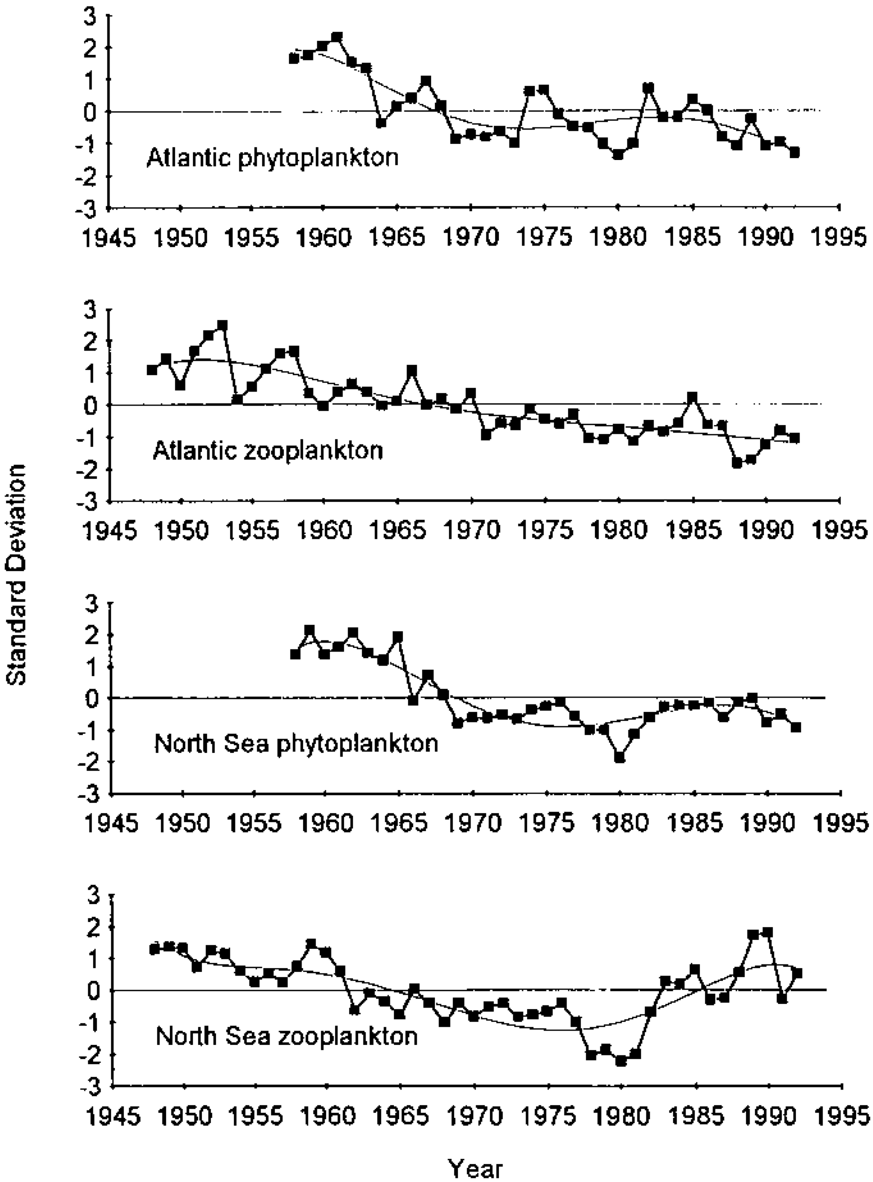



Fig. 5. First principal component of the fluctuations in abundance (standardised to zero mean and unit variance) of phytoplankton and zooplankton in the northeast Atlantic around the British Isles and the North Sea. Fifth order polynomial fitted to data.

# Report on the session: New Methods in the Study of Biodiversity

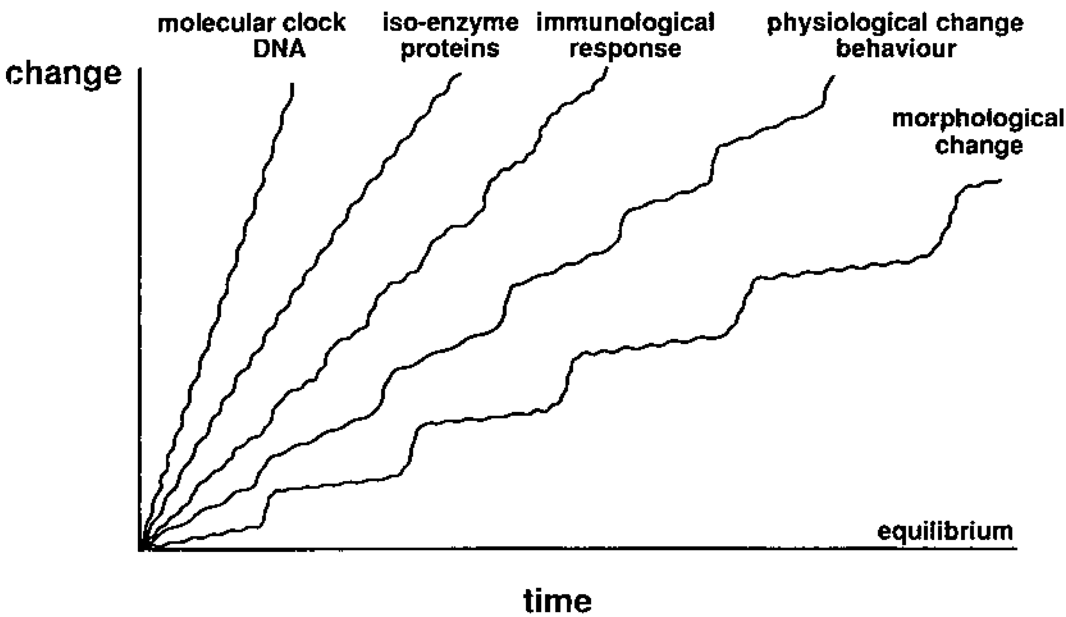
Vibeke Brock (Chairperson)
Viborg Amtsgymnasium
Viborg, Denmark

John A. Beardmore (Rapporteur)
School of Biological Sciences
University College of Swansea
Swansea, United Kingdom

Molecular techniques are now being increasingly used to address salient points of biodiversity and production. There is a growing interest on the part of biological oceanographers, fishery scientists, and marine biologists to find new means of answering major scientific questions concerning

- the identification of morphologically cryptic, sibling species,
- the amount and spatial structure of genetic diversity at the species level,
- temporal genetic change,
- the analysis of historical collections,
- reconstructing phylogenetic and phylogeographic histories,
- the development of analytical tools to interpret molecular data.

The session was opened with a diagram relating changes at molecular, physiological and morphological levels (Fig. 6). The diagram provided a common conceptual framework for geneticists, ecophysiologists and ecologists, and was referred to by several speakers.



The talks of this session provided many examples of how these techniques have been incorporated into studies of marine organisms. Francois Bonhomme opened the session with a provocative talk designed to bring together ecologists and geneticists. The talks by Sbordoni, Medlin and Patarnello provided examples of how ecologists have used molecular techniques to answer questions about taxonomic affinity and genetic diversity in marine fish and phytoplankton. Marta Estrada concentrated on the complex inter-relationships between diversity and production. The general consensus was that we need a full system approach to study comprehensively these complex marine communities.

### *Molecular Approaches to Genetic Diversity: Methodological and Theoretical Aspects.*

Francois Bonhomme
Laboratoire Genome et Population
University of Montpelier, Montpelier, France

Geneticists and ecologists need to come together in their study of marine biodiversity. Ecologists are interested in dynamics and want to quantify the biodiversity, whereas geneticists are interested in relative numbers, i.e. polymorphism's. Molecular geneticists have the right tools for objective frameworks to study marine problems but they still need precise fieldwork.

Biodiversity has a time element, therefore the molecular techniques used should reflect the resolution obtainable in the time scale of interest. For example, DNA sequence analyses are best used for phylogenetic studies, whereas RAPD, VNTR and fingerprinting techniques should be used for studies of gene flow and population structure. Molecular trees are trees of relatedness and are static descriptors. They do not give information about function, although there are some recent advances in the study of genes controlling quantitative characters.

Biodiversity also has a biogeographical element. There is a need to recognise differences in the "bauplan" of different systems. There are important questions about how generation time, population size and the evolution of specialists affect the fitness of the species in the community and the community's biodiversity, which must be answered.

Techniques, such as PCR, have greatly facilitated the application of molecular techniques to ecological problems. Databases for DNA and protein sequence storage and acquisition are essential and are increasing.

## *Genetic Diversity and Fitness*

Valerio Sbordoni
Department of Biology
University of Tor Vergata, Rome, Italy

Molecular biology provides the opportunity to study processes of evolutionary history and adaptation and to discriminate between them. Two examples are provided.

In certain crustacean species, different kinds of genetic structure are present in different environments, which suggests that the species is able to adapt genetically to its environment.

In a study of genetic relatedness of seabass using mtDNA; RAPD's and allozymes, results indicate that not all genes will produce the same phylogenetic tree. Some loci operate under selection, while others are neutral. Fst values show very high differentiation between populations of seabass within the Mediterranean Basin (0.18) and overall within the species (0.27). Significant selection appears to be taking place within this very mobile species. Experiments on the adaptation of the seabass to freshwater systems have identified loci that are under selection and contributing the most to Fst values. Mediterranean and Atlantic populations may be regarded as cases for separate specific status.

## *Applications of Molecular Approaches to Genetic Diversity.*

Linda K. Medlin
Alfred-Wegener-Institute
Bremerhaven, Germany

Molecular techniques can now address many important questions concerning taxonomic affinity, genetic diversity, gene flow and dispersal, and physiological states, of which all have an impact on the assessment of biodiversity and production. There is growing evidence that speciation and dispersal mechanisms in the marine environment are very different from terrestrial systems and occur at different rates. We have examined species/genetic diversity in three ecologically important members of the marine phytoplankton: the prymnesiophytes *Phaeocystis* and *Emiliania huxleyi* and the diatom *Skeletonema costatum*. All are high dispersal taxa. Differences among *Phaeocystis* species as measured by 18S rRNA sequence comparison indicate that extant *Phaeocystis* species

probably arose from a cosmopolitan warm-water ancestor. Speciation events in this genus appear to have responded to major global cooling events. Two species complexes are apparent: one corresponds to taxa from polar regions and the other to taxa from temperate to tropical regions. *Emiliania huxleyi*, a much younger species, has dispersed across many oceanographic barriers during much colder climatic conditions (Fig. 2).
Sequence data from coding and non-coding regions confirm that it is a single taxon, whereas RAPD techniques reveal extreme genetic diversity within short-term spatial and temporal resolution. Sequence comparison of isolates of *Skeletonema costatum*, a cosmopolitan neritic form, reveals at least one cryptic species, which can be differentiated by certain morphological features, and a cluster of strains, which may be sibling species.

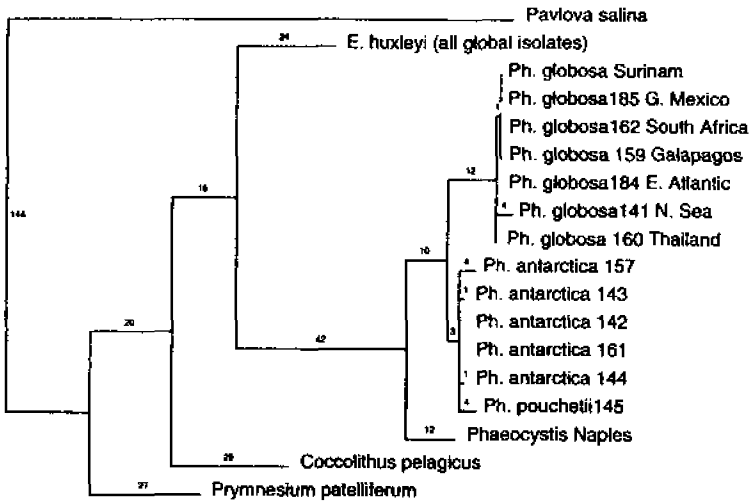



Fig. 7. Phylogenetic representation of the genetic distance among strains of *Emiliania huxleyi* and *Phaeocystis*. All isolates of *E. huxleyi* are identical, whereas isolates of *Phaeocystis* fall into two distinct species complexes found either in warm or cold waters.

Molecular biology provides tools to

1) identify multi-species complexes and define a species limits,
2) interpret the taxonomic level to which physiological and morphological differences should be applied,
3) interpret gene flow and dispersal mechanisms, and
4) depict the phylogenetic history of a group and interpret its biogeographic distribution.

## *Case Studies of Biodiversity and Production*

Marta Estrada
Institut de Ciencies del Mar, Barcelona, Spain

Marine phytoplankton species are often cosmopolitan or distributed over very wide areas. Intensive surveys of the phytoplankton in a particular region reveal the presence of numerous taxa, whose overall relative abundances may be related to characteristics of the corresponding ecosystems. However, most studies deal with measurements of diversity, considered (Margalef, this conference) as an estimate of the effective biodiversity in a particular situation, more or less limited in space and time; thus, diversity values, whether based on number of species or on indices which take into account the relative abundance of the different taxa, depend not only on ecosystem characteristics, but also on other sources of variability, such as sampling methodology and observer bias.

Comparison of diversity measurements for phytoplankton data sets from several upwelling areas, the Southern Ocean, the Mediterranean, and laboratory microcosm experiments, shows that similar diversity values can be found in different ecological situations and that direct correlations between diversity and primary production estimates must be interpreted with caution. These difficulties reflect various problems affecting the usual determinations of diversity. Some of them are listed below.

- Biodiversity and production need to be considered as a function of the temporal and spatial scales. This affects not only any conceptual relationships between biodiversity and production, but also the interpretation of quantitative estimates in practice. Diversity values for a particular collective depend on the area or volume sampled. The shape of the diversity spectra obtained for progressively larger sampling areas or volumes may be a valuable indicator of the community structure. However, no general rules can be given for minimum sampling areas and obtaining spectra is time-consuming and may be misleading in patchy environments.

- The need to take into account the dynamics of the community. According to Margalef, variations in diversity should be correlated with the acceleration or deceleration of production, rather than with the actual production values.

- The need of adequate censuses. Even when dealing only with a subset of the components of a community, it may be impossible, in practice, to make a complete census of the collective under study. This is particularly important in the case of microbial assemblages.

A simple way of gaining some insight into the relationships between diversity and biomass (often used as an indicator of production), for a particular data set, may be plotting scatter diagrams of diversity versus chlorophyll concentration or some other estimate of phytoplankton biomass. This approach has been used with data from several cruises carried out in the Catalano-Balearic Sea. As a rule, within each cruise, diversity showed a peak at intermediate values of biomass. A likely explanation is that, for low biomass samples, many species may be missing, so that the corresponding diversity values are not representative. On the other side, high biomass samples, probably resulting from growth pulses, presented low diversity due to the stronger dominance of some species. When different cruises were compared, diversity was generally lower for the samples corresponding to the most productive period.

The problem of the inadequate censuring may be approached by means of alternative measurements of diversity, based for example on molecular biology techniques or on analyses of a certain group of chemical compounds. As an example, photosynthetic pigment diversity (as determined from HPLC analyses) and taxonomic diversity of the phytoplankton were compared for samples from two cruises in the Catalano-Balearic Sea. Although scatter was large within the same cruise, both indices showed the same patterns when between-cruise variability was examined.

At present, it is not feasible to make accurate predictions concerning biodiversity and production. In this context, it may be preferable to consider levels of organisation such as functional types or assemblages, rather than the species. The classification of phytoplankton functional groups on the basis of their response to environmental parameters expressing growth potential (availability of light and nutrients) on one side, and turbulence on the other, has permitted in a number of case studies to find consistent associations between environmental characteristics and the dominance of major taxonomic groups of phytoplankton.

The delimitation of species assemblages or the identification of trends of variability among them can be approached by means of multivariate statistical methods. Studies in marine areas such as the Catalan Sea and the Peruvian upwelling have shown that it is possible to identify persistent regularities in the composition of phytoplankton assemblages in a particular ecosystem. These results suggest that a search for patterns at the assemblage level is likely to provide better prediction chances than the simple consideration of species lists.

## *Molecular Aspects of Biodiversity in Fish*

Tomaso Patarnello
Dipartimento di Biologia, Padova, Italy

Phylogenetic relationships among organisms and their systematic status have been based so far solely on morphological characters. These represent the main tool in defining the degree of biological diversity existing in terrestrial and marine environments. Although the large increase in the use of molecular techniques such as the amplification by polymerase chain reaction (PCR) and direct sequencing of both nuclear and mitochondrial genes, very few studies have approached biodiversity issues employing DNA sequences.

This is true also for the teleost fish group which is one of the most represented group of vertebrates in terms of number of species. Due to this high diversification, the evolutionary events underlying the phylogenetic relationships among some fish taxa are still unclear. Such is the case of the Italian salmonids belonging to the genus Salmo. According to the morphological systematics, there are at least three good species inhabiting the Italian freshwater, namely: *Salmo trutta trutta* (the brown trout), *S. caripo* and *S. fibreni*. Moreover, there are three morpha of the *S. trutta trutta* species which are named fario, marmoratus and macrostigma. They differ by one another mostly on the base of coloration pattern, size and meristic characters and their systematic status has been long debated but not yet established.

By means of PCR amplification and direct sequencing of two mitochondrial genes, namely cytochrome b and 16S rRNA, we have analysed about 700 bp for all the taxa described above, including a sample of *S. trutta trutta* collected in Ireland. On the base of the mtDNA sequences, very little genetic variation was found among the Italian salmonids despite their large phenotypic differentiation. The mean number of nucleotide substitution per site ranged between 0.2% and 0.5% also when *S. carpio* and *S. fibreni* were taken into account. Therefore, on the bases of the DNA data the systematic status of the two latter taxa as good species is questionable.

An opposite situation was observed in another group of teleost fish belonging to the family of Mugilidae (the grey mullets). The systematics of the species inhabiting the Mediterranean Sea was recently revised. The difficulty in establishing phylogenetic relationships among them is due to the very similar morphology displayed. The sequence analysis of the cytochrome b mitochondrial gene revealed that one of the six species investigated, *Mugil cephalus*, is highly divergent from all the other taxa having a mean number of nucleotide substitution per site ranging between 20,6% and 24,5% and about 10% of amino acid substitution.

These results strongly suggest the need of combining molecular and morphological data, which sometime may be quite different, in establishing the phylogenetic relationships among organisms as well as in defining their systematic status. Moreover, considering that phenotypic characters such as coloration pattern, size or other morphological features, may be under strong selective constrains, it would be better to base the understanding of the evolutionary pattern of nucleotide substitution in neutral evolving sites. In this sense, information gained at the molecular genetics level will certainly help in addressing questions concerned with biodiversity.

**Summary of the Discussions**

There was a recognised need to integrate molecular techniques into marine studies to enhance our understanding of this complex ecosystem. There was general agreement that marine ecosystems operated very differently from terrestrial systems and it was not sensible to extrapolate from one to the other. Marine systems have both low and high dispersal taxa. Barriers to dispersal are also not so well known. It is not well established how this affects the genetic diversity of the species and the question of dispersal versus genetic diversity seemed to be a recurring issue. A diagram was produced that summarised our understanding of how functional change relative to genetic change changes over time with different genes. A multidimensional species concept incorporating as many descriptors as possible was considered essential.

# Report on the session: Anthropogenic effects on diversity and production

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Laboratoire Arago
Banyuls-sur-mer
France

Paul Nival (Rapporteur)
Station Zoologique
Villefranche-sur-mer
France

## *Anthropogenic Effects on Biodiversity and Production*

Richard Warwick
Plymouth Marine Laboratory, Plymouth, U.K.

Coastal and shelf ecosystems are under the most immediate threat from man's activities, e.g. industrialisation, agricultural practices, fishing and tourism. Recent work suggests that macrobenthic communities on the shelf are equally as diverse as those from the deep-sea: data from the continental shelf of Norway (J.S. Gray, in press) indicates that species, family and phyletic diversity are similar to recently published deep-sea data, and species / area curves have almost identical slopes. Species diversity is reduced when the levels of pollution or disturbance are high, but appears to be very resilient to low levels. However, at these low levels of disturbance, community changes are taking place which are reflected in the results of multivariate analysis.
One example concerns changes in community structure of the soft-bottom benthic macrofauna in relation to oil-drilling activity at the Ekofisk platform in The North Sea. Sampling stations were positioned at different distances around active platforms. Species diversity was significantly reduced only in the inner zone, closer than 250 m from the rig, and three outer zones did not differ from each other in diversity. Also, k-dominance curves indicate a significant effect only in the inner zone, the curves for the three outer zones being closely coincident. However in a non-metric Multidimensional Scaling (MDS) analysis community composition in all of the zones were distinct, and was confirmed by a multivariate significance test (ANOSIM). Thus, changes in community structure were detectable 3.5 km from the rig. Similar insensitivity of diversity to perturbations in contrast to the sensitivity of multivariate community analyses, has been shown for several other types of communities, e.g. fish and corals. These multivariate changes in community structure do not simply result from replacements of closely related species, but are reflected at very high taxonomic levels, i.e. in the phyletic composition of communities. Moreover, changes in phyletic composition, at least for the macrobenthos, are very consistent when considered in relation to the intensity of perturbation, apparently regardless of the nature of that perturbation. A "meta-analysis", combining a number of pollution / disturbance studies in a single ordination, shows a clear sequence of change in phyletic composition

from unperturbed to grossly perturbed situation. Clearly, better ways of measuring biodiversity, which incorporate multivariate information of this kind and which in some way reflect the community changes which are taking place, need to be devised. Species diversity alone seems to be insensitive and inadequate.

In order to protect and conserve biodiversity we should protect habitats rather than species. We need integrated coastal management plans that incorporate not only scientific but also socioeconomic aspects so that the integrity of coastal habitats is preserved.

## *Effects of Beam Trawl Fisheries on the Benthic Ecosystem*

Han Lindeboom
Netherlands Institute foe Sea Research
Texel, The Netherlands

There are many signals that a number of human activities do affect the marine ecosystem on local and sometimes regional scales. Fisheries is one of these activities. On the Dutch continental shelf, this activity is now so intensive that each square meter is trawled, on an average, once to twice a year.
Furthermore, it has been shown that trawling causes direct damage to the marine ecosystem. The following conclusions have been drawn:

- A commercial beam trawl disturbs hard-sand sediment to a depth of 4-8 cm.
- Trawlings induce a significant decrease in density (40-65%) of starfish (*Asterias rubens* ), small-sized heart urchins (*Echinocardium cordatum*) and polychaetes (*Lanice conchilega, Siophanes bombyx*). An insignificant decreasewas found for small crustaceans, various bivalves and larger heart urchins.
- The chance of survival for benthos which is returned to the sea after catch is only 10-15% for Cancer and Arctica, 40% for other crabs and molluscs, 70-80% for starfish and approximately 100% for whelks and hermit crabs.
- 100% of discard fish returned to the sea after processing the catch will die.
- Depending on the studied area, sole fisheries produced 4-10 kg discard fish and 0.5-4 kg dead benthos per kg marketable sole.

This indicates that the "natural" North Sea ecosystem under study is already a heavily influenced system.

To be able to study the natural trends in the marine ecosystem and to answer the question which human activity (fisheries, pollution, eutrophication, climatic changes or a combination of causes) has influenced the ecosystem the most, there is a strong need for protecting areas to be established. The size of such protected areas must be determined by:

- the behaviour of the species characteristic for the area,
- the possibility to control the area,
- the scientific question to be answered. In such areas where fisheries and local pollution will be forbidden or very limited, scientific research on species composition and age distribution of different populations should be carried out and trends should be established.

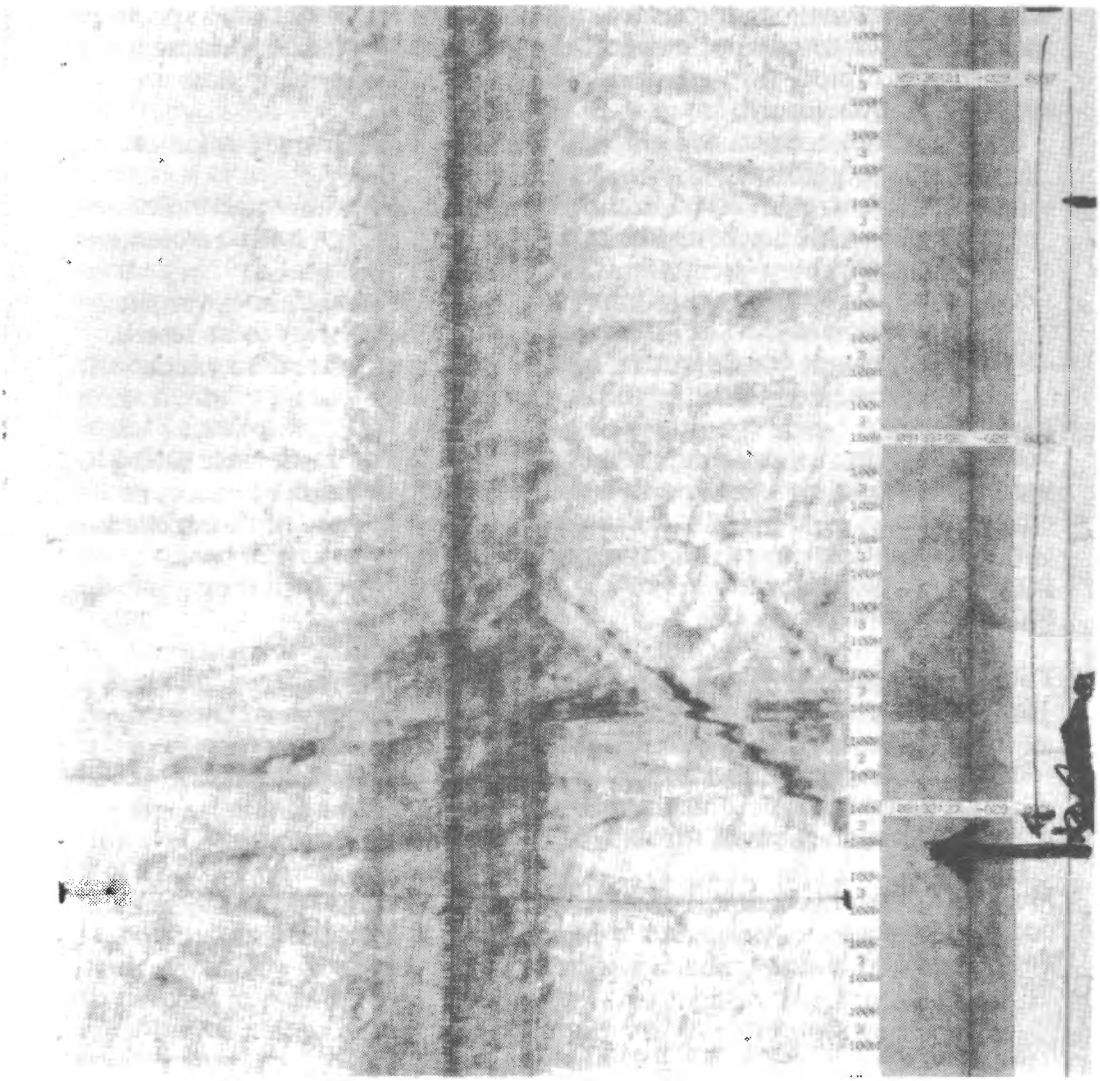

Fig. 8. Trawl marks in an area which was used as an unfished reference area on recommendation by fishermen. Side-scan sonar recording

## *Implications of Transplantations to Aquaculture and Ecosystem*

Harald Rosenthal
Institute of Marine Research, University of Kiel
Kiel, Germany

Increasing aquaculture activities occur primarily in areas where support and supply for the developing industry are available, e.g., close to main shipping routes and harbours. Because intensive aquaculture operations often provide ideal conditions for initial establishment of exotic species, the chances for transfer of non-indigenous species increase. Diseases have spread rapidly through multiple transfer of major candidate species for aquaculture.

- important deleterious side effects accompanying transplantation of aquatic organisms
- general pathways involved in transplantation of harmful and unwanted species (transfer of aquatic species with ballast water in bulk carrier)
- control measures and regulations (ICES -International Council for the Exploration of the Sea - Code of Practice) hypotheses to be tested. An important consideration might be the grid system on which data have been collected in the past.

Such monitoring programmes need to be carried out for at least 5-10 years. Additional process oriented studies to understand the causes of changes observed should be executed inside and outside the controlled (closed) area (settlement, biodiversity on species and genetic levels, production/biomass ratio, foodwebs, habitat structure including sediment characteristics.

There is a need

- for studying appropriate methods to describe and evalutate the effective cost of ecosystem change
- for developing guidelines for adequate regulations to safeguard, biodiversity structures in healthy ecosystems and mimimise risks of dramatic changes through human activities.

More than merely economic motivation is required for success. A close cooperation between basic and applied research together with environmental management is needed.

## *Natural Variability of the Deep-Sea Floor, Benthos Diversity and Anthropogenic Disturbances*

Hjalmar Thiel
Institute of Hydrobiology and Fisheries Science
University of Hamburg, Hamburg, Germany

Deep sea benthos is characterised by small species and their small ambits. As in other environments, niches occur nested in different sizes, but the deep sea is structured specifically by organismal and environmental grain below human visibility. Organic matter turn-over is dominated by these invisible organisms, and therefore they need careful determination, observation and consideration.
Diversity should be studied on all levels of organism sizes in the frame of basic investigations. However, for impact evaluation a subset of indicator taxa is essential. We need to learn which size group can give us the information for the evaluation of community changes, specially those induced by human activites. These applied questions of impact evaluation can certainly not consider the total size spectrum and the basic investigations must help to develop the right biological tools.

Human impact from waste dumping and from metal resource mining must be investigated, although the use of the deep sea floor may be many years (dumping) or several decades (mining) ahead. The slow pace of biological processes in the deep sea deserve long-term studies. Dumping and mining activities will create large scale impacts because all uses of the deep sea will be characterised by immense masses of wastes to be dumped, or resources and sediment to be mined, and tailings to be discharged.

We have to ensure that the results of our impact experiments will be extrapolatable to full scale industrial actions, and, therefore, we need environmental studies on small (metre) and large (kilometre) scales, and the development of innovative tools for the on line (video) manipulation of experiments and for long term observations on the deep sea floor.

However, environmental changes cannot be studied only through biochemically summarising parameters. Ecological units are the species and they are to be determined and described by professional taxonomists. They must be an integral part in a project together with oceanographers of the different disciplines. Basic studies are to be conducted in parallel with the impact experiments on different scales. It must be the aim to understand structure and function of deep sea communities and to apply the basic knowledge gained to the evaluation of human impact.

**Summary of the Discussions**

The marine environment is very dispersive in nature, this implies that the space scales of "marine" problems can be much larger than on the continents. Mankind must be clearly considered as a part of the ecosystems, actively structuring them. Community structures reflect human activities much more than the diversity indices do. Our perceptions and methods for measuring biodiversity are embryonic at best. A question is to known if diversity of one size class is relevant to the diversity of all other size classes (meiofauna vs. megafauna)?

For all size classes, multivariate approaches are strongly recommended. Impacts of human activities occur, or will occur, at all depths, on organisms of all sizes. Human activity on the deep sea floor will modify the community structure. Is there a need for the total description of communities - or, tailored to the problem, for a description of a targeted group of species? How to minimize the effect of human activities? (Species preservation vs. habitat preservation). At what scale?

It is hypothesised that current fishing activity induces reversible changes in biota and the establishment of areas closed for fisheries would lead to directional changes in:
- biomass
- species and size compositions of benthic and demersal fish communities (reduction of mortality caused by fishing)
- changes in settlement patterns
- changes in behavioural responses of species to decreased disturbance.

Diseases and parasites are a component of species composition and species diversity, despite the fact that they play a controlling role in ecosystem health and species performance. Human impacts due to transfers and introductions of non-indigenous species via shipping (e.g., ballast water, ship hulls, oil rigs) and via aquaculture (e.g. transfers of juveniles and brood stocks) can alter natural communities. Prophylaxis is, therefore, necessary. Some epizootic population explosions as well as subtle penetrations of ecosystems by introduced species can be considered as model cases to be studied for a better understanding of the mode and of the reasons for changes in biodiversity. Technological progression increases transport of species through natural barriers between ecosystems (e.g. the tropics for cold-water species or the open ocean for coastal forms). This results in substantial disruption of ecosystems and great economic losses to other human activities. Intensified ecological studies are needed to assess the impact of such activities and to assist in deriving realistic control measures (economic interest vs. ecology).

There is a need for diversity preservation management in coastal, shelf and deep seas through:
- observations under controlled conditions in
- preserved reference areas
- impact reference areas
- experimentation under natural conditions vs. mesocosms
- basic research (taxonomy at different levels of diversity expression)
- identification of the habitats to preserve

Controlled areas must be selected depending on representativeness, homogeneity, sensitivity of communities, fishing intensity, presence of reference areas, presence of historic data.

The size and the shape of controlled areas depends on the type of hypotheses to be tested. An important consideration might be the grid system on which data have been collected in the past.

Such monitoring programmes need to be carried out for at least 5-10 years. Additional process oriented studies to understand the causes of changes observed should be executed inside and outside the controlled (closed) area (settlement, biodiversity on species and genetic levels, production/biomass ratio, foodwebs, habitat structure including sediment characteristics.

There is a need
- for studying appropriate methods to describe and evaluate the effective cost of ecosystem changes
- for developing guidelines for adequate regulations to safeguard biodiversity structures in healthy ecosystems and minimise risks of dramatic changes through human activities.

More than merely economic motivation is required for success. A close cooperation between basic and applied research together with environmental management is needed.

# Recommendations

1. As for the most effective management of marine living and non-living resources, it is essential to understand the nature of any coupling between biodiversity and productivity. Research on this is urgently required. The research will need to accommodate spatial and temporal dimensions and a multivariate approach to estimating biodiversity.

2. Methods for assessing production (particularly at higher trophic levels) and biological diversity have to be improved. Genetic and molecular tools must be incorporated in order to characterize "cryptic" diversity (e.g. sibling species). Such methods are also of great importance for the characterisation of diversity in bacteria, picoplankton and so-called cosmopolitan species, as existing methods are grossly inadequate. New technologies are needed for extracting information relevant to studies of biodiversity over wide ranges of time and space scales.

3. Our ability to understand changes in production and biodiversity of an ecosystem in time and space must be enhanced. The use of multivariate data analysis and the development of simulation models of complex systems, including submodels of species competition, trophic interaction, species life cycles and genetic structure is recommended. The development of theoretical studies of complex systems should be encouraged with the aim of interpreting the variations and maintenance in the biodiversity of marine systems.

4. We recommend the further development of an integrated information system to store ecological, taxonomical, and functional characteristics of species. This system must be made easily accessible and widely known for an extensive and optimal use.
The flow of matter through an ecosystem as well as its production and its structure depends on the external energy it receives. Nowadays, human activity also adds a significant amount of energy through fishing, mining, or any other use of the marine environment. As a consequence, human impact on the production as well as on the diversity of living organisms must be urgently considered.

5. Taxonomy is absolutely necessary for biodiversity studies. We recommend increasing efforts in taxonomy using the most appropriate of the wide range of techniques available.
Existing taxonomic skills and knowledge as well as the care of taxonomic and ecological collections should be maintained and improved in order to:
- integrate morphological and molecular approaches,
- integrate evolutionary history and recent ecological conditions through phylogenetic studies, and
- study the relationship between genetic characteristics and ecological responses.

6. Marine habitats in coastal, shelf, and deep sea areas should be identified for risk assessment for the purpose of:
- conservation and habitat rehabilitation. These areas should be exposed to a minimum of human impact and used for research in order better to understand community (ecosystem) structure and changes in them. This refers in particular to coastal and shelf seas where human influence is strongest. Time and space scales should be appropriate to the geographical area and scientific problems in question.
- experimental research, in order to improve our knowledge of the resilience of the ecosystem in relation to human induced perturbances (deep-sea mining, dumping, etc.). This involves changes in species composition at all trophic levels, recolonization of disturbed areas, etc.

7. Introduced and transferred species/stocks often proliferate in their new environments to the detriment of native species and the system. Such phenomena should be studied to assess abiotic and biotic controls (competition, predation, diseases, etc.) operating within the respective systems.
Comparative studies with unaffected areas need to be carried out at an early stage to elucidate the impact of introduced species. Such studies would help in assessing the environmental risks associated with transfers and introductions and provide guidance for management to minimize these risks.

8. Pelagic ecosystems, which are of fundamental importance to the generation of global oceanic production, are not amenable to in situ experimentation or manipulation. However, existing monitoring programmes have established a close coupling between changes in planktonic ecosystems, hydrographic regimes, and climatic patterns. We recommend that continued efforts should be made to enhance and extend monitoring programmes to elucidate spatial and temporal patterns in the dynamics of marine ecosystems.

# Annex 1

European Research Conference on

## Oceanography:

## Biodiversity and Production in the Ocean

San Feliu de Guixols, Spain, 3-8 May 1994

Chairman: Prof. J.-O. Strömberg
Vice-Chaiman: Prof. V. Smetacek

### Programme

**Tuesday, 3 May 1994**

**Afternoon:** Registration: hotel reception and conference secretariat

19.30 DINNER
21.30 GET TOGETHER, DRINKS

**Wednesday, 4 May 1994**

**"Why is our understanding of biodiversity and production in the ocean important?"**

09.00 Jarl-Ove STRÖMBERG and Representatives of the ESF and CEC
Opening remarks.
Presentation of the purpose of the conference: *The identification of the most important scientific problems at the European level to promote multidisciplinary approaches for the study of biodiversity and production in the ocean with appropriate tools and to identify common targets.*

**"Biodiversity in the ocean"**
*Chair: Annelies C. PIERROT-BULTS*
*Rapporteur: Victor SMETACEK*

Introductory lectures of 30 minutes, followed by 10 minutes of discussion

09.40 Ramon MARGALEF (Spain)
*"Biodiversity, Diversity and production*
10.20 John A. BEARDMORE (United Kingdom)
*"Dimensions of biodiversity"*
11.00 COFFEE BREAK
11.30 Siebrecht VAN DER SPOEL (The Netherlands)
*"Assessment of biodiversity"*
12.10 Paul NIVAL (France)
*"Physical factors influencing biodiversity"*
13.00 LUNCH
14.30 Martin ANGEL (United Kingdom)
*"Biological factors influencing biodiversity"*

15.10 General discussion on biodiversity
16.30 COFFEE
19.30 DINNER
21.30 Possibility for Poster session

**Thursday, 5 May 1994**

**"Production in the ocean"**
*Chair: Jarl-Ove STRÖMBERG*
*Rapporteur: Richard WARWICK*

Lectures of 30 minutes, followed by 10 minutes of discussion

09.00 Andrew CLARKE (United Kingdom)
*"Is there a link between production and diversity"*
09.40 Frédéric PARTENSKY (France)
*"New methods for assessing marine primary productivity"*
10.20 Victor SMETACEK (Germany)
*"Biological factors controlling production"*
11.00 COFFEE BREAK
11.30 Ulrich BATHMANN (Germany)
*"Physical factors controlling production"*
12.10 John GAMBLE (United Kingdom)
*"Global change and effects on biogeographic patterns"*
13.00 LUNCH
14.30 Discussion on production in the ocean
16.30 COFFEE
19.30 DINNER

## Friday, 6 May 1994

**"New methods in the study of biodiversity"**
*Chair: Vibeke BROCK*
*Rapporteur: John A. BEARDMORE*

Lectures of 30 minutes, followed by 10 minutes of discussion

| | | |
|---|---|---|
| 09.00 | | Valerio SBORDONI (Italy)<br>*"Genetic diversity and fitness"* |
| 09.40 | | François BONHOMME (France)<br>*"Molecular approaches to genetic diversity: methodological and theoretical aspects"* |
| 10.20 | | Linda MEDLIN (Germany)<br>*"Applications of molecular approaches to genetic diversity"* |
| 11.00 | COFFEE BREAK | |
| 11.30 | | Marta ESTRADA (Spain)<br>*"Case studies of biodiversity and production"* |
| 12.10 | | Tomaso PATARNELLO (Italy)<br>*"Molecular aspects of biodiversity in fish"* |
| 13.00 | LUNCH | |
| 14.30 | | Discussion on genetic aspects on diversity and production. |
| 16.00 | COFFEE | |
| 19.30 | DINNER | |

## Saturday, 7 May 1994

**"Anthropogenic effects on diversity and production"**
*Chair: Jean-Pierre FERAL*
*Rapporteur: Paul Nival*

Lectures of 30 minutes, followed by 10 minutes of discussion

| | | |
|---|---|---|
| 09.00 | | John S. GRAY (Norway)<br>*"Anthropogenic effects on biodiversity and production"* |
| 09.40 | | Han LINDEBOM (The Netherlands)<br>*"Effects of beam trawl fisheries on the benthic ecosystem"* |
| 10.20 | | Harald ROSENTHAL (Germany)<br>*"Implications of transplantations to aquaculture and ecosystems"* |
| 11.00 | COFFEE BREAK | |

11.40 Hjalmar THIEL (Germany)
*"Natural variability of the deep-sea floor, benthos diversity and anthropogenic disturbances"*
12.10 Discussion on anthropogenic effects on biodiversity and production
13.00 LUNCH
14.30 Continued discussion
16.00 COFFEE
16.30 Meeting of the planning committee
19.30 CONFERENCE DINNER

**Sunday, 8 May 1994**

09.00 Final discussion, synthesis and recommendations
Chairpersons: John A. BEARDMORE and Jarl-Ove STRÖMBERG

13.00 LUNCH

**DEPARTURE**

# Annex 2

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