



# EUROGLOBEC

## Science plan



A great deal of additional information on the European Union is available on the Internet.  
It can be accessed through the Europa server (<http://europa.eu.int>).

Cataloguing data can be found at the end of this publication.

Luxembourg: Office for Official Publications of the European Communities, 1998

ISBN 92-828-3516-2

© European Communities, 1998

Reproduction is authorised provided the source is acknowledged.

*Printed in Italy*

PRINTED ON WHITE CHLORINE-FREE PAPER

## ECOSYSTEMS RESEARCH REPORT 27

# EUROGLOBEC — SCIENCE PLAN

Report of an international workshop organised jointly  
by the MAST Programme of the European Commission,  
DG XII/D-3, and the Baltic Sea Research Institute Warnemünde

Warnemünde, Germany, 13-15 October 1997

Edited by

J. Alheit, K.-G. Barthel, K. Brander, F. Carlotti, R. Harris, C. Koutsikopoulos, B. MacKenzie, G. Paffenhöfer, H. Roe and K. Tande

February 1998

ENVIRONMENT



## **EUROGLOBEC — SCIENCE PLAN**

Edited by

Alheit, Jürgen  
Baltic Sea Research Institute  
Seestr. 15  
D-18119 Warnemünde, Germany

Barthel, Klaus-Günther  
MAST Programme, DG XII/D-3  
European Commission, SDME 7/83  
Rue de la Loi 200  
B-1049 Brussels, Belgium

Brander, Keith  
ICES/GLOBEC Secretary  
ICES  
Palaegade 2-4  
DK-1261 Copenhagen K, Denmark

Carlotti, Francois  
Station Zoologique  
P.O. Box 28  
F-06230 Villefranche-sur-Mer, France

Harris, Roger  
Plymouth Marine Laboratory  
Prospect Place, West Hoe  
GB-Plymouth, PL1 3DH, United Kingdom

Koutsikopoulos, Constantin  
University of Patras  
Dept. of Biology  
GR-26500 Patras, Greece

MacKenzie, Brian  
Danish Institute for Fishery Research  
Kavalergaden 6  
DK-2920 Charlottenlund, Denmark

Paffenhöfer, Gustav  
Skidaway Institute of Oceanography  
10 Ocean Science Circle  
Savannah, Georgia 31411, USA

Roe, Howard  
Southampton Oceanography Centre  
Empress Dock  
GB-Southampton SO14 3ZH, U.K.

Tande, Kurt  
The Norwegian College of Fishery Science  
University of Tromsø  
N-9037 Tromsø, Norway



# CONTENTS

EXECUTIVE SUMMARY	4
<b>1. INTRODUCTION</b>	<b>6</b>
<b>2. GOAL AND OBJECTIVES</b>	<b>8</b>
<b>3. EUROPEAN CONTEXT</b>	<b>10</b>
<b>4. SCIENCE PROGRAMME</b>	<b>15</b>
4.1 FOCUS: RETROSPECTIVE STUDIES	18
4.1.1 Rationale	18
4.1.2 Background	20
4.1.3 Approach	25
4.2 FOCUS: PROCESS STUDIES	27
4.2.1 Rationale	27
4.2.2 Background	28
4.2.3 Approach	35
4.3 FOCUS: MODELLING	39
4.3.1 Rationale	39
4.3.2 Background	40
4.3.3 Approach	43
<b>5. TECHNOLOGY DEPLOYMENT AND DEVELOPMENT</b>	<b>50</b>
5.1 RATIONALE	50
5.2 BACKGROUND	51
5.3 APPROACH	51
5.3.1 Time and space scales	52
5.3.2 Coupled observations and modelling	53
5.3.3 Quality control	53
5.3.4 European strengths	53
5.3.5 Technology development	55
<b>6. DATA MANAGEMENT</b>	<b>57</b>
<b>7. LINKAGES TO OTHER PROGRAMMES</b>	<b>58</b>
<b>8. REFERENCES</b>	<b>60</b>
Appendix (Acronyms)	71
List of Participants	73

## Executive Summary

**The goal of EUROGLOBEC is to advance our quantitative understanding of the functioning of marine pelagic ecosystems in relation to physical forcing to develop the capability of predicting the effects of climate variability and change on such ecosystems. This goal consists of two components:** First, to develop through retrospective analysis, short- and long-term process studies, application of new technologies and modelling an understanding of the effects of physical forcings on ecosystem functioning and its natural interannual variability. Second, to create through advanced modelling of key physical, biological and chemical variables techniques to predict ecosystem modifications due to climate variability and change. Using data collected previously and data from this proposed study EUROGLOBEC expects to develop capability in the analysis of long-term time-series which, by coupling real-time data and progressive modelling, will allow prediction of ecosystem responses and their variability.

The analyses of retrospective data collected over the past decades by meteorologists and fisheries scientists and the various oceanographic disciplines will provide valuable information on variability of ecosystem functioning due to natural forcing. These data could already indicate variables critical to global change. Some retrospective analyses have shown that longevity/strength of westerly winds affect the abundance of a dominant copepod in the north Atlantic. Clear causal relationships, however, cannot be established from such data. Thus, the design of process studies should be organised in a manner that causal relationships can be developed. This implies that environmental physical and biological variables should be recorded at similar frequencies with sufficient resolution.

Measurement of all relevant variables by EUROGLOBEC would be an insurmountable task. We envision that various meteorological and hydrodynamic variables could be obtained through CLIVAR which is close to presenting its implementation plan. ESA/JRC could provide sea surface imagery, and ELOISE other relevant variables. It would be a top priority to establish as soon as possible a working relationship with the above mentioned programmes.

Participating in EUROGLOBEC will be of major significance for European countries. First, the results from the initial 3-year study, in

conjunction with retrospection, will enhance our understanding of the function of selected marine ecosystems, and with this provide additional knowledge on the causality of changes in various fish stocks.

Additionally, starting to reveal causal relationships between physical forcing and ecosystem functioning should provide the momentum towards a predictive capability for anthropogenically-caused changes in ecosystem dynamics in parts of the marine environment adjacent to European countries.

## 1. INTRODUCTION

GLOBEC (GLOBal ocean ECosystem dynamics) is a Programme Element of the International Geosphere-Biosphere Programme (IGBP) being developed by oceanographers and fisheries scientists to address the question of how global climate change may affect the abundance and production of animals in the sea. Zooplankton are a primary focus because they are the key link in the food web between phytoplankton and higher trophic levels.

GLOBEC aims to advance understanding of the structure and functioning of the global ocean ecosystem, its major subsystems, and its response to physical forcing so that a capability can be developed to forecast the responses of the marine ecosystem to global change. It will combine retrospective and process studies with new technology and coupled physical-biological models to provide a better basis for 1) the sustainable exploitation and management of marine resources, 2) understanding causes of observed changes in the plankton ecosystem and 3) the likely consequences of long term climate variability and change on fisheries and other marine life, such as marine mammals and seabirds.

An integrated and coherent understanding of natural forcing and its interactions with human populations is limited by current understanding of marine ecosystem dynamics, the focus of GLOBEC. Equally limited is our current ability to differentiate anthropogenic from naturally occurring effects in marine ecosystems. There are three major gaps in our knowledge of marine ecosystem dynamics:

- the dynamics of zooplankton populations both relative to phytoplankton and to their major predators;
- the influence of physical forcing on these population dynamics, particularly at the mesoscale; and
- the estimation of biological and physical parameters associated with the dynamics of zooplankton relative to phytoplankton.

Identifying the need for a co-ordinated international approach to these and other related questions pertaining to higher trophic levels GLOBEC was established by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) in late 1991. An initial workshop noted the need “to understand how changes in the global environment will affect the

abundance, diversity and production of animal populations comprising a major component of ocean ecosystems". It also recognised the importance of zooplankton in "shaping ecosystem structure... because grazing by zooplankton is thought to influence or regulate primary production and... variations in zooplankton dynamics may affect biomass of many fish and shellfish stocks." GLOBEC is cosponsored by IGBP, SCOR and IOC. The International Council for the Exploration of the Sea (ICES) and the North Pacific Marine Science Organisation (PICES) contribute specific regional programme components.

GLOBEC focuses on herbivores and primary carnivores - those trophic levels where primary production is processed to provide energy and nutrients for longer-lived species, which constitute the world's fisheries. The organisms in these groups include a great diversity of species and exhibit many adaptive strategies. For a specific purpose, such as studies of carbon cycling, treatment of this group as a single subset of variables may be possible. However, given the great number of transfer pathways to higher trophic levels, GLOBEC requires a more complex approach. Study of the entire global ocean is not feasible so the selected sites must be chosen with sufficient care so that they can serve as proxies for major ocean zones. One of the challenges for a EUROGLOBEC programme is to discover where generalisations may be made and where, conversely, attention to detail is essential. In order to meet this challenge, EUROGLOBEC must focus on specific processes and appropriate sites. These are selected to best test and improve upon the generalisations that relate structure to dynamics in European seas. They represent, at the same time, important subsystems of the global ocean ecosystem.



## 2. GOAL AND OBJECTIVES

### \* GOAL

The goal of EUROGLOBEC is to advance our quantitative understanding of the functioning of marine pelagic ecosystems in relation to physical forcing to develop the capability of predicting the effects of climate variability and change on such ecosystems.

### OBJECTIVE 1

**Quantify and understand the effects of physical forcing on pelagic marine ecosystems over a wide range of spatial and temporal scales.**

Various physical processes significantly affect the dynamics of marine pelagic ecosystems at scales ranging from a few mm and less than a second to hundreds of kms and months to years. Major components of pelagic ecosystems include zooplankton, their prey and their predators. At the smallest and shortest scales, small scale turbulence can affect predator-prey interactions. Physical forcing on large and long scales ranges from intermittent atmospheric events over hours to days to seasonal changes and decadal climate variability. These forcings should manifest themselves in mixing and circulation processes with various effects on pelagic ecosystems. For example, intermittent wind forcing will dissipate food patches but enhance primary productivity in coastal regions. Interannual temperature changes will affect species composition and abundance.

Although we possess some information on the effects of physical variables on the dynamics of a few zooplankton species from experimental and field studies, such data are clearly insufficient to arrive at an understanding of ecosystem functioning, especially under changing physical forcing. The scarcity of information is partly the result of a lack of truly interdisciplinary design and execution of ecosystem studies. Early results from the first US GLOBEC study in the Northwest Atlantic have shown that both, co-ordinated planning and *in situ* observations by physicists and biologists in conjunction with modelers, are extremely productive. To arrive at such an understanding requires quantitative information on individual and population rate processes for the major species contributing to the functioning of the respective ecosystem. Whereas such results are

usually obtained through short-term, small-scale studies, long-term and large-scale continuous (time-series) observations are needed to quantify the response of populations of zooplankton, their prey and their predators to physical (mesoscale) forcing.

## OBJECTIVE 2

**Determine past and future effects of global change on zooplankton and ichthyoplankton using linked models and observation systems, with the aim of predicting future impacts and potential feedback processes.**

Determining the effects of climate variability and change on the structure and functioning of a pelagic ecosystem and its major components requires empirical information over extended periods (decades) with adequate resolution and the application of models which link physical and biological variables. Objective 1 is a precursor to Objective 2 because quantitative understanding of pelagic ecosystem function and natural variability has to be achieved in order to develop a predictive capability. Retrospective analyses of time-series through biological-physical modelling will provide insights into natural ecosystem variability in relation to atmospheric or hydrodynamic forcing. Time-series around the British Isles, off California and Peru and in the Benguela Current have shown dramatic changes in zooplankton abundance over decades and these may be related, directly or indirectly, to one or possibly several physical variables. Modelling will help to understand the causes of such changes and to distinguish between the effects of natural physical and of anthropogenic factors.

Modelling will be most effective if data on the required variables can be collected simultaneously at the appropriate level of resolution. Technology designed to achieve rapid, high resolution measurement of physical and chemical variables already exists and is being developed for zooplankton abundance and distribution. The aim within the GLOBEC programme will be to synthesise physical and biological data rapidly through advanced modelling to provide near real-time information to guide ongoing studies. Rapid data analysis and synthesis should also provide information on imminent changes in ecosystem function without any delay. The quality of predictions of changes in the marine ecosystem will inevitably depend on the quality of predictions of changes in biological variables to physical forcing, but scenario modelling will give an indication of the magnitudes of the likely impact.

### 3. EUROPEAN CONTEXT

The European seas extend from the high latitudes of the Arctic to the southern Mediterranean ecosystems, covering a wide range of environmental features. Marine ecosystems play an important role in the economy and culture of European countries. In several cases these links are so strong that entire societies depend on the health of the marine ecosystems.

Increasing concern has been expressed from a scientific, economic and social point of view about the state of the marine environment and its continuing health, functioning, diversity and productivity, but the means of defining, describing, monitoring and predicting such characteristics are not yet adequate. Europe has a particular opportunity and responsibility to play a major role in developing the tools for improved understanding of the marine ecosystem because of its scientific capabilities and the diversity of its marine environment. Consequently, EUROGLOBEC should concentrate on those issues which are particularly important in a European context and in which European scientists are likely to make a significant contribution. Areas of interest include not only European seas, but also the Southern Ocean and other areas.

The central focus of EUROGLOBEC is on zooplankton dynamics, because this is a major, under-studied part of the trophic system which is critical in understanding the effects of changing physical forcing on system properties and production at higher trophic levels. The programme makes explicit connections between climate variability and change studies and ongoing work on fisheries dynamics and marine environment management. Unless the effects of varying physical forcing are understood it is difficult or impossible to distinguish the effects of anthropogenic factors on the marine system. The programme aims to complement other work on the state of the marine ecosystem; sustainable use of marine resources; limits to marine productivity; effects of global change on the marine ecosystem; design and interpretation of monitoring of the marine ecosystem.

European marine ecosystems are characterised by a remarkable variety in their fundamental characteristics. This diversity in physical and biological characteristics offers opportunities for the development of co-operative research to test the influence of particular parameters over a wide range of values and to observe the reaction of several



ecosystems with different structures to a given environmental forcing. The latitudinal range of Europe provides a gradient in the amount of energy supplied to the ecosystems. Topography varies from open oceanic areas to semi-enclosed seas, regions with wide continental shelves, deep sea areas, relatively shallow seas, passages and straits. Interactions between geographic position and continental topography influence the meteorological conditions which are of major importance for the dynamics of marine ecosystems. Terrestrial influence ranges from high in the case of large estuaries to low in offshore areas. There are great differences in the amounts of nutrients supplied to the ecosystems which vary from the rich and very productive continental shelves to oligotrophic seas. Differences also exist in the types of enrichment mechanism, with regular tidal mixing and upwelling phenomena having marked seasonal character and enrichment from wind mixing events occurring with variable frequency.

A range of European scientific activities over the past decade and earlier is relevant to the future development of GLOBEC, the data sets which they provide (some of which may not have been analysed previously), the development of sampling and modelling tools and the formation of trained personnel and teams. Some main relevant EU programmes are listed in Table 1. The capability for high quality pan-European oceanographic research is well demonstrated by these programmes and there are particular skills in population dynamics and ecosystem modelling, coupled with physical models at a range of scales.

**Table 1. Relevant European research programmes.**

Acronym	Title
BASYS	Baltic Sea System Study (MAST III)
CANIGO	Canary Islands Azores Gibraltar Observations (MAST III)
CINCS	Pelagic-Benthic Coupling in the Oligotrophic Cretan Sea (MAST II)
CORE	Baltic Cod Recruitment Project (AIR)
ELOISE	European Land-Ocean Interaction Studies (MAST II)
ERSEM	European Regional Seas Ecosystem Model (MAST II)
ESOP	European Sub-Polar Ocean Programme (MAST III)
EURAPP	The impact of Appendicularia in European marine ecosystems (MAST III)
FLEX	Fladen Ground Experiment
HELCOM BMP	Baltic Monitoring Programme
ICOS	Investigations of Calanus finmarchicus Migrations between Oceanic and Shelf Seas off Northwest Europe (MAST II)
MARE-COGNITUM	Marine Ecology of the Nordic Seas
MATER	Mediterranean Targeted Project II - Mass Transfer and Ecosystem Response (MAST III)
NOWESP	North European Shelf Project (MAST II)
OMEGA	Observations and Modelling of Eddy Scale Geostrophic and Ageostrophic Circulation
OMEX	Ocean Margin Exchange Project (MAST III)
PEP	Impact of a Climatic Gradient on the Physiological Ecology of a Pelagic Crustacean (MAST III)
PEX	Patchiness Experiment
POEM	Physical Oceanography of the Eastern Mediterranean
PROVESH	Processes of Vertical Exchange in Shallow Seas (MAST III)
SEFOS	Shelf Edge Fisheries and Oceanography Studies (AIR)
SOMARE	
TASC	Trans-Atlantic Study of Calanus finmarchicus (MAST III)
VEINS	Variability of Exchanges in the Northern Seas (MAST III)

## Research approach

It may be advantageous to focus on particular areas, including large oceanic regions. The comparative approach, concentrating on sites with particular natural characteristics, can be a powerful organising principle for research, but the numbers and types of sites and the processes and parameters to be studied must be carefully defined in a common framework of theory and observation. Simple systems, which are characterised by a restricted species diversity and trophic structure, may be easier to model and understand.

On the other hand there is also a case for focusing on areas which offer a wide dynamic range in some of the important physical factors (depth, mixing, density gradients, mesoscale features, etc.) affecting energy flow, the marine food web, population dynamics and species diversity. Such sites may allow lower cost sampling of a range of ecosystem states and better opportunities to test hypotheses about different critical processes. Whatever the approach, the main objective in the frame of EUROGLOBEC is the development of studies which could not be realised outside this context. The research effort will be organised in a way which ensures an efficient and effective use of all available resources.

## Criteria for selecting study areas

### Structural Criteria

- particular physical oceanographic structures (fronts, eddies, gyres, upwellings)
- degree of continental influence
- level of biological productivity
- the nature of the boundaries and the relative importance of fluxes through them
- area typifies a particular region or ecosystem
- feasibility of controlled experiments

### Forcing Criteria

- regional climatic characteristics
- characteristics of external forcings (large scale versus local, regular versus accidental)
- vulnerability of the area to large scale environmental changes

- enrichment mechanisms - tidal mixing (regular), upwelling phenomena (seasonal character), wind mixing (variable frequency)
- influences the dynamics of adjacent sensitive marine ecosystems

#### **Knowledge Criteria**

- past studies on major pathways of energy transfer in the ecosystem; biological structure at different trophic levels; modelling physics and biology
- availability of historical records
- facilities and human resources available including low cost monitoring

#### **Economic and Social Criteria**

- socially or economically important pressure of human activities

## 4. SCIENCE PROGRAMME

### Scale-based biological-physical interactions in the plankton

Interactions between physical and biological processes in the plankton occur on a variety of spatio-temporal scales (for examples see 4.2.2.2). All the scales discussed are relevant to the understanding of plankton abundance and dynamics and they need to be addressed by different techniques; hence, it is relevant to first define these scales and discuss potential interactions and gaps in our knowledge and next define relevant projects.

- **$\mu\text{m}$ -cm, s-min scales: Small-scale physical forcing of interactions within the plankton**

At the smallest scale ( $\mu\text{m}$ ) material transport is limited by diffusion. Thus, nutrient uptake in phytoplankton cells and bacteria is typically nutrient limited. A quantitatively important implication of turbulent shear is that it may cause suspended particles to collide and, hence, coagulate into large marine snow aggregates with high settling velocities (Jackson 1990); this is believed to be one of the most important processes driving vertical particle fluxes in the ocean. Marine snow aggregates may also provide an important food source for zooplankton. The significance of these processes and their implications for zooplankton population dynamics and pelagic food web structure are not well explored.

Behavioural responses (such as feeding and prey detection, orientation and aggregation, avoidance of predators, mate detection and tracking) are mirrored by the species capability to adapt to the physical and chemical environment. Chemical cues mediate a variety of responses which ultimately could play a major role in determining the success of the species.

Zooplankton live in a flow environment at low Reynolds numbers, where viscous forces predominate. Chemotaxis can be an effective orientation mechanism, which indicates that zooplankton are susceptible to odour production and the physical mediation of the signals. Our future success in understanding how the physical environment determines encounter rates, rests ultimately on quantifying prey detection by the predators. As encounter rate of a



predator is extremely sensitive to slight changes in perceptive volume, more accurate predictions of encounter rates, and hence feeding rates, of predators on their prey are needed. Therefore small scale mechanistic approaches are necessary to understand large scale processes in aquatic ecosystems.

At slightly larger scales, near or around the Kolmogorov length scale (mm-cm), ambient turbulence may significantly enhance prey encounter rates in planktivorous predators (Rothschild and Osborn 1988). Experimental and empirical evidence is now accumulating, that this is in fact quantitatively important in copepods and in larval fish (Sundby et al. 1994, Saiz & Kiorboe 1995, Dower et al. 1997) while unimportant in both larger (e.g. fish) and smaller (e.g. ciliates) predators.

- **cm-10's of m vertical scales, m-10's of km horizontal scales; day to weeks: Mesoscale physical forcing and responses of plankton food webs**

Physical processes at mesoscales include fronts, upwellings, eddies, and thermoclines. A common feature for these processes is that they separate water masses and therefore provide hydrographic structure to the pelagic environment. Transition zones such as these are usually places which have high rates of plankton production due to favourable light, nutrient and turbulence conditions (Kiorboe 1993), or where interactions between plankton behaviour and mesoscale circulation patterns result in local plankton aggregations (LeFevre 1986, Franks 1997). Moreover, the high abundances of plankton in such regions often coincide with high abundances (Munk et al. 1995, Coombs et al. 1997) and good condition (St. John and Lund 1996) of fish larvae, suggesting that processes that affect boundary integrity could have a role in determining recruitment to fish populations (Lasker 1975). Also, intermittent atmospheric forcing (one to several days) can have a profound effect on secondary production (e.g. Nielsen and Kiorboe 1991); storm events cause resuspension in neritic regions leading subsequently to phytoplankton production and zooplankton reproduction.

In the context of climatic variability, the vertical and geographic positions and seasonal development of hydrographic boundaries are likely to vary. Given the impact of such processes on plankton (including young fish stages), boundary-related processes at the mesoscale should be investigated by EUROGLOBEC.

- **> 100 km, weeks-years: Large-scale transport and shelf-edge processes**

Processes at spatial scales in excess of 100 km and spanning time periods from weeks to years include regional circulation patterns, seasonal warming and stratification processes, and latitudinal gradients in ocean properties. Such processes will affect the seasonal development of zooplankton populations such as copepods which often are the main prey of larval and juvenile fish. The annual abundance of phyto- and zooplankton has decreased over decades with an increase of northerly winds near the British Isles (Dickson et al. 1988). Over the same period, the abundance of the copepod *Calanus finmarchicus* was directly related to the North Atlantic Oscillation (NAO) index, i.e. its abundance decreased with an increase in strong mid-latitude westerly winds (Fig. 1) (Fomentin and Planque 1996). Yet the direct cause(s) of these relationships still have to be determined. Also, the long-term geographical distributions of individual species can be altered by such processes. Through the modelling of realistic transport patterns it may be possible to describe the effects of atmospheric forcing on reproduction and transport of copepod populations (e.g. Backhaus et al. 1994, Hays 1995).

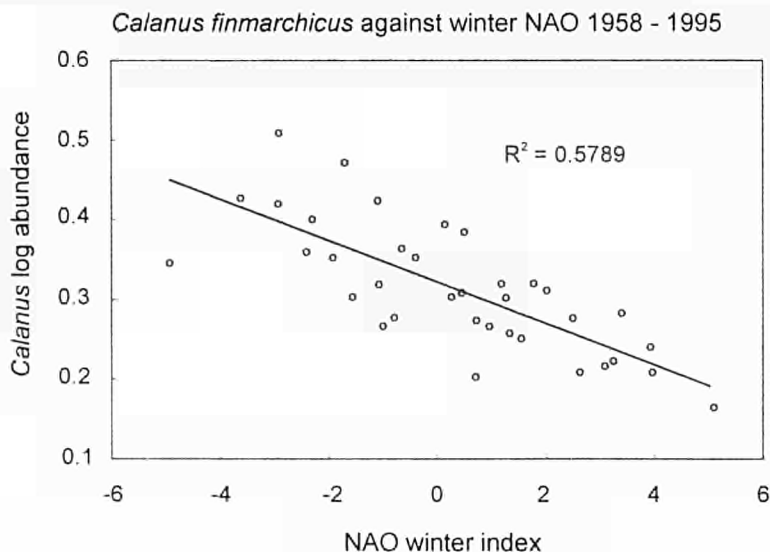


Fig. 1

Correlation between the changes in the North Atlantic Oscillation (NAO) index and the abundance of *Calanus finmarchicus* in the northeast Atlantic. Modified after Fomentin and Planque 1996.

Large scale circulation variability can also modify the distributions of abiotic factors that may control growth, survival and distribution of organisms in local areas. One European example of such a process is the intermittent occurrence of inflows of saline oxygen - rich water into the Baltic Sea (Matthäus and Franck 1992), which directly benefits cod recruitment (Sparholt 1996). Alternatively species can relocate to environments more physiologically suitable in response to oceanographically induced changes in local habitat conditions (e. g., temperature, salinity).

## 4.1 Focus: Retrospective Studies

### 4.1.1 *Rationale*

A key aim of GLOBEC is to differentiate anthropogenic from naturally occurring effects on marine ecosystems. Natural variability, occurring over a variety of time scales, is inherent in the functioning of marine ecosystems and understanding its role is essential if we are to manage marine living resources. Natural climate variability has substantial impact on marine ecosystems as shown for the North Atlantic (Cushing 1982), the North Pacific (Beamish 1995) and eastern boundary upwelling systems (Bakun 1996). It can reorganise marine communities and trophic relationships and induce regime shifts where the dominant species replace each other on decadal time scales (Bakun 1996).

One way to predict how ecosystems will react to global changes is to look at causal relationships of past patterns of natural variability by means of retrospective studies. Such retrospective analysis in the context of large-scale climatic changes and variability is one of the four research foci of GLOBEC (IGBP 1997). Its objective is the identification and improved understanding of the characteristic, natural modes of physical forcing and the response of marine ecosystems over a range of temporal and also large spatial scales. The approach is to develop and examine historical information on marine ecosystem characteristics at interannual, decadal and centennial time scales from a variety of sources.

Retrospective analyses of observations are currently the only method available to identify characteristic temporal scales of ecosystem variability and their rates of change due to both natural and natural



plus anthropogenic forcing (GLOBEC Implementation Plan, in prep.). In the future, models will likely be used in association with observations to assess the levels and characteristics of natural ecosystem variability.

With our growing capabilities to make synoptic observations of oceanographic conditions over large areas and advances in coupled atmosphere-ocean models, we are now starting to understand the causes of coherent changes in marine ecosystems over large scales. The challenge is to predict such events or, at least, to recognise them when they occur (Sissenwine 1997). A EUROGLOBEC Programme will contribute to hindcasting, nowcasting and forecasting the impact of climate variability (such as the NAO) on North Atlantic ecosystems. Retrospective studies (i) will help us to better understand why marine populations exhibited decadal-scale fluctuations in the past and which atmospheric-hydrographic mechanisms caused these fluctuations (hindcasting), (ii) will enable us to identify in which regime (NAO mode) we are at a given time (nowcasting) and (iii), using the results of the planned studies of CLIVAR (Climate Variability and Predictability), may allow us to predict regime shifts and future fluctuations of marine populations. The contribution to prediction will come about through direct climate-ecosystem empirical prognostic relations, and through the contribution of retrospective studies to an ability to model the impact of physical forcing on marine ecosystems. Despite difficulties in simulating NAO variations from SST forcing, recent modelling studies have suggested that the North Atlantic Ocean may have climate predictability on the order of a decade or longer (Griffies and Bryan 1997) and any tendency for the NAO to undergo structured long-period change over years to decades must have predictive value, if it can be rigorously established (CLIVAR ms.). Evidence for predictability is accumulating in new data on deep-rooted oceanic temperature anomalies which seem to propagate around the Atlantic Basin on decadal or longer time scales with a clear potential to affect air-sea interaction. It is expected that the large heat capacity of the ocean is the probable memory of this coupled ocean-atmosphere system (WCRP 1997).

The results of retrospective analysis in conjunction with modelling (see Focus 3: Modelling) will indicate which are the critical processes to be investigated by EUROGLOBEC (see Focus 2: Process Studies).

### 4.1.2 Background

#### 4.1.2.1 Knowledge of past variability in a European context

Lamb (1972, 1977, 1982) gives examples of the wealth of long-term climatological data derived from a variety of sources. Naturally, the largest marine ecosystem data bases are national and international fishery records. A compilation of many historical data series from the marine realm is to be found in Cushing's (1982) excellent book on Climate and Fisheries which is a rich data source for later studies. The proceedings of several meetings contain much information on long-term data from hydrography and fisheries (Wyatt and Larraneta 1988, Dickson et al. 1992, Astthorsson et al. 1993, Caan et al. 1996). The long-term data on the Bohuslän herring fishery (10th-20th century; Alheit and Hagen 1997) (Fig. 2), the Russell Cycle in the English Channel (since 1920s; Russell et al. 1971) and results of the Continuous Plankton Recorder (CPR, since 1940s; Reid and Budd 1979) are already classic examples of long-term data time series. The CPR Survey, introduced 65 years ago, is the only ocean basin-wide and long-term operational survey of plankton in the world. Hydrometeorological forcing of plankton variability as evidenced by strong associations with the North Atlantic Oscillation (Fomentin and Planque 1996) (Fig. 1) and the Gulf Stream Index (Taylor 1995) indicate the relevance of this data set to the aims of a EUROGLOBEC Programme.

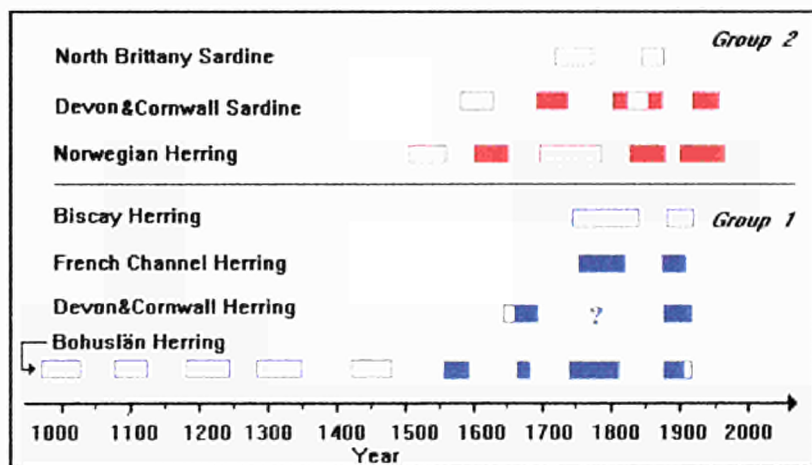


Fig. 2

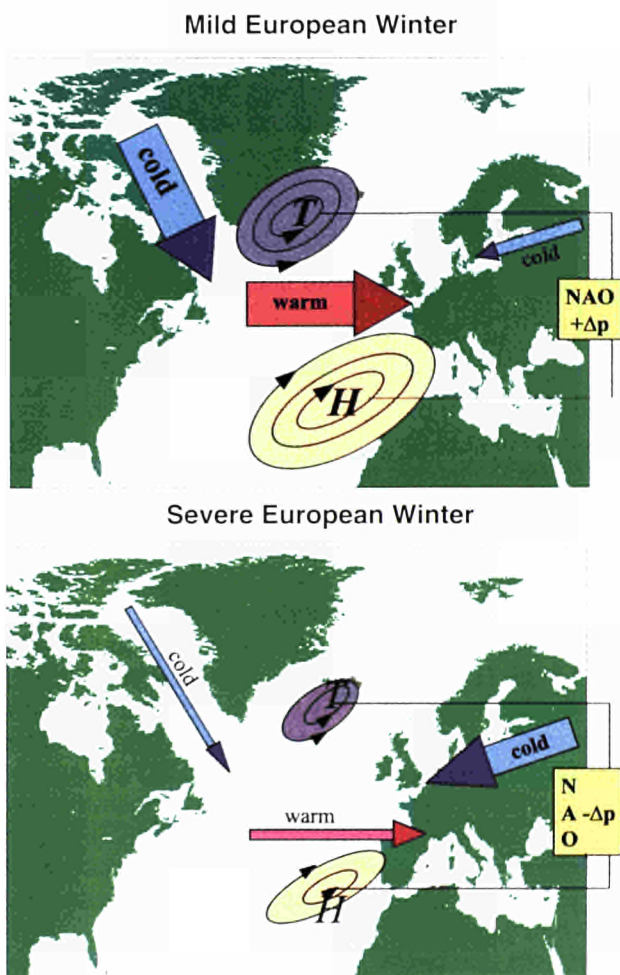
Historical periods of European herring and sardine fisheries. Open rectangles depict periods where the extensions are not precisely known. Modified after Alheit and Hagen 1997.

For the physical climate, a range of data sets exists. Data from ships are archived in computerised data sets starting in the mid-1850s. The Comprehensive Ocean-Atmosphere Data Set (COADS) contains a range of ship-reported variables including sea-surface temperature (SST), sea-level pressure (SLP) and near-surface wind. The NACD (North Atlantic Climatological Data set) is a data source for atmospheric variables over the North Atlantic area. The United Kingdom Meteorological Office (Hadley Centre, Bracknell) has processed the SST observations into quality controlled historical data sets, and more recently, these data sets have been transformed into fully gridded products (the Global Ice and SST data sets GISST). Similar products are available from the National Centres for Environmental Prediction (NCEP), Washington DC. Since the early 1980s, the surface-based ship and buoy observations are blended with satellite remotely-sensed ocean-skin temperature estimates. Other satellite data sets of such variables as wind and precipitation are also available for the last decade or so.

The strongest climate signal in the North Atlantic is the North Atlantic Oscillation (Walker and Bliss 1932, Lamb and Pepler 1987, Hurrell 1995, Dickson et al. 1996, CLIVAR ms.). In the positive phase, westerly winds across the North Atlantic are stronger, and stronger than normal storms are steered into Northern Europe (Fig. 3), while the reverse occurs in the negative NAO phase. The winter NAO pattern contributes the largest fraction of the northern hemisphere temperature variability of any mid-latitude or tropical mode of fluctuation (WCRP 1997). The NAO is associated with systematic large amplitude patterns in the anomalies of wind speed, latent and sensible heat fluxes and, hence, sea surface temperature over much of the extratropical North Atlantic (Cayan 1992a,b, CLIVAR ms.). Its influence domain sometimes extends further eastward into Europe, while at other times, a similar phenomenon is confined to European longitudes. Its character may vary depending on time scale (interannual, decadal). These are major research issues for CLIVAR and EuroCLIVAR.

For marine ecology, some of the most direct physical ocean changes associated with the NAO include: ocean temperature and salinity anomalies (Buch 1995, Reverdin et al. 1997.), the transport of the Labrador Current (Myers et al. 1989, Marsh 1997), Arctic sea-ice (Fang and Wallace 1994, Mysak et al. 1996). Also, it has recently been suggested that decadal changes in the NAO control and co-ordinate the intensity of deep convection between the three main



**Fig. 3**

*Scheme of the atmospheric winter circulation over the northern Atlantic Ocean indicating the two distinct modes of the North Atlantic Oscillation (NAO), which is described by the difference in sea level air pressure between the Icelandic Low in the north (T) and the Azores High in the south (H) ( $\pm \Delta P$ ) (a)  $+\Delta P$  (NAO) corresponds to:*

- mild European winters;
- a strong inflow of cold air masses over the Alaska-Greenland region;
- warming air masses over the north-west Atlantic Ocean;
- intensification of westerly winds transporting relatively warm air masses to western Europe;
- a relative northward migration of the belt of westerly winds reducing the inflow of cold Siberian air masses over north-eastern Europe.

*(b)  $-\Delta P$  (NAO) corresponds to:*

- severe European winters;
- reduced inflow of cold air masses over the Alaska-Greenland region;
- reduction in the intensity of westerly winds transporting relatively warm air masses to western Europe;
- a relative southward migration of the belt of westerly winds favouring a strong inflow of cold Siberian air masses over north-eastern Europe.

*Modified after Alheit and Hagen 1997.*

Atlantic sites (Greenland Sea, Labrador Sea and Sargasso Sea) (Dickson et al. 1997), thus driving decadal change to considerable depths in the ocean (CLIVAR ms.).

There is already evidence that the physical ocean changes associated with the NAO do indeed strongly affect marine ecosystems. The recent ICES/GLOBEC Workshop on "Prediction and Decadal-Scale Ocean Climate Fluctuations of the North Atlantic" clearly demonstrated that the dynamics of phytoplankton, zooplankton, fish populations and top predators such as herring-feeding sea birds are governed by annual, decadal and centennial oscillations of the NAO and associated processes of the coupled ocean-atmosphere system. The ecosystem changes include: regime shifts of herring and sardine fisheries over centuries (Cushing 1982, Southward et al. 1988, Binet 1988, Alheit and Hagen 1997) (Fig. 2), parallel trends across several trophic levels in the North Sea (Aebischer et al. 1990), rise and fall of the West Greenland cod fishery (Buch and Hansen 1988), stock fluctuations of Barents Sea cod (Sundby, pers. comm.), dynamics of *Calanus finmarchicus* and *C. helgolandicus* (Fomentin and Planque 1996) (Fig. 1) and phytoplankton production in the Skagerrak (Belgrano, pers. comm.). Whereas correlations of the NAO with a large number of biological variables are obvious, mechanisms of the impact of the coupled ocean-atmosphere on marine populations are far from understood. Thus, retrospective studies now need to be framed in ways that lead to hypothesis formation for testing in models.

While the main thrust of retrospective work in the European context will involve the NAO and related climate variability, the influence of some other sources of climate variability over the European region has also been found and should be considered by EUROGLOBEC retrospective studies. These include some evidence for an ENSO (El Niño Southern Oscillation) influence in the European region at certain times, and interactions between European climate and other tropical variability such as the West African and Southeast Asian monsoons.

#### 4.1.2.2 On-going activities

At the present time, a number of institutions, programmes and projects are involved in continuing long-term sampling for physical, chemical and biological parameters and in processing and analysing the resulting data: national and international fisheries agencies, the Sir Alister Hardy Foundation (CPR survey) and monitoring programmes

such as HELCOM in the Baltic. The different regional and national programme components of GLOBEC in Europe apply different approaches to analyse time series.

For the North Atlantic, the Cod and Climate Change (CCC) initiative has organised a series of successful ICES/GLOBEC workshops. The Database Workshop set out the basis for a user driven data and information system for Cod and Climate Change (Anon. 1996a). The 2nd Backward-Facing Workshop considered the incidence, causes and ecosystem effects of extremely cold years in the marine environment of the Barents Sea and the Baltic Sea (Anon. 1996b). The Workshop on Prediction and Decadal-Scale Ocean Climate Fluctuations of the North Atlantic discussed particularly the impact of the North Atlantic Oscillation on Northeast Atlantic ecosystems.

The EU-funded TASC Project (Trans-Atlantic Study of *Calanus finmarchicus*) analyses long-term data sets in relation to zooplankton dynamics. The objective of this analysis is to determine trends and seasonal cycles in abundance of *Calanus* in different regions of the NE Atlantic and examine evidence for correlations between regions. This is being done by extending the statistical time series analysis of data from the CPR surveys carried out for the North Sea during ICOS (Investigations of *Calanus finmarchicus* Migrations between Oceanic and Shelf Seas off Northwest Europe) to include a wider area of the North Atlantic and Norwegian Sea, and draw this together with an analysis of historical time series data from Iceland, Færoese, Norwegian and published Russian sources.

The Small Pelagic Fishes and Climate Change (SPACC) programme, one of the four major GLOBEC regional initiatives, investigates the impact of climate variability on those ecosystems in which small pelagics play an important role (Hunter and Alheit 1995). It operates through a number of Retrospective Working Groups on (i) Decadal Changes of Ecosystems, (ii) Comparative Population Dynamics, (iii) Paleoecology, and (iv) Genetics (Hunter and Alheit 1997). Its Baltic Sea component is funded by the EU MAST Programme BASYS (Baltic Sea System Study).

In the Norwegian GLOBEC Programme MARE COGNITUM in the Nordic Seas, historical data sets are a prerequisite for the study of ocean climate and the mechanisms which generate climate fluctuations (Skjoldal et al. 1993).



The sister programme of the IGBP, the World Climate Research Programme (WCRP) maintains several initiatives the results of which will be tremendously important for retrospective studies within GLOBEC, especially the DecCen (Decadal to Century variability) CLIVAR initiative, with a major focus on the NAO and its predictability. A European CLIVAR programme (EuroCLIVAR) is expected to focus on Atlantic and European climate variability, in particular on the NAO. Many coupled ocean-atmosphere model experiments are expected. The conclusions on NAO character and variability are essential inputs to EUROGLOBEC retrospective studies. In addition, the CLIVAR model output itself will form data sets for comparison with observed data compiled by EUROGLOBEC. A specific African component to EuroCLIVAR is also anticipated. Thus EUROGLOBEC and EuroCLIVAR can be expected to lead to highly complementary research.

#### 4.1.3 Approach

##### 4.1.3.1 Development and compilation of background data

- *Compilation of existing data*

The building of comprehensive data bases will be the key basis for retrospective studies. This includes the search for, and the rescue of, long-term sample and data sets, as is being done within the EU-BASYS project in the Baltic Sea. All data sets should be subjected to a strict quality control, and checked for internal consistency where possible.

- *Compilation and creation of proxy time series*

Understanding of decadal-scale variability is central to a EUROGLOBEC Programme. The length of conventional data sets often does not allow reliable estimates of decadal variability. Therefore there is a need to utilise proxy data sets to improve estimates of decadal variability. Examples of such proxy data include tree rings, varved sediments and shells of marine organisms. The particular aim is to better describe the decadal-scale variability of the marine ecosystem and its response to physical forcings over the last few hundred years.

- *Construction of climatologies for regional European seas*

There is a need for background climatologies of the key variables for EUROGLOBEC, both mean values for recent decades and

interannual variability. Where possible, the climatologies will be constructed by drawing on work in related programmes, such as CLIVAR. CLIVAR's main goal is to study seasonal-interannual-decadal variability of climate including ocean-atmosphere interactions, with the goal to eventually predict climate variability. However, for many variables, especially within the marine ecosystem, the responsibility will lie with GLOBEC.

#### 4.1.3.2 Analysis of interrelationships

- *Interrelationships between atmospheric, hydrographic and biological data series*

The interrelationships between atmospheric variability (e.g. patterns of NAO), physical characteristics of the ocean (e.g. temperature, salinity, circulation, convection) and ecosystem response (e.g. plankton and fish populations) will be studied using statistical methods. Multivariate statistical methods such as empirical orthogonal function (EOF) analysis (Preisendorfer 1988, von Storch 1995), canonical correlation analysis (CCA) (von Storch 1995) and singular value decomposition (SDV) (Bretherton et al. 1992) need to be applied to describe the principle spatial and temporal patterns of physical and biological variability and also the coupled modes. The use of non-parametric tests like Pettitt's test (Sneyers 1975, Pettitt 1979) will be helpful in detecting significant regime shifts in both biological and physical time series. These statistics will (i) form bench marks to which the variability generated by models can be compared and the models realism assessed and (ii) also provide basic evidence for the construction of hypotheses.

- *Documentation of relationships on different time scales (interannual, decadal, centennial)*

Analysis on different time scales will assist greatly in the interpretation of underlying processes. Inter alia, the following questions should be particularly considered: What controls the population variability that is observed at time scales of decades (regimes)? Are the processes similar to or distinct from those processes generating interannual variability? At what trophic level is decadal-scale variability driven? Is climatic forcing based on single events or more gradual trends through habitat change? How do marine ecosystems respond to episodic climate events in contrast to more gradual trends (regime shifts)? Cross spectral analysis may be useful in isolating characteristics of the relationships between biological and physical variables on



particular time scales. In addition, prefiltering variables on the time scale of interest should also prove useful.

- **Comparison of results from different regional seas**

It is important for process and modelling studies to identify if interrelationships amongst physical and biological variables are the same in different locations or whether certain relationships vary geographically. Given the strong global connectivity of climate anomalies it is necessary to assess if marine ecosystems display similar large scale teleconnections. Questions to be asked are: Is there regional/global coherence in climate variability over multi-decadal time scales which tends to produce synchronicity in variability in the ocean environment among different ecosystems/regional seas? If true, how do the regional and local processes which regulate ecosystem structure and function respond to the synchronous changes in climate?

- **Retrospective modelling**

Models shall be developed to provide insight into the key questions listed above. In the hindcast–diagnostic mode, models shall be run retrospectively and compared with the data. Discrepancies between simulated conditions and actual data are used to diagnose and correct model deficiencies. Once a credible model has been developed, it shall be used in the hindcast mode to infer mechanisms responsible for historical variation and in the forecast mode to make predictions on the future effects of climate change using information on current conditions. The interaction between modelling and retrospective analysis is particularly crucial not only because of the limited observational records, but also because of the need to synthesise sparse data sets.

## **4.2 Focus: Process Studies**

### *4.2.1 Rationale*

Understanding ecosystem functioning requires initial knowledge of its components. The first section provides background information on the significant physical and biological variables which govern processes of various ecosystems and their components down to individuals, and particularly points out gaps in our knowledge. The section, Approach, outlines the various essential process studies in conjunction with

retrospective and modelling efforts, to achieve the main goal, i.e. that of understanding ecosystem function, and eventually its prediction. Only an interdisciplinary and concerted quantification of respective physical and biological variables will result in obtaining environmentally-realistic process rates. These data will form the basis for developing near real-time models of *in situ* processes for EUROGLOBEC.

#### 4.2.2 Background

##### 4.2.2.1 General

The identification within a EUROGLOBEC programme of key environmental processes affecting plankton production and their impact on fish populations is consistent with other recent European developments in the fields of fisheries assessment. One of these developments is the attempt to begin the integration of fisheries and environmental management in the North Sea (e. g., Anon. 1997). A EUROGLOBEC Science Plan is a potential vehicle to begin extending some of these developments to other European seas.

Some of the issues relevant to the impacts of climate variability on the distribution and production of both plankton and fish that a EUROGLOBEC programme should consider include the following:

- Which hydrographic and biological processes are most important in determining growth, survival and reproduction in zooplankton and young fish, and which of these processes are most sensitive to climate variability in different European waters?
- How sensitive are pelagic food webs to climate variability?
- Which processes should be investigated to yield the most understanding and predictability of how marine ecosystems will react to climate variability, in relation to expected research effort.
- How does variation in pelagic food webs between areas affect sampling and modelling techniques?
- Do fisheries, by significantly influencing the abundance of zooplanktivorous fish, also impact zooplankton dynamics?

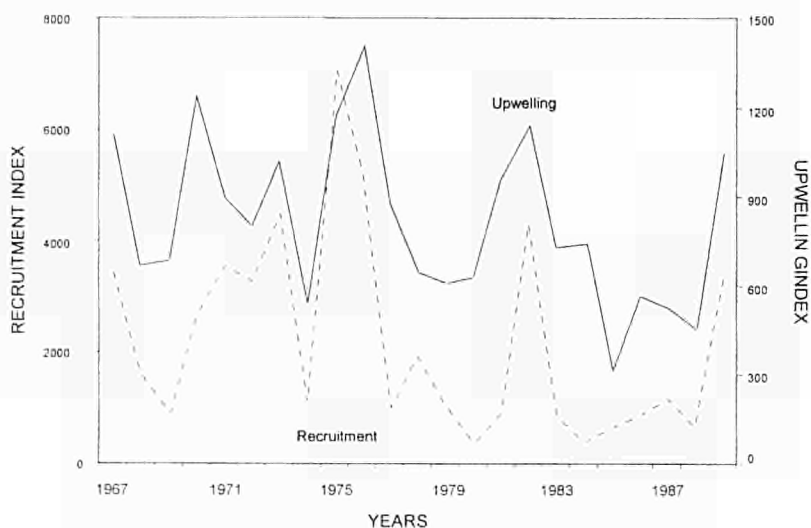
The solution of some of these questions could be considerably facilitated by respective results from retrospective studies and modelling. Two examples of potential links between plankton

production, ecosystem variability and fish recruitment are given as part of the Background to this document, and other examples are being developed within EU programmes (e.g. ICOS, TASC).

#### 4.2.2.2 Links between ecosystem variability, plankton production and fish recruitment

- *Upwelling areas*

Statistical analyses have shown that recruitment variability in the Bay of Biscay sardine population is related to hydrographic variability during the first year of life (Fig. 4) (Borja et al. 1996). A similar pattern of recruitment variability exists for sardine and anchovy populations in several other major upwelling ecosystems around the world (Cury and Roy 1989, Ware and Thomson 1991, Roy et al. 1992). This result suggests that there may be common and strong environmental components to recruitment variability for pelagic species inhabiting upwelling ecosystems (Bakun and Parrish 1990, Hunter and Alheit 1995).



**Fig. 4**

Anchovy (*Engraulis encrasicolus*) recruitment and upwelling indices in Bay of Biscay between 1967 and 1989. Modified after Borja et al. 1996.

The key hydrographic component involved in these relationships is the intensity of upwelling and oceanic turbulence, with recruitment usually being maximal at an intermediate level of upwelling and turbulence. Turbulence and upwelling have several direct and indirect effects on larval fishes. The direct effects of turbulence relate to encounter rates between larval fish and their prey, which increase with turbulence intensity (Sundby et al. 1994, MacKenzie and Kiorboe 1995), and the ability of larvae to pursue and capture encountered prey, which decreases at high turbulence (MacKenzie et al. 1994, Saiz and Kiorboe 1995). When the effects of turbulence on encounter and pursuit success are combined, the overall effect of turbulence on larval food consumption rate will be a dome-shaped response (Gallego et al. 1996, Dower et al. 1997).

The indirect effects of oceanic turbulence relate to its role in plankton production, pelagic food web structure (reviewed by Kiorboe 1993), and the role of food web structure on larval growth and condition (St. John and Lund 1996). In general, turbulent water columns are characterised by diatom-dominated phytoplankton communities and homogeneous plankton distributions, and stratified water columns are characterised by dinoflagellate-dominated phytoplankton communities and heterogeneous plankton distributions.

Upwelling may have other effects on recruitment that are less direct, but which nevertheless may still impact growth and survival. For example, years of strong upwelling could transport eggs and larvae away from normal nursery areas and therefore result in a loss of reproductive effort (Sinclair 1988). The effects of transport on larval growth and survival may therefore also contribute to the dome-shaped relation between recruitment and upwelling/turbulence intensity. The relative importance of these processes and their sensitivity to climate variability is presently unclear, but is relevant to a potential EUROGLOBEC Programme.

- *Frontal regions*

These areas occur at mesoscales and have been identified as larval nursery sites for several larval fish species (Sabates and Maso 1990, Munk et al. 1995, St. John and Lund 1996, Coombs et al. 1997) in European seas (e. g., North, Irish, Skagerrak/Kattegat, Adriatic, Mediterranean). Recent evidence shows that pelagic 0-group cod at a front in the North Sea have higher lipid condition indices and are those



which have been feeding on a diatom-based food web (St. John and Lund 1996). This suggests that the food web characteristics of frontal environments may be nutritionally superior to those of neighbouring environments. In general frontal zones have higher production and concentrations of zooplankton than neighbouring areas (LeFevre 1986, Kiorboe et al. 1988), and field and modelling studies show that these areas are moderately turbulent environments (Horne et al. 1996). It can be hypothesised therefore that frontal regions, and especially their food environment (e. g., prey abundance, prey nutritional quality, patch characteristics, turbulence), serve the same functional role (for many but not all species of larvae) as upwelling systems do for sardine and anchovy larvae, and that in both instances, growth and condition of larvae in the intermediate-type environment will be higher than in other places.

#### 4.2.2.3 Trophic interactions: zooplankton as predators and as prey

Trophic interactions of zooplankton include:

(1) (micro)zooplankton species/stages preying on phytoplankton;  
(2) omnivorous zooplankton species/stages preying on (micro)zooplankton; (3) planktivorous fish species/stages preying on (micro)zooplankton.

- *Evidence of bottom-up controls: feeding strategies, growth, reproduction and mortality in relation to food quality and quantity*

During upwelling events and spring blooms, the classical food chain (diatoms-copepods-fish) was thought to predominate, i.e. copepods would be almost exclusively herbivorous. Yet, recent evidence suggests that even during high diatom abundance, calanoid copepods prefer to eat ciliates and heterotrophic dinoflagellates (e.g. Fessenden and Cowles 1994, Verity and Paffenhöfer 1996) clearly showing omnivorous behaviour. As also shown by Ohman and Runge (1994) calanoids can obtain sufficient food for reproduction from heterotrophs, thus indicating that much, or all, of their energy demands can be derived from protozoa which in turn ingest bacteria and small phytoplankton cells which cannot be directly captured by copepods. Thus, the microbial loop can be of significance for juvenile fish which prey heavily on copepods.

Behavioural responses involved in omnivorous feeding such as prey detection, orientation and aggregation and predator-prey interactions (Paffenhöfer and Lewis 1990) are mirrored by the species capability to respond to the physical and chemical environment. The chemical cues involved mediate a variety of responses (Cowles et al. 1988) which ultimately may play a major role in determining species success. Sensory ecology on a small scale will also have implications on larger scale processes for secondary production.

While juvenile and adult copepods are highly selective in the presence of abundant food, they become far less selective in times of food scarcity (e.g. Paffenhöfer 1984). Not only food abundance, but also its composition affects growth, reproduction and mortality (e.g. Kleppel 1992, Uchima and Hirano 1986). The ability to select certain types of food particles is a function of a copepod's perceptive and capture abilities (e.g. Paffenhöfer and Lewis 1990). A major challenge in this area of research is to develop methods of accurately quantifying feeding rates of abundant zooplankton species in the ocean, and develop models to estimate feeding rates from zooplankton species and stages and food abundance and composition. This has been problematic because most copepods possess a wide food spectrum which changes as they grow (e.g. Paffenhöfer 1984). However, some methods have recently been employed which allow the quantification of growth (Peterson et al. 1991) and food consumption of copepods (Verity and Paffenhöfer 1996) by creating conditions close to those *in situ*. These rate quantifications can then later be used in models in conjunction with copepod stage and food abundances to estimate growth and feeding impacts of the same copepod species at other times and locations. Eventually near real-time data may be obtained by applying such models to abundances of vertical distributions of food and feeders (copepods) obtained with automated image analyses (for cells) and acoustics/optics (for copepods).

The linkage between microbial and classical food webs will also influence physiological rates in zooplankton due to differences in the quality of prey consumed. Although it is well known that a functional relationship exists between food quantity and copepod production rates, the influences of food quality on copepod biology (e. g., hatching success of eggs, development rates of all stages) is much less well known. However, poor food can reduce clutch size, inter-clutch period, and retard embryogenesis and generation time to adulthood. Other food characteristics may include deterrent

compounds that modify feeding (Huntley 1988), fecundity and hatching success (Ban et al. 1997). Hence, changes in the environment that alter phytoplankton species composition or the feeding strategy of copepods (herbivores vs. omnivores) may potentially induce significant changes in copepod reproduction and shifts in community structure.

One of the most difficult variables to quantify in the ocean is that of mortality (e.g. Marine Zooplankton Colloquium 1, 1989, Ohman and Wood 1995). The continuous advection of water at different velocities vs. depth is just one of the factors which contribute to the dispersion of zooplankton populations making it almost impossible to follow a population in the ocean unless one operates in a restricted environment such as a lagoon (Landry 1978). Nevertheless, new theories and technologies are about to enable us to study mortality in zooplankton on ranges up to mesoscale in open waters. This is especially true for “physiological mortality” driven by food availability and composition of the diet. It is well known that a functional relationship exists between food quantity and copepod production rates, and field studies have demonstrated that in many areas copepods show food-limited growth for prolonged periods of the year. Much less is known on how food quality determines the successful hatching of eggs and development from egg to adulthood. Measurements of egg viability in the sea have only recently been initiated; the available data indicate that egg hatching success is variable over the course of the reproductive season (Laabir et al. 1995). Hatching success is therefore an important factor determining the timing and duration of copepod recruitment. The causes of high egg mortality are uncertain but laboratory studies have shown that the fatty acid composition of the diet and the presence of deterrent compounds blocking embryonic development such as those described in diatom cells (Ban et al. 1997 and references therein) may modify fecundity and hatching success.

- *Evidence of top-down control of zooplankton*

Inter alia, GLOBEC focuses on the importance of predation and competition forcing the structure and population dynamics of zooplankton populations (IGBP 1997). One of the key questions for a comparative process study of the linkages between zooplankton and small pelagic fish production is whether predation by fish regulates zooplankton abundance (GLOBEC Small Pelagic Fishes and Climate Change Program) (Hunter and Alheit 1995). Evidence for the impact of



predation on the next lower trophic level, and for cascading effects of predator introductions (imported by man) and removals (e.g. advection or migration out of the area, extinction by natural or man-made causes, fishery activities) is accumulating.

Studies of the impact of predation by planktivorous fishes on the seasonal dynamics of specific zooplankton populations and structure of the zooplankton community have been conducted mainly in freshwater systems (e.g. Mills et al. 1987) and coastal areas (e.g. Hansson et al. 1990). Studies in larger sea areas indicate that predation on zooplankton communities by both vertebrate and invertebrate predators can be intense and hence influence zooplankton population dynamics. Studies in the Baltic Sea have indicated that (1) fish predators actively select certain zooplankton species; (2) these copepod species show a stronger vertical migration than others to avoid a high predation pressure; (3) the annual consumption of zooplankton may reach 70% of the production; and (4) the increase in planktivory in summer coincides with a decrease in zooplankton biomass (Rudstam et al. 1994). There is considerable evidence for the importance of invertebrate predators in controlling and structuring zooplankton communities. Especially medusae and ctenophora have been identified as controlling predators, e.g. in the western Baltic (Schneider and Behrends 1994), Black and Azov Sea (Vinogradov et al. 1996), German Bight (Greve 1981), Nova Scotia (Suthers and Frank 1990), Georges Bank (Davis 1984) and Chesapeake Bay (Purcell 1992).

Mechanistic outlines of sensory processes are likely to reveal physical factors that determine risks of mortality and foraging opportunities in marine systems. The optical properties of water masses are a central factor governing the outcome of predatory and competitive dynamics in pelagic communities. The competition between gelatinous zooplankton and fish in particular is strongly influenced by the turbidity of the water, and a shift towards more jelly-dominated situations is often observed in turbid and eutrophic areas. The causal mechanisms for such transitions are probably linked to the visual feeding mode of fish and fish larvae; major reductions of reactive distance occur at lower levels of light (Aksnes and Utne 1997).

Global change may have rapid effects on distributions, migrations and phenology (time of appearance) of organisms, as these are easily modified by the organism (Miller et al. 1991). Predation and resource



availability act through morphologies and life history strategies to structure pelagic ecosystems, and hence drive biogeochemical cycles (Verity and Smetacek 1996). Therefore, if we understand variability in behaviour, morphology and life history, we are in a better position to predict effects of global change.

#### 4.2.3 Approach

##### 4.2.3.1 Structure and function of pelagic food webs: response to physical forcing

The characteristics of physical forcing (frequency and intensity of external energy inputs) are important factors determining the structure of planktonic food webs. This forcing contributes motion over a wide range of spatial and temporal scales which in turn has numerous direct and indirect effects on plankton food webs at both the levels of individual plankters and entire populations. Moreover, the nature of the physical forcing (e.g., periodic or aperiodic) affects the coupling between the temporal scales of physical variability and the response time of the different elements of the food web. Investigations of how physical forcing due to climate variability affects pelagic food webs should address the following issues:

- *Direct effects of physical forcing on pelagic food webs*

Turbulent motion at the scale of individual plankters (mm-cm) affects particle - particle interactions in ways relevant to their growth, reproduction and mortality. Coagulation of phytoplankton cells, sedimentation of marine aggregates, mate-finding in zooplankton, predator-prey interactions (e. g. encounter rates), and zooplankton feeding strategies (e. g. filter feeding vs. raptorial feeding) are known from limited theory and empirical observations to be sensitive to turbulent motion. However, the direct biological response to this motion in the few cases studied is often highly non-linear (e. g. positive or negative effects depending on turbulence intensity) and depends strongly on organism size and behaviour in complex ways. Generalisations about the effect of small-scale turbulence on many types of interactions between organisms are therefore not yet possible and require further study in order to estimate and model the impact of climate variability and change on vertical fluxes, pelagic food web structure and zooplankton (including larval fish) ecology. Such

investigations should involve behavioural, feeding, growth and reproduction studies in both, the field and the laboratory.

- *Indirect effects of physical forcing on pelagic food webs, with particular reference to mesoscale processes*

Physical forcing influences the species composition of phytoplankton plankton communities and the rate of new production of phytoplankton cells. It also affects the maintenance and dissipation of patches. Hence climatically-induced variability in phytoplankton species composition and abundance will affect the nutritional quality, toxicity and abundance of prey for both primary and secondary consumers. This will in turn impact zooplankton growth, reproduction and mortality rates, which subsequently will affect food availability and quality for higher consumers (e. g. larval and juvenile fish).

The second indirect consequence of physical forcing on pelagic food webs is its potential role on the transfer and flow of matter and energy from primary producers to higher consumer levels. Dominance of the microbial or the classical herbivorous food webs has important consequences for the efficiency of the link between primary producers and fish via the role of copepods as omnivores or herbivores.

The third indirect consequence of physical forcing on pelagic food webs is its role in creating transition zones or boundaries in pelagic ecosystems. These zones occur at mesoscales and are important sites of zooplankton production and aggregation (ICES 1994), and as such are probably key habitats in the early life history of many commercially important fish species. However, the temporal and spatial stability of their geographic positions in response to climate variability are uncertain. The effects of physical forcing on pelagic marine ecosystems can only be understood through long-term time-series observations in the ocean (e.g. Dickson et al. 1988) in conjunction with sophisticated shorter term experiments in the field and the laboratory. Such studies represent an essential element of EUROGLOBEC.

#### 4.2.3.2 Climatically induced temperature fluctuations: effects on biological and successional processes in pelagic food webs

Perhaps one of the earliest signs of climatic variability in marine ecosystems will be changes in water temperature. These variations

might occur gradually or rather suddenly depending on the nature of the physical forcing. Since both the rate and magnitude of temperature change can be crucial to zooplankton development success, understanding how physiological processes respond to temperature variability will be necessary for developing models of zooplankton production and distribution. In addition, temperature changes will have direct effects on biological rates (e.g. feeding, growth, reproduction, mortality) in ways which are not presently understood, particularly for zooplankton exposed to fluctuating temperatures, and may include a high degree of plasticity. As a result, some species may alter their distributional ranges, migration routes and aspects of life history (e.g., overwintering timing and duration, timing and location of spawning) in attempts to remain within ranges of thermal optima.

Temperature also affects zooplankton distribution via its effects on seasonal species succession. Since different species have different temperature optima, climatically-induced variations in long-term seasonal warming and cooling trends will alter the seasonal succession within zooplankton communities. A more advanced understanding of temperature effects on zooplankton succession is essential for interpreting long-term changes in zooplankton seasonality that might become apparent from retrospective and future data analyses.

Temperature changes caused by climatic variations may have even more complicated effects on the structure and functioning of pelagic ecosystems. For example, one of the preconditions for high recruitment of Arcto-Norwegian cod is warm temperatures during the larval phase. During these years, cod larvae usually experience high concentrations of copepod prey and presumably feed and grow at higher rates than in cold years. In general, within a certain range, rising water temperatures could be expected to increase stratification of the water column and suppress phytoplankton production, whereas decreasing water temperatures will have the opposite effects. However, the degree of this suppression will vary widely across European marine ecosystems, and its effect will depend on second order considerations such as the rates, timing and magnitude of temperature changes both within and between years.



#### 4.2.3.3 Ocean circulation: role of climate variability and its effects on the distribution, life history and habitat linkages of key species of European pelagic ecosystems

Pelagic life is adapted to large-scale ocean circulation. Long-term studies are required to find out how zooplankton and fish are adapted to present pelagic ecosystems, and how changes in circulation will affect their production. Such studies have been few and include the ongoing Northwest Atlantic GLOBEC study on Georges Bank (U.S. GLOBEC Report No. 6, 1992). That study relates the seasonal changes in abundance of copepods, larval and juvenile fish to circulation and other hydrographic variables. A similar GLOBEC study is being initiated off the west coast of the U.S. (U.S. GLOBEC Report No. 17, 1996). In each case, close co-operation between physical and biological oceanographers is essential.

Impacts of climate variability on zooplankton will be investigated through empirical and model studies, the former requiring large-scale long-term observations including satellite imagery. Climate variability may result in changes in water mass properties and current structure which could have a profound influence on zooplankton communities and fish populations via altered life history patterns. For example the timing and completion of overwintering stages, migration routes, and the timing and location of major spawning grounds are likely to be sensitive to major climatically induced changes in large-scale circulation. These changes will also alter the present temporal and spatial patterns of overlap between zooplankton (prey) and fish (predators), thereby affecting the degree to which zooplankton populations may be regulated by predators.

A major issue is how the large scale circulation patterns transport and redistribute individuals within the system so that successive generations experience different environmental conditions in the different regions they are transported to. Outside their main large-scale habitats these species may occur more or less successfully in smaller habitats. This provides an excellent opportunity to test the hypothesis relating to the extent of linkages among different ecosystems, by studies of the population genetic structure in prey and predators that are distributed over several ecosystems. Recent studies have provided some evidence of the usefulness of molecular genetic markers as tags of transport pathways and as tools to identify and discriminate species (Fevolden & Pogson 1997). The approach

may assist in understanding of plankton dynamics and, by interference, functional linkages among ecosystems, pollutant impact and the effect of global change.

### 4.3 Focus: Modelling

#### 4.3.1 Rationale

The purpose of modelling in EUROGLOBEC is first to synthesise understanding of how mesoscale physics modulate the interactions among small- and large-scale ecosystem processes and second to develop predictive capabilities. GLOBEC modelling efforts must resolve the effects of physical forcing on ecosystem dynamics at fundamental spatial and temporal scales. Regional and large-scale models may require combinations of nesting, process-oriented approaches and parameterisations derived by up- and down-scaling. EUROGLOBEC modelling strategies must rather include a suite of approaches than searching for one single generic model.

During the last decades, biogeochemical models have been developed to simulate nutrients and lower trophic dynamics in regional

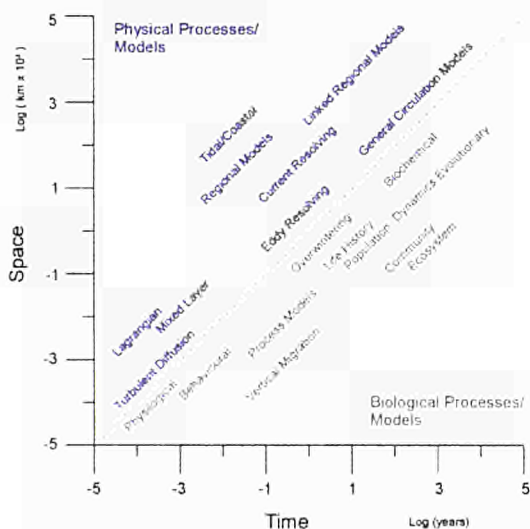


Fig. 5

The temporal and spatial scales over which particular physical and biological models apply. Modified after Murphy et al. 1993.



seas around the European coasts and for different parts of the Atlantic Ocean. Many of these models have largely ignored higher trophic levels, i.e. macro-zooplankton and their predators. Modelling of higher trophic levels (zooplankton and ichthyoplankton) presents particular challenges due to the organisms' adaptive (and complex) behavioural traits, the length of their life cycle, and the large range in body sizes. Fig. 5 indicates the range of time and space scales which should be considered in GLOBEC models.

A new generation of coupled models is needed if we are to understand how changes in the global environment will affect the abundance, distribution, diversity and production of zooplankton populations, and consequently the dynamics of predators. Ultimately, such multi-scale biological-physical models must resolve meso-scale features and integrate structured and unstructured individual- and population-based approaches.

#### *4.3.2 Background*

The GLOBEC programme concentrates in particular on dynamics of critical zooplankton populations and their responses to physical forcing. In doing so, it bridges the gap between phytoplankton studies and predator related research. Models of zooplankton population dynamics related to (i) physical forcing at the mesoscale, (ii) to phytoplankton and (iii) to their predators are required.

A variety of so-called "N-P-Z" (nutrients-phytoplankton-zooplankton) models exists where the biological constituents are represented by bulk biomass state variables (e.g. Evans and Parslow 1985; Fasham et al. 1990; Baretta et al. 1995; Ross et al. 1993). In comparison to such biogeochemical models, food web models have been rarely developed during the last decades. A major contribution to the design of model food webs was made by Steele (1974). Biogeochemical models have concentrated on the physics-nutrient-phytoplankton systems; they subdivide the ecosystem into large functional units (e.g. limiting nutrient, phytoplankton, zooplankton) and simulate energy flows through these units. Food web models try to represent the feeding relations between groups of organisms in order to estimate their production.

During the last decade, biogeochemical models have been coupled with 3-D physical models and simulated results have been compared

with remote sensing and field data. An important aim of this research effort (including modelling) has been to show that the main productive areas are characterised by hydrographic mesoscale features such as eddies, fronts or upwelling (e.g. Fennel and Neumann 1996) where the effect of mesoscale features on biological dynamics was illustrated by means of high resolution circulation models coupled with a chemical-biological model. Thus, the link between physical processes and biological production appears to be the base of the food-web.

Studies on zooplankton species have shown the link between species' life cycles and physical structures. A major problem for zooplankton modelling compared to nutrient, phytoplankton and microzooplankton modelling is that these organisms go through different developmental stages, change in form, behaviour and function and that their body size varies by at least two orders of magnitude during their life time, with associated allometric scaling of physiological rates. Stage- and weight-structured population models are a way to represent realistic growth and development of zooplankton populations, and then their role in the ecosystem dynamics. Steele and Mullin (1977) showed that numbers of individuals rather than biomass is a good description of population dynamics. Recent development of structured representations of population dynamics integrate both biomass and numbers of individuals by taking into account the processes involved in individual growth and by linking bioenergetical processes to demographic processes (Carlotti and Nival 1992). A major difficulty in building realistic models of zooplankton population dynamics is that relatively little data on growth and reproduction have been published. Attempts to couple such models with biomass based ecosystem models have been made (Carlotti and Radach 1996; Heath et al. 1997), but simulations ignore often the spatial dimension. These first attempts at modelling population dynamics demonstrated the difficulty of obtaining adequate data to construct and test complex models of zooplankton and to verify the response to short term spatio-temporal variations in physical forcing.

In parallel to this approach for studying zooplankton dynamics in food webs, some work has been done to study the dynamics of zooplankton species in relation to physical processes at small or meso-scales. Copepod production response to storms has been predicted by some models (Wroblewski and Richman 1987). Structured population models are difficult to incorporate in 3-D resolved models as age and/or size resolved representation of a

particular species requires a high number of variables for simulation. For this reason, few simulations of structured population models have dealt with spatial distribution in time (Davis 1984; Slagstad and Tande 1996; Bryant et al. 1997). Further development will need to simplify structured population models while retaining their essential dynamic properties to an extent that a three dimensionally resolved model becomes feasible.

Another task concerns the representation of the entire zooplankton community: Present models deal with one copepod species as the herbivore in the food chain, i.e. the seasonal succession of species is ignored. It is not possible to simulate the dynamics of all the species or to model the entire zooplankton community as if it were a simple metapopulation. First attempts consider one or two main species explicitly, and the rest of the community as a bulk biomass group (Heath et al. 1997).

Few dynamic models of fish exist, and modelling has mainly served to study growth and survival processes in a given environmental setting. During recent years, spatial distributions of fish have been studied by two methods: life history theory (e.g. Giske and Aksnes 1992) and dynamic optimisation focusing on the behaviour of individuals. Results of these process-oriented models are supposed to deliver simpler expressions in later generations of ecological models (Giske et al. 1997). Complex interactions between zooplankton species and fish larvae have not been modelled, although the role of predation in the control of plankton demography has been suggested (Davis 1984, Steele and Henderson 1995).

A key feature of the population dynamics of higher metazoans (e.g. mesozooplankton, early life stages of fish) is that the survivors at any stage in the life cycle rarely seem to be drawn at random from the initial population. Individual survival probability can often be related to, for example, parental origin, growth rate, or spatial and temporal characteristics. As a result, the average properties of the population over a period of time do not necessarily reflect the average properties of the survivors. The consequences for modelling are that approaches which are formulated in terms of the development of a population of average individuals will fail to capture an important element of the dynamics. One solution is to formulate Individual Based Models (IBM) which incorporate the essential aspects of individual variability in the exposure of animals to the environment and the responses of



individuals to exposure (Heath and Gallego 1997). Strategic IBM modelling, in which the environment is represented as a series of time varying, but spatially homogeneous properties is well established (see review by van Winkle et al. 1993).

Individual-based models (IBM) coupled with spatially resolved physical models have been recently attempted (Hinckley et al. 1996, Werner et al. 1996). These schemes could integrate more complex biology (Carlotti and Hirche 1997; Hinckley et al. 1996). The value of models that incorporate IBM and physical habitat modelling techniques consists in increasing our understanding of the link between spatial and temporal dynamics of zooplankton/fish populations as well as in allowing exploration of potential environmental habitat variations on these populations.

The present particular strengths of research in Europe are:

- (1) the existence of hydrodynamic models (2-D, 3-D) for many of the European seas which form a good basis for developing coupled biological and circulation models within EUROGLOBEC
- (2) the existence of different types of structured and IBM population models.

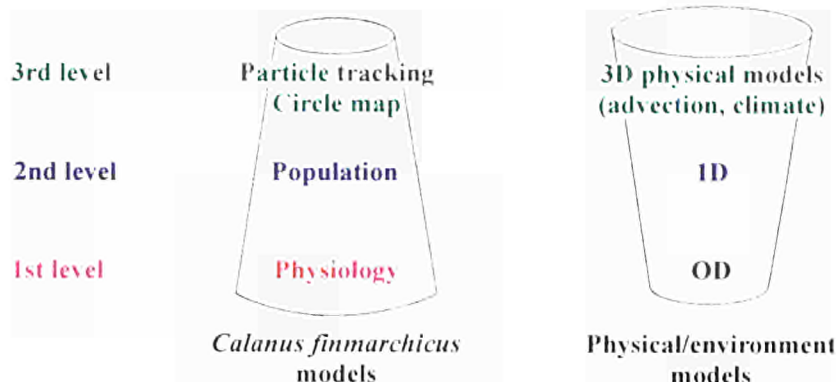
#### 4.3.3 Approach

##### 4.3.3.1 Coupled physical and biological model formulations

To understand the coupling between physical forcing and marine ecosystems, a suite of modelling approaches have to be combined. In many instances, frameworks for the models already exist in various stages of development but the key element is the coupling between models at the relevant scales (see for instance coupling of physical and biological models in the TASC project in Fig. 6).

- *Circulation models*

Circulation models which describe the oceanic response to atmospheric forcing play a key role in interdisciplinary modelling. They provide three-dimensional, time-evolving flow fields which determine the transport of dissolved and particulate matter, as well as the levels of energy (temperature), stratification and turbulent mixing within the water column. Circulation models are needed to address GLOBEC's



**Fig. 6**

*Biological and physical modelling in TASC where the base of the cone represents the highest degree of model complexities (from TASC leaflet edited by K. Tande)*

objective of understanding how the physical environment, and its variability, affect marine ecosystems. Mesoscale currents may control biological processes by aggregation of individuals, by altering their feeding environment, or by affecting the regional dispersal, distribution or retention of populations. Small scale turbulence in the upper mixed layer, driven by atmospheric and thermodynamic forcing, and mixing in the bottom boundary are important processes that affect stratification and vertical fluxes within the water column, as well as predator-prey interactions at the individual level. Circulation models need to resolve biologically and physically relevant spatial and temporal processes, if they are to provide the basis for model-data comparison, evaluation and integration of processes.

Advanced marine ecosystem models must integrate physical, chemical, and biological processes. To foster a close co-operation between theory and observations, the use of community models should be considered. The model results should be made publicly available for use by field and laboratory researchers. Within EUROGLOBEC, the implementation of modular versions of regional or large-scale circulation models would allow to combine most advanced circulation models and chemical-biological models in a clear way.



As a complement to time-dependent prognostic models used in studying temporal variability explicitly, diagnostic models are valuable to GLOBEC objectives related to retrospective studies where model results can help to represent conditions within a particular climate scenario or in the study of mean conditions observed in the past. Diagnostic model studies also provide a baseline against which variability or events can be evaluated.

- *Models of lower trophic levels*

An important precursor to the development of models of zooplankton and fish larval population dynamics is the establishment of robust, operational schemes for simulating the underlying nutrient-phytoplankton dynamics. This should necessarily include a coarse representation of the bulk zooplankton community grazing pressure on the phytoplankton. Various "N-P-Z"-type models (with more than 3 compartments) are capable of providing a reasonable simulation of the spatially resolved seasonal dynamics of the base of the food chain in a variety of physical settings. It will be necessary in EUROGLOBEC to implement and assess the performance of a standard version of one of these systems across the range of regional study areas to provide a background for the development of a variety of higher trophic level models. The basic N-P-Z results should be archived and made widely available as forcing data for more advanced models, and the models themselves should be freely available for operational use, and for dynamic coupling to explicit models of target species.

- *Models of higher trophic levels*

Fundamentally different approaches are required to model higher trophic levels compared to nutrients and phytoplankton. These differences arise from the sophistication of behavioural responses of higher organisms to the environment, and from the wide range (orders of magnitude) of changes in body size of individuals within their life cycle. Both structured population and individual based models may be appropriate under different circumstances. Multi-species models may be constructed from combinations of bulk-biomass representations, structured population models, and Individual Based Models. These may operate on different spatial and temporal scales, presenting particular technical challenges. Evaluating the results of such models will also be carried out on a variety of scales from laboratory cultures and mesocosms to regional scale assessments.

### Structured population models

Structured population models (SPM) are required to simulate seasonal and annual dynamics of successive cohorts of targeted species with multistage development. By coupling them with spatially resolved ecosystem models, they provide an Eulerian approach to the stage distributions of the studied populations. This approach is particularly convenient for studying the trophic links between lower trophic levels and the target species at the mesoscale. In these models, mortality remains a key process of variable population dynamics to be determined. Critical developmental stages (i.e. with high mortality rates or particular behaviour) should be represented as single variables whereas other less critical stages should be aggregated. SPM of zooplankton could also provide the prey field for the IBM of fish larvae.

### Individual based models

The approach is to track individuals through time modelling their growth and survival probability in terms of their exposure to environmental forcing conditions. Major research challenges in the development of spatially explicit IBMs of marine organisms are in relation to the formulation of individual survival probability, and feedback between population density and individual survival. The biological basis for the interaction between predation, internal sources of mortality, and population feedback is only poorly understood for the majority of species. This is one of the main areas of necessary interaction between model development and process orientated biological studies. Individual based modelling is most applicable to modelling the early life history dynamics of ichthyoplankton since there are methods to determine the individual growth histories of animals sampled in the field from otolith microstructure. Thus, it is possible to parameterise and test models in a field setting. Another key area for development is the representation of so-called sub-grid scale processes (predator-prey interactions at scales relevant to individuals, i.e. micrometers-centimetres) at the typical resolution scales of most hydrodynamic models (1-20 kilometres).

#### 4.3.3.2 Applications of models in process-oriented and site-specific situations

- *Process oriented studies*

#### Sub-grid scale analysis

Research on the effects of up- and downscaling could provide important insights. Process-specific model development should be

accompanied by studies on parameterisation of these processes at the larger scales where their effects are emergent. Also, predator-prey interactions involve several sets of small-scale processes. Process models integrating sub-scale processes should be developed.

#### Strategic modelling for the development of functional forms

The study of statistically and physiologically based formulations of processes including their parameterisation needs to be developed before inclusion into structured population models and individual based models. Processes at the level of individuals which relate vital rates of pelagic organisms with physical parameters such as light, turbulence, temperature, advection need further development. Both, laboratory and field measurements, as well as experiments are needed for model development of process studies and for testing. Short-term and mid-term experiments in fluctuating environments should be designed for testing simple process models. Biological processes are usually studied in a steady state environment which is never the case in the natural environment. These experiments should attempt to relate to what occurs in the field. Individual variability in bioenergetic, development and mortality processes as well as behaviour, life history and phenology should be estimated and integrated in population models. Individual behavioural processes (feeding, swimming, prey selectivity, etc.) are important to study and represent in models as they influence the dynamics between zooplankton/fish and their prey. Understanding of behavioural patterns and life history of marine organisms is required to understand how individuals and populations are adapted to environmental variability (as opposed to mean conditions.) Vertical as well as horizontal processes should be investigated by interaction of models.

#### Development of evolutionary models

Theoretical studies are also required to investigate the response of various formulations of processes and in understanding complex non-linear processes. Theoretical studies have a strong place in IBM development. Many important couplings are non-linear and should be explored in detail to improve our understanding in this area. Theoretical work is required to investigate the response of various formulations of marine ecosystem models to broad-band physical forcing. For these objectives, new modelling techniques such as neural network methods, object-oriented design, dynamic modelling, etc. should be developed. Through evolutionary mechanisms, zooplankton are well adapted to their present environmental



conditions and their variations. It will be useful to clarify how the processes of natural selection, flexible behaviour and life strategies may compensate environmental change, and to investigate whether the time scale of global change is sufficient to allow evolutionary modifications to take place. To accommodate such studies, many methods from evolutionary ecology are available. The use of optimal models (life history theory, ideal free distribution, game theory, dynamic programming) and the emerging adaptation models (genetic algorithms, neural networks) will be appropriate. Evolutionary models have the potential to derive biological forcing functions from the concept of fitness, by making assumptions of optimal behaviour under physical and physiological constraints.

- *Site-specific studies*

#### Synthesise the results from observational programmes

The links between observations and modelling will act in two ways. First, numerical models are required for the analysis of observations and for filling gaps in observations. Second, observations are necessary to first deliver correct climatological and physical forcing to test the order of magnitude of model variables, and second to test the interrelationships among models' variables. The analysis of existing data and modelling should be a starting point to allow a better focus for field studies. Consistency between data and model results must be developed by using new procedures for collecting data in the field and assimilating data into dynamical models that are adapted to specific sites.

#### Development of strategies of operational modelling for data assimilation and ship board use

Data assimilation in GLOBEC-type models should enable the stochasticity in processes to be constrained or to give values of non-accessible parameters via experiments. Data assimilation techniques provide a mathematically formal way to incorporate field measurements (physical and/or biological) into model hindcasts and "nowcasts". As such they can keep model solutions from deviating too far from the system's expected response that could occur due to incomplete internal dynamics or incomplete specification of the forcings. Data assimilation techniques can also provide estimates of unknown model parameters in space and time (by requiring the model to stay "on track") and hence can provide (for certain parameters) bounds that are based on dynamical constraints of the models'



formulation. Data assimilation techniques can be useful in retrospective studies where the systems' boundaries and initial conditions are likely to be known only partially. They can also provide a guide to the design and placement of long-term moorings, and to the type of measurements that are most critical to model predictions. Shipboard "real time" modelling techniques are a valuable tool for designing sampling schemes at sea. Experience with these approaches has proven useful (in programmes such as the Canadian OPEN programme) where sampling of larval patches was based on predicted positions over a number of days allowing sampling (for larval growth; feeding environment; etc.) in a Lagrangian sense. This technique is particularly useful (although challenging) when the flow structure in the vertical is not uniform and where drogued drifters may not capture the details of the underlying flow field. Shipboard forecasts are natural components of regional studies. Sampling and observational strategies need to be considered in the initialisation of these models in the field and hence appropriate links to technological capabilities need to be made a priori. These will vary depending on the site being studied.

#### Prediction

Expected results of the new models will improve our understanding on how changes in the global environment will affect the abundance, diversity and production of animal populations, and consequently the dynamics of many fish stocks. The improved representation of the higher trophic levels will yield a much better understanding of the world ocean ecosystem dynamics related to physical variability. The predicted responses of the ecosystem to climate variability can be envisaged on the basis of coupled models which involve the resolution of mesoscale features and the inclusion of advanced biological models. Anticipated scenarios of climate variations, which may be provided by other programmes such as, e.g. CLIVAR, can be used to establish the atmospheric forcing fields as well as the large scale circulation patterns. These fields could be used to drive high resolution regional models in order to predict the response of zooplankton and its prey and predators in relation to mesoscale circulation patterns.

## 5. TECHNOLOGY DEPLOYMENT AND DEVELOPMENT

### 5.1 Rationale

To address the objectives identified in EUROGLOBEC it will be necessary to bring together efficiently and effectively the various observational systems which already exist within the European community. Bringing these capabilities together and co-ordinating their deployment, data collection and data management will advance not only EUROGLOBEC but also make significant contributions to wider international programmes such as International GLOBEC and GOOS (Global Ocean Observing System).

The observational programme will be based primarily on existing proven technology. EUROGLOBEC will not be a major technology development programme. However existing technology will be modified and use will be made of new techniques which are currently being developed within other national and international programmes (including MAST) to ensure that EUROGLOBEC benefits from state of the art technology in addition to well tried techniques. Limited developments to aid understanding and data interpretation will also form part of EUROGLOBEC. These developing technologies and the bringing together of different observational tools will have additional benefits for future programmes. The European community will be better placed, for example, to recommend appropriate sensor packages and measuring strategies for future GOOS programmes, including the establishment of core measurements to ensure international comparability.

The observational programme must be managed and co-ordinated to maximise use of resources. This will require appropriate infrastructure both nationally and centrally within the European community. It is likely that observational systems will be deployed in a variety of European waters. To ensure comparability of data, a core series of essential measurements will be established, and the collection, quality control and management of the resultant data will be co-ordinated. EUROGLOBEC will also promote the sharing of complex on-off observational techniques and platforms to maximise their usefulness to the European community. It will similarly encourage non-European scientists to collaborate - again to enhance the total programme.

## 5.2 Background

The scientific problems inherent in understanding ecosystem dynamics, and the observational strategies to meet these, have been discussed and well documented in recent years (e.g. Dickey 1991, GLOBEC 1993, IGBP 1997). The various developing national and international GLOBEC programmes have considered these issues both generally and specifically in terms of technology requirements (e.g. GLOBEC 1993, US GLOBEC 1991, 1993). Similar reports are available for other developing programmes, e.g. GOOS and EuroGOOS (SCOR in prep, Woods et al 1996). The implementation strategy for EUROGLOBEC builds upon this previous experience and tunes these strategies to particular European needs.

## 5.3 Approach

EUROGLOBEC will co-ordinate the deployment of technologies and the development and use of new technologies. It will co-ordinate and manage the resultant data and rigorously control the quality of the

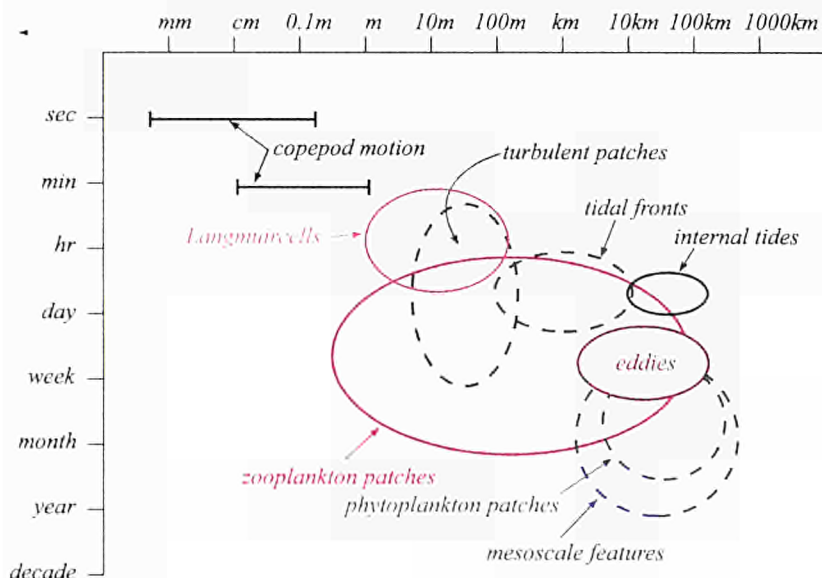


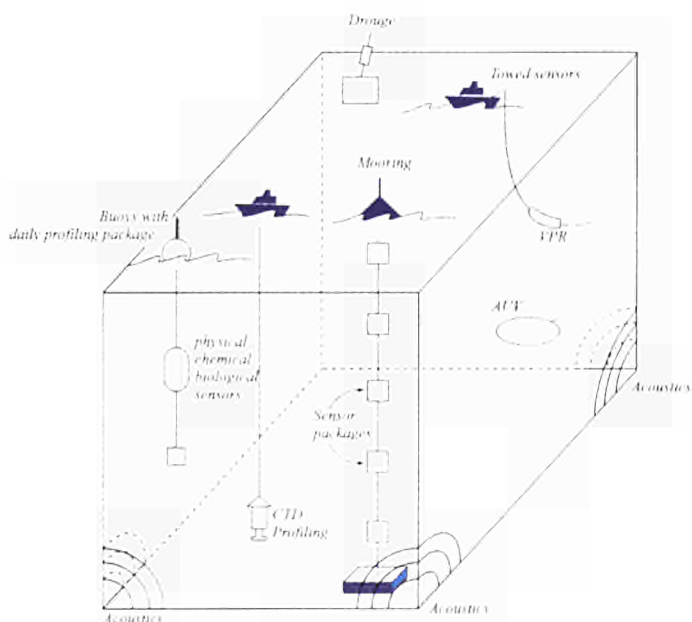
Fig. 7

Schematic presentation of the temporal and horizontal spatial ranges of physical and biological oceanographic variables in ocean margins (produced after an idea of Dickey 1991).

data - especially that from the core measurements. These data will be important to EUROGLOBEC, but also to concurrent global programmes and to the future development of such programmes. The precise strategy and the technology to be deployed will depend upon the particular scientific questions being asked, and the areas in which these can best be addressed. It is likely that the strategy will include the following elements.

### 5.3.1 Time and space scales

The range of problems identified by EUROGLOBEC cover a very wide spectrum of time and space scales - from molecular processes on one hand to global/basin scales on the other (Dickey 1991) (Fig. 7). To



**Fig. 8**

*Presentation of various types of oceanographic instrumentation to quantify physical and biological variables over short and long temporal, and small and large spatial ranges (after an idea of Dickey 1991). Abbreviations AUV - Autonomous Underwater Vehicle, VPR - Video Plankton Recorder, CTD - Conductivity Temperature Density Profiler. The acoustics instrumentation are upward-oriented ADCP - Acoustic Doppler Current Profiler to be used for quantification of (a) current velocity and direction, and (b) vertical distribution of zooplankton abundance.*



address these wide-ranging problems technology will be needed to observe appropriate scales; and to maximise both scientific utility and cost effectiveness multidisciplinary and multisensor arrays and platforms will be used wherever possible and appropriate. Nested sensor arrays ranging from satellites to microscale observations will be deployed (Fig. 8).

### *5.3.2 Coupled observations and modelling*

Observations must be focused on the scientific questions and must be closely coupled to modelling in an iterative way. Models will be used to direct observations efficiently and the resultant data will be used to retune and improve the models. Coupled observational modelling strategies of this kind have been well developed in the International GLOBEC programme (GLOBEC 1997), and this experience will be used to determine appropriate strategies for EUROGLOBEC.

### *5.3.3 Quality control*

Quality control of both measuring systems and the resultant data is extremely important. Particular attention will be paid to ensuring the stability of long term sensor packages, and EUROGLOBEC will draw on the experience gained in other programmes.

### *5.3.4 European strengths*

There are considerable European strengths in the various technologies required for EUROGLOBEC. It is convenient to outline these according to the scale of the observation.

- *Satellite remote sensing*

Remote sensing from satellites or aircraft will provide large scale observations putting more focused observations in context. They will also provide specific data for particular processes, e.g. colour sensors for primary productivity, AVHRR and SAR imagery for information on environmental parameters and features such as fronts and eddies. EUROGLOBEC will use ESA (European Space Agency) and CEOS (Committee on Earth Observation Satellites) to ensure that maximum use is made of such data (CEOS 1995)

- *Research vessels*

The European fleet of research ships is a tremendous asset, being both large and varied. These ships provide the capability to validate remotely sensed parameters, to deploy observational arrays and to carry out specific sampling. Formal arrangements already exist to facilitate ship sharing between the UK, France and Germany, and the current MAST programme has greatly enhanced the communal usage of ships from various countries. Greater use should be made of research ships on passage as ships of opportunity, through the regional seas or ocean basins. An example is the RRS James Clarke Ross used in the Atlantic Meridional Transect project

- *Ships of opportunity*

Similarly there is great experience within Europe of using ships of opportunity. These include weather stations, ferries and commercial ships. Their use is extremely valuable for obtaining observations at times and places not available to research ships, and they are essential for the continuation and establishment of long term observational and monitoring programmes such as the Continuous Plankton Recorder in the NE Atlantic and North Sea (Warner and Hays 1994), and the Algaline Project in the Baltic Sea (Leppänen et al. 1994, 1995) - which again will link to future GOOS programmes. The Undulating Oceanographic Recorder (UOR) (Aiken 1985) was developed in Europe as a ship-of-opportunity survey system which can carry a large sensor payload.

- *Autonomous underwater vehicles*

Future cost effective use of ships will be significantly enhanced by the concurrent use of autonomous underwater vehicles. These will be able to carry out routine physical, chemical and biological measurements - freeing up expensive ship time to carry out sampling which cannot yet be done autonomously. AUVs will also have a critical role in defining the boundary conditions of sampling areas within which more detailed observations take place. Europe is particularly well placed to take advantage of this new technology - the UK's AUTOSUB vehicle has been successfully tested and has already carried out inshore science missions (Millard et al. 1997, in press).

- *Towed sensor platforms*

Europe is also particularly strong in the development and availability of towed multidisciplinary, multisensor arrays and platforms. These provide detailed synoptic surveys over wide areas. Undulating towed

vehicles, e.g. the UOR (Aiken et al. 1995), are available which carry a range of physical, chemical and biological sensors and which collect data over time and space scales ranging from seconds to weeks, and metres to hundreds of kilometres (SAHFOS 1996, Allen et al. 1994).

- *Moored floating platforms*

Within the areas surveyed by AUVs and towed sensors, multisensor moorings and buoys will be deployed. These provide long term data sets at very fine vertical resolution on, for example, current vectors, hydrography, nutrient and chemical parameters, primary productivity and zooplankton size and numbers. Again there are a number of such sensor buoys already within Europe, some of which are linked together via communication networks, e.g. the BSH German Fixed Monitoring Network.

- *Biological quantification*

In addition to these strengths in deployment strategies and multisensor platforms, there is particular expertise in other technologies appropriate to EUROGLOBEC. For example, there are well developed net and pump systems for sampling small fish, zooplankton and phytoplankton (Williams et al. 1983, Dunn et al. 1993). These systems are themselves instrumented so that they not only sample the biota but also place these within their environmental context. Remote sensing within the sea using acoustic and optical techniques is also a strength. Such remote sensing provides a range of quantitative and qualitative data in real time without the problems of net avoidance. It also allows targeting of conventional sampling and collection of data from inhospitable areas such as continental slopes where the risk of losing conventional trawls is very high (e.g. Roe et al. 1996, Foote 1993).

### *5.3.5 Technology development*

These existing strengths will be complemented and enhanced by new technologies which are being developed within Europe. Self-profiling multisensor moorings; coupling shear turbulence probes with fast repetition rate fluorometers; multifrequency and broad band acoustic sensors; coupled acoustic/ optical sensors are all being developed (e.g. European Commission 1996) and will be available within the lifetime of EUROGLOBEC. Incorporation of these new technologies will be accompanied by the development of robust, autonomous sensor packages capable of providing data over long periods with

minimal human intervention. Some sensor development will be needed to enhance the interpretation of some of the measurements. For example, quantification of ichthyoplankton and zooplankton by acoustics and optics requires knowledge of the physical properties of the animals. This knowledge is generally lacking and may require specific developments in micro-instrumentation. In addition the influence of the act of observation on animal behaviour must be quantified.

EUROGLOBEC will co-ordinate the deployment of technologies and the development and use of new technologies. It will co-ordinate and manage the resultant data and rigorously control the quality of the data - especially that from the core measurements. These data will be important to EUROGLOBEC, but also to concurrent global programmes and to the future development of such programmes.



## 6. DATA MANAGEMENT

Data will be collected in a range of areas and disciplines during the GLOBEC programme. The availability, standardisation, integration and archiving of data will be essential to the success of the programme and will be given a high level of importance at all stages from the initial design onward.

Since one of the foci of the Science Programme for GLOBEC is retrospective studies, accessing and rescuing historic data is a high priority. Within the relatively short time frame proposed for EUROGLOBEC, these historic data sets and other reconstructions of past physical and biological changes provide the only means of identifying long term trends in ecosystem structure and functioning and relating these to global change.

Many historic records are only available from national sources and there are often technical or financial restrictions on access which will need to be overcome. A number of regional data centres, such as EDMED and ICES should be actively involved in assisting with both historic and current aspects of data management, but there are likely to be special problems in dealing with biological data as the data structures for handling these are not yet well developed. This is a major area in which a EUROGLOBEC programme can carry out valuable work which should extend beyond the time frame of the programme.

There should be a EUROGLOBEC data management facility whose tasks would include developing and implementing data communication codes and formats; receiving storing and distributing data among participants; maintaining quality control and meta data; developing and disseminating tools for accessing, comparing and integrating information throughout the programme, including the use of models, making data available from remote sensing, meteorological data sets and ocean climate models.

The data management facility should work closely with existing international data management systems and collaborate with them where possible. Participants in EUROGLOBEC should network by electronic means as far as possible and should use electronic access to data and information tools.

## 7. LINKAGES TO OTHER PROGRAMMES

There are a large number of potential linkages with other international, national, regional and individual programmes. The most obvious are with the other marine programmes in the IGBP; both JGOFS (Joint Global Ocean Flux Study) and LOICZ (Land-Ocean Interactions in the Coastal Zone) have research programmes closely related to GLOBEC.

GLOBEC already co-ordinates activities with JGOFS. GLOBEC's emphasis on zooplankton population dynamics complements the JGOFS primary focus, which is on primary production, carbon flux and the oceanic carbon budget. Both process and ecosystem approaches are necessary to formulate a complete picture of ocean ecosystem functioning. GLOBEC and JGOFS are both interested in the relationships between primary production and zooplankton but JGOFS investigates interactions of carbon and other important biogenic matter in the ocean whereas GLOBEC is concerned with the effects of climate change on upper trophic levels via changes in ocean circulation and mixing at different scales. GLOBEC will make use of new JGOFS results on the influence of physical conditions on lower trophic level carbon cycling.

GLOBEC and LOICZ plan to co-ordinate their activities, since both will benefit considerably from formal ties. LOICZ is not designed to study coastal pelagic ecosystem structure, or the impact of the changes on resources such as fish stocks. GLOBEC will thus complement, not overlap with LOICZ.

Future oceanographic ecosystem studies now in the planning stages would benefit from co-ordination and integration with GLOBEC, as well as with JGOFS and LOICZ. For example, SOLAS may focus upon fluxes between the atmosphere and the ocean and continue the development of upper ocean models suitable for incorporation in a new, advanced generation of coupled ocean-atmosphere models. GLOBEC, with its emphasis on physical-biological interactions and interdisciplinary models will be a significant source of input for future projects.

Links to the WCRP (World Climate Research Programme), and especially to oceanographic projects such as WOCE (World Ocean Circulation Experiment) and CLIVAR, will contribute significantly to the

GLOBEC perspective. The atmospheric and ocean data sets on climate variability produced by CLIVAR will provide input to retrospective studies on physical forcing for marine ecosystems. CLIVAR will also result in a better understanding of ocean processes to link with marine ecosystems and modelling to assess predictability of the physical forcing for marine ecosystems. Studies carried out by CLIVAR will help assess anthropogenic versus natural variability for the physical climate, which forces the marine ecosystem. In the context of EUROCLIVAR it is expected that an emphasis on European/Atlantic variability and the North Atlantic Oscillation (NAO) will provide a strong link with GLOBEC research.

GLOBEC will also contribute to the design of the planned Global Ocean Observing System (GOOS) by providing information on critical parameters to be measured and on time and space scales that are best suited for predictive capabilities in such a system. GLOBEC is also concerned with continuing development of technology suitable for continuous sampling of biological and chemical parameters in the ocean, and these are critical to the development of GOOS, especially its module on Living Marine Resources, which specifically recognises the significance of GLOBEC in its planning documents (GOOS-LMR Report, 1997).

Strong linkage with remote sensing agencies such as ESA and NASA will be necessary.

The International Council for the Exploration of the Sea (ICES) is co-ordinating the GLOBEC Cod and Climate Change Programme (CCC), the major Regional Programme in the North Atlantic. ICES has a Regional Co-ordination Office for this programme.

The research proposed would utilise and extend the expertise developed by European scientists within a number of recent and ongoing projects supported by the EU and other European science funding agencies. These projects include, ELOISE, ERSEM, ICOS (MAST II), TASC (MAST III), BASYS (Baltic Sea System Study), SEFOS (AIR), Gadoid Recruitment Project (FAIR), CORE (Baltic Sea Recruitment Project, AIR), MARENOR/MARECOGNITUM (Norwegian Nordic Seas Projects), OMEX, OMEGA and the Baltic, MATER and CANIGO, Regional Seas projects (Table 1).



## 8. REFERENCES

- Aebischer, N.J., J.C. Coulson and J.M. Colebrook. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347: 753-755.
- Aiken, J. 1985. The Undulating Oceanographic Recorder Mark 2, a multirole oceanographic sampler for mapping and modelling the biophysical marine environment. *In: Mapping Strategies in Chemical Oceanography*. Ed. by A. Zirino. American Chemical Society, 209: 315-332.
- Aksnes, D. and A.C.W. Utne. 1997. A revised model of visual range in fish. *Sarsia* 82: 137-147.
- Alheit, J. and E. Hagen. 1997. Long-term climate forcing of European herring and sardine populations. *Fish. Oceanogr.* 6 : 130-139.
- Allen, J.T., D.A. Smeed and A.C. Chadwick. 1994. Eddies and mixing at the Iceland-Faeroes Front. *Deep-Sea Res.* 41: 51-79.
- Anon. 1996a. Report of the ICES/GLOBEC Cod and Climate Database Workshop. ICES CM 1996/A:7.
- Anon. 1996b. Report of the Cod and Climate Backward-Facing Workshop. ICES CM 1996/A:9
- Anon. 1997. Statement of conclusions of the Intermediate Ministerial Meeting on the Integration of Fisheries and Environmental Issues 13-14 March 1997, Bergen, Norway. Fifth Intl. Conf. on the Protection of the North Sea. 13 pp.
- Astthorson, O.S., R.J.H. Beverton, B. Bjornsson, N. Daan, K.T. Frank, J. Meincke, B. Rothschild, S. Sundby and S. Tilseth. 1993. Cod and Climate Change. ICES Marine Science Symposia 198: 693 pp.
- Backhaus, J.O., I.H. Harms, M. Krause and M.R. Heath. 1994. An hypothesis concerning the space-time succession of *Calanus finmarchicus* in the northern North Sea. *ICES J. mar. Sci.* 51: 169-180.
- Bakun, A. and R.H. Parrish. 1990. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*). *J. Cons. int. Explor. Mer* 46: 269-283.
- Bakun, A. 1996. Patterns in the Ocean – Ocean Processes and Marine Population Dynamics. California Sea Grant College System, 323 pp.
- Ban, S., C. Burns, J. Castel, Y. Chaudron, E. Christou, R. Escribano, S.F. Umani, S. Garsparini, F.G. Ruiz, M. Hoffmeyer, A. Ianora, H.K. Kang, M. Laabir, A. Laxcoste, A. Miralto, X. Ning, S. Poulet, V. Rodriguez, J. Runge, J. Shi, M. Starr, S. Uye and Y. Wang. 1997. The paradox of diatom-copepod interactions. *Mar. Ecol. Prog. Ser.* 157: 287-293.



- Baretta J.W., W. Ebenhöf and P. Ruardij. 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model. *Neth. J. Sea Res.* 33, 233-379.
- Beamish, R.J. (ed.) 1995. Climate Change and Northern Fish Populations. *Can. Spec. Publ. Fish. Aquat. Sci.* 121, 739 pp.
- Binet, D. 1988. French sardine and herring fisheries: a tentative description of their fluctuations since the eighteenth century. *In: Long Term Changes in Marine Fish Populations. Proc. Int. Symp., Vigo, Spain, 18-21 November 1986. Ed. by T. Wyatt and M.G. Larraneta. Imprenta Real, Bayona, pp. 345-364.*
- Borja, A., A. Uriarte, V. Valencia, L. Motos and A. Uriarte. 1996. Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in Bay of Biscay. *Scientia Marina* 60 (Suppl. 2): 179-192.
- Bretherton, C.S., C. Smith and J.M. Wallace. 1992. An intercomparison of methods for finding coupled patterns in climate data. *J. Climate* 5: 541-560.
- Buch, E. 1995. A Monograph on the Physical Oceanography of the Greenland Waters. Royal Dan. Admin. of Nav. and Hydrog., Copenhagen, 405 pp.
- Buch, E. and H.H. Hansen. 1988. Climate and cod fishery at West Greenland. *In: Long Term Changes in Marine Fish Populations. Proc. Int. Symp., Vigo, Spain, 18-21 November 1986. Ed. by T. Wyatt and M.G. Larraneta. Bayona, pp. 345-364.*
- Bryant A., M. Heath, W. Gurney, D.J. Beare and W. Robertson. 1997. The seasonal dynamics of *Calanus finmarchicus*: development of a three-dimensional structured population model and application to the northern North Sea. *Neth. J. Sea Res.* (in press).
- Caan, N., K. Richardson and J. Pope. 1996. Changes in the North Sea ecosystem and their causes: Aarhus 1975 revisited. *ICES J. Mar. Sci.* 53: 879-883.
- Carlotti F. and P. Nival. 1992. Model of growth and development of copepods: study of moulting and mortality related to physiological processes during the course of individual moult cycle. *Mar. Ecol. Prog. Ser.* 84: 219-233.
- Carlotti F. and G. Radach. 1996. Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled one-dimensional model. *Limnol. Oceanogr.* 41: 522-539.
- Carlotti F. and H.J. Hirche. 1997. Growth and egg production of female *Calanus finmarchicus*: an individual-based physiological model and experimental validation. *Mar. Ecol. Prog. Ser.* 149: 91-104.

- Cayan, D.R. 1992a. Variability of latent and sensible heat fluxes estimated using bulk formulae. *Atmos.-Ocean* 30: 1-42.
- Cayan, D.R., 1992b. Latent and sensible heat flux anomalies over the northern oceans: the connection to monthly atmospheric circulations. *J. Climate* 5, 354-369.
- CEOS 1995. Coordination for the next decade. 1995 CEOS Yearbook. European Space Agency. 133pp.
- CLIVAR. Implementation Plan (Ms.)
- Coombs, S., O. Giovanardi, D. Conway, L.S. Manzueto, N. Halliday and C. Barrett. 1997. The distribution of eggs larvae of anchovy (*Engraulis encrasicolus*) in relation to hydrography and food availability in the outflow of the river Po. *Acta. Adriat.* 38(1): 33-47.
- Cowles, T.J., R.J. Olson and S.W. Chisholm. 1988. Food selection by copepods: discrimination on the basis of food quality. *Mar. Biol.* 100: 41-49.
- Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* 46: 670-680.
- Cushing, D.H. 1982. *Climate and Fisheries*. London: Academic Press, 363 pp.
- Davis, C.S. 1984. Predatory control of copepod seasonal cycles on Georges Bank. *Mar. Biol.* 82: 31-40.
- Dickey, T. 1991. The emergence of concurrent high-resolution physical and bio-optical measurements in the upper ocean. *Rev. of Geophysics* 29: 383-413.
- Dickson, R.R., P.M. Kelly, J.M. Colebrook, W.S. Wooster and D.H. Cushing. 1988. North winds and production in the eastern North Atlantic. *J. Plankton Res.* 10: 151-169.
- Dickson, R.R., P. Maelkki, G. Radach, R. Saetre and M.P. Sissenwine. 1992. Hydrobiological Variability in the ICES Area, 1980-1989. *ICES Marine Science Symposia* 195, 514 pp.
- Dickson, R.R., J. Lazier, J. Meincke, P. Rhines and J. Swift. 1996. Long-term co-ordinated changes in the convective activity of the North Atlantic. *Prog. Oceanog.* 38: 241-295.
- Dower, J.F., T.J. Miller and W.C. Leggett. 1997. The role of microscale turbulence in the feeding ecology of larval fish. *Adv. Mar. Biol.* 31: 169-220.
- Dunn, J., C.D. Hall, M.R. Heath, R.B. Mitchell and B.J. Ritchie. 1993. ARIES - a system for concurrent physical, biological and chemical sampling at sea. *Deep-Sea Res.* 40: 867-878.
- European Commission 1996. Marine science and technology (MAST III) 1994-98. Catalogue of contracts - July 1995. Ed. by M.

- Weydert. Luxembourg: Office for Official Publications of the European Communities. 1996-XXIV, 101pp.
- Evans G.T. and J.S. Parslow. 1985. A model of annual plankton cycles. *Biol. Oceanogr.* 3: 327-347.
- Fang, Z. and J.M. Wallace. 1994. Arctic sea-ice variability on a time-scale of weeks and its relation to atmospheric forcing. *J. Clim.* 7: 1897-1914.
- Fasham, M.J.R., H.W. Ducklow and S.M. McKelvie. 1990. A nitrogen based model of plankton dynamics in the ocean mixed layer. *J. Mar. Res.* 48: 591-639.
- Fennel W. and T. Neumann. 1997. The mesoscale variability of nutrients and plankton as seen in coupled models. *Deutsche Hydrographische Zeitschrift* 48: 49-71.
- Fessenden, L., and T.J. Cowles. 1994. Copepod predation on phagotrophic ciliates in Oregon coastal waters. *Mar. Ecol. Prog. Ser.* 107: 103-111.
- Fevolden, S and G.H. Pogson. 1997. Genetic divergence at the synaptophysin ((Zyp(1) locus among Norwegian coastal and North East Arctic population of Atlantic cod. *J. Fish. Biol.* 51: 895-908.
- Fiksen, O., J. Giske and D. Slagstad. 1995. A spatially explicit fitness-based model of capelin migrations in the Barents Sea. *Fish. Oceanogr.* 4: 193-208.
- Fomentin, J.-M. and B. Planque. 1996. Calanus and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Progr. Ser.* 134: 111-118.
- Foote, K.G. 1993. Application of acoustics in fisheries, with particular reference to signal processing. In: *Acoustic Signal Processing for Ocean Exploration*. Proceedings of the NATO Advanced Study Institute. Ed. by J.M.F. Moura and I.M.G. Lourtie. D. Reidel, Dordrecht, Holland, pp 371-390.
- Franks, P.J.S. 1997. New models for the exploration of biological processes at fronts. *ICES J. Mar. Sci.* 54: 161-167.
- Gallego, A., M.R. Heath, E. McKenzie, and L.H. Cargill. 1996. Environmentally induced short term variability in the growth rates of larval herring. *Mar. Ecol. Prog. Ser.* 137: 11-23.
- Giske, J. and D.L. Aksnes. 1992. Ontogeny, season and trade-offs: vertical distribution of the meso-pelagic fish *Maurolicus muelleri*. *Sarsia* 77: 253-261.
- Giske J., H.R. Skjoldal and D. Slagstad. 1997. Ecological modelling for fisheries. In: *Multispecies Management*. Ed. by T. Rodseth. Springer Verlag (in press)



- GLOBEC 1993. Report of the first meeting of the International GLOBEC working group on sampling and observational systems. Paris, France, March 30 - April 2, 1993. GLOBEC Report No. 3, 99 pp.
- GLOBEC 1997. An Advanced Modelling/observation System (AMOS) for Physical-biological-chemical Ecosystem Research and Monitoring (Concepts and Methodology). GLOBEC Special Contribution No. 2, 155 pp.
- Greve, W. 1981. Invertebrate predator control in a coastal marine ecosystem: the significance of *Beroe gracilis* (Ctenophora). Kieler Meeresforsch., Sonderh. 5: 211-217.
- Griffies, S.M., and K. Bryan. 1997. Predictability of North Atlantic multidecadal climate variability. Science 275: 181-184.
- Hansson, S., U. Larsson & S. Johansson. 1990. Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. J. Plankton Res. 12: 1099-1116.
- Hays, G.C. 1995. Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*. Limnol. Oceanogr. 40: 1461-1465.
- Heath M., W. Robertson, J. Mardaljevic and W. Gurney. 1997. Modelling the population dynamics of *Calanus* in the Fair Isle current off northern Scotland. Neth. J. Sea Res. (in press)
- Heath, M.R. and A. Gallego. 1997. From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. J. Fish Biol. 51 (Suppl. A). (in press)
- Hinckley, S., A.J. Hermann and B.A. Megrey. 1996. Development of a spatially explicit, individual-based model of marine fish early life history. Mar. Ecol. Prog. Ser. 139: 47-68.
- Horne, E.P.W., J.W. Loder, C.E. Naimie, and N.S. Oakey. 1996. Turbulence dissipation rates and nitrate supply in the upper water column on Georges Bank. Deep Sea Res. II, 43: 1683-1712.
- Hunter, J.R. and J. Alheit (eds). 1995. International GLOBEC Small Pelagic Fishes and Climate Change program. Report of the First Planning Meeting. La Paz, Mexico. June 20-24, 1994. GLOBEC Report No. 8. 72 pp.
- Hunter, J.R. and J. Alheit (eds.). 1997. Small pelagic Fishes and Climate Change Program – Implementation Plan. GLOBEC Report No. 11. 36 pp.
- Huntley, M. 1988. Feeding biology of *Calanus*: a new perspective. Hydrobiologia 167/168: 83-99.
- Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269: 676-679.



- IGBP 1997. Global Ocean Ecosystems Dynamics Science Plan. IGBP Report 40, 83pp.
- Jackson, G.A. 1990. A model of the formation of marine algal flocs by physical coagulation processes. *Deep Sea Res.* 37: 1197-1211.
- Kiorboe, T. 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Adv. Mar. Biol.* 29: 1-72.
- Kiorboe, T., P. Munk, K. Richardson, V. Christensen and H. Paulsen. 1988. Plankton dynamics and larval herring growth, drift and survival in a frontal area. *Mar. Ecol. Prog. Ser.* 44: 205-219.
- Kleppel, G.S. 1992. Environmental regulation of feeding and egg production by *Acartia tonsa* off California. *Mar. Biol.* 112: 57-65.
- Laabir, M., S.A. Poulet and A. Ianora. 1995. Measuring production and viability of eggs in *Calanus helgolandicus*. *J. Plankton Res.* 17: 1125-1142.
- Lamb, H.H. 1972. *Climate: Past, Present and Future. I. Fundamentals and climate now.* London: Methuen, 613 pp.
- Lamb, H.H. 1977. *Climate: Past, Present and Future. II. Climate history and the future.* London: Methuen, 835 pp.
- Lamb, H.H. 1982. *Climate History and the Modern World.* London: Methuen, 387 pp.
- Lamb, P. and R.A. Peppler. 1987. North Atlantic Oscillation: Concept and Application. *Bull. Am. Meteor. Soc.* 68: 1218-1225.
- Landry, M.R. 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. *Int. Rev. Ges. Hydrobiol. Hydrogr.* 63: 77-120.
- Lasker, R. 1975. Field criteria for the survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *U.S. Fish Bull.* 73: 453-462.
- LeFevre, J. 1986. Aspects of the biology of frontal systems. *Adv. Mar. Biol.* 23: 163-299.
- Leppänen, J.-M., E. Rantajärvi, M. Maunumaa, M. Larinmaa and J. Pajala. 1994. Unattended algal monitoring system - a high resolution method for detection of phytoplankton blooms in the Baltic Sea. - In: *Oceans 94 : proceedings.* - IEEE, New York 1: 461-463.
- MacKenzie, B.R., T.J. Iller, S. Cyr, and W.C. Leggett. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnol. Oceanogr.* 39: 1790-1799.
- MacKenzie, B.R., and T. Kiorboe. 1995. Encounter rates and swimming behaviour of pause-travel and cruise of larval fish

- predators in calm and turbulent laboratory environments. *Limnol. Oceanogr.* 40: 1278-1289.
- Marine Zooplankton Colloquium*. 1989. Future marine zooplankton research - a perspective. *Mar. Ecol. Prog. Ser.* 55: 197-206.
- Marsh, R.* 1997. Cooling in the Northwest Atlantic due to Labrador Current strengthening at minima of the North Atlantic Oscillation. *J. Clim.* (in press)
- Matthäus, W. and H. Franck.* 1992. Characteristics of major Baltic inflows - a statistical analysis. *Cont. Shelf. Res.* 12: 1375-1400.
- Millard, N., S. McPhail, M. Peabody, J. Perrett, P. Stevenson, and A. Webb.* 1997. AUTOSUB-1. From test-tank to autonomy and the science beyond. Seventh International Conference in Electronic Engineering in Oceanography - technology transfer from research to industry. Southampton 23-25 June 1997. IEE London. ISBN 0 85296 689.
- Millard, N.W., G. Griffiths and G. Finnegan.* A versatile autonomous submersible - the engineering challenges of realising and testing a practical vehicle. *Underwater Technology.* (in press).
- Miller, C.B. T.J. Cowles, P.H. Wiebe, N.J. Copley and H. Grigg.* 1991. Phenology in *Calanus finmarchicus*; Hypothesis about control mechanisms. *Mar. Ecol. Progr. Ser.* 72: 79-91.
- Mills, E.L., J.L. Forney and K.J. Wagner.* 1987. Fish predation and its cascading effect on the Oneida Lake food chain. *In: Predation: Direct and indirect impacts on aquatic communities.* Ed. by W.C. Kerfoot and A. Sih, pp. 118-131. Univ. Press of New England, Hanover, New Hampshire.
- Munk, P., P.-O. Larsson, D. Danielsen and E. Moksness.* 1995. Larval and small juvenile *cod Gadus morhua* concentrated in the highly productive areas of a shelf break front. *Mar. Ecol. Prog. Ser.* 125: 21-30.
- Murphy, E.J., J. Field, B. Kagan, C. Lin, V. Ryabchenko, J. Sarmiento and J. Steele.* 1993. Global extrapolation. *In: Towards a model of ocean biogeochemical processes.* Ed. by G.T. Evans and M.J.R. Fasham. NATO ASI series. Vol. 10, Springer Verlag.
- Myers, R.A., J. Helbig, and D. Holland.* 1989. Seasonal and interannual variability of the Labrador Current and West Greenland Current. *ICES CM* 1989/C:16, 18 pp (mimeo).
- Mysak, L.A., R.G. Ingram, J. Wang, and A. van der Baaren.* 1996. The anomalous sea-ice extent in Hudson Bay, Baffin Bay and the Labrador Sea during three simultaneous NAO and ENSO episodes. *Atmos-Ocean* 34(2): 313-343.

- Nielsen, T.G. and T. Kiorboe. 1991. Effects of a storm event on the structure of the pelagic food web with special emphasis on planktonic ciliates. *J. Plankton Res.* 13: 35-51.
- Ohman, M.D. and J.A. Runge. 1994. Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. *Limnol. Oceanogr.* 39: 21-36.
- Ohman, M.D. and Wood, S.N. 1995. The inevitability of mortality. *ICES J. mar. Sci.* 52: 517-522.
- Paffenhöfer, G.-A. 1984. Food ingestion by the marine planktonic copepod *Paracalanus* in relation to abundance and size distribution of food. *Mar. Biol.* 80: 323-333.
- Paffenhöfer, G.-A. and Lewis, K.D. 1990. Perceptive performance and feeding behaviour of calanoid copepods. *J. Plankton Res.* 12: 933-946.
- Peterson, W.T., P. Tiselius and T. Kiorboe. 1991. Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. *J. Plankton Res.* 13: 131-154.
- Pettitt, A.N., 1979. A non-parametric approach in the change-point problem. *Appl. Statist.* 28, 2: 126-135.
- Preisendorfer, R.W. 1988. Principal component analysis in meteorology and oceanography. Elsevier, 425 pp.
- Purcell, J.E. 1992. Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. *Mar. Ecol. Prog. Ser.* 87: 65-76.
- Reid, P.C. and T.D. Budd. 1979. Plankton and environment in the North Sea within the period 1948-1977. *ICES C.M.* 1979/L:26.
- Reverdin, G., D.R. Cayan and Y. Kushnir. 1997. Decadal variability of hydrography in the upper northern North Atlantic in 1948-1990. *J. Geophys. Res.* 102: 8505-8531.
- Roe, H.S.J., G., Griffiths, M. Hartman and N. Crisp. 1996. Variability in biological distributions and hydrography from concurrent Acoustic Doppler Current Profiler and SeaSoar surveys, *ICES J. mar. Sci.* 53: 131-138.
- Ross A.H., W.S.C. Gurney, M.R. Heath, S.J. Hay and E.W. Henderson. 1993. A strategic simulation model of a fjord ecosystem. *Limnol. Oceanogr.* 38: 128-153.
- Rothschild, B.J. and T.R. Osborn. 1988. Small-scale turbulence and plankton contact rates. *J. Plankton Res.* 10: 465-474.
- Roy, C., P. Cury and S. Kifani. 1992. Pelagic fish recruitment success and reproductive strategy in upwelling areas: environmental compromises. *S. Afr. J. mar. Sci.* 12: 135-164.



- Rudstam, L.G., G. Aneer and M. Hilden. 1994. Top-down control in the pelagic Baltic ecosystem. *Dana* 10: 105-129.
- Russell, F.S., A.J. Southward, G.T. Boalch and E.I. Butler. 1971. Changes in biological conditions in the English Channel off Plymouth during the last half-century. *Nature* 234: 468-470.
- Sabates, A. and M. Maso. 1990. Effect of a shelf-slope front on the spatial distribution of mesopelagic fish larvae in the western Mediterranean. *Deep Sea Res.* 7A: 1085-1098.
- SAHFOS 1996. Sir Alister Hardy Foundation for Ocean Science. Annual Report 1996. 39pp.
- Saiz, E. and T. Kjørboe. 1995. Predatory and suspension feeding of the copepod *Acartia tonsa* in turbulent environments. *Mar. Ecol. Prog. Ser.* 122: 147-158.
- Schneider, G. and G. Behrends. 1994. Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. *ICES J. mar. Sci.* 51: 359-367.
- SCOR (in prep.) Report of the GOOS LMR Planning Workshop, University of Massachusetts, Dartmouth, March, 1-5 1996. (in prep.)
- Simpson, J.H., W.R. Crawford, T.P. Rippeth, A.R. Campbell, and J.V.S. Cheok. 1996. The vertical structure of turbulent dissipation in shelf seas. *J. Phys. Oceanogr.* 26: 1579-1590.
- Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Washington Sea Grant Program, University of Washington Press, Seattle, 252 pp.
- Sissenwine, M. 1997. Watching history being made: a personal view of the 1996 ICES Annual Science Conference. *ICES Newsletter*, Issue no. 29, 16 pp.
- Skjoldal, H.R., T.T. Noji, J. Giske, J.H. Fossa, J. Blindheim and S. Sundby. 1993. Mare Cognitum Science Plan for research on Marine Ecology of the Nordic Seas (Greenland, Norwegian, Iceland Seas). Institute of Marine Research, Bergen, Norway, 162 pp.
- Slagstad D. and K. Tande. 1996. The importance of seasonal vertical migration in across shelf transport of *Calanus finmarchicus*. *Ophelia* 44: 189-205.
- Sneyers, R. 1975. Sur l'analyse statistique des series d'observations. O.M.M. Note Technique 143. Geneva, 192 pp.
- Sparholt, H. 1996. Causal correlation between recruitment and spawning stock size of central Baltic cod? *ICES Jour. Mar. Sci.* 53: 771-779.



- Southward, A.J., G.T. Boalch and L. Maddock. 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *J. mar. biol. Ass. U.K.* 68: 423-445.
- Steele, J., 1974. The structure of marine ecosystem. Harvard University Press, Cambridge.
- Steele J.H. and Henderson E.W. 1995. Predation control of plankton demography. *ICES J. mar Sci.* 52: 565-573.
- Steele, J.H. and M.M. Mullin. 1977. Zooplankton dynamics. In: The sea, ideas and observations on progress in the study of the seas, pp. 6 and 857-890. Ed. by E.D. Goldberg. John Wiley, New York. 1031 pp.
- St. John, M.A. and T. Lund. 1996. Lipid biomarkers: linking the utilisation of frontal plankton biomass to enhanced condition of juvenile North Sea cod. *Mar. Ecol. Prog. Ser.* 131: 75-85.
- Sundby, S., B. Ellertsen, and P. Fossum. 1994. Encounter rates between first-feeding cod larvae and their prey during moderate to strong turbulent mixing. *ICES mar. Sci. Symp.* 198: 393-405.
- Suthers, I.M. and K.T. Frank. 1990. Zooplankton biomass gradient off south-western Nova Scotia: near shore ctenophore predation or hydrographic separation. *J. Plankton Res.* 12: 831-850.
- Taylor, A.H. 1995. North-south shifts of the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. *ICES J. mar. Sci.* 52: 711-721.
- Uchima, M. and R. Hirano. 1986. Food of *Oithona davisae* (Copepoda: Cyclopoida) and the effect of food concentration at first feeding on the larval growth. *Bull. Plankton Soc. Japan* 33: 21-28.
- US GLOBEC. 1991. GLOBEC workshop on acoustical technology and the integration of acoustical and optical sampling methods. US GLOBEC Report No. 4.
- U.S. GLOBEC. 1992. Northwest Atlantic Implementation Plan. US GLOBEC Report No. 6.
- US GLOBEC. 1993. Optics Technology Workshop Report. US GLOBEC Report No. 8.
- U.S. GLOBEC. 1996. US GLOBEC Northeast Pacific Implementation Plan. Report No. 17.
- van Winkle, W., K.A. Rose and R.C. Chambers. 1993. Individual-based approach to fish population dynamics: an overview. *Trans. Am. Fish. Soc.* 122: 397-403.
- Verity, P.G. and G.-A. Paffenhöfer. 1996. On quantification of feeding rates of zooplankton. *J. Plankton Res.* 18: 1767-1779.

- Verity, P.G. and V. Smetacek. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Progr. Ser.* 130: 277-293.
- Vinogradov, M.E., E.A. Shushkina, Y.V. Bulgakova and I.I. Serobaba. 1996. Consumption of zooplankton by the comb jelly *Mnemiopsis leidyi* and pelagic fishes in the Black Sea. *Oceanology* 35: 523-527.
- von Storch, H. 1995. Spatial patterns: EOFs and CCA. *In: Analysis of climate variability: applications of statistical techniques*. Ed. by H. v. Storch, and A. Navarra. Springer, pp. 227-258.
- Walker, G.T., and E.W. Bliss. 1932. World weather. V. *Mem. Roy. Meteorol. Soc.* 4: 53-84.
- Ware, D.M. and R.E. Thomson. 1991. Link between long-term variability in upwelling and fish production in the Northeast Pacific Ocean. *Can. J. Fish Aquat. Sci.* 48: 2296-2306.
- Warner, A.J. and G.C. Hays 1994. Sampling by the Continuous Plankton Recorder Survey. *Prog. Oceanography*, 34: 237-256.
- Williams, R., N.R. Collins and D.V.P. Conway. 1983. The double LHPR system, a high speed micro- and macroplankton sampler. *Deep-Sea Res.* 30: 331-342.
- WCRP. 1997. *CLIVAR - A Research Programme on Climate Variability and Prediction for the 21st Century*. International CLIVAR Project Office, Hamburg, 48 pp.
- Werner, F.E., R.I. Perry, R.G. Lough and C.E. Naimie. 1996. Trophodynamic and advective influences on Georges bank larval cod and haddock. *Deep Sea Res. II.* 43: 1793-1822.
- Woods, J.D., H. Dahlin, L. Droppert, M. Glass, S. Vallergera and N.C. Flemming. 1996. The strategy for EUROGOOS. EUROGOOS Publication No. 1. Southampton Oceanography Centre, Southampton. ISBN 0 -904175-22-7.
- Wroblewski J.S. and J.G. Richman. 1987. The non-linear response of plankton to wind mixing events-implications for survival of larval northern anchovy. *J. Plankton Res.* 9: 103-123.
- Wyatt, T. and M.G. Larraneta (eds.). 1988. Long Term Changes in Marine Fish Populations. *Proc. Int. Symp.*, Vigo, Spain, 18-21 November 1986. Imprenta Real, Bayona, 554 pp.

## Appendix

### Acronyms

AIR	Agro-Industrial Research Programme of the European Union
AUV	Autonomous Underwater Vehicle
BASYS	Baltic Sea System Study
CANIGO	Canary Islands Azores Gibraltar Observations
CCC	Cod and Climate Change
CEOS	Committee on Earth Observation Satellites
CINCS	Pelagic-Benthic Coupling in the Oligotrophic Cretan Sea
CLIVAR	Climate Variability and Predictability
COADS	Comprehensive Ocean-Atmosphere Data Set
CORE	Baltic Sea Recruitment Project
CPR	Continuous Plankton Recorder
ELOISE	European Land-Ocean Interaction Studies
ENSO	El Niño Southern Oscillation
ERSEM	European Regional Seas Ecosystem Model
ESA	European Space Agency
ESOP	European Sub-Polar Ocean Programme
EURAPP	The impact of Appendicularia in European marine Ecosystems
EUROGLOBEC	European GLOBEC
EuroGOOS	European GOOS
FAIR	Agriculture and Fisheries Programme of the European Union
FLEX	Fladen Ground Experiment
GISST	Global Ice and SST data sets
GLOBEC	Global Ocean Ecosystem Dynamics
GOOS	Global Ocean Observing System
HELCOM BMP	Baltic Monitoring Programme
IBM	Individual Based Models
ICES	International Council for the Exploration of the Sea
ICOS	Investigations of Calanus finmarchicus Migrations between Oceanic and Shelf Seas off Northwest Europe
IGBP	International Geosphere Biosphere Programme

IOC	Intergovernmental Oceanographic Commission
JGOFS	Joint Global Ocean Flux Study
LOICZ	Land-Ocean Interactions in the Coastal Zone
MARE COGNITUM	Norwegian Nordic Seas Projects
MAST	Marine Science and Technology Programme of the European Union
MATER	Mediterranean Targeted Project II - Mass Transfer and Ecosystem Response
NACD	North Atlantic Climatological Data set
NAO	North Atlantic Oscillation
NASA	National Aeronautics and Space Administration (USA)
NCEP	National Centers for Environmental Prediction (USA)
NOWESP	North European Shelf Project
OMEGA	Observations and Modelling of Eddy Scale Geostrophic and Ageostrophic Circulation
OMEX	Ocean Margin Exchange Project
PEP	Impact of a Climatic Gradient on the Physiological Ecology of a Pelagic Crustacean
PEX	Patchiness Experiment
PICES	North Pacific Marine Science Organisation
POEM	Physical Oceanography of the Eastern Mediterranean
PROVESH	Processes of Vertical Exchange in Shallow Seas
SCOR	Scientific Committee on Oceanic Research
SEFOS	Shelf Edge Fisheries and Oceanography Studies
SPACC	Small Pelagic Fishes and Climate Change
SPM	Structured population models
SST	Sea Surface Temperature
TASC	Trans-Atlantic Study of Calanus finmarchicus
VEINS	Variability of Exchanges in the Northern Seas
WCRP	World Climate Research Programme
WOCE	World Ocean Circulation Experiment



## List of Participants

Alcaraz, Miguel  
 Institut de Ciencies de Mar, CSIC  
 P. Joan de Borbo S/N  
 08039 Barcelona, Spain  
 Tel.: +34 3 221 64 16  
 Fax: +34 3 221 73 40  
 e-mail: miquel@icm.csic.es

Alheit, Jürgen  
 Baltic Sea Research Institute  
 Seestr. 15  
 D-18119 Warnemünde, Germany  
 Tel.: +49 381 5197 208  
 Fax: +49 381 5197 440  
 e-mail: juergen.alheit@io-  
 warnemuende.de

Astthorsson, Olafur  
 Marine Research Institute  
 P.O. Box 1390  
 Skulagata 4  
 121 Reykjavik, Iceland  
 Tel.: +354 1 55 20 240  
 Fax: +354 1 56 23 790  
 e-mail: osa@hafro.is

Barthel, Klaus-Günther  
 MAST Programme, DG XII/D-3  
 European Commission, SDME  
 7/83  
 Rue de la Loi 200  
 B-1049 Brussels, Belgium  
 Tel.: +32 2 295 12 42 / 296 79 02  
 Fax: +32 2 296 30 24  
 e-mail: klaus-guenther.barthel@  
 dg12.cec.be

Bodungen, Bodo von  
 Baltic Sea Research Institute  
 Seestr. 15

D-18119 Warnemünde, Germany  
 Tel.: +49 381 5197 100  
 Fax: +49 381 5197 105  
 e-mail: bodo.bodungen@io-  
 warnemuende.de

Bojariu, Roxana  
 National Institute of Meteorology  
 & Hydrology  
 SOS. Bucuresti Ploiesti No. 97  
 71552 Bucharest, Romania  
 Tel.: +40 1 230 31 16  
 Fax: +40 1 230 31 43  
 e-mail: bojariu@meteo.inmh.ro

Brander, Keith  
 ICES/GLOBEC Secretary  
 ICES  
 Palaegade 2-4  
 1261 Copenhagen K, Denmark  
 Tel.: +45 33 15 26 77 (tone) 238  
 Fax: +45 33 93 42 15  
 e-mail: keith@ices.dk

Carlotti, Francois  
 Station Zoologique  
 P.O. Box 28  
 06230 Villefranche-sur-Mer,  
 France  
 Tel.: +33 493 76 38 39  
 Fax: +33 493 76 38 34  
 e-mail: carlotti@ccrv.obs-vlfr.fr

da Silva, Antonio  
 Instituto Hidrografico  
 Rua das Trinitas, 49  
 1296 Lisboa Cedex, Portugal  
 Tel.: +351 1 39 5119  
 Fax: +351 1 39 60515  
 e-mail: -

Fennel, Wolfgang  
 Baltic Sea Research Institute  
 Seestr. 15  
 D-18119 Warnemünde, Germany  
 Tel.: +49 381 5197 110  
 Fax: +49 381 5197 440  
 e-mail: wolfgang.fennel@io-  
 warnemuende.de

Fiksen, Oyvind  
 Dept. of Fisheries and Marine  
 Biology  
 University of Bergen  
 HiB  
 N-5020 Bergen, Norway Tel.: +47  
 55 58 46 24  
 Fax: +47 55 58 44 50  
 e-mail: oyvind.fiksen@ifm.uib.no

Foote, Kenneth G.  
 Institute of Marine Research  
 P.O. Box 1870 Nordnes  
 N-5024 Bergen, Norway  
 Tel.: +47 55 23 84 56  
 Fax: +47 55 23 85 32  
 e-mail: ken@imr.no

Hansson, Sture  
 Department of Systems Ecology  
 Stockholm University  
 106 91 Stockholm, Sweden  
 Tel.: +46-8-164248  
 Fax: +46-8-15 84 17  
 e-mail: STURE\_H@system.  
 ecology.su.se

Harris, Roger  
 Plymouth Marine Laboratory  
 Prospect Place, West Hoe  
 Plymouth, PL1 3DH, United  
 Kingdom  
 Tel.: +44-1752-633-400

Fax: +44-1752-633101  
 e-mail: r.harris@pml.ac.uk

Heath, Mike  
 SOEAFD  
 Marine Laboratory  
 P.O. Box 101, Victoria Road  
 Aberdeen, AB9 8DB, U.K.  
 Tel.: +44 12 24 87 65 44  
 Fax: +44 12 24 29 55 11  
 e-mail: heathmr@31G.dnet.  
 marlab.ac.uk

Ianora, Adrianna  
 Station Zoologica 'A Dohrn'  
 Villa Comunale  
 80121 Naples, Italy  
 Tel.: +39  
 Fax: +39 81 76 41 355  
 e-mail: ianora@alpha.szn.it

Koutsikopoulos, Constantin  
 University of Patras  
 Dept. of Biology  
 26500 Patras, Greece  
 Tel.: +30 61 99 61 00  
 Fax: +30 61 99 75 21  
 e-mail: ckouts@upatras.gr

Leppänen, Juha-Markku  
 Finnish Institute of  
 Marine Research  
 P.O. Box 33  
 SF-00931 Helsinki, Finland  
 Tel.: +358 861 38 41  
 Fax: +358 961 39 44 94  
 e-mail: jukkis@fimr.fi

Linkowski, Tomasz  
 Sea Fisheries Institute  
 Dept. of Oceanography  
 ul. Kollataja 1  
 81-332 Gdynia, Poland

Tel.: +48 58-21 71 95  
 Fax : +48 58-20 28 31  
 e-mail: tlink@miryb.mir.gdynia.pl

MacKenzie, Brian  
 Danish Institute for Fishery  
 Research  
 Kavalergården 6  
 DK-2920 Charlottenlund,  
 Denmark  
 Tel.: +45 3396 3403  
 Fax: +45 3396 3434  
 e-mail: brm@dfu.min.dk

Neves, Ramiro  
 Department of Mechanical  
 Engineering  
 Instituto Superior Tecnico  
 Av. Rovisco Pais 1  
 P-1096 Lisboa Cedex, Portugal  
 Tel.: +351 1-841-73-97  
 Fax: +351 1-841-73-98  
 e-mail: ramiro.neves@hidrox.  
 ist.utl.pt

Paffenhöfer, Gustav  
 Skidaway Institute of  
 Oceanography  
 10 Ocean Science Circle  
 Savannah, Georgia 31411, USA  
 Tel.: +1 912 598 2489  
 Fax: +1 912 598 2310  
 e-mail: vicki@skio.peachnet.edu

Proctor, Roger  
 Proudman Oceanographic Lab  
 Bidston Observatory  
 Birkenhead  
 Merseyside L43 7RA, U.K.  
 Tel.: +44 151 653 8633  
 Fax: +44 151 653 6269  
 e-mail: rp@pol.ac.uk

Reid, Philip Chris  
 Sir Alister Hardy Foundation  
 for Ocean Science  
 Walker Terrace, The Hoe  
 Plymouth, England PL1 3BN  
 Tel.: +44 1752 22 11 12  
 Fax: +44 1752 22 11 35  
 e-mail: PCRE@wpo.nerc.ac.uk

Roe, Howard  
 Southampton Oceanography  
 Centre  
 Eripress Dock  
 Southampton SO14 3ZH, U.K.  
 Tel.: +44 1428 68 41 41  
 Fax: +44 1428 68 38 24  
 e-mail: hsr@soc.soton.ac.uk

Sabates, Ana  
 Inst. Cienc. del Mar (CSIC)  
 Paseo Juan de Borbon s/n  
 08039 Barcelona, Spain  
 Tel.: +34 3 22 16 416  
 Fax: +34 3 22 17 340  
 e-mail: anas@icm.csic.es

Tande, Kurt  
 The Norwegian College of  
 Fishery Science  
 University of Tromsø  
 9037 Tromsø, Norway  
 Tel.: +47 77 64 45 24  
 Fax: +47 77 64 60 20  
 e-mail: kurt@nfh.uit.no

Tselepidis, Anastassios  
 Institute of Marine Biology of  
 Crete  
 P.O. Box 2214  
 71003 Heraklion, Greece  
 Tel.: +30-81-24 20 22 /24 66 47  
 Fax: +30-81-24 18 82  
 e-mail: ttse@imbc.gr

Ward, M. Neil  
IMGA-CNR  
Via Gobetti 101  
Bologna 40129, Italy  
Tel.: +39 51 639 8040  
Fax: +39 51 639 8132  
e-mail: neil@imga.bo.cnr.it

Werner, Cisco  
Marine Science Program  
University of North Carolina  
12-7 Venable Hall CB 3300  
Chapel Hill NC 27599-3300,  
U.S.A.  
Tel.: +1 919 962 0269  
Fax: +1 919 962 1254  
e-mail: cisco@marine.unc.edu



European Commission

**EUROGLOBEC — Science plan**

Luxembourg: Office for Official Publications of the European Communities

1998 — 76 pp. — 16.2 x 22.9 cm

ISBN 92-828-3516-2

Price (excluding VAT) in Luxembourg: ECU 6.5









**BELGIE/BELGIË**

**Jean De Lannoy**  
Avenue du Roi 202/Koningslaan 202  
B-1900 Bruxelles/Brussel  
Tel. (32-2) 538 43 08  
Fax (32-2) 538 08 41  
E-mail: jean.de.lannoy@infoboard.be  
URL: http://www.jean-de.lannoy.be

**La librairie européenne/De Europese Boekhandel**

Rue de la Loi 244/Watstraat 244  
B-1040 Bruxelles/Brussel  
Tel. (32-2) 295 26 39  
Fax (32-2) 735 08 60  
E-mail: mail@libeurop.be  
URL: http://www.libeurop.be

**Moniteur belge/Belgisch Staatsblad**

Rue de Louvain 40-42/Louvenseweg 40-42  
B-1200 Bruxelles/Brussel  
Tel. (32-2) 552 22 11  
Fax (32-2) 511 01 84

**DENMARK**

**J.H. Schultz Information A/S**  
Herstedvang 10-12  
DK-2620 Albertslund  
Tel. (45) 43 63 23 00  
Fax (45) 43 63 19 69  
E-mail: schultz@schultz.dk  
URL: http://www.schultz.dk

**DEUTSCHLAND**

**Bundesanzeiger Verlag GmbH**  
Vertriebsabteilung  
Amsterdamer Straße 192  
D-50735 Köln  
Tel. (49-221) 97 66 80  
Fax (49-221) 97 66 82 78  
E-mail: vertrieb@bundesanzeiger.de  
URL: http://www.bundesanzeiger.de

**EMMAGREECE**

**G.C. Eleftheroudakis SA**  
International Bookstore  
Piraeus 107  
GR-10564 Athens  
Tel. (30-1) 331 41 80/12/3/4/5  
Fax (30-1) 323 98 21  
E-mail: elebooks@net.gr

**ESPAÑA**

**Boletín Oficial del Estado**  
Tratado, 27  
E-28071 Madrid  
Tel. (34) 915 38 21 11 (Libros)/  
913 84 17 15 (Suscripciones)  
Fax (34) 915 38 21 21 (Libros)/  
913 84 17 14 (Suscripciones)  
E-mail: clientes@com.boe.es  
URL: http://www.boe.es

**Mundi Prensa Libros, SA**  
Castelló, 37  
E-28001 Madrid  
Tel. (34) 914 36 37 00  
Fax (34) 915 75 39 98  
E-mail: libreria@mundiprensa.es  
URL: http://www.mundiprensa.com

**FRANCE**

**Journal officiel**  
Service des publications des CE  
26, rue Desaix  
F-75727 Paris Cedex 15  
Tel. (33) 140 58 77 31  
Fax (33) 140 58 77 00

**IRELAND**

**Government Supplies Agency**  
Publications Section  
45 Harcourt Road  
Dublin 2  
Tel. (353-1) 661 31 11  
Fax (353-1) 475 27 60

**ITALIA**

**Icoso SpA**  
Via Duca di Calabria, 1/1  
Casella postale 552  
I-20125 Firenze  
Tel. (39-55) 64 54 15  
Fax (39-55) 64 12 57  
E-mail: icoso@fbcc.it  
URL: http://www.fbcc.it/icoso

**LUXEMBOURG**

**Messageries du livre SARL**  
5, rue Raffaisen  
L-1411 Luxembourg  
Tel. (352) 40 10 20  
Fax (352) 49 06 81  
E-mail: mdl@pt.lu  
URL: http://www.mdl.lu

**Abonnements:**

**Messageries Paul Kraus**  
11, rue Christophe Plantin  
L-1339 Luxembourg  
Tel. (352) 49 98 68-8  
Fax (352) 49 98 68-444  
E-mail: mpk@pt.lu  
URL: http://www.mpk.lu

**NETHERLAND**

**SDU Servicecentrum Uitgevers**  
Christoffel Plantijnstraat 2  
Postbus 20014  
2500 EA Den Haag  
Tel. (31-70) 378 98 80  
Fax (31-70) 378 97 83  
E-mail: sdu@sdunl  
URL: http://www.sdu.nl

**ÖSTERREICH**

**Manz'sche Verlags- und  
Universitätsbuchhandlung GmbH**  
Kohlmarkt 16  
A-1014 Wien  
Tel. (43-1) 53 16 11 00  
Fax (43-1) 53 16 11 67  
E-mail: bestellen@manz.co.at  
URL: http://www.austria.eu.net/81/manz

**PORTUGAL**

**Distribuidora de Livros Bertrand Ld.ª**  
Grupo Bertrand, SA  
Rua das Terras dos Vales, 4-A  
Apartado 60037  
P-2700 Amadora  
Tel. (351-2) 496 90 50  
Fax (351-2) 496 02 55  
Imprensa Nacional-Casa da Moeda, EP  
Rua Marquês Sá da Bandeira, 16-A  
P-1050 Lourenço Codex  
Tel. (351-1) 353 03 99  
Fax (351-1) 353 02 94  
E-mail: del.ncm@mail.telepac.pt  
URL: http://www.ncm.pt

**SUOMI/FINLAND**

**Akateeminen Kirjakauppa/Akademiska  
Bokhandeln**  
Keskuskatu 1/Centralgatan 1  
P.O. Box 123  
FIN-00101 Helsinki/Helsingfors  
P.O. Box (358-9) 121 44 35  
F. Fax (358-9) 121 44 35  
Sähköposti: akatila@stockmann.fi  
URL: http://www.akateeminen.com

**SVERIGE**

**BTJ AB**  
Traktorvägen 11  
S-221 82 Lund  
Tfn. (46-46) 18 00 00  
Fax (46-46) 30 79 47  
E-post: btjeu-pub@btj.se  
URL: http://www.btj.se

**UNITED KINGDOM**

**The Stationery Office Ltd**  
International Sales Agency  
51 Nine Elms Lane  
London SW8 5DR  
Tel. (44-171) 873 90 90  
Fax (44-171) 873 84 63  
E-mail: puenquiries@theso.co.uk  
URL: http://www.the-stationery-office.co.uk

**ÍSLAND**

**Bokabud Larusar Blöndal**  
Skólavörðustíg, 2  
IS-101 Reykjavík  
Tel. (354) 551 56 50  
Fax (354) 552 55 60

**NORGE**

**Swets Norge AS**  
Ostenjovøien 18  
Boks 6512 Etterstad  
N-0606 Oslo  
Tel. (47-22) 97 45 00  
Fax (47-22) 97 45 45

**SCHWEIZ/SUISSE/SVIZZERA**

**Euro Info Center Schweiz**  
c/o OSEC  
Stampfenbachstraße 85  
PF 492  
CH-8035 Zürich  
Tel. (41-1) 365 53 15  
Fax (41-1) 365 54 11  
E-mail: eics@osec.ch  
URL: http://www.osec.ch/eics

**BĂLGARIA**

**Europress Euromedia Ltd**  
59, blvd Vitoshka  
BG-1000 Sofia  
Tel. (359-2) 980 37 66  
Fax (359-2) 980 42 90  
E-mail: Milena@mbocit.bg

**ČESKÁ REPUBLIKA**

**USIS**  
NIS-prodávna  
Havekova 22  
CZ-130 00 Praha 3  
Tel. (420-2) 24 23 14 86  
Fax (420-2) 24 23 13 14  
E-mail: nkpcap@dec.nis.cz  
URL: http://www.nis.cz

**CYPRUS**

**Cyprus Chamber of Commerce  
and Industry**  
PO Box 1455  
CY-1509 Nicosia  
Tel. (357-2) 66 95 00  
Fax (357-2) 66 10 44  
E-mail: info@ccci.org.cy

**ESTI**

**Eesti Kaubandus-Tööstuskoda (Estonian  
Chamber of Commerce and Industry)**  
Toom-Kooli 17  
EE-0001 Tallinn  
Tel. (372) 646 02 44  
Fax (372) 646 02 45  
E-mail: einfo@koda.ee  
URL: http://www.koda.ee

**MAGYARORSZÁG**

**Euro Info Service**  
Európa Ház  
Margitsziget  
PO Box 475  
H-1396 Budapest 62  
Tel. (36-1) 350 80 25  
Fax (36-1) 350 90 32  
E-mail: euroinfo@mail.mata.vu  
URL: http://www.euroinfo.hu/index.htm

**MALTA**

**Miller Distributors Ltd**  
Malta International Airport  
PO Box 25  
Luqa LQA 05  
Tel. (356) 66 44 88  
Fax (356) 67 67 99  
E-mail: gwinth@usa.net

**POLSKA**

**Ars Polona**  
Krakowskie Przedmieście 7  
Skł. pocztowa 1001  
PL-00-950 Warszawa  
Tel. (48-22) 826 12 01  
Fax (48-22) 826 62 40  
E-mail: ars\_pol@bevy.hsn.com.pl

**ROMÂNIA**

**Euromedia**  
Str. G-ral Berhelot Nr 41  
RO-70749 Bucuresti  
Tel. (40-1) 315 44 03  
Fax (40-1) 315 44 03

**SLOVAKIA**

**Centrum VTI SR**  
Nám. Slobody, 19  
SK-81223 Bratislava  
Tel. (421-7) 531 83 64  
Fax (421-7) 531 83 64  
E-mail: europ@tbl.sk.stuba.sk  
URL: http://www.slk.stuba.sk

**SLOVENIA**

**Gospodarski Vestnik**  
Dunajska cesta 5  
SLO-1000 Ljubljana  
Tel. (386) 611 33 03 54  
Fax (386) 611 33 91 28  
E-mail: repasek@gvestnik.si  
URL: http://www.gvestnik.si

**TÜRKİYE**

**Dünya Infotel AS**  
100, Yıl Mahallesi 34440  
TR-80350 Bağcılar-Istanbul  
Tel. (90-212) 629 46 89  
Fax (90-212) 629 46 27

**AUSTRALIA**

**Hunter Publications**  
PO Box 404  
3067 Abbotsford, Victoria  
Tel. (61-3) 94 17 53 61  
Fax (61-3) 94 17 51 54  
E-mail: jpdavies@ozemail.com.au

**CANADA**

**Renout Publishing Co. Ltd**  
5369 Chemin Canotek Road Unit 1  
K1J 9J3 Ottawa, Ontario  
Tel. (1-613) 745 26 65  
Fax (1-613) 745 76 60  
E-mail: order.dept@renoutbooks.com  
URL: http://www.renoutbooks.com

**EGYPT**

**The Middle East Observer**  
41 Sherif Street  
Cairo  
Tel. (20-2) 393 97 32  
Fax (20-2) 393 97 32

**HRVATSKA**

**Mediatrade Ltd**  
Pavla Hatza 1  
HR-10000 Zagreb  
Tel. (385-1) 43 03 92  
Fax (385-1) 43 03 92

**INDIA**

**EBIC India**  
3rd Floor, Y. B. Chavan Centre  
Gen. J. Bhosale Marg.  
400 012 Mumbai  
Tel. (91-22) 282 60 64  
Fax (91-22) 285 45 64  
E-mail: ebic@glasbmd1.vsnl.net.in  
URL: http://www.ebicindia.com

**ISRAËL**

**ROY International**  
PO Box 13056  
61130 Tel Aviv  
Tel. (972-3) 546 14 23  
Fax (972-3) 546 14 42  
E-mail: roy@netvision.net.il

Sub-agent for the Palestinian Authority:

**Index Information Services**  
PO Box 19502  
Jerusalem  
Tel. (972-2) 627 16 34  
Fax (972-2) 627 12 19

**JAPAN**

**PSI-Japan**  
Asahi Sanbancho Plaza #206  
7-1 Sanbancho, Chiyoda-ku  
Tokyo 102  
Tel. (81-3) 32 34 69 21  
Fax (81-3) 32 34 69 15  
E-mail: books@psi-japan.co.jp  
URL: http://www.psi-japan.com

**MALAYSIA**

**EBIC Malaysia**  
Level 7, Wisma Hong Leong  
18 Jalan Perak  
50450 Kuala Lumpur  
Tel. (60-3) 262 62 98  
Fax (60-3) 262 61 36  
E-mail: ebic\_kl@ml.net.my

**PHILIPPINES**

**EBIC Philippines**  
19th Floor, PS Bank Tower  
San. Gil-J. Puyat Ave. cor. Tindalo St.  
Makati City  
Metro Manila  
Tel. (63-2) 759 66 80  
Fax (63-2) 759 66 90  
E-mail: ecpcpm@globe.com.ph  
URL: http://www.ecpcpm.com

**RUSSIA**

**CECE**  
60-Ilyiya Oktyabrya Av. 9  
117312 Moscow  
Tel. (70-95) 135 52 27  
Fax (70-95) 135 52 27

**SOUTH AFRICA**

**Safto**  
Safto House  
NO 5 Esterhysen Street  
PO Box 782 706  
2146 Sandton  
Tel. (27-11) 883 37 37  
Fax (27-11) 883 65 69  
E-mail: emalstar@ide.co.za  
URL: http://www.safto.co.za

**SOUTH KOREA**

**Information Centre for Europe (ICE)**  
204 Woo Sol Parktel  
395-185 Seogyong Dong, Mapo Ku  
121-210 Seoul  
Tel. (82-2) 322 53 03  
Fax (82-2) 322 53 14  
E-mail: euroinfo@shinbiro.com

**THAILAND**

**EBIC Thailand**  
29 Vanissa Building, 8th Floor  
Soo Chifrom  
Ploenchit  
10330 Bangkok  
Tel. (66-2) 855 06 27  
Fax (66-2) 855 06 28  
E-mail: ebicbk@ksc15.th.com  
URL: http://www.ebicbk.org

**UNITED STATES OF AMERICA**

**Bernan Associates**  
4611-F Assembly Drive  
Lanham MD20706  
Tel. (1-800) 274 44 47 (toll free telephone)  
Fax (1-800) 865 34 50 (toll free fax)  
E-mail: query@bernan.com  
URL: http://www.bernan.com

**ANDERE LÄNDER/OTHER COUNTRIES/  
AUTRES PAYS**

Bitte wenden Sie sich an ein Büro Ihrer  
Wahl / Please contact the sales office of  
your choice / Veuillez vous adresser au  
bureau de vente de votre choix

---

Price (excluding VAT) in Luxembourg: ECU 6.5

ISBN 92-828-3516-2



OFFICE FOR OFFICIAL PUBLICATIONS  
OF THE EUROPEAN COMMUNITIES

L-2985 Luxembourg



9 789282 835166 >