



GLOBAL OCEAN ECOSYSTEM DYNAMICS

GLOBEC REPORT NO. 2

POPULATION DYNAMICS AND PHYSICAL VARIABILITY

ISSN 1066-7881

POPULATION DYNAMICS AND PHYSICAL VARIABILITY

Report of the First Meeting of an International GLOBEC Working Group

St. John's College, Cambridge University

February 1 - 5, 1993

PREFACE

The international program on Global Ocean Ecosystem Dynamics (GLOBEC) is sponsored by the Scientific Committee on Oceanic Research (SCOR) with the co-sponsorship of the Intergovernmental Oceanographic Commission, the International Council for the Exploration of the Sea and the North Pacific Marine Science Organization. GLOBEC is dedicated to understanding the effects of physical processes on predator-prey interactions and population dynamics of zooplankton and their relation to ocean ecosystems in the context of the global climate system and anthropogenic change.

The GLOBEC Core Program is being developed through a series of scientific working groups and regional planning efforts. This report results from the first of a series of meetings of these groups leading to the development of an international Science Plan for GLOBEC. The Working Group on Population Dynamics and Physical Variability met at St. John's College, Cambridge University in early February 1993.

This meeting was chaired by Dr. David Cushing to whom the international sponsors of GLOBEC wish to express their gratitude for his leadership and for the effort he expended in producing and editing this report.

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EXECUTIVE SUMMARY

INTRODUCTION

Concerns for global climate change emphasize the need to understand how changes in the global environment affect the abundance, diversity, and production of animal populations comprising the ocean ecosystems. Among these animal populations, zooplankton play a pivotal role 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 (IOC, 1991).

Yet despite the importance of zooplankton in the ocean ecosystem, very little is known about the population dynamics of zooplankton. The problem derives from three sources:

- **conceptual,**
- **measurement,** and
- **integration**

involving description, explanation, and prognostication.

Conceptual

The population dynamics framework involves the dynamical equations linking mortality, growth, and reproductive rates into a dynamical setting. What are the "right" equations and how should they be linked together in either continuous or stage structured systems? What are appropriate trophodynamic, physiological, and physical parameterizations? What is the best way to parameterize stage structured populations? How can nonstage structured equations be interpreted? How are zooplankton linked to the other taxa in the ocean?

Measurement

Given some set of dynamical equations, what field measurements should be made in order to estimate the parameters? How can the "intrinsic rates of increase" and the "carrying capacity" of dynamic models be linked to the actual ecosystem? What is the most appropriate suite of sensors that can be used to estimate parameters? What are the appropriate sampling theoretic issues.

Integration

How can the concepts, their quantitative articulation, and the measurement and sampling systems be fully articulated into the dynamical models to provide synthetic descriptions, explanations and prognostications given observed phenomena and various environmental scenarios?

Clearly it would be desirable to interrelate the conceptual issues with the measurement and integration systems. However, before this can be done, it is necessary to more fully articulate the conceptual issues which lie at the intersection between the density-dependence inherent in the population dynamics process and the density-independent destabilizing processes that are driven by ocean physics.

There are several key issues which lie at this intersection. These issues focus on the interrelationships among the zooplankton, their prey, and their predators. These basically trophodynamic interrelationships drive the vital rates of growth, mortality and reproduction which are essential components to the dynamics of not only the populations of interest, but of the prey and predator populations as well.

Deliberations preceding the workshop considered the role of each major taxa (e.g. "jellyfish", arrow worms, etc.). However, for the sake of concreteness, we decided to focus initially on copepods because they are one of the most abundant forms of zooplankton in the ocean and in some sense the best understood. Because of the abundance and the level of understanding, the copepods provide the ideal "proof of concept", point-of-departure for the study of the other taxa.

Accordingly, considerable attention was given to our understanding of the trophodynamics of copepods. A number of species of copepods are thought of as grazers feeding only on phytoplankton cells; yet these copepods are generally omnivores feeding not only on phytoplankton cells, but on copepod nauplii and detritus for example. This discussion suggested the need for considerable work on diet components; the dynamics that generate diet changes; the nutritional value of various diet items, and the transformation of various food items into somatic and reproductive biomass.

In addition to studying how copepods function with fixed amounts of food partitioned into various diet items, it is also necessary to consider the quantity of "food delivered" to a copepod. This has to do with the interactive dynamics of the predator and the prey. Key among these dynamics are the density-dependent non-linear response to food quantity in the copepod, in the predator and in the prey. These responses involve, for example, shading in phytoplankton and the functional feeding response. Stress was placed on the need to have much better estimates of growth and mortality rates and more

measurements of reproductive rates (both recruitment rate and egg production rate) in a trophodynamic setting. Experimental studies are needed to establish maximal growth rates at temperature on given biochemically replete diets. It would be desirable to estimate growth rates at sea as proportions of such maximal rates. It was also absent that the quantity grazed, estimated at sea, should be partitioned into that due to the mesoplankton, such as copepods, and that due to the tiny grazers characteristic of the microbial food loop. Additional stress was placed upon the fact that a better understanding of copepod population dynamics requires a better understanding of phytoplankton dynamics which has received relatively little attention in the literature. This specifies an important opportunity for interaction with JGOFS.

Estimation of growth and mortality is a non-trivial problem requiring considerable research into the factors that control stage duration. The estimation problem is generally statistical and might involve stage structured models and simulation. The estimation of the range of population dynamics requires a much better understanding of the predators and trophodynamics of copepodites and nauplii. A focus on nauplii places the traditional zooplankton problem, which is generally viewed as a large plankton problem, in the context of the very small plankton. How nauplii interact with the small plankton is a critical problem for future study.

The classical population dynamics formalisms are often phrased in temporal rather than spatial or spatial-temporal terms. In this regard there is a considerable amount of work that needs to be

done regarding the genesis and dissipation of patches.

In one context, the generation of spatial, temporal, or velocity patches can be thought of in strictly biological terms. However, it is now well known that hydrodynamic flow interacts with and may even cause patch structure. In this regard required research ranging from feeding currents, the interaction of these and between predator and prey as influenced by small-scale turbulent flow, to the effects of mesoscale eddies was identified. In addition to these essentially two-dimensional flow problems a better understanding of the factors determining stratification and mesoscale "hot spots" seemed to be key elements in furthering the understanding of the biophysical coupling.

Moving forward will require considerable work in the above areas which again focus on how the population dynamics of predator prey populations interact in a trophodynamic setting. The work required includes a wide spectrum of laboratory, field, and theoretical studies. Some studies are routine and have perhaps only been implemented at few times because of great sampling and specimen identification costs. However, these can now be accomplished at greatly reduced cost by using modern technology. A modern revisiting of "old" experiments is regarded as having a high payoff.

The greatest efficiency in moving forward, however, will derive from the GLOBEC Core Program model explicitly linking in an interactive fashion the fundamental ideas of physics/population dynamics interactions with numerical

models which are data assimilative for the major ecosystem types. This means the numerical models and the sampling technology (hardware, software, and theory) are linked together in a specific sampling and observation system.

The development of such systems will lend greater insights to the functioning of the major ecosystem types of the world oceans such as the HNLC, Southern Ocean, and North Pacific or the spring bloom, or the upwelling systems. For example, the onset of stratification in each year can now be described with turbulence closure methods, which allow greater vertical sampling within the mixed layer. Then Lagrangian models of grazing by, and predation on, the populations of zooplankton (and hence of phytoplankton) can be envisaged. Consequently, detailed descriptions of the biological processes of production in spring should become possible as function of the physical processes in each year. The methods for investigating the onset of stratification can be used to describe the degree of decoupling between the algal production and the grazing zooplankton. It arises because of the delay in time between them. From year to year, the differences in the degree of decoupling can be estimated as function of the physical factors, the agents of climatic change. There is no spring outburst in the North Pacific as there is in the North Atlantic and the contrast between the processes in the two oceans deserves a comprehensive approach in modelling. The workshop considered that understanding the array of ecosystem types is critical to understanding the boundary conditions associated with shelf ecosystems. The workshop considered that the deployment of sampling

and observation systems in these ecosystems combining lagrangian, eulerian and population dynamics measurements which could be assimilated in near real time in numerical models at various laboratories around the world would provide major increments in our understanding of global change phenomena, such as the coupling - decoupling contrast between the North Atlantic and the North Pacific fisheries, and the fate and effect of anthropogenic substances.

SUMMARY

The introductory papers:

Net primary production can be calculated in the mixed layer as function of the average depth, the time averaged irradiance and a generalized loss term. *From such estimates may be derived the net rate of increase and the critical depth* (it might be desirable to repeat and extend the work of Eppley, 1972 on the maximal division rates of algae). Flow cytometry has considerable advantages, particularly if linked with Lagrangian modelling, not only as shown in Figures 1 and 2, but in the detailed study of grazing.

Two dramatic videos were shown of the behaviour of copepods. To analyze such behaviour in a turbulent environment, a Lagrangian model of different forms of turbulence will be used with observations on the distribution of animals.

The major zooplankton field programs are listed in Table 1. Experimental methods to estimate ingestion are listed in Table 2 and in Table 3 are given the new developments in zooplankton methods.

The important point here is that *there is a broad array of programs already, potentially part of GLOBEC.INT.*

The feeding of copepods is not as simple as has sometimes been suggested (Figures 3 and 4). Laboratory experiments on feeding are somewhat artificial, but the proposition of solely temperature dependent growth suggests that copepods can detect non-limiting food concentrations in micropatches. Further, *laboratory experiments should be integrated with field systems in an interactive manner.*

Copepods are omnivores and their food should be investigated, its nature, size and quality, or discontinuities and micropatches. They need a variety of amino acids, fatty acids, sterols and vitamins and, therefore, a variety of foods. They eat the protozoa in the microbial food loop and much experimental work is needed on the variety of food they eat. Because the food is so diverse, *there is a case for estimating growth rate as proportion of the maximal growth rate (see Figure 1).*

An extensive review was given of the models used to describe the population dynamics of copepods. The simplest is a predator/prey model, but more complex ones are needed to take into account differences due to transport and diffusion. Stages can be expressed as ages, assuming the dependence of development rate on temperature and size distributions can be used (Figures 8 - 11). The egg method might be used to estimate the variability of populations in space and time (Figure 7).

It is no longer possible to assume that mortality is constant during the period of production of a developmental stage. The

problem is to smooth the data in time and in the course of the life history. A cubic spline was supported with cross validation splines which optimized the smoothing. *Information is needed on the stage duration and so observations are needed for the cross validation method.*

Mesoscale eddies of 50 - 300 km across were described and it was suggested that the spatial spectra of zooplankton were flatter (or more random) than those of the phytoplankton. *But the distributions of the zooplankton may actually reflect the mesoscale structure.*

Biological processes:

1. Food

Copepods are omnivorous and their intake depends on the array of particles presented to them. The diverse diet affects their growth, development, mortality and reproduction. The growth rate and species composition of the algae are controlled by physical variables and so is their chemical composition. The protozoa comprise another food component and their ingestion in the field should be studied. *Work needs to be done on the feeding processes in patchy or discontinuous feeding regimes.*

More generally, how do growth and egg production vary with the diversity of diet? It should be pointed out that many laboratory measurements have been biased by artifacts and new techniques are needed to describe the varied diet eaten. It is possible that the maximal ingestion rate varies with the size and abundance of the food items. *The biochemical components of the diet needed for growth and reproduction should be established.*

The possible Carlotti effect attracted some attention, that animals in a developmental stage might have to reach a critical mass before moulting or reproducing. If true, this could generate a density dependent mortality, particularly if the food were patchy. *The Carlotti effect should be investigated more fully.* Another possible form of density dependence may lie in the occurrence of barren females. It is now well known that food affects fecundity directly, *but the effect of food on development rate has not been much studied;* recent work suggests that as consequence, growth is density dependent.

Many aspects of the effects of food abundance on reproduction and on egg viability require firm, quantitative work.

Copepod nauplii remain a neglected field in the study of microzooplankton.

2. Experimental studies

Experimental studies are needed on the predator prey interaction. Generation times should be established as function of temperature and food and there should be standardized techniques for determining egg viability in the field. *The maximal growth rates and egg production rates are needed for target species.*

3. Variation in populations

Variation is expressed in the vital rates of the population. Birth rate may be estimated by the egg ratio method or by incubation experiments. Recruitment rate is essentially the moulting rate (perhaps at a late copepodite stage). Estimates of mortality rate differ between birth pulse and birth flow populations; perhaps Simon Wood's method of splining will be useful. Prey and predator should be sampled on

the same time and space scales. *To obtain per capita rates properly, accurate measurements are needed of copepod abundance (which is a sampling problem).*

4. Trends in populations

Trends in the populations need 15 - 20 years of observations before they are revealed. There are advective events, like the flow of cold low salinity water from the north in the California current or the increase in abundance of dinoflagellates in the North Sea with the incursion of low salinity water from the Baltic. There are climatic events like the increase in zooplankton in the North Pacific or the decline off Peru.

Existing long term pelagic sampling series should be supported. New ones should be developed and there should be a unified data base.

5. The maximal growth rate

Perhaps the most important conclusion is that maximal growth rates on diverse diets should be established in the laboratory and that growth rates in the field should be expressed as proportions of the maximum.

Physical processes

1. The mixed layer depth

A principal source of variation in the populations of zooplankton originates in changes in the mixed layer depth, for example, shoaling in spring in the North Atlantic and deepening slowly in the offshore Ekman transport, amongst many other productive regions. In the integral models of the mixed layer commonly used today, the layer is assumed uniform in temperature. But the *study of biological processes in the sea demands more vertical*

detail in the mixed layer. Turbulence closure models provide such details and with them it should be possible to describe the onset of stratification in any given year, but changes from year to year are at the moment inaccessible.

Because the nearest neighbour distances are excessive, *Lagrangian models will be needed at least for the zooplankton* and so perhaps should also be used for the phytoplankton as well. This is particularly true for the details of grazing and of predatory behaviour. But the ecological modellers will have "to resort to sub grid scale parameterization of small scale processes". Then the physicists propose to develop adequate models for the use of the GLOBEC.INT community.

2. Decoupling

The decoupling of algal and zooplankton production arises from the delay in time between the development of the algal reproductive rate and significant algal mortality due to grazing. Productions of algae and grazers are decoupled in the North Atlantic spring bloom and in upwelling processes, but they are coupled in the oligotrophic ocean and in the subarctic North Pacific. The shoaling of the mixed layer in spring is an intermittent process which is variable in time and the grazing capacity is mobilized during that period. The physicists propose to model the annual cycle of the mixed layer depth and hence the degree of decoupling. *The contrast between the processes in the North Atlantic and North Pacific deserves a comprehensive modelling approach as proposed.*

3. Turbulence

The cascade of turbulence is generated by shear at all scales and ends at the

Kolmogorov length scale and many animals of the zooplankton live there. Turbulence may be correlated or uncorrelated (Figure 2).

The contact rate with food particles increases with turbulence and within the correlated structures the copepods may receive chemical and mechanical signals from a certain range. But the uncorrelated component of turbulence may disturb such signals. Then the animals could make use of that component to reduce predation.

The Rothschild/Osborn thesis should be tested in the laboratory more fully and the effect of turbulence on growth rate should be examined. There should be numerical simulations of the correlated structure of turbulence and it is possible that the vertical distribution of the zooplankton is linked to turbulence.

4. The physics of grazing

Contact and ingestion rates have been examined but the searching and handling processes need more study. The animals distinguish edible from non edible food. They can detect particles at a range of at least two body lengths and at all directions within the feeding current. *More experimental work is needed.*

5. Transport and diffusive processes

The separation of transport and dispersion depends on the scales at which the processes are averaged in space. Physical losses may be determined horizontally, but in the vertical dimension biological processes may predominate. The area sampled is a function of generation time and the physical properties should be sampled vertically as well as horizontally.

The target animals should be sampled at the same time and space scale as the food and the predators (together with their buoyancy and vertical migration). Two particular new tools are needed: first, drifters with vertically programmable behaviour, and; secondly, large drifting enclosures to estimate growth and mortality.

Planktonic predators encounter the same transport and diffusion as their prey, but fishes will aggregate and disperse. Over a bank, tidal mixing generates inflow at the surface with outflow over the seabed, but buoyant and vertically migrating animals may concentrate at the stratified layer. Storms could flush out a fraction of the population or at least reduce the food resources.

If the population lives in a well defined area, bank, bay or a section of the continental shelf, numbers can be estimated (with transport and dispersion) with the use of current meters, drifters and ADCP profilers. But in the open ocean, where transport predominates, a Lagrangian approach is needed, with an array of drifters to estimate horizontal dispersion.

6. Physical structures

Ideally, a physical structure should endure for more than one generation of the animals (say, a month) and it should be small enough to be within the range of present logistics (say, 300 km across). But with data assimilation methods this restriction need no longer apply. Such are the rings, topographically trapped gyres, estuarine circulations, shelf break fronts and upwellings of all types. Fjords are special cases where physical and biological

processes can be described fairly readily and where indeed much classical work has already been carried out.

There are regions where research is already in progress. The first is the front in the Western Mediterranean between Catalonia and the Italian Riviera which forms the northern edge of a gyre with a jet current. A second is the Agulhas Bank off the southern coast of South Africa where there is a cyclonic circulation around the bank. Work is being planned in a third region, in the gyres of the Subarctic North Pacific. An attractive proposal is to sample distinct regions of the North Atlantic (for example, the Norwegian Sea), where exchange is low and which can be sampled for long periods within logistic requirements.

LIST OF RECOMMENDATIONS

Biological processes

A. Food

1. Work needs to be done on interactions with patchy and discontinuous regimes.
2. The Carlotti effect, that a critical weight should be reached to moult and reproduce, should be investigated.
3. The biochemical components in the diet essential for growth and reproduction should be investigated.
4. The effects of food abundance and composition on reproduction, diapause, egg viability and on sex ratio should be investigated.
5. Further quantitative work on the role of food in naupliar biology is needed to advance our understanding of zooplankton population dynamics.

B. Experimental studies

1. Investigate the role of small scale turbulence on predator-prey interaction.
2. Investigate the generation times of target species as functions of temperature and appropriate food.
3. Establish a standardized technique for determination of egg viability in the field.
4. Determine growth and reproductive rates on a diverse diet including the microzooplankton.
5. Establish maximal growth and egg production rates for target species, the highest mean rate for various food combinations.

C. Sources of variation

1. Development rates should be estimated as functions of food and temperature.
2. Mortality rates may be estimated by splining, based on information on food satiated development rates at various temperatures and on moulting rate derived from incubations in natural sea water.
3. Studies on predation rates should be made on carnivorous zooplankton (including the gelatinous ones) and planktivorous fish and injury frequency analysis should be encouraged.
4. As the rate terms are per capita, accurate measurements of copepod abundance are needed.
5. Prey and predator must be sampled on the same time and space scales and hence acoustic methods are needed for sampling the fish.
6. There should be a close partnership with fish ecologists from conception to

completion of GLOBEC studies; this is needed to close the mortality terms.

D. Trends

1. The long term pelagic time series should be supported.
2. Targeted investigations should be integrated with the long term time series.
3. New planktonic time series should be encouraged on a world wide scale.
4. A unified data base should be established for long term series.
5. The Sampling and Observations Working Group should consider specification of a new generation of Plankton Recorders which maintains the integrity of the present system but includes new and wider sensing and storage capabilities.

E. Maximal growth rates

1. There should be an investigation of the maximal growth rates in the laboratory at various temperatures and on diverse diets as basis for a study of growth rates in the field. This is the quickest way of dealing with the problem of the diverse diet in the field.

Physical processes

A. Variation in the mixed layer depth

1. A turbulence-closure model of mixed layer depth should be made available to the GLOBEC community as a vehicle for modelling the seasonal cycles of phytoplankton/zooplankton coupling.
2. An analysis of suitable time series distributions should be made to provide statistics on interannual

variations of mixed layer depths and the onset of spring time stratification.

3. A theoretical/modelling study should be carried out to determine the best sub-grid scale parameterizations for phytoplankton and zooplankton.

B. The Physics of Decoupling

1. A comprehensive modelling study should be made to investigate all the alternative hypotheses (and combinations thereof) for the differences between the North Atlantic and the North Pacific seasonal production studies. To be acceptable a model result must be robust to reasonable variability in either the parameters or the physical forcing and so special attention should be given to the sensitivity of the models to stochastic fluctuations.

C. Turbulence

1. An experimental test of the Rothschild and Osborn idea is recommended. Generating turbulence in the laboratory in a way that realistically imitates the situation in the field is not a trivial problem, although a qualitative assessment of the Rothschild and Osborn model is judged possible. However, laboratory experiments should preferentially be followed up by field studies. In situ video techniques that allow simultaneous observations of turbulence and copepod feeding behaviour are currently being developed. These techniques should be applied to thoroughly examine the plankton encounter rate hypothesis.
2. We need to test interaction of food concentration with turbulence. At high food concentrations (greater than

saturating) there may be no effect on ingestion although there **may be an** effect on gross growth efficiency. The effects of turbulence on the estimation of growth rate may be an **interesting** experiment to design.

3. The effects of the structured component of turbulence **should** be further examined. There are **as yet** no techniques available to approach this experimentally, but numerical simulation studies may **help** us explore this. The effect on zooplankton behaviour should be included in these models.
4. There are some observations to suggest that the vertical distribution of zooplankters is related to the distribution of turbulence (Haury et al., 1990). There is a need to increase the observational data base, by doing simultaneous measurements of vertical distributions of zooplankton and dissipation rate (pumps, Remote Observation Vehicles or acoustics with a free fall turbulence profiler).

D. The physics of grazing

1. In conjunction with the physical aspects of the searching process we *must stress the importance of the animal's ability to detect a target particle, prey, predator and mate.* We recommend developing an experimental plan taking both aspects into consideration.

E. Transport and dispersion

1. There is a need for careful studies of evolution in time of the population structure and physical patterns at selected sites, the sizes of which are related to the generation time of the target species. The area should be

carefully selected so that a hydrodynamic survey and a continuous monitoring of the species be feasible. The time and space scale should be carefully defined for the set of species under consideration.

2. It is important that the target species is studied at the same time as its food and predators. This is necessary to estimate the transport and mortality components of the population dynamics.
3. There is a need for small scale studies of transport processes which directly affect the population dynamics as well as the vertical distribution of physical properties.
4. There is a need to define the processes involved in the change of vertical distribution of species (buoyancy, diurnal and ontogenetic migration).
5. There is a need to develop new tools to monitor spatially a large water mass and to monitor short term events which might drastically affect the population dynamics. Accurate drifters with vertically programmable behaviour have to be designed to investigate the effect of 3D physical structure on the space time development of zooplankton species and fish larvae.
6. Mesoscale models of physical structures which could integrate biological processes should be developed.
7. It is necessary to study the feasibility of drifting large size enclosures in order to separate physical processes and estimate growth and mortality in short periods of time.

Biological Processes

1. The role of food in the population dynamics of zooplankton

(Roger Harris, Mark Huntley, Mike Roman, Serge Poulet, Brian Rothschild, Jarl-Ove Stromberg)

In this report, zooplankton are considered to be synonymous with copepods, and copepods are considered as omnivores.

a. The relation between population dynamics and food requirements

The essential components of copepod population dynamics are growth, reproduction, mortality and development time. Population dynamics can be thought of as the study of the temporal change of population abundance or weight. Population dynamics is important because the variability in the dynamics of populations that comprise an ecosystem drives the variability in ecosystem production.

In turn, to understand the variability in the dynamics of populations it is necessary to understand the trophodynamics associated with each population. In order to illustrate this point consider the well known virtual linkage between any two populations, a grazing copepod P , and its phytoplankton prey, N , for example,

$$\begin{aligned} \frac{dN}{dt} &= N \{ r (1 + N/K) + BP/(N+D) \} \\ \frac{dP}{dt} &= P \{ s (1 + hP/N) \} \end{aligned}$$

These coupled differential equations are basically logistic with a grazing functional response. The logistic components

involve r and s which are the "intrinsic rates of increase" of the phytoplankton and the copepods respectively; K is the carrying capacity of the phytoplankton and h is a constant that modifies the "carrying capacity". The grazing component is $B/(N+D)$, where B is the asymptotic ingestion of algal cells and the constant D refers to the rate at which the asymptote is reached.

Despite the fact that these equations are almost metaphors of the true predator - prey relationships, they can lend considerable insight into the dynamics of the population. This insight is obtained by an analysis of the meaning of the parameters.

It can be seen that each parameter is implicitly or explicitly related to "food":

1. the constants r and s refer to the rate of increase, and each relates to the difference between intrinsic rate of growth and birth. These are well known to depend upon food resources.
2. The carrying capacity constant, K , depends among other things on the "food" available to the phytoplankton.
3. The constants h , B and D relate to the actual trophic interaction between the predator and the prey or grazer and the phytoplankton. So it is clear that the dynamics of the populations, (i.e. dN/dt and dP/dt) depend on food in so far as the equations above are concerned.

Each parameter thus needs to be studied and evaluated in terms of food density,

variance in density (i.e. patch structure), nutrition and nutritional requirements etc.

Carrying the analysis to its completion involves evaluating the equations above in the context of the physical environment. Physical variability affects them in distinctly different ways. For example, changes in temperature speed up or slow down the physiology of the predators and prey. Advection modifies the initial conditions and turbulence affects the functional response and the carrying capacity, *h*, directly.

b. The characteristics of food

As omnivores, copepods potentially feed on a complex mixture of phytoplankton, detritus, microzooplankton, and other copepods, in the case of carnivores. The major features of this food assemblage are food abundance, food composition, size and motility.

The specific nutritional requirements of copepods are not well known. Overall energy demands (calories) have been estimated from respiration measurements. However, we know little of the carbohydrate, lipid and protein requirements of copepods and virtually nothing concerning their essential vitamins, amino acids and fatty acids.

Why do different species of phytoplankton and different types of detritus vary in their ability to support copepod production?

What is role of protozoa in copepod production?

What are optimum ratios of dietary protein, carbohydrate and lipid for maximum copepod growth rate and egg production?

What amino acids and fatty acids are essential in copepod diets?

Research which answers these questions is necessary to understand the causes of variability in the production of copepods.

The suspended particulate matter in the ocean is a complex mixture of inorganic particles, bacteria, phytoplankton, protozoa and detritus in varying concentrations, sizes and chemical compositions. Thus zooplankton which feed on this particulate matter potentially experience a wide range of dietary diversity which can vary both in space and time over the life of the animal. Because the diet can directly influence the growth, development, mortality and reproduction of copepods, the role of food is a critical variable in understanding zooplankton population dynamics.

The biochemical composition of phytoplankton varies with the algal group (diatoms vs. dinoflagellates vs. chlorophytes, etc.), algal species within the group, phase of growth, ambient light field and availability of inorganic nutrients. Thus phytoplankton contain different amounts of: bulk constituents such as carbon, nitrogen and calories; major biochemical classes such as proteins, carbohydrates and lipids; and, specific macro and micronutrients such as amino acids, fatty acids and vitamins. Because these elements can vary widely in algal cells, gross measurements of chlorophyll do not give an accurate representation of

the "available" food of zooplankton. Algal growth rate and phytoplankton species composition is controlled by physical variables such as water column stability, mixing rates and eddy diffusivity. Thus, physics to a large extent controls the chemical composition of phytoplankton.

Protozoa are a dominant component of the seston. Numerous studies have demonstrated that copepods ingest protozoa (Stoecker and Egloff, 1987; Stoecker and Sanders, 1985; Gifford and Dagg, 1988; Kleppel et al., 1988) and that protozoa can support copepod egg production and growth (Klein Breteler, 1980; Kleppel 1991; White and Roman, 1992). In general, the C:N ratio in protozoa is lower than the ratio in phytoplankton, (Stoecker and Capuzzo, 1990), implying that they have relatively more protein per unit mass than phytoplankton. Marine ciliates contain high intracellular concentrations of free amino acids (Kaneshiro et al., 1969). Protozoa may have more long polyunsaturated fatty acids (PUFA) than phytoplankton (Phillips, 1984) and thus be an important dietary element for zooplankton which cannot synthesize PUFA. Because of difficulties in both the collection and culture of protozoa, there is a paucity of data on their biochemical composition. Since protozoa are an important group in the marine food web and are a dominant food item of interest, future efforts should be made to characterise the factors affecting their biochemical composition. We clearly need more estimates of the ingestion of protozoa by copepods in nature and to relate these ingestion rates to copepod production.

Detritus dominates the suspended particulate matter of the open ocean and

coastal waters (Parsons, 1963; Riley, 1970; Wangersky 1978). There are many types of detritus (i.e. faecal pellets, macrophyte detritus, marine snow, etc.) which vary widely in their chemical composition depending on both the detrital source and age (e.g. Riley, 1970; Rice and Tenore, 1981; Roman, 1983). Zooplankton have been shown to ingest faecal pellets (Paffenhofer and Knowles 1979); dead algae (Paffenhofer and Strickland, 1970; Paffenhofer and Van Sant, 1985); macrophyte detritus (Roman, 1977, 1984) and coral mucus detritus (Gottfried and Roman, 1983). The ability of detritus to support zooplankton growth is largely speculative.

The chemical composition of particulate matter affects copepod production over a range of scales. For example, the chemical composition of particles can determine how far a copepod perceives and actively grazes a particle (Paffenhofer and Van Sant, 1985). Once caught the chemical composition or "taste" of a particle can determine whether the particle is consumed or rejected (Poulet and Marsot, 1980). There are probably specific compounds such as amino acids which stimulate copepod feeding (Heinen, 1980; Poulet and Marsot 1980). Thus ingestion rates of particles of higher nutritional value (more protein) are often greater than the ingestion rate of particles of lower nutritional value (Houde and Roman, 1987; Cowles et al., 1988). Once ingested, a number of studies have shown that the chemical composition of the ration affects both somatic growth and reproduction. Unfortunately, because of compounding variables (presence or absence of a particular amino acid and fatty acid), we have little data on how

specific organic compounds affect copepod production. One possible way to elucidate the nutritional requirements of copepods is to measure copepod production on biochemically defined diets (Conklin and Provasoli, 1977). The ability of copepods to synthesise specific compounds (amino acids, fatty acids) could be assessed by the use of radio-labelled precursors (Kanazawa and Teshima, 1977; Morono et al. 1979).

c. Relations between food and ingestion

The primary influence of food on population dynamics is in feeding. A consideration of current knowledge of the influence of the four major characteristics of food, abundance, size, composition and motility, on ingestion rate is summarised in the table below.

	abundance	size	composition	motility
ingestion rate	++	++	++	+

(+ some knowledge, ++ extensive knowledge)

Each of these interactions is reviewed briefly below.

1. The effect of food abundance on ingestion rate

During their ontogenic development, copepods utilise a great variety of prey. Consequently, omnivory provides some adaptive advantages when food is scarce, while it induces a strong variability in the functional responses, in terms of growth and egg production (Huntley and Lopez, 1992). It is probably one of our most challenging objectives to estimate this variability and understand why it is so. Our next task is then to find how this type of

physiological variability influences the population dynamics of copepods.

Abundance of food determines ingestion rate, following a Michaelis - Menten relationship. This factor is coupled to the species and nature of prey (phytoplankton, heterotrophs, detritus) and to their intrinsic biochemical characteristics. It is likely that maximum ingestion rate (I_{max}) for a given food compound (i.e. proteins) varies with the abundance and size of the prey. This point will have to be verified. Furthermore, we still do not know if copepods select food, through behavioral mechanisms in order to maximise absorption or to obtain essential compounds required for growth and egg production.

New developments should be oriented towards a better identification of food heterogeneity and patchiness, which are some of the important aspects of food concentration in nature. These characteristics should be identified in relation to the specific requirements of copepods.

2. The effect of food composition on ingestion rate

Precursors in the food, which are essential, for example in hormones, vitamins or vitellogenesis metabolism, should be one of the next issues in studying the relation between food and ingestion. Toxic compounds, as well as inhibitors produced by phytoplankton, which have direct influence on feeding, or indirect effects on production, should also be identified. Their effect on growth and egg viability as well as on juvenile stages, should be estimated.

Neither chlorophyll a, nor carbon is a satisfactory index of food characteristics in our trophodynamic context. Food compounds, such as proteins or fatty acids, which have a direct influence on the metabolism should be used to identify food "quality", parallel to these classic indices.

3. *The effect of food size and motility on ingestion rate*

Behavioral aspects of feeding, and feeding mechanisms in copepods are influenced by size and motility of prey. The latter is related to carnivory and raptorial feeding and is probably the least known of food characteristics influencing ingestion rate.

Even though the relationships between food and ingestion have been studied in great detail from a qualitative point of view, it is considered that there is no satisfactory method to measure in situ ingestion. Moreover, measurements of ingestion have been biased by many artifacts in laboratory experiments. Consequently, results are difficult to extrapolate to trophodynamic models or to natural conditions. One of the major issues will be to improve our techniques and methods for accurately measuring both food characteristics and ingestion in the field.

d. Food and population dynamics

The effects of food on population dynamics are mediated by the feeding process, and in turn influence somatic growth, reproduction, development rate and mortality. A consideration of current knowledge of the influence of the four major characteristics of food: abundance,

size, composition and motility, on these four components of zooplankton population dynamics is summarized in the table below.

	abundance	composition
growth (somatic)	++	+
reproduction	+	+
development rate	+	+
mortality	0	+

(0 = no knowledge, + = some knowledge, ++ extensive knowledge)

Each of these eight interactions are reviewed briefly below.

1. Effects of food abundance on growth

The functional response of individual growth rate to food abundance has been studied extensively in the laboratory. It is well known that, below some critical concentration, metabolic costs exceed assimilatory gains and growth is negative; growth rate then increases with food availability to an asymptote (Vidal, 1980). This principle holds for all species that have been studied and, although the absolute values of the parameters may change from species to species, the phenomenon appears not to merit further intensive study.

2. Effects of food abundance on mortality

Food concentration could have very significant effects on mortality rates in natural populations of zooplankton, but the relevant mechanisms have received little attention and remain to be quantified. Possible mechanisms include starvation and increased susceptibility to predation.

The most extreme case of food availability leading to mortality is starvation. The complete absence of food obviously leads to starvation and ultimately to mortality; although a laboratory experiment is not required to demonstrate such an effect, it is not clear whether zooplankton experience complete absence of food in nature. Another mechanism that could lead to starvation is cell toxicity; certain phytoplankton produce chemical compounds that inhibit feeding and therefore, although food may be apparently abundant when measured as chlorophyll, the zooplankton may not be ingesting any of it. Such an effect has been demonstrated for *Phaeocystis pouchetii* (Weisse, 1983) as well as for certain dinoflagellate species (Sykes and Huntley, 1987).

A more subtle effect of food availability on mortality could be caused by partial starvation. Carlotti and Nival (1992) cite work on macrocrustaceans showing that, within each developmental stage, a certain critical weight must be attained in order to moult to the next stage. The accumulation of body weight depends upon cumulative ingestion. If the critical weight is not achieved in some critical period of time, the probability that the individual will moult to the next stage begins to decrease rapidly, until finally moulting becomes impossible and the individual is lost from the population. This mechanism is entirely unexplored in zooplankton. However, it could be a significant mechanism for causing mortality in natural populations. In an inherently patchy food environment, it seems reasonable that some fraction of the population might be unable to locate

sufficient food to acquire the critical weight necessary to moult to the next stage.

Another possible result of partial starvation is an increase in the susceptibility to predation. Individuals that are inadequately fed may be weaker, more sluggish, and hence less capable of escaping from predators. Furthermore, the longer an individual remains in a given developmental stage the greater the probability that it will be subject to predation, because early instars of zooplankton are disproportionately susceptible to predation (Lopez 1991 and references therein).

It has generally been thought that density dependence in zooplankton population dynamics was exerted entirely through effects on individual growth rate. In other words, reduced food concentrations should lead to reduced individual growth rate, which in turn would manifest as reduced productivity of the entire population. However, it is clear that this need not be the only mechanism of action. Density dependent effects could just as well be manifest through increased mortality resulting directly from low food availability. Such mechanisms remain almost entirely unexplored among the zooplankton.

3. Effects of food abundance on reproduction

It is well documented that food abundance has a direct effect on fecundity (Runge, 1984), with the functional response being asymptotic. However, there may be other effects that have not yet been elucidated. For example, there is reason to believe that a certain critical

amount of food needs to be ingested by any female in order to attain reproductive capability. This might account for observations that a large proportion of females in natural populations produce few or no eggs (R. Harris, M. Huntley, unpubl. data). This would be another example of how density dependence could control population dynamics without having any effect on individual growth rates; rather, it would exert effects through the control of reproduction.

Yet another mechanism which has only recently received attention is egg viability (Ambler, 1986; Ianora & Poulet, submitted), which directly affects reproductive success. It may be that the proportion of viable eggs produced by a given female depends on the amount of food it has ingested. A failure to acquire an adequate amount of food could result in eggs which do not have the necessary lipids or other essential chemical constituents required for normal development. This phenomenon requires attention.

4. Effects of food abundance on development rate

Food availability may directly affect development rate, although the importance of this mechanism in natural populations is not well studied. Laboratory populations exhibit such an effect, although only at very low food concentrations (Harris and Paffenhofer, 1976; Green, Harris and Duncan, 1991). The "Carlotti effect" of food availability on moulting success, alluded to earlier, may rapidly remove from the population a number of individuals which develop slowly within a given developmental stage.

Because these animals are taken from the population by mortality, their reduced development rates might not have a large effect on the apparent development rate of the population. However, if a large fraction of the population were on the threshold of starvation, yet were able to acquire sufficient food for continued development, the overall development rate could be significantly reduced. The magnitude of such effects in nature is not well known.

5. Effects of food composition on growth

In the absence of certain essential dietary components, it is clear that individual growth will suffer. While it is reasonable to believe that this is so, the specific nutritional requirements of zooplankton are not well known, and therefore the effects of a given diet on the dynamics of natural populations are difficult to predict.

6. Effects of food composition on mortality

Chemical composition of food could have a direct effect on mortality, but again, knowing so little about the dietary requirements of zooplankton makes it difficult to predict how common such effects might be.

7. Effects of food composition on reproduction

It is clear that fecundity is directly related to food composition. Laboratory experiments have established that egg production varies in accordance with the type of phytoplankton food presented (Gill and Harris, 1987; Uye and Takamatsu, 1990). Whether such a mechanism has an

important influence on natural populations is largely unknown, given that natural particulate assemblages rarely consist of a single species of food particle.

8. Effects of food composition on development rate

Chemical composition of food can have a significant effect on the development of nauplii reared in saturating concentrations of ten different dinoflagellate species exhibited a wide range of difference in development rate, over almost one order of magnitude (Huntley, Lopez and Ciminiello, 1987). However, the importance of such effects in field populations is not well known. Again, the generally wide variety of food particles available in any marine environment suggests that such effects may not be as important in nature as they are in artificial environments created for laboratory experiments.

e. Research priorities

A list of priorities for GLOBEC research on the role of food in the population dynamics of copepods is given below. The list is not in order of priority.

Inter - and intra - patch functional response

Following the work of Dagg (1977) and Sciandra, Gouze and Nival (1990) considerable further work needs to be done on interactions with patchy and discontinuous feeding regimes if the significance of micro scale patchiness for population dynamics is to be understood.

Effects of food abundance on mortality

Carlotti and Nival (1992) have shown that, in some cases, within each developmental stage, a certain critical weight must be attained in order to moult to the next stage. Accumulation of body weight depends upon cumulative ingestion. If the critical weight is not achieved in some critical period of time, the probability that the individual will moult to the next stage begins to decrease rapidly, moulting becomes impossible and the individual dies.

Nutritional requirements of copepods

A concerted effort needs to be made to define biochemical components of the diet that are essential for copepod growth and reproduction.

Effects of food abundance and composition on reproduction

Despite the existing body of work (e.g. Runge, 1984; Ambler, 1985) many aspects of these relationships require firm quantification.

Nutritional induction of diapause

Many key copepod genera have complex life-histories, which involve diapause, or resting stages. The influence of food conditions on this important aspect of population dynamics is generally unknown.

Egg viability : relations with food

The work of Ianora and Poulet (submitted) indicates that this is a priority research topic.

Critical mass for fecundity

In the same way that, during growth, a copepod may need to achieve a certain body mass before it can move to the next

stage, an adult female may not reproduce unless a critical mass is achieved.

Food effects on sex ratio

The availability of males, and hence sex ratio, must be an important component of population dynamics. There are indications of nutritional effects on sex ratio, and this subject deserves further attention.

Trophodynamics of nauplii

Despite some recent studies (Fernandez, 1979; Green, Harris and Duncan, 1991; Paffenhofer and Lewis, 1989) copepod nauplii remain a neglected field of study. These early developmental stages form a largely unknown proportion of the microzooplankton, and it is likely that many effects of food on mortality and development rate are particularly significant during these critical early life history stages. Further quantitative work on the role of food in naupliar biology may be of major importance in advancing our understanding of zooplankton population dynamics.

2. Experimental studies related to PDPV objectives

(Jeffrey Runge)

Field and modelling components of the GLOBEC PDPV program will require experimental studies for conceptual development, interpretation of observations at sea, and determination of coefficients in model equations. Focus of the experimental work should be on the processes and coefficients implicit in the fundamental equation:

$$dN / dt = N (\text{birth} - \text{swimming} - \text{advection} + \text{diffusion} - \text{death})$$

Several questions warranting immediate study have been identified:

1. What is the role of small-scale turbulence on predator-prey interactions? Development of experimental techniques and improvement of physical understanding of turbulence at small scales will accelerate testing of the relevant hypotheses.
2. What are the generation times of species of interest as a function of temperature and appropriate food?
3. What factors determine egg viability? Biochemical composition of the diet, bacteria and contaminants in the water column may be important sources of variability in hatching success. The sensitivity of egg viability to experimental manipulation should be investigated, with the aim of establishing a standardized technique for determination of egg viability in field populations.
4. What are the functional relationships of growth and reproduction to food concentration? There is an important problem regarding the measurement of appropriate food concentration, as the biochemical composition of the optimal diet for any particular zooplankton species is not known. Determination of growth and reproduction rate using a single food species is not sufficient; a variety of concentrations and mixtures of food, either natural particulate material or cultured algal and microzooplankton species must be tried.

Two levels of experimental studies could be undertaken:

- a. measurement of maximum growth and egg production rates only for species of interest. The maximum rate could be defined as the highest mean rate from the various food combination experiments.
 - b. functional relationships of growth and egg production, involving determination of threshold and critical concentrations, using an appropriate food combination. Experiments of this nature should be done with continuous collaboration of modellers, in order to ensure that they provide the knowledge essential to the modelling effort.
5. What are the physiological mortality rates of laboratory-reared copepods? These data will allow understanding of the importance of physiological mortality in the field populations.

3. Sources of variation in the populations of zooplankton

(Larry Hutchings, Mark Ohman, Gus Paffenhof, Jeffrey Runge)

Introduction

Zooplankton populations vary on many time scales. Here we focus on the scale defined by the generation time of the animals. We recognize that GLOBEC is also interested in variability on considerably longer scales, in the context of global change research. Our premise is that the mechanisms of action of longer time scale variations (e.g., El Niño to Climate Oscillations) can be understood

from the way a changing physical environment interacts with the population processes that we describe here. Because advective and diffusive terms are addressed by another working group, we focus our attention on biological sources of population variability.

Simplified description of population growth

A generalized description of population growth of a holoplanktonic animal can be considered as follows:

$$dN/dt = (\text{birth} - \text{death} - \text{behavioral migration} - \text{advection} + \text{diffusion}) N$$

where each of the terms in parentheses is expressed as a per capita rate. (Examples of behavioral migration are the ontogenetic ascent of copepods that have recently emerged from diapause in deep waters, the horizontal migration of Antarctic krill from beneath the pack ice to open water, etc.)

To focus attention on biological sources of variation within a population we need to define a "population" on a large enough scale such that the advective and diffusive fluxes are relatively small, or at least tractable. Consider a control volume in which the population of interest will be studied. Ideally the control volume will be large enough that the residence time of water and animals (τ) is long relative to the generation time (T_{gen}) of the animals of interest. That is, we seek to meet the condition that:

$$\tau > T_{\text{gen}}$$

T_{gen} is defined operationally as the time from egg to egg.

Approximate generation times for zooplankton taxa in mid-latitudes are:

	T_{gen}
Calanoid copepods	20-40 (180) days
Salps	3 - ? days
Euphausiids	4 - 12 months

In the case of calanoid copepods the generation time can increase markedly if there is a diapause phase of the life history. Thus, having chosen the target species of interest, the physical dimensions of the control volume can be chosen to meet the criteria of given above. Operationally, one may need to relax these criteria to some extent or to shorten the study period to some fraction of the generation time (e.g., the active growth season of a diapausing population). However, two other considerations are that:

- one may be interested in several multiples of T_{gen} , to examine intergeneration differences in processes regulating the population, and
- that for coupled prey - predator studies, T_{gen} of the planktivorous predator (e.g., ctenophore or fish) must also be taken into account.

Stage structured population growth

If we consider a planktonic copepod population the birth and death rate terms must be expressed for a stage-structured population.

Schematically this can be expressed as:

$$dN_{(i)} / dt = (R_{(i)} - R_{(i+1)} - d_{(i)}) * N_{(i)}$$

where: $N_{(i)}$ is abundance of the i th developmental stage

$i = 1 = \text{egg}$
 $i = 2 = \text{nauplius I}$
 \vdots
 $i = 13 = \text{copepodid VI}$

$R_{(i)}$ is recruitment rate to the i th developmental stage

$R_{(1)}$ = birth rate

$d_{(i)}$ is death rate for the i th developmental stage

Population growth, and variability can then be considered in terms of the Input ($R_{(i)}$) and the Mortality terms ($d_{(i)}$) that vary with stage of development.

Input terms

Input terms may, in principle, be density-dependent. Although density - dependence of birth and recruitment rates is of considerable theoretical interest (e.g., Rothschild, 1986), we do not explicitly consider population density as an independent variable below because the evidence for density-dependence is scant for marine zooplankton populations in nature. This subject warrants additional attention.

$R_{(1)}$ --- Birth Rate

Variations in $R_{(1)}$, the birth rate term, take on considerable importance for GLOBEC studies. Copepod fecundity needs to specified as a function of:

- temperature
- concentration of appropriate food(s)
- in situ distribution of food (e.g., vertical layers and horizontal patches)
- size distribution of females
- stage structure of the female part of the population

The last factor -- female stage structure -- is important because there may be periods of several days before newly moulted females begin to produce eggs, and there may be appreciable periods of time between clutches.

Resting (or "diapause") eggs are produced by some taxa and must be considered as a separate input term to the population. For shallow continental shelf and estuarine study sites, where copepod taxa that produce diapause eggs sometimes occur, the factors regulating the production of and subsequent emergence from resting eggs need to be considered (e.g., Marcus 1990).

$R_{(2...4)}$ --- Recruitment to NI... NIII
(where NIII is often the first feeding stage)

For many species, recruitment rate to stages NI - NIII can be expressed as a function of temperature alone. This rate is proportional to (1 / stage duration).

$R_{(5...13)}$ --- Recruitment to NIV...CVI

For developmental stages that continue development without entering a period of dormancy, recruitment rate can be expressed as a function of:

- temperature
- concentration of appropriate food(s)

If animals do not develop continuously but undergo a period of seasonal dormancy, then predictive relationships are needed for the seasonal timing of the onset of and emergence from dormancy. These dormancy responses might be

predictable as a function of daylength and temperature.

Mortality terms

We consider mortality rates as having 2 primary components: physiological mortality (arising from inadequate nutrition, deficiency of essential metabolites, exceeding thermal optima, pollution, etc.) and predation mortality. Physiological mortality is likely to be independent of population density. The predation component may or may not be density-dependent.

$d_{(1)}$ --- Egg Mortality

Mortality of eggs may occur from lack of fertilization. In addition, egg mortality needs to be expressed as a function of:

- physiological state
- predation
- cannibalism
- parasitism

$d_{(2...13)}$ --- Mortality of NI...CVI

Mortality rates of postembryonic developmental stages need to be expressed as a function of:

- physiological state
- invertebrate predation
- vertebrate predation
- parasitism

For feeding stages, physiological state may be influenced by the nutritional history and lipid content of previous developmental stages.

It is essential to note that there is usually a strong stage-specific and

size-specific component to mortality. The types of predators may vary markedly for different developmental stages of copepods (e.g., invertebrate predators could be more important for younger developmental stages and planktivorous fish more significant for older developmental stages).

There are also important inter-specific contrasts in sources of mortality. For example, in some environments small copepods may be more susceptible to carnivorous zooplankton and large copepods more prone to capture by planktivorous fish.

Measurements needed

We will point very briefly to the techniques that are available to measure the functional relationships identified above. More importantly, we identify the areas where concepts and measurement techniques are not available and require substantial infusions of new ideas to become useful for GLOBEC field studies. The areas where new developments are particularly sorely needed are:

- parameter estimation techniques to obtain mortality rates for natural populations and
- quantifying rates of predation on copepod populations in situ.

The mortality side of the population dynamics equation has historically seen much less attention than growth and development in marine zooplankton studies and will require major new efforts.

Birth rate

The two general approaches that are available for birth rate estimation are:

- incubation experiments and
- the Edmondson egg ratio method

Elsewhere this workshop report identifies specific refinements and improvements needed to make accurate measurements of egg production rates from these two methods. Overall we find that these methods are relatively mature, do not require advanced technologies to perform, and will be widely accessible for GLOBEC studies.

Recruitment rate

For "recruitment rate" measurements, generally equivalent to the moulting rate from developmental stage to stage, we again feel that suitable techniques are available. Development rates as a function of temperature and food concentration can be determined from laboratory incubations. Moulting rates have been determined for a number of natural populations. Although there are assumptions of the moulting rate method that require further attention, these are probably resolvable in the foreseeable future.

Mortality rate

Total mortality, encompassing both physiological and predation mortality, needs to be quantified because we cannot decide a priori which will be the most significant component.

Methods for estimating mortality rates are best developed for two extreme cases:

- where there are discrete, nonoverlapping cohorts, or
- continuously reproducing populations that have attained a stable age distribution.

In practice most copepod populations fall between these two extremes, where parameter estimation techniques are the least well developed. Techniques in current use derive partly from freshwater zooplankton studies or from the insect literature, and require more refinement for application to marine populations. We wish to call attention to the need for:

- **Mortality Estimation Models**
(from horizontal life tables)
Techniques based on the von Foerster equation, after smoothing raw data (Wood and Nisbet, 1991), may prove useful. Other approaches need also to be developed with specific applicability to the sampling constraints for marine zooplankton populations.
- **Unbiased estimates of stage duration**
(for incorporation in mortality rate estimations)
Models for mortality rate estimation generally require independent knowledge of durations of developmental stages (Hairston and Twombly 1985) and tend to be quite sensitive to these values. For populations developing at temperature - dependent, food - satiated rates, these can be estimated from laboratory experiments. Otherwise stage durations can be estimated from moulting rate incubations in natural seawater.
- **Vertical Life Tables**
Even populations that grow discontinuously may have time intervals when the assumptions of stationarity apply (Mullin, 1991). Vertical life tables may be useful for

parameter estimation over these intervals, and need further exploration.

- **Evolutionary Stable Strategy (ESS) approach**
In some cases variation in mortality rates over time may be consistent with the ESS approach tested by Myers and Runge (1983). Mortality rate is predicted from life history traits (including body size, weight at maturity, temperature-body size relationships, etc.). There is a critical need for sensitivity analyses to be conducted prior to field studies to address the following questions vis-a-vis mortality rate estimation:
 - What level of simplification of the stage structure of a population (i.e., developmental stage aggregation) can be made while retaining stable estimates of mortality?
 - What frequency of sampling and extent of replication are required to obtain sufficiently precise mortality rates?

Predation rate

A multitude of studies, weighted toward limnology, have illustrated that aquatic predators are highly selective and have significant consequences for structuring assemblages of zooplankton (e.g., Kerfoot and Sih, 1987). Predation studies need to assess sources and rates of predation on copepod populations in situ. Special attention is needed to address the roles of carnivorous zooplankton and planktivorous fish. Different sampling techniques and technologies are needed

for these two disparate groups of predators.

Where the important carnivorous zooplankton are gelatinous and difficult to capture by conventional pump and net technologies (e.g., ctenophora, medusae, siphonophora), specialized means will be needed to obtain accurate estimates of their abundance and vertical distribution, and to characterize their foraging behaviour and prey selectivity in situ. These might include diving, remotely operated vehicles, and other submersibles.

Injury frequency analysis has been explored in freshwater (Murtaugh 1981) and marine (Ohman 1986, Beyer 1992) zooplankton studies and may prove useful in inferring either mortality rates or seasonal timing of attacks.

Fish Predation

A strong linkage is needed between zooplankton and fish studies. We feel that understanding the variability of zooplankton populations will be severely compromised in the absence of serious attention to predation by fishes, as well as by carnivorous zooplankton. The most significant sources of predation may be from juvenile or adult fishes, rather than from larval fishes alone. Moreover, commercially important fish may not be the only (or even most significant) source of fish predation, requiring attention to the dominant planktivores in the ecosystem of interest as a problem in fish ecology rather than fisheries management alone.

Specific highlighted concerns

1. Since all of the rate terms of interest are expressed per capita, they also

require accurate measurements of copepod abundance. Both numbers of animals and their vertical distributions need to be well resolved, since the latter influence the temperature values required for many rate functions.

2. Sampling of prey and predators needs to be conducted on the same time and space scales. This is currently feasible for copepods and some carnivorous zooplankton taxa, but not for planktivorous fish. New technological approaches are needed because existing fish trawling techniques are not adequate and acoustic methods rarely resolve both fish and zooplankton simultaneously and unambiguously. Optical techniques will probably be best suited to resolving target zooplankton species in the same water column where fish are being censused by acoustic means.

3. We wish to call for a close partnership with fish ecologists, from conception through the completion of GLOBEC field studies. Without this partnership we will not properly close mortality terms.

4. Sources of trends in the populations of zooplankton

(John Gamble and Geoff Laurence)

Time Frame

It is possible to discern interannual trends in populations of zooplankton which in themselves should be regarded as the long term resolution by the populations of short term variability. In the first instance the problem is how to recognise such a trend in a multispecies population and, in particular, what is the time frame necessary for establishing its

presence? Experience with the Continuous Plankton Recorder (CPR) Survey, which is concerned with describing the spatio-temporal patterns of about 200 zooplankton taxa, suggests that 15 - 20 years of data are required before trends become apparent, i.e. we are considering a decadal time base.

Causes of Trends

Once established, the immediate question must relate to the cause of the trend, or at least what independently observed change in the environment correlates with the trend? As most trends are observed on large scales, either in time or in both time and space, most explanatory causes must be in the same context.

1. Anthropogenic influence.

The long term impact of pollution and exploitation of resources on pelagic populations are not easy to establish although, intuitively, such effects must exist. They are only likely to be discernible on small scales and particularly in localised situations. There has been a change in the phytoplankton population structure off Helgoland, North Sea (Radach et al, 1990) which correlates with increasing nutrient loading in the German Bight.

2. Hydrographic effects

It has long been recognised that specific plankton assemblages can be associated with different water masses and, as such, are indicators of alterations in the customary hydrographic regimes of specific areas. The CalCOFI time-series, which was initiated in 1949, has shown that zooplankton biomass in the California Current is strongly correlated with the

mass transport of cold, low-salinity water from the north (Chelton et al., 1982). These zooplankton fluctuations may reflect advective input of the higher northern zooplankton biomass into the area and/or local changes in response to flow - related nutrient input (Chelton et al., 1982). Such effects are characterised by their relatively short term nature and the rapid reversion (within a year) to normality after the passing of an event. Dickson et al. (1992) were able to associate increases in the abundance of dinoflagellates in the northern North Sea with an incursion of low salinity water from the Baltic. This was manifest over three years after which the dinoflagellate abundances declined to normal levels.

3. Climatic Effects

While the consequences of anthropogenic impact (when related to environmental contamination) and hydrographic change are potentially reversible within a season, true long term changes, which are interannually persistent and spatially coherent at the oceanic basin scale, can only be attributed to climatic change. Such climatic effects are not immediately reversible although the direction of the trend can change; in fact cyclical responses are characteristic of climate induced trends. The long term decline in the abundance of the trend of North Atlantic zoo and phytoplankton (CPR, 1992), the changes observed in the zooplankton of the North Pacific (Venrick, et al., 1987; Brodeur and Ware, 1991) and the coincidental declines in the zooplankton (Carrasco and Lozano, 1989) and anchoveta (Pauly and Palomares, 1989) off Peru have all been attributed to pelagic ecosystem responses to climate change.

4. Trophic Displacement

It is also probable that some long term trends in zooplankton populations can be attributed to the change in species dominance as a consequence of interspecific competition, i.e. changes do not necessarily have to be attributed to a specific external cause. Such changes will take place mostly over evolutionary time but where alien introductions are implicated, e.g. ctenophores in the Black Sea (Mee, 1992), the change in the structure of the pelagic population can occur with great rapidity.

Relevance to GLOBEC

GLOBEC seeks to understand some of its major objectives (discussed elsewhere in this Report) in the context of the global climate system and anthropogenic change. Most of the target studies will be of relatively short duration so, to establish the global climate context, we need evidence that observed changes in marine pelagic ecosystems can be attributed to climate change. This can only come from the assiduous monitoring of plankton populations over a wide scale. However the current understanding as to how climate affects plankton populations is largely conjectural as most claims at climatic effects are based on correlations and the causative mechanisms are subsequently assumed. It should be an aim of GLOBEC to provide a better understanding of the short-term processes and interactions between physics and biology which inevitably sum up to the long term climatic consequences.

Recommendations

GLOBEC must:

- support existing long term pelagic time series
- integrate the results of targeted investigations with those from long term time series
- encourage the development of new planktonic time series on a world wide scale
- promote the development of unified global data bases for long term time series

Methodology

- the global plankton monitoring system must be seen to be an integrated balance between basin scale spatio-temporal systems and fixed point monitoring programmes
- new generation CPR monitoring systems need to be developed which maintain the integrity of the existing data bases but which provide additional information for integrating with short term targeted process studies.

5. Population variability in the North Atlantic

(John Gamble)

Support should be given for further examination of the multidecadal data base of the Continuous Plankton Recorder (CPR) Survey of the North Atlantic. While much information has been derived from this survey on biogeographical patterns, basin-scale seasonal changes and long term trends of mixed layer plankton populations, much more information resides in the database. In particular, use

of past and current CPR data by GLOBEC during the planning and execution of programmes in the North Atlantic will provide a unique opportunity to define their context and widen their scope. In addition to applying new analytical techniques for evaluating archival CPR data, it is recommended that the Sampling and Observations Systems Working Group of GLOBEC consider specification for the design of a new generation of Plankton Recorder which maintains the integrity of the existing system but includes new and wider sensing and storage capabilities.

6. Copepod grazing rates (Bill Peterson)

One of the fundamental measurements that must be made in any study of energy flow or trophodynamics is the rate at which carbon is transferred through each trophic level. In marine food chain research, hundreds of studies have been made on the rate at which copepods graze phytoplankton. From all of this work, one would hope that it would be possible to write a general equation for copepod grazing in any trophodynamics model. Several such equations have been written; one popular form is the Ivlev equation:

$$I = I_{\max} (1 - e^{-aP})$$

where:

- I is the ingestion rate (mass of phytoplankton ingested per expressed in terms of carbon);
- I_{\max} is the maximum ingestion rate,
- a is the Ivlev constant describing the curvature;

- P is the concentration of phytoplankton (units of carbon per unit volume).

It is fairly easy to estimate the Ivlev parameters in the laboratory by measuring ingestion rate at several different food concentrations, using unialgal cultures and a Coulter Counter. The parameters of this equation have been determined for a number of copepod species in laboratory studies (Mullin et al., 1975; Peterson, 1988). The equation is commonly used in models (Franks, Wroblewski and Flierl, 1986).

In principle, it should be easy to combine the laboratory results of grazing by different copepod species on various algal sizes into one single equation by adding coefficients that account for differences in ingestion rate as a function of body weight. Thus, I_{\max} and a could be multiplied by coefficients that correct for differences in body weight between species and developmental stages. However, these coefficients are not known and no such general equation exists.

Another challenge is to develop equations that can be applied to populations in the field. In practice it is extremely difficult to describe copepod grazing in situ because a large number of variables can affect parameter estimation (Huntley, 1988). These include not only food concentration, but also (among others) species composition, size, nutritional quality, and possibly turbulence. In the sea, copepods do not live in a unialgal culture, rather they live in a soup of particles including phytoplankton cells, protozoan cells and other small microzooplankton. At this point in time,

we cannot measure the total amount of material a copepod in the sea ingests each day; there are too many technical difficulties (including, for example, the delicate nature of many single-celled organisms). Modelling the very sophisticated behavioral responses to the wide diversity of food particles and environmental conditions is also problematic. As a consequence, reliable general models of copepod ingestion rates in the sea do not exist.

There is, however, a simple way to estimate and model the total amount of mass ingested by copepods each day. The method involves estimation of ingestion from measurements of growth rate. The two are related by the gross growth efficiency in the following manner:

$$\delta W = k I$$

where δW is the amount of weight that all individuals of a given developmental stage gain each day (production), k is the gross growth efficiency, and I is the mass of material ingested daily. Growth rate, g , for stage i can be estimated from

$$g_i = \ln [(W_i + \delta W) / W_i]$$

Growth rate can also be estimated from incubations in which the proportion of animals moulting per day is measured. Once the moulting rate is known, the growth rate is calculated as follows:

$$g_i = \ln (W_{i+1} / W_i) M$$

where g is the growth rate, W is the weight of adjacent developmental stages and M is the moulting rate. Growth of all

individuals in a developmental stage is given by:

$$P = g_i B_i$$

where P is production rate, g is the growth rate and B the biomass. Once production is estimated for all species and stages, total copepod ingestion can be calculated, provided the gross growth efficiency, k , is known (Peterson et al., 1991). Gross growth efficiency appears to be remarkably constant (0.35 - 0.45) in copepods (Mullin and Brooks 1970; Checkley, 1980; Berggreen et al., 1988; Kiorboe, 1989).

The maximal growth rate of copepods

Huntley and Lopez (1992) have shown that the growth rate, g , of copepods can be displayed as function of temperature, T , ($g = 0.0445 \exp 0.1117 T$) in both field observations and laboratory experiments (where the animals were probably well fed). Figure 1 shows the relationship (a) for the laboratory material (b) for the field observations and (c) for both. There is no difference between the two regressions.

In Figure 1 b, which represents the field data there are differences in growth rate at any one temperature which may be due to food. This confirms the general view that differences in the growth rate of copepods may be rather low. But on spatial scales of hundreds of km, temperature may be a sufficient predictor of growth rate.

Our purpose is a bit different, to investigate variation in the vital parameters. It might be desirable to continue laboratory determinations of maximal growth rate from a **diverse diet** at

fixed temperatures and to investigate growth rate at sea as function of food and temperature.

Physical processes

1. Modelling Physical Processes

(T.Dickey, M.J.R. Fasham & T.Platt)

1. Modelling the annual cycle of mixed layer depth

One of the most important variables for ecosystem models is the mixed layer depth. During the 1970's and 1980's considerable efforts were devoted to both the modelling and observation of the mixed layer. Early models were based on fundamental conservation equations in integral form. These so-called "integral" models (Krauss & Turner, 1967; Nüiler et al., 1977; Price et al., 1986; Gaspar, 1988) utilise empirical data for entrainment parameterisation. These models require initial temperature profile data and surface boundary conditions for heat and momentum fluxes. A major assumption is that the mixed layer is uniform in temperature. These models are quite computationally economical and are often used in 3-D models for this reason. However, for ecological models it may preferable to have several computational grid points within the mixed layer. During the 1970's, 1-D mixed layer models of a different variety evolved. So-called "turbulence closure" models were developed for engineering, atmospheric, and oceanographic applications (Mellor & Yamada, 1974, 1982). These models solve the fundamental thermodynamic and momentum conservation equations using finite difference schemes. The number of grid points in the vertical dimension can be selected to be as great as desired and

the distribution can be taken to be logarithmic (i.e. more grid points near the surface) to optimise resolution where desired. The fundamental closure is accomplished by using empirical constants derived from laboratory experiments (i.e. not tuned to oceanic conditions); initial and boundary conditions must be provided as for the integral models. While integral models treat the mixed layer as a slab, which may rotate uniformly, the turbulence models produce vertical structure in all properties.

Several comparisons of these classes of mixed layer models have been done by simulation of seasonal forcing (Martin, 1985). The basic features modelled, sea surface temperature and mixed layer depth, are well represented using either class of model. The trade-offs are:

- integral models are simpler to use and computationally more efficient, and
- turbulence closure models are more amenable to ecological applications which need to represent vertical structure in biological variables and currents. It should be noted that with advances in computing power the use of turbulence closure models is not particularly burdensome in terms of CPU time.

2. Inter-annual variability in mixed layer depth

Inter-annual variability in onset of thermal stratification is well-known to any oceanographer who has tried to study the onset of the spring bloom. As this variability is directly linked to the variability in meteorological conditions it is unlikely that a model of this process will be possible in the near future. However,

suitable time series observations can be studied (e.g. Bermuda Hydrostation "S", Bermuda Atlantic Time series, BATS, Ocean Weather stations "India", "Lima", and "Papa") to determine the statistics of the variability in mixed layer depth for use in model sensitivity studies.

3. 3D Model and sub-grid scale parameterisations

Few attempts have been to model 3-D physical processes on scales of direct relevance for individual zooplankton. Presumably, models on space scales of mm (or less) to at least a few kilometres in the horizontal and a few hundred metres in the vertical are needed. The number of grid points required for such a direct numerical integration of the conservation equations is indeed computationally prohibitive at this time. Even simulation of a volume of 1 m^3 requires several hours of supercomputer time. Thus, it is likely that ecological modellers, like their physical compatriots, will have to resort to sub-gridscale parameterisations of small scale processes. This is particularly annoying as we attempt to model zooplankton and their interactions with phytoplankton and each other. While treatments of phytoplankton in a continuum sense may be reasonably acceptable (Lande and Lewis, 1989), the same is clearly not true for mesozooplankton and higher trophic level organisms and so Lagrangian models may be required (Wolf and Woods, 1987).

Mesoscale physical models are clearly important for GLOBEC interests and models with a resolution of 30-40 km have been developed (Webb et al, 1991). However, local upwelling and downwelling need to be well-represented as do

convergences and divergences and so models with space scales down to 0.1 km will need to be developed (Onken, 1992). One may think of the vertical mixed layer and mesoscale models as providing the template for the nutrient, phytoplankton and zooplankton distributions and their evolution in a gross sense. However, the important individual organismal information cannot be obtained or modelled using continuum approaches as nearest neighbour distances are excessive (Rothschild, 1992). Further, behavioral effects are likely to be important as are motility attributes.

Just as 1-D models can simulate physical and diurnal seasonal cycles quite well on coarse time-scales, it may be that bulk biological models may do well for phytoplankton and, to a lesser extent, zooplankton. However, it will be extremely difficult to model zooplankton populations which may wax or wane in response not only with physical conditions but also inherent variations in mortality, grazing pressure etc. Clearly, good fidelity of physical models is required to at least provide nutrient, phytoplankton and zooplankton transport information, as other sources and sinks (predation, mortality) within a given control volume will be difficult to estimate observationally. Complications to be considered include vertical and horizontal advection, sinking rates, and differential motion of large versus small organisms.

4. Recommendations

- A turbulence-closure model of mixed layer development should be made available to the GLOBEC community as a vehicle for modelling the seasonal cycles of phytoplankton zooplankton coupling.

- An analysis of suitable time-series observations should be made to provide statistics on inter-annual variation of mixed layer depths and the onset of springtime thermal stratification.
- A theoretical/modelling study should be carried out to determine the best sub-gridscale parameterisations for phytoplankton and zooplankton.

2. The Physics and Biology of Decoupling (M. J. R. Fasham, T. Platt, and T. Dickey)

Decoupling is defined as any situation in which a predator population is unable to increase its grazing pressure to match an increase in the prey growth rate with the result that there is a large increase in prey population. An example is the spring phytoplankton bloom in the temperate North Atlantic, the result of which is that summer nitrate levels are invariably less than 1 milli Mole m^{-3} . In contrast, in the subarctic North Pacific the zooplankton appear to match the increase in algal growth with the result that a spring bloom never occurs and nitrate levels remain high throughout the summer. Note that the grazing pressure on the prey is the product of the predator grazing rate and its biomass and so this matching could either be brought about by the grazers having a high growth rate or high biomass. The latter case could be attained if conditions are such that over-wintering zooplankton concentrations are significantly higher in the North Pacific compared to the Atlantic. The various hypotheses that have been advanced for the dramatic differences between the two oceans have been the subject of number of recent reviews (Parsons & Lalli, 1988; Miller et

al., 1991 a, b; Cullen, 1991). The theories may be summarised as below.

1. Differences in physical structure

The differences in meteorological conditions and basin structure mean that there is no Atlantic type deep mixing in the North Pacific so that there is a permanent halocline at c. 150m (Warren, 1983). Evans and Parslow (1985) suggested that this meant that a significantly higher winter primary production was possible in the North Pacific compared to the Atlantic with the result that over-wintering zooplankton levels were sufficiently high at the time of the spring stratification for grazing rates to match algal growth rates. This hypothesis has much to commend it as it relies on an obvious and permanent physical difference between the two oceans.

2. Difference in the algal growth rates

Martin & Fitzwater (1988) suggested that algal growth in the subarctic Pacific is limited by iron not nitrogen. This would explain the high summer nutrients although it is unclear as to whether this would explain the lack of a spring bloom. In contrast, iron does not seem to be limiting in the subarctic North Atlantic (Martin et al., 1993). However recent results have not conclusively shown that the common algae in the North Pacific have significantly lower growth rates and they do not seem to be iron limited (Morel et al., 1991). However, there is evidence that iron deficiency may militate against larger phytoplankton and that may have important food web implications (see hypothesis 3).

3. Differences in the zooplankton grazing rates

Frost (1987) has shown from model studies that it is possible to reproduce the Pacific seasonal cycle by assuming a strong role for protozoan grazers with grazing rates that match algal growth rates (ca 2 d⁻¹). The major question that must be asked is why are protozoan grazers more important in the North Pacific compared with the North Atlantic? It may be that the lack of iron favours smaller phytoplankton and thereby a greater role for protozoan grazers (Miller et al., 1991 a). However the results from the JGOFS North Atlantic Bloom Experiment showed that the microplankton were also the dominant grazers of the spring bloom in the North Atlantic. It is possible, however, that the lack of iron limitation in the North Atlantic means that the phytoplankton population there consists of larger cells, compared to the North Pacific, that are less efficiently grazed by microzooplankton.

4. Differences in zooplankton mortality rates

Steele & Henderson (1992) studied a simple P-Z-N model and showed that if a quadratic zooplankton mortality function was assumed (in contrast to a linear function) then it was possible to generate either Pacific or Atlantic seasonal cycles by varying the constant of the mortality function. Other model results (Fasham, 1993; Slater et al., 1993) have shown that improved agreement between models and observations was obtained using a Michaelis - Menten function for the specific mortality rate. While these results have important implications for modelling in general they can only provide an explanation for the Atlantic - Pacific

difference if it can be shown why there are significance differences in herbivore mortality between the two oceans.

5. Differences in zooplankton life histories.

One of the early explanations for the difference was that the ontogenetic migration of Pacific *Neocalanus* populations was such that it enabled them to exploit the spring increase in algal growth rate as soon as it occurred (Frost, 1987). The work of the SUPER program showed that the biomass of *Calanus* was insufficient to account for the estimated grazing of phytoplankton in the spring (Miller et al., 1991 a).

Recommendation

A comprehensive modelling study should be made to investigate all the alternative hypotheses (and combinations thereof) for the differences between the North Atlantic and North Pacific seasonal production studies. To be acceptable as an explanation a model result must be robust to reasonable variability in either the parameters or the physical forcing and so special attention should be given to the sensitivity of the models to stochastic fluctuations.

3. Effects of turbulence

(T. Kiorboe, C. Marassé and H. Yamazaki)

1. What is turbulence and why worry about it ?

Oceanic turbulence is generated by shear due to winds, tides and currents or convective processes, such as night time cooling. Turbulence modifies the physical and chemical environment of plankters, and may have both direct and indirect effects on the zooplankton. The indirect effects are mediated by the effects of

effects are mediated by the effects of turbulence on the phytoplankton while the potential direct effects are due to enhanced predator prey contact rates, the potential roles of organized structures associated with turbulence and the possibility of receiving mechanical and chemical signals properly. Turbulence cascades the kinetic energy from large to small scale eddies. This scale is a minimum size of eddies, commonly referred to the Kolmogorov length scale, below which all turbulent kinetic energy dissipates as heat, and water motion can be characterized as laminar shear. Turbulence may have both organized (the correlated flow field) and unorganized (the uncorrelated flow field) components; these different components may have different implications to the zooplankters. Isotropic turbulence can be characterized solely by the energy dissipation rate, epsilon, and by the velocity spectrum, which tends to be almost universal (i.e., independent of how the turbulence was originally generated). In the following we shall first consider the potential indirect effects, then the direct effects and finally we shall recommend on possible research relevant to GLOBEC.

2. Indirect effects mediated by the phytoplankton

There is ample evidence that the size and species composition of the phytoplankton community is related to the vertical structure of the water column and, hence, to turbulence (Kiorboe 1993). Thus, dinoflagellates and small sized phytoplankters normally dominate in vertically structured, stable water columns while larger diatoms characterize partially mixed and, presumably, more turbulent water columns. Turbulence partly erodes vertical water column structure and, thus,

transport of inorganic nutrients from below the pycnocline into the euphotic zone. Turbulence also enhances nutrient uptake in phytoplankters by increasing the advective transport of nutrients to the cell surface. This effect is most pronounced for large cells. These two processes together relaxes the competitive pressure for small cell size in a turbulent environment. Finally, turbulence may be a prerequisite for nonmotile large cells to remain suspended. These potential effects of turbulence on the size and species composition of the phytoplankton have important implications to the availability of phytoplankton cells to mesozooplankton grazers, as is evident from previous chapters. There is also at least one potentially negative indirect effect of turbulence, in that turbulence may dissipate patches of elevated food concentration on which the copepods may depend.

3. Direct effects of turbulence

Copepods have three main obligations during their life span: to feed, to reproduce and to avoid being eaten by predators. The contact rates between copepods and their prey, between mates, and between copepods and their predators may all potentially be modified by turbulence. Also, transmission of "signals", whether chemical or mechanical, between plankton organisms may be modified by turbulence. There are both potentially beneficial and potentially detrimental effects of turbulence to these processes.

Turbulence may express itself in two fundamental ways, as uncorrelated flow field and correlated flow field (Yamazaki, 1993). The uncorrelated flow field can be

represented by the conventional random walk and is the model used by Rothschild and Osborn (1988). The correlated field is the source of organized structures. Students of fluid dynamics have found that such structures are dynamically important and have found associations of high dissipation associated with such structures. From a biological point of view, we suggest that such structures may act as a "landmark". For example, helical structures are known to persist in space and may help to transport chemical signals over a long distance (Figure 2).

3.1 Potential positive effects

With respect to feeding, both uncorrelated and correlated flow fields may increase feeding rate. The theoretical calculations of Rothschild and Osborn (1988) suggest that uncorrelated flow fields lead to higher particle encounter rates due to the superposition of swimming and the flow field via random walk. Subsequent modelling exercises (Yamazaki et al. 1991) have verified this, and have found that plankton encounter rates may be increased by as much as a factor of 10 by turbulence (MacKenzie & Leggett, 1991). In these models there is no behaviour component and no structure to the flow field.

In the case of a correlated component of the flow field, we suggest that copepods may seek out structures in the flow field and receive a benefit from chemical signals. They may be able to locate chemical cues from leaky phytoplankton cells in these structures. Another possibility is that they orientate themselves in the flow such that they may search a larger volume of water than they would if they were not in that flow and thus derive an energetic bonus.

Similarly, pheromone signals may be retained in organized structures and facilitate the location of a receptive female by the male. The uncorrelated component of the turbulence may disturb mechanical and chemical signals. In a turbulent environment zooplankters may thus hide from predators utilizing such signals to localize their prey (e.g. chaetognaths and predatory copepods). On the other hand, if the predators are larger invertebrates and planktivorous fish, using visual or acoustic cues, turbulence does not provide a refuge from predation. A special consideration of size dependence on the effects of turbulence may be considered as another important issue. However, we leave this size dependence problem open to a future consideration.

3.2. Potential negative effects

Feeding may be disturbed by strong turbulence. Also, the uncorrelated component of turbulence may disturb chemical and hydrodynamical signals from prey organisms. Finally, turbulence may interfere with the feeding currents of copepods in an as yet unknown way.

Microcosm experiments of Alcaraz et al. (1988) showed that in mixed chambers, copepod ingestion rates were higher and egg production rate lower (i.e. gross growth efficiency declined). We are not clear on the physics of all this but the suggestion is that copepods simply expend more energy trying to maintain orientation within the turbulence or to escape from the turbulent medium (Marrasé et al., 1990). In the ocean they simply drop down below the turbulent layer they cannot do this in a microcosm or mesocosm.

There are, thus, potentially opposing effects of turbulence.

4. Recommendations

There is very limited empirical evidence of the potential effects of turbulence (reviewed by Kiorboe, 1993) and thus a need to examine these experimentally. Future research should include:

- An experimental test of the Rothschild & Osborn idea. Generating turbulence in the laboratory in a way that realistically mimics the situation in the field is not trivial, although a qualitative assessment of the R&O model is judged possible. However, laboratory experiments should preferentially be followed up by field studies. In situ video techniques, that allow simultaneous observations of turbulence and copepod feeding behaviour are currently being developed. These techniques should be applied to thoroughly examine the plankton encounter rate hypothesis.
- Need to test interaction of food concentration with turbulence. At high food concentrations (greater than saturating) there may be no effect on ingestion although there may be an effect on gross growth efficiency. The effects of turbulence on the estimation of growth rate may be an interesting experiment to design.
- The effects of the structured component of turbulence should be further examined. There are as yet no techniques available to approach this experimentally, but numerical simulation studies may help us explore

this. The effect of zooplankton behaviour should be included in these models.

- There are some observations to suggest that the vertical distribution of zooplankters is related to the distribution of turbulence (Haury et al. 1990). There is a need to increase the observational data base, by doing simultaneous measurements of vertical distributions of zooplankton and dissipation rate (pumps, ROVs or acoustics with a free fall turbulence profiler).

4. Physics of grazing (Hide Yamazaki)

It is practically impossible to estimate the in situ grazing rate for a target copepod. However, conceptual models and laboratory cinematography observations help us to better understand the grazing physics of this animal. The grazing process can be decomposed into the following steps:

- searching;
- particle contact;
- handling;
- ingestion;

Rothschild (1992) considers the second and the fourth processes in his food signal theory which is a point of departure from simple particle contact rate arguments (Gerritsen and Strickler, 1977; Rothschild and Osborn, 1988). However, the searching and the handling processes have not received much attention.

Clearly, the searching process can significantly increase the particle contact rate if the animal uses "intelligent" tactics. The handling strategy can also alter significantly the total ingested amount. Therefore, all of four processes are significant for the total ingestion; as a result, the growth rate is also affected from the combination of these processes.

High-speed cinematography (Strickler, 1982) can reveal a striking moment in which copepods handle spiny alga in order to eat it properly. The whole process takes place in a blink of an eye. Two messages are clear from this observation: 1. the animal knows exactly how to handle the food; 2. the animal lives on a much shorter time scale than that of the human beings. Strickler (personal communication) also shows that the animal can differentiate between non edible and edible food. In general, copepods generate feeding currents in order to actively capture food. They can sense the existence of food at least within a distance of two body lengths in the feeding current, and can detect food in all directions within the feeding current.

Can we extend these findings to the real world, because the experiments were conducted in still water using a tethered animal? Two points in field conditions can potentially alter such an extrapolation:

- there exists small-scale flows due to turbulence around the animal;
- the animal is in a free swimming condition.

Although the interaction between the flow created by the animal and the existing physical flows is probably negligible, one may need to consider some animal may

have adapted to create a combined flow between its own flow field and the physical flow field. On the other hand, it is certainly important to study how turbulence plays a role in both searching and handling processes. In conjunction with the physics aspect of the searching process we must stress the importance of the animal's ability to detect a target particle, i.e. prey, predator and mate. We recommend developing an experimental plan taking both aspects into consideration.

When the Strickler film was shown, two physicists immediately suggested the use of queuing theory. Another point is that the array of hairs which are linked to mechanosensors around a copepod suggests that the animal may be able to detect deformations in the water at some range ahead.

If true, this would have consequences both for the detection of prey and for the avoidance of predators. A conclusion would be that a physical study of the microphysical field around a copepod would be very profitable. Indeed the boundary layer around the animal must be a place where particles collect.

5. Transport and dispersion processes

(P. Nival, T. Sugimoto and K. Hirakawa)

1. General comments

The size of a population depends on reproduction rate, natural mortality, mortality by predation and the flux of emigration and immigration.

$$dN/dt = r.N - m.N - V.dN / dx + K.d^2 N/dx^2$$

where:

N is the number of animals;
r is the reproductive rate;
m is the mortality rate;
V is the loss by advection;
k is the coefficient of dispersion in the x dimension.

Separation of the transport and dispersion terms depends on the scale at which processes are averaged which in turn depends on the spatial scale of the population under consideration. In order to estimate the growth and mortality of a population the physical loss terms must be known.

The generation time for a species (10 days to one year) is the time scale of interest. The spatial extent of the population, that is, the area which has to be studied, is related to the time scale and the current pattern.

In order to be able to estimate the population size (total number of organisms by stages) it is necessary to know the area over which the population extends. The characteristic length scale could be evaluated. Losses in the X, Y dimensions are mainly related to physical processes. In the Z dimension, however, the losses depend on the combination of animal behaviour (ontogenic or diurnal migration) and those physical processes which determine the advection and the vertical shear affecting turbulence profiles. The combination of behaviour changing during along the life cycle and 3D physical patterns are able to disperse and advect a population in a very complex way. The overall diffusion coefficient (D) could be very different from the turbulent diffusion

coefficient evaluated for a passive particle at a specific depth.

Description of the population:

The Eulerian approach is useful in areas where there is a permanent physical structure (for example, over an bank) or where the topography encloses part of the population. It is necessary to evaluate and monitor the fluxes at the boundary.

The Lagrangian approach is necessary when the transport dominates the hydrodynamics of the area in which the population lives.

2. Effect of Transport and Dispersion on growth and mortality

The long lived hydrodynamic structures, such as rings, fronts, etc. are places where the export term is either measurable or reduced and therefore growth and mortality terms could be evaluated.

2.1 Vertically mixed area in a stratified sea

Tidal mixing over banks is favourable to the growth of food and consequently to the development of zooplankton populations and fish larvae. The secondary circulation associated with the tidal mixing over the bank (inflow at the surface and outflow in the bottom waters) induces a dispersion of passive particles. However buoyant particles and vertical migrators could be concentrated in this structure.

The balance between the dispersion and retention depends on the intensity of stratification which varies with seasons. The behaviour of plankton is in this respect important. Passive young stages

could be more affected by dispersion than older stages which migrate.

2.2 Short term events

Aside from constant processes such as tidal currents, events like storms and intrusion of offshore water have to be studied. In some situations these short but energetic impulses to the system could flush out a large fraction of the population or at least decrease its food resource. These events could, in some situations, be more important to the long term variation of the population size than a constant transport or dispersion.

2.3 Jets and frontal structures

Frontal structures are usually associated with jet currents which are able to export part of the population under consideration. However, the perturbations of the fronts and the associated circulation can create favourable situations which reduce dispersion of populations able to migrate vertically.

2.4 Prey and predators

The physical pattern could affect the predatory mortality. In many cases plankton predators suffer the same transport and diffusion and hence predator mortality can be evaluated. However, depending on the behaviour of the animals the population of the species and its predators are dispersed differently. It is important to investigate simultaneously the prey and its predator and to study the matching of the spatial distribution of both categories of organisms.

It is important to know to what extent the area over which a population spreads is related to the features detected by thermal or visible imagery.

3. Estimation of mortality and growth in the field

Depending on the site and species of interest two methods are possible.

3.1 Eulerian approach

At a specific site (a bank, a bay, a section of continental shelf) the population could be estimated with an array of sampling stations. If the area is closed by a well defined boundary (semi-closed circulation and water body) the transport and dispersion could be possibly estimated with current meters and drifters. Moored current meters give the time change of current at selected depths and ADCP profiles should be used to assess the vertical pattern of the current.

3.2 Drifting population structure, where advection dominates

The Lagrangian approach is necessary in the open ocean where transport is dominant. The population should be surveyed on a spatial grid. The persistent horizontal dispersion term could be evaluated with an array of drifters. It is also necessary to evaluate the effect of storm events so some drifters should be used to investigate the trajectory of water masses and to calculate the export term.

The Transport and dispersion terms could be estimated from the study of the physical structure. On the other hand the feasibility of using large floating enclosures to estimate predatory and natural mortality over a short period of time might be evaluated.

Recommendations:

- There is a need for careful studies of the evolution in time of population

structure and physical patterns at selected sites, the size of which are related to the generation time of the target species. The area should be carefully selected so that a hydrodynamic survey and a continuous monitoring of the species be feasible. The time and space scale should be carefully defined for the set of species under consideration.

- It is important that target species, is studied at the same time as its food and predators. This is necessary to estimate the transport and mortality components of the population dynamics.
- There is a need for small scale studies of transport processes which directly affect the population dynamics, as well as the vertical distribution of physical properties.
- There is a need to define the process involved in the change of vertical distribution of species (buoyancy, diurnal and ontogenic migration).
- There is a need to develop new tools to monitor spatially a large water mass and monitor the short term events which might drastically affect the population dynamics. Accurate drifters with vertically programmable behaviour have to be designed to investigate the effect of 3D physical structure on space - time evolution of zooplankton species and fish larvae.
- Mesoscale models of physical structures which could integrate biological processes should be developed.
- It is necessary to study the feasibility of drifting large size enclosures in order to separate physical processes from biological

processes and estimate growth and mortality on short periods of time.

6. Persistent physical structures in relation to plankton population dynamics (Svein Sundby and Janet Grieve)

Whereas the geographical ranges of fish stocks are fairly well defined, the distribution of zooplankton may appear to be continuous from defined coastal regions up to the basin scale. Whereas fishes migrate back to their spawning grounds, zooplankton spawn where they find themselves; presumably the most successful are those that are transported by the flow field to environments favourable to egg production and recruitment. The question of how plankton populations are maintained within a favourable environment from generation to generation is not well understood.

Another major problem in zooplankton population dynamics is the measurement of rates of mortality. It would be easier to estimate mortality if defined cohorts could be followed through at least one generation. In order to do this we have to identify physical structures of a certain duration and manageable size. The minimum duration would have to be on the order of one month, depending on the temperature and species. The choice of the particular size of the physical structure will depend on the available logistical capabilities; the preferred length scale would be on the order of 10-300 km.

Of the listed features in Table 4, only a few permanent physical structures satisfy the above criteria: rings generated from baroclinic frontal instabilities,

topographically-trapped gyres, estuarine circulations, shelf break fronts, coastal upwelling zones of permanent character, and upwelling zones downstream of islands. For all structures the exchange of plankton across the boundaries has to be estimated.

Baroclinic eddies / rings and topographic gyres are closed systems (i.e., they define a specific water mass and its contained plankton population). The remaining structures allow advection of plankton populations in a way that is more difficult to follow. Although it could be of interest to follow populations in open systems, the two closed systems have many advantages for the estimation of variables determining population growth rates. It must be borne in mind, however, that both baroclinic eddies / rings and topographic gyres also have characteristics that may complicate interpretation of zooplankton population dynamics. For example, in topographic anticyclonic gyres new plankton may be transported continuously into the surface layers and be concentrated there. In addition, if the water column should become strongly stratified, the upper layer decouples from the lower layer and may be swept away.

In the case of an anticyclonic eddy/ring, in situ processes could unpredictably change the composition of the plankton populations. For example warm-core eddies in the Gulf Stream, in the East Australian Current, and east of New Zealand have been observed to become dominated by salps after a period of deep winter mixing and some form of spring phytoplankton growth.

7. Some characteristics of fjords

(G. Paffenhofer and S. Sundby)

Many fjords contain water masses below the thin brackish surface layer that resemble those of the nearby ocean. Lateral exchange is unidirectional and its magnitude and frequency are affected by the height of the sills. The sub surface water of the fjords with deep sills is strongly influenced by the dynamics of coastal processes outside the fjords. Shallow - sill fjords have calm deep water where replenishment by new oceanic water occurs in the order of years. All exchange processes may be monitored in the sill region and consequently the biological and physical variables are relatively easy to observe and to model. Fjords suitable for study of zooplankton population dynamics may be found in Norway (Balsfjorden), the Pacific Northwest (Dabob Bay; Saanich Inlet), Great Britain (Loch Striven), Québec (Saguenay fjord) and Chile.

In deep northern fjords (e.g.: fjords of northern Norway and the Pacific Northwest) there may be overwintering populations of *Calanus*. The northernmost fjords in Norway are spawning areas for coastal cod stocks; fjords in the Pacific Northwest may contain larvae of numerous fish species. Larvae of Norwegian cod stocks remain in the fjords for a longer time and prey mainly on *Calanus*, *Oithona*, and other microzooplankton species. In many fjords the zooplankton populations are sustained by immigration in deep up-fjord flow (which compensates for run off displaced towards the coast). A very high percentage of zooplankton may therefore originate from outside the fjord.

8. Globec Studies in the Mediterranean Sea

(*P. Nival and C. Marrasé*)

The northern part of the Western Mediterranean basin is an excellent place for a project to study the interaction between population dynamics and physical processes.

Oceanographic context:

A jet current, some distance off the coast, flows from Italy (Gulf of Genoa) to the Catalan Sea off Spain (Font et al. 1988). A frontal structure along the offshore boundary persists throughout the year. However, during the summer the front does not extend to the sea surface, but rather stops at the thermocline and lies under the mixed layer. Strong local northerly winds (the Mistral) can introduce perturbations in the front structure.

The physical mechanisms work at two different scales. At the basin scale, advection is one of the major processes to consider, but at a smaller scale periodic variations of the circulation induce pulses of nutrients which can affect phytoplankton dynamics (Estrada and Margalef 1988).

The distribution of plankton biomass, species composition, and plankton activities in relation to physical structures have been studied in this area (among others: Alcaraz 1985, 1988, in press; Boucher et al. 1987; Estrada and Margalef 1988; Gill et al. 1988; Sabates et al. 1989; Estrada 1991; Saiz et al. 1992; Delgado et al. 1992). However the spatial extent of these studies is limited.

Fish larvae have also been intensively studied in the Catalan sea. The front retains the populations living in the coastal waters, for example fish larvae in the Catalan sea (Sabates and Maso, 1990, 1992) and sea urchin larvae in the Ligurian sea (Pedrotti et al. 1992).

Peculiarities in the mesoscale circulation in the Western Mediterranean Sea are used by different larvae and post larvae of various fish species as they disperse to offshore waters and later return to concentrate along the coastal side of the frontal area. Mechanisms which facilitate dispersion and the return of life history stages also govern the exchange of water masses between the continental shelf and slope.

Scientific activity

Several research cruises have been made in this area, especially in the Ligurian and Catalan seas, and regular surveys along transects are still carried out. Detailed studies of the frontal structure have been undertaken during the last 10 years (Estrada and Margalef 1988; Delgado et al. 1992, Sabates and Maso 1990, 1992; Saiz et al. 1992; Sournia et al. 1992).

Other studies include:

- ongoing survey programs for plankton along a transect (Ligurian Sea, Catalan Sea);
- ongoing survey of the distribution of plankton and fish larvae in the Catalan Sea;
- study of the carbon budget in the Golfe du Lyon (French PNOC program);

- modelling of the western Mediterranean Sea (MEDMODEL project);
- study of biological dynamics in the frontal zone and phosphorus cycle (MEDIPELAGOS in Mast II, Mediterranean targeted program).

Proposed studies:

- determine the timing and scale of spatial patterns of development of the population dynamics for selected species.
- study the population dynamics of a small set of plankton species by comparing time series of life stage abundances in different segments of the frontal zone:
Species group 1: copepods (*Centropages typicus*; *Calanus helgolandicus*, *Temora stylifera*);
Species group 2: gelatinous zooplankton (siphonophore species: *Muggiaea atlantica* and *Chelophyes appendiculata*; medusae: *Aglaura hemistoma* and *Lyriope tetraphylla*; chaetognath: *Sagitta setosa*).
Species group 3: fish larvae (*Diplodus sargus*, *Engraulis encrasicolus*, *Sardina pilchardus*).
- Relate the changes of phytoplankton and microzooplankton biomass and species composition to the population dynamics of the targeted species.
- Establish the feasibility of estimating the growth rate and predation rate of fish larvae on the prey species of zooplankton.
- Develop a model of coupled population dynamics for the 3 groups of species.
- Conduct a mesoscale survey to detect the spatial extent of the selected

species and compare patterns with remote sensing observations.

A workshop will be organized this year to consolidate the project.

9. North Atlantic zooplankton study (S. Sundby)

The composition of mesozooplankton in the Atlantic Subarctic Gyre is characterized by low diversity and dominance by the planktonic copepod *Calanus finmarchicus* (e.g. Wiborg 1955; Matthews 1967; Bainbridge and Corlett 1968; Pavshits and Timokhina, 1972; Anderson 1990). A study of the population dynamics of *Calanus* in the subarctic gyre could contribute substantially to understanding of the influence of climate change on zooplankton population dynamics and its role in recruitment processes. The spatial scale of the system is large but well-defined, and meteorological and oceanographic variables characterizing climate change are fairly well described. For example, long-term fluctuations (< 10 yr) seem to be inversely correlated between the east and west sides of the system, due to a strong inflow of Atlantic water to the Nordic seas and a compensatory strong flow of Arctic water down the coasts of Greenland and northern North America. *Calanus finmarchicus* is distributed over the wide range of temperatures (-1° to 15° C) in the gyre system. It is not known whether the species constitutes a single stock or comprises a number of substocks between which intermixing is limited. Given the circulation in the subarctic gyre, a single *Calanus* population could be carried around the gyre within a period of about

one decade, if it does not utilize deeper return currents to maintain itself within a more limited habitat. It is not known whether changes in temperature and circulation patterns will influence the growth, reproduction and distribution of *Calanus* within the system. Since the recruitment to the major fish stocks of the system is strongly linked to climate fluctuations (Ellertsen et al. 1989; Saetersdal, G. and Loeng, H. 1987; Hansen and Buch, 1986) and it is hypothesized that this linkage is transferred through zooplankton production, a future Cod, Climate and Copepods program should receive GLOBEC guidance and cooperation.

10. The Agulhas Bank as a GLOBEC study site.

(L. Hutchings)

The Agulhas Bank is a productive broad shelf region at the southern tip of Africa at latitudes 34° - 37° S. The Bank supports a high biomass of pelagic and mesopelagic fish. The circulation on the shelf is dominated during summer months by the cyclonic circulation of water around a subsurface ridge of cool water. Here, a high standing stock of zooplankton, dominated by a single species, *Calanus agulhensis*, has a centre of abundance which is coherent over all development stages. This ridge appears to be a semi-permanent feature and only occasionally does it disappear, which results in substantial changes to the currents and to the distribution patterns of the *Calanus* population. This disappearance is associated with the intrusion of Agulhas Current eddies on to the shelf. Stratified conditions on the shelf are occasionally

disrupted by the passage of storm events which temporarily erode the thermocline and mix phytoplankton subsurface maxima through the upper mixed layer.

The area is currently subject to an intensive study as part of Phase III of the Benguela Ecology Program (1992 - 1996), a multidisciplinary study focusing on variations in the distribution and recruitment strength of pelagic fish and squid. Variations in the productive capacity of the Bank are related to the density, condition and egg production of anchovy and sardines during the spawning season. Parameters currently being measured on the Bank during hydroacoustic fishery surveys in November (the peak spawning period) include fluorescence and temperature profiles of the water column, nutrients, size-fractionated chl *a* and particle spectra, phytoplankton species composition at the surface and at subsurface fluorescence maxima, and mesozooplankton biomass and species composition. Copepod egg production and moulting rates of stages N6 to CV are measured at 60 to 80 stations in order to calculate turnover times.

Eggs and larvae spawned on the Bank are advected to the upwelling dominated west coast and recruit to the reduction fishery 6 to 9 months later. Interannual variations in recruitment strength are being related to a number of potentially important biological and hydrographical variables with the aim of predicting the relative strength of recruitment each year.

The location of the study site in the mixing area between the Benguela and Agulhas Current systems on the boundary

of the westerly and subtropical weather systems enhance the sensitivity of the area in terms of climate change. The integrated study of physical factors, plankton distribution and productivity and variation in fish distribution and recruitment strength appear to be closely related to the GLOBEC program aims and objectives.

11. The problem of the high nutrient/low chlorophyll areas

(Takashige Sugimoto)

The circulation of the Subarctic North Pacific and the productivity in the Gulf of Alaska and the Western Subarctic gyres are considered to be sensitive to atmospheric forcing. Recent evidence indicates that interannual variability in the biomass of zooplankton in the Gulf of Alaska is linked to the intensity of the Aleutian flow during the winter.

Japanese surveys indicate that the biomass of the plankton in the Gulf of Alaska doubled in the 1980s compared to the levels measured in the 1960s. The mechanism of these changes, including the similarity with that in the Western Subarctic, should be examined. The trophodynamic and population dynamic models will be used to assess how changes in meteorological and oceanic conditions affect primary and secondary production as well as species composition of the pelagic fish community.

Regional studies on the dynamics of the marine ecosystem in the North Pacific Subarctic water focusing on the linkage between the populations of key species, such as Walleye pollock and Salmon, and climate changes through mixed layer

processes, primary and secondary production are now being planned by scientists from Japan, Canada and the U.S. Intensive field experiments off the east coast of Japan and in the Subarctic gyre with a few university vessels are now being planned, focusing on a spring bloom period. We are also planning to monitor continuously the seasonal and year to year variations of physical environment, phytoplankton, zooplankton and pelagic fish abundance across the Pacific Subarctic gyres with the use of a commercial ferry fitted with XBTs, ADCPs and an intake water type of Continuous Plankton Recorder. The observation will be combined with satellite monitoring and mooring systems.

12. High Nutrient Low Chlorophyll areas in the Antarctic

(Janet Grieve)

Currently we do not have a clear understanding of the role of phytoplankton in the production cycle in the Southern Ocean nor of the mediating influence of zooplankton. Under the GLOBEC umbrella we have an excellent opportunity to understand the interaction of zooplankton and phytoplankton populations in both the Subantarctic and Antarctic regions, and the role of physical processes in structuring this interaction. The Southern Ocean is the major region of the global ocean where phytoplankton biomass is relatively low in spite of an oversupply of macronutrients. This region has subregions with physical, chemical, and biological characteristics which, if compared and contrasted, should provide insight into the relative dominance of physical and biological processes in governing phytoplankton biomass, and into

the way oceanic ecosystems will respond to changing climate.

South of the Antarctic Convergence the ocean is characterised by large seasonal differences in light, a very unstable water column and an abundant supply of nutrients. Surface waters of this water mass are inhabited by a characteristic fauna dominated by a few large species of copepod (for example the copepods *Calanoides acutus*, *Rhincalanus gigas*, *Metridia gerlachei*, and to a lesser extent *Calanus propinquus*; see Vervoort 1957). Most of these species survive the winter by vertical migration to deeper water as late copepodites. For example Atkinson (1991) finds that *Calanoides acutus* mates below 750 m in middle to late winter and the summer generation develops rapidly to either CIV or CV. Its life span seems typically 1 year but those individuals who fail to moult in winter survive into their second summer; their subsequent fate is uncertain. Huntley & Escritor (1991) observe that egg production in *C. acutus* is unrelated to ambient chlorophyll concentrations so presumably egg laying is fuelled by lipids stored the previous summer. *Rhincalanus gigas* on the other hand mates in the top 750 m in spring in a protracted breeding season (Atkinson 1991). Stages CIII and CIV are reached by the first autumn and further development resumes the following spring. *Calanus propinquus* lives nearer the surface than the other species at all times of the year and shows much less evidence of seasonal migration.

The zooplankton communities of the Antarctic region are also influenced by the seasonal sea ice. It appears that some species prefer the habitat provided by the

pack ice, where carnivory is dominant (Hopkins and Torres, 1989). During the seasonal melting of the pack ice not only do the ice algae become available to the water column communities but the stratification, derived from the lowered salinity, reduces mixing in the photic zone (see e.g. Niebauer, 1991). Species such as *Euphausia superba* (Marr, 1962) and the hyperiid amphipods *Paralanceolata anomala*, *Mimoscina setosa*, *Hyperia antarctica*, and *H. macronyx* (Hurley 1969) have distributions which are related to the seasonal sea ice. It is not clear whether copepods have similar distributions although Atkinson (1991) records *C. propinquus* as rare in all but the coldest waters near the Weddell-Scotia confluence. Copepods of the genus *Paraeuchaeta*, taken beneath the ice off McMurdo Station in the Ross Sea (Bradford 1981), include species which seem to have life histories some how connected with the ice; these species lay their eggs in winter with a timing that differs slightly from species to species. The suggestion that the life cycle of species such as *E. superba* are linked to the melting of the sea ice is further corroborated by Meguro et al. (1992). They observed that the sea ice community drifts from west to east with the pack ice in coastal currents and concentrates on the eastern side of peninsulas and banks (such as in the western Weddell Sea). Meguro et al. believe this explains the regionally higher productivity around the Antarctic Peninsula where the largest concentration of *E. superba* are found (Marr 1962). Considerable interannual variability has been noted in the Antarctic marginal ice zone (Smith et al. 1988). The impact of this variability on water column is not known.

Subantarctic water is more variable in its characteristics than water south of the Antarctic Convergence. In the north, where subantarctic water meets subtropical water at the Subtropical Convergence, some nutrients can become depleted. Here the production season is prolonged by the stability that subtropical water imparts to the nutrient - rich subantarctic water and cross frontal mixing in the form of baroclinic eddies takes place (Lutjeharms et al. 1985).

Subantarctic Surface Water also has an actual excess of nitrate over silicic acid (Zentara & Kamykowski, 1981) with implications for the growth of diatoms. The subantarctic region is characterised by strong seasonal changes in light, in vertical stability of the water column, and in nutrients, and by a distinct fauna. In subantarctic waters there are three large seasonally dominant subantarctic copepod species (*Calanus simillimus*, *Neocalanus tonsus*, and *Calanoides macrocarinatus*) which have similar vertical migration strategies to the Antarctic species for surviving winter. Most is known about *N. tonsus* (Ohman, 1987; Ohman et al. 1989; Bradford et al. 1988) and *C. simillimus* (Atkinson 1991) but hardly anything is known of the life history of *C. macrocarinatus*.

There is agreement that much of the Southern Ocean phytoplankton community is dominated by cells which would pass through a 20 μm mesh net (flagellates) (Weber & El-Sayed 1987, Kopczynska, 1992). Is the dominance of flagellates the result of zooplankton grazing or the physiological characteristics of flagellates in relation to their environment? Kopczynska (1992) notes the positive

correlation between krill abundance and the flagellate/diatom ratio which she interpreted as evidence of the effects of krill grazing on phytoplankton composition. She also notes that flagellate concentrations exceed those of diatoms when phytoplankton population numbers were low, although both algal groups increased in numbers with growing stability of the water column. Therefore she concluded that both deep vertical mixing and krill grazing act together to suppress diatom blooms in the Antarctic. Additional insight into the reasons for the dominance of flagellates may be gained from observations in south-west Pacific, New Zealand waters. In a relatively high-nutrient, deeply mixed environment, near the southern boundary of subtropical waters, picoplankton dominate but with a low ratio between prokaryotic and eukaryotic cells (Hall & Vincent 1990). The results of modelling the growth and mortality of three different size fractions of autotroph, based on the above work, indicate that the dominance of the small phytoplankton fraction may be the result of continual disturbance of the water column, resulting in conditions which favour their growth in low average light intensities, and which suppress substantial grazing pressure (Kumar et al. 1991). Therefore there seems to be a body of evidence that supports the contention that the low stability of the upper water column is the major limitation to the accumulation of phytoplankton biomass in Antarctic waters (see also Dugdale & Wilkerson 1989, Sakshaug et al. 1991, Hong et al., 1991); zooplankton grazing seems to have a secondary affect.

The role that zooplankton play in the production cycle in the Southern Ocean is

hardly known. It is important that the region from mid to high latitudes be considered so that a full range of combinations of environmental and biological characteristics can be investigated. The following are some of the important questions that need to be answered (not in order of priority).

- How do the population dynamics of antarctic and subantarctic species of copepods affect and how are they affected by the biomass of phytoplankton and the physical regime in spring and summer in the Southern Ocean? Is there a spring bloom in any part of the Southern Ocean, as in the North Atlantic? Through modelling we should evaluate our understanding of the impact of physical and chemical processes and grazing on phytoplankton species and size - class composition and productivity. What is the impact on zooplankton of a silica deficit in Subantarctic waters and potential deficit in Antarctic waters? Follow up experimentally on any discrepancies between models and field observations. What is the role of microheterotrophs in the Southern Ocean and their importance as food for zooplankton?
- What are the life histories of all major species in antarctic and subantarctic waters, especially in winter? What is the significance for survival in a changing climate of the different methods of fuelling egg production in large southern ocean copepods: based on stored lipids (*Neocalanus tonsus* and *Calanoides acutus*?), or based on spring plankton

growth (e.g. *Calanus simillimus*, *Rhincalanus gigas*)?

- There is only limited quantitative knowledge of zooplankton population dynamics in the Southern Ocean and hardly any information for winter months.
- Detailed knowledge is needed for food, feeding, growth rates, mortality etc. for all major species.

13. Warm Core Rings (D.H. Cushing)

The Warm Core Rings shoreward of the Western Boundary Currents persist for many months. They can be described in physical terms and there is upwelling in their centres. It is likely that cyclopoids dominate the input populations but calanoids may well appear in the exchanges across the boundary in the surface layer; indeed, sometimes salps "invade" the ring [a very recent paper is of some value:- Paffenhofer, 1993]. A study of the population dynamics of the zooplankton in the warm core rings would be desirable, off the Gulf Stream, off the Kuroshio and off the East Australian Current.

14. The oligotrophic ocean (D.H. Cushing)

In the oligotrophic ocean the algae and the grazers are probably in a quasi-steady state where the division rate of the algae approximately equals the mortality due to grazing. There is the advantage that the algae do not sink and the disadvantage that the copepods are so very diverse, but they may not be the predominant grazers. The microzooplankton are so small that from

the point of the study of physical variability, they may be treated in the same way as the algae, that is, simply.

Two problems

In the course of discussion within and outside the group two problems arose, the first on the nature of zooplankton populations and the second on the estimation of the quantity grazed.

The nature of zooplankton populations

Populations have been classified as reproducing continuously (or birth flow) or in distinct cohorts (birth pulse). In the oligotrophic ocean or the eastern tropical Pacific, the animals reproduce continuously (Mullin and Brooks, 1970) and then the problem is merely to sample the vital parameters, recruitment, egg production, growth and mortality (a problem not to be underestimated). In contrast, animals that spawn in a short season form cohorts that remain distinct (birth pulse).

Mark Ohman suggested that copepods lived between birth flow and birth pulse conditions. Indeed, there were three cohorts of *Calanus* in Loch Striven (described by Marshall and Orr, 1955; figure 28) which were quite distinct as nauplii but there were only two subsequently as spawning females. Dr Caswell told me that the distinction between birth flow and birth pulse lay in the projection interval (in the terminology of population matrices, this is the time interval for model estimates). If the projection interval is short with respect to the generation time (say a day or a week), the animals reproduce by birth flow. If it is long with respect to the generation time, (say a year), the animals reproduce by

birth pulse. So on the face of it, copepods reproduce by birth flow.

If this were the simple truth, there is perhaps less need to sample distinct cohorts within persistent physical structures. Then, as in the oligotrophic ocean, the problem is to sample the vital parameters. Dr Caswell also noted that there is a problem that needs investigation. So the question remains open.

Mark Ohman writes "Population processes might be profitably studied in a series of intensive bursts. Then ten days of sampling three or four times a day in subtropical areas or twenty days of sampling once or twice a day in subpolar environments, combined with short projection intervals, would keep parameter estimation in the 'birth flow' domain. If this approach obeys assumptions for parameter estimation models, then the question becomes 'has one chosen the right ten days and a representative patch of copepods'".

The quantity grazed

The quantity grazed may be estimated experimentally or in model calculations. The latter are based on the numbers of algae, their reproductive rate and sinking rate, and the algal mortality due to grazing (which is included in the ingestion rate). There appears to be a deficit in the quantity grazed as estimated experimentally compared with the model calculations. According to estimates taken round the table it might amount to as much as 30% to 40%. There is a case for bringing the two estimates closer together.

APPENDICES

Welcome *Brian Rothschild*

Introductory Papers

1. Primary production *Trevor Platt*
2. Minutes from Strickler's Laboratory: quest for the bottom up approach *Hide Yamazaki*
3. Major zooplankton field studies throughout the world *Tom Kiorboe*
4. Present and future laboratory and shipboard experiments related to the dynamics of pelagic copepods; the "egg method" approach *Serge Poulet*
5. The role of food *Roger Harris*
6. Characteristics of copepod food *Mike Roman*
7. Zooplankton models *Paul Nival and Francois Carlotti*
8. Estimating production and mortality surfaces for zooplankton *Joe Horwood*
9. Mesoscale physical variability and zooplankton spatial structure *Mike Fasham*

Welcome by Brian Rothschild

On behalf of GLOBEC.INT. SSC, welcome to the first meeting of the GLOBEC.INT. Population Dynamics and Physical Variability Working Group (PDPV.WG), chaired by David Cushing, and affectionately known as "Fizzy Pop".

The SSC is looking forward to a productive meeting and to your report, particularly with regard to your insights on the influence of the physical environment on zooplankton population dynamic variability in a global setting. We hope that you will provide us with guidance with respect to specific steps that need to be undertaken during the next decade.

By way of background, GLOBEC.INT. is an international program motivated by a request from IOC to SCOR and endorsed by SCOR, IOC, ICES and PICES. Preliminary planning activities have been articulated in IOC Working Group Report 75 and GLOBEC Report No. 1 (SCOR, 1992).

In essence, these planning activities have been established an initial template for (1) direction (2) research strategy and (3) a mechanism intended to launch a major global ocean ecosystem dynamics research component (complementary with other global programs, such as JGOFS) during the next decade. As you will see, at this point in time, the initial template is being used to organize substantive contributions by the ocean ecosystem dynamics community into a detailed scientific plan for Globec.Int research.

Your Fizzy Pop meeting is the first of several GLOBEC.INT international

workshops which will be held in the next several months which are intended to shape the GLOBEC.INT detailed scientific plan.

You can be sure that your workshop proceedings will be studied in detail and the future of Globec.Int will depend on your deliberations

Direction

The direction is established in the goal of GLOBEC.INT which is, "To understand the physical processes on predator prey interactions and population dynamics of zooplankton, and their relation to ocean ecosystems in the context of the global climate system and anthropogenic change".

In other words, the SSC sees GLOBEC.INT as focusing on fundamental scientific issues associated with zooplankton population dynamics and its variability in a physical setting. Important applications involve "climate change" issues, fisheries, and the waste-sink capacity of the ocean.

On occasion the question is asked as to why the SSC chose to focus on zooplankton (including ichthyoplankton). The reasons are that 1) the study of zooplankton dynamics is scientifically "ready" 2) the focus on zooplankton dynamics in a physical setting is needed as a complement to other "global" programs such as JGOFS, and 3) the study of zooplankton dynamics is such a large undertaking, that the concentration on zooplankton was about as large a task as the SSC could handle at the present time. This certainly does not mean that other

major taxa will not be considered (particularly since the predators and prey of zooplankton are often non zooplankton, or even particulate matter). Indeed, any classical population dynamics study of grazing zooplankton would need to take into account the population dynamics of the phytoplankton that are ingested by the zooplankton. Further, the present focus on zooplankton also does not mean that the taxonomic scope of GLOBEC will not be broadened, eventually.

The fact that other taxonomic groups necessary to generate a complete understanding of the ocean ecosystem are being studied in other programs necessitates full coordination of Globec.Int with other global programs that are more concerned with phytoplankton and the very small plankton. Discussions on how to effectively coordinate global programs, now, and more importantly, into the future, are under way.

Strategy

The GLOBEC.INT. SSC has established a research strategy which is intended to serve as a basis for the implementation of a ten year research program. This research strategy has as its fundamental component the GLOBEC Core Program (GCP). The GCP is intended to be a framework by which international programs and regional programs, whether or not they are initiated as a GLOBEC.INT. activity can link together toward a common goal of understanding zooplankton dynamics in a physical and ecosystem setting.

To achieve these aims, the GCP needs to be sufficiently general and applicable (with some modification, of course) to the

major ecosystem types (e.g. HNLC, upwelling systems, mid ocean gyres, spring bloom etc). At the same time, the GCP must contain sufficient substance to serve as a "point of attachment" for any national or regional program. This does not mean that all contributing and associated programs will have to be completely identical to the GCP. On one hand, the SSC expects the major increments to understanding to come from the unifying strength afforded by a GCP. On the other hand, the SSC expects innovational departures from the GCP which will eventually modify and strengthen the direction of research.

Please appreciate that the GCP and national and regional programs cannot be mirror images of one another. The GCP and national and regional programs have different motivations. The national and regional programmes are intended to implement research while the GCP is intended to provide a framework to develop coherence among national and regional research efforts.

At present the GCP is evolving as separate but coordinated activities. These activities can be partitioned into two types of programs. The first involves issues related to a general approach, searching for commonality and generality among ecosystems. The second involves applications to specific ecosystems. The "general approach" is being implemented by the Population Dynamics and Physical Variability Working Group, the Numerical Modelling Working Group; the Sampling and Observation System Working Group and the GLOBEC Prudence Working Group.

The Population Dynamics and Physical Variability Working Group is charged with problem definition and the development of population dynamic, behavioral, trophodynamic mathematical and conceptual models. We see a major function of this working group to sharpen our understanding of the population and trophodynamics processes particularly in a physical setting. The Numerical Modelling Working Group will be incorporating zooplankton population dynamics models into realistic physical fields. The Numerical Modelling Working Group has a major challenge of specifying the right class(es) of physics population dynamics model. The Sampling and Observation Systems Working Group is charged with the responsibility of specifying and facilitating the development of advanced and innovative sampling systems. We see that this Working Group will bring modern technology to bear on estimating parameters which are deemed critical by the Population Dynamics and Physical Processes and Numerical Modelling Working Groups. The GLOBEC Prudence Working Group will be mining data that have been collected in the past but are not now available for analysis. Inasmuch as these data appear to be extensive, it might be that the availability of some heretofore unavailable data might contribute to a substantial increment in understanding. The ecosystem approach is being implemented by the Southern Ocean Working Group, the North Atlantic Cod and Climate Working Group, the Subarctic Pacific Working Group and the Upwelling Systems Working Group. The details of approach in these working groups is continuing to evolve.

The Sampling and Observation Systems Working Group is scheduled to meet in Paris in early April, the Southern Ocean Working Group in Norfolk in June, the North Atlantic Cod and Climate Working Group in Lowestoft in June and the Numerical Models Working Group in Villefranche in July.

Again, as you see, the GCP as it presently stands is a device intended to organize the various activities of GLOBEC.INT into a coherent program. The scientific details remain to be established in the course of the next year. The evolution of these details by the scientific community will in fact sharpen the relation between the GCP and ocean ecosystem dynamics science.

It would have been ideal to develop the interactions among the various working groups in a temporally more coordinated fashion. As a practical matter, this has been difficult. However, as we progress through our scientific planning, we will bring the aims of the various working groups into closer harmony.

Mechanisms for moving ahead

The SSC has developed a mechanism for moving ahead. The mechanisms are both scientific and administrative. From a science point of view the development of a detailed scientific plan has the highest priority. Reports of the working groups will be assembled to contribute to the detailed scientific plan.

To do this the SSC will most likely invite the working groups to evaluate progress and to develop substantive mechanisms for the ten year program.

Near the end of the year the working groups will meet jointly to evaluate progress and complete the components associated with the working groups. Also, near the end of the year, we will schedule an administrative meeting to discuss how we might implement GLOBEC.INT involving both scientists and leaders of national and regional programs. This will involve not only new activities but a meeting of ways to facilitate ongoing GLOBEC programs in countries such as Japan, China, New Zealand, Korea, the USA, Canada and Norway; helping to develop national and regional programs as required ; and interrelating with various bodies concerned with "global ecosystem dynamics ".

We intend that major elements of the GLOBEC.INT plan will be complete by the end of the year.

There follow a number of papers presented on the first two days of the meeting by way of introduction to the problems facing the Working Group.

Introductory Papers

1. Primary Production

(Trevor Platt)

We restrict the discussion to the mixed layer, assumed to be vertically homogeneous, the first in terms of biomass, the second in terms of individual cells (which may be more useful for further calculations of grazing by zooplankton).

1. Description in terms of pigment biomass

- (a) In broad band illumination, assuming a static water column, daily production for the mixed layer can be calculated easily using the analytic results in (Platt et al., 1990).
- (b) A better calculation accounts also for spectral effects. No analytic solution exists for this case. However, it is shown in Platt and Sathyendranath (1991), how the spectrally weighted result may be estimated from the broad band result.
- (c) Where the water column is mixing actively, it may be preferred to force the calculation of daily production with the depth and time averaged irradiance (Sverdrup, 1953). The resultant correction is computed in Platt et al. (1991).
- (d) With a generalized loss term (respiration, *sensu lato*), net production of the mixed layer can be estimated, leading to expressions for intrinsic rate of increase of the autotrophic biomass (Platt et al., 1991) and critical depth (Sverdrup, 1953).
- (e) Criteria for the initiation of phytoplankton blooms can thus be

derived. But how do blooms form? Does the surface mixed layer develop from the surface downwards or does it work its way towards the surface from the seasonal thermocline? Probably both processes occur, but with different time scales.

- (f) There is a growing body of evidence, especially from Norwegian fjords, of vernal blooms in the apparent absence of any stratification (Eilertsen and Taasen, 1984, Eilertsen et al., 1989). These need to be understood.

2. Description in terms of individual cells

- (a) Rather than the Eulerian descriptions referred to above, Lagrangian descriptions have also been used, where the calculations follow the migration of individual cells as they move through the mixed layer and experience a corresponding change in irradiance. This approach, expensive in computing time, is logically more defensible (Woods and Onken, 1982), but some workers (Lande and Lewis, 1989) consider that the difference between the two approaches is negligible in the final result. In any case, no comparison between the two methods has dealt with spectral effects: more needs to be done.
- (b) The properties of individual cells can be assessed rapidly by means of flow cytometry. Statistical moments of distributions in photoadaptive properties can be estimated, for example as function of depth (Olson et al., 1991), as the mixing rate changes. These provide the best demonstration of the fine control of ecosystem dynamics by physical forcing. Change in photoadaptive

properties with change in mixing rates is a further complication for comparisons of Eulerian and Lagrangian approaches to computations of primary production.

3. (the following section is taken from Olson et al., 1991).

The biological responses of phytoplankton cells to changes in their environment can be used to provide information on physical processes such as water column mixing and nutrient supply. If we know how fast cells can respond to changes in light levels, we can get an idea from the depth distribution of their properties how fast they have been moved from one depth to another. A variety of bulk water parameters, such as photosynthesis vs irradiance characteristics (Falkowski, 1983) and carbon:chlorophyll ratio (Cullen and Lewis, 1988) have been proposed as potential candidates for investigating vertical mixing. Flow cytometric analyses offer the potential for added specificity since discrete components of the community can be followed, which reduces the potential for interference by changes in community composition. We have observed, for example, that the shape of the depth distribution of the mean fluorescence of protochlorophytes at a station in the Sargasso Sea changed over a diel cycle (Figure 3), from a homogeneous distribution in the upper water column (i.e. the cells were being mixed faster than they could photoacclimate) to one in which the surface cells were dimmer and the deeper cells were brighter. The timing of this change coincided with a shoaling of the mixed layer caused by surface heating, suggesting that cessation of mixing allowed the cells at various depths to

photacclimate to their ambient light levels (Dusenberry et al., 1990).

Since the flow cytometer makes measurements on individual cells, we also have access to information contained in the distribution of properties within each population. In the illustration above, the distributions as well as the means in fluorescence per cell show some dramatic changes with depth, including skewing of the distribution near the seasonal thermocline (Figure 4). This skewness is predicted to occur at a reflecting boundary layer using a single cell mixing model (Dusenberry et al., 1990). We have also seen bimodal distributions in the prochlorophytes near the nitracline, which we hypothesize to reflect a transition from nutrient-limited growth to light limited growth. A record of each cell's trajectory through its environment represented by these measurements may provide insights into complex processes, such as mixing, that are not possible in any other way.

2. Minutes from Strickler's Laboratory: quest for the bottom-up approach (Hide Yamazaki)

I presented the needs of the bottom up approach using two pieces of field data sets. One set (Haury et al., 1990) suggests that there is a threshold turbulence intensity separating "strong" and "weak" swimming capability of copepods. Another data set (Mackas et al., 1993) suggests that for a given swimming ability, some species may have adapted well to a turbulent environment but some do not. In order to quantify these aspects we need to develop a Lagrangian model in a "realistic" turbulent condition. I have been using a Direct Numerical Simulation code which

solves the Navier-Stokes equations directly. So the simulated flow field is "real" in the sense that we do not use any sub grid scale model. I have studied the importance of "coherent structures" in turbulent flows. Animals may have been adapted to such structures.

In order to develop a right Lagrangian model for the purposes of Globec.Int, I recommend:-

- To establish a data base for the distribution of zooplankton taxa with high resolution physical data including turbulence.
- We need to harmonize Lagrangian oriented modelling efforts with laboratory observations, and both numerical and laboratory approaches and both numerical and laboratory approaches must be linked to the field data base.

[Drs Yamazaki and Paffenhofer showed remarkable video recordings of the behaviour of copepods]

3. Major zooplankton field studies throughout the world (Tom Kiorboe)

1. Most "major" zooplankton field studies are integrated parts of interdisciplinary projects/programmes.
2. Some of the studies address very specific questions of topical (e.g. the "Antarctic paradox") or regional interest (e.g. aggregation of *Calanus* and whales in the same region). However most are more descriptive/observational projects dealing with less specific topics.

3. Although there is an over representation of projects in temperate/boreal regions, projects in colder and warmer climates are on average much larger. Contrary to the expectation, the effort, thus, seems to be fairly well distributed.
4. About half of the studies are relevant to or part of JGOFS. The other half of the studies are of direct relevance to Globec.Int. Thus, Globec.Int is already to a large extent operational, though uncoordinated.

Please see Table 1

4. Present and future laboratory and shipboard experiments related to the dynamics of pelagic copepods; the "egg method" approach.
(Serge Poulet)

Recently, the ICES Study Group on Zooplankton (1992) has listed the experimental methods used to estimate ingestion, assimilation, egestion, metabolism and growth as displayed in Table 2. In Figure 5 are given the factors and functions needed in the study of the population dynamics of zooplankton. Then, in Table 3 is given an overview of new developments in zooplankton methods.

Please see Table 2, Table 3 and Figure 5

All kinds of techniques are already in use by copepodologists and it is likely that improvements will be related to the adaptation of methods of the following groups:- Optical microscopy, fibre optics, neural networks, flow cytometry, SEM-TEM, image analysis, electrophysiology, spectrophotometry,

HPLC, mass spectrometry, immunology, radio labelling and tracers and in molecular biology.

According to the type of objectives, new improvements could be inspired from existing classic, "low" and "high" tech. methods, such as, for example:

Classic:

Elemental analyzer
Video, cine camera
Labelled tracers
Scintillation counter
SEM, TEM

Low Tech:

Electrophoresis
Immunology
Image Analysis
Cultivation
Biometry

High Tech:

Mass Spectrometry
Flow cytometry
Electrophysiology
Confocal microscopy

The egg method of studying copepod dynamics

The general equation for production is:

$$P = \sum_{i=1}^j N_i \cdot W_i$$

where N and W are the number and weight of individuals in the classes, *i* to *j*.

The copepod life cycle is divided into four components (egg, nauplii, copepodites

and adults) within which there are twelve developmental stages. Because the identification of the stages and the estimation of biomass, growth and mortality within each class needs immense amounts of time and are generally not accurate, the classic methods have proved impractical for estimating production.

Classic methods have stipulated that:-

- variability of biomass is six orders of magnitude greater than the variability in individual growth rate;
- growth rate is isochronal, or independent of body size or of species;
- food and feeding do **not alone** govern secondary production.

Assumptions 2 and 3 tend to underestimate the contributions of various biological factors (see Figure 5), although a best fit to a production model can be based on temperature alone (Huntley and Lopez, 1992). In fact, the variability of growth (both somatic and reproductive) is highly species and food dependent, as shown in works defining food in terms of chemical compounds relevant to growth, other than chlorophyll a.

The "egg method" is an alternative approach, where each factor can be accurately measured, either in the lab or in the field.

$$\text{Let } P = F.v$$

where:

F is number of eggs/volume/time;
v is the viability of the eggs.

This approach is based on simple measurements of the number of viable eggs. Experimental observations demonstrate that F and v are related to food quantity and quality (see Figures 6 and 7). The production of the cohort can be obtained from:-

$$P_c = F. \Sigma Mt$$

$$\text{and } M = (\ln e - \ln A)/t$$

where:

ΣMt is the total mortality rate of the cohort;
e and A are the numbers of viable eggs and adults respectively.
t is the generation time.

The method is illustrated in Figure 8.

We consider that the mortality of the cohort includes all causes, that t, the generation time is temperature dependent and that F and v are food dependent.

The "egg method" is species specific and gives a method of the "potential production" or of the "instantaneous recruitment". The measurements of F and v can be extremely accurate and reliable, through laboratory or ship board experiments implying short term incubations (hours). The *in situ* measurements of e, A and t are known for several common and "strategic" species but estimates of M remain a problem.

5. The role of food

(Roger P. Harris)

An extensive body of laboratory studies demonstrates that food concentration affects the growth,

development rate, and reproduction of copepods. These results, obtained under defined environmental conditions, provide valuable information on interspecific comparisons, and are critical for studies of population dynamics. However, the use of unialgal diets, and relatively uniform food concentrations introduces a degree of artificiality into the laboratory - derived data set, and extrapolation to the field situation must be viewed with caution.

In contrast to these laboratory experiments, some field studies have concluded that copepod growth is not limited by food in the sea. If this is the case, a temperature - dependent model may be a valid generalisation, which could be appropriate for large - scale comparisons. The possible discrepancy between the laboratory results and those *in situ* may be resolved if copepods are capable of detecting dependable, non - limiting food concentrations in micro - scale patches in the sea, and hence grow at maximal growth rates. This issue needs to be resolved.

A major limitation to the study of copepod population dynamics is the lack of a direct *in situ* method for measuring production, such as the ^{14}C technique for phytoplankton. Where *in situ* measurements have been made, particularly of egg production, a poor relationship between production and phytoplankton biomass (chlorophyll) or primary production (^{14}C) is often observed. In addition, many laboratory experiments have shown the importance of algal species in influencing egg production, and there is mounting evidence that the nutritional composition of the diet can have significant effects on production.

Hence chlorophyll alone can no longer be considered to be a good predictor of the food available for copepods. All copepods should be considered to be omnivores and the role of microzooplankton in the diet deserves further study. It is concluded that a proper consideration of the role of food is essential in future work on modelling zooplankton population dynamics in relation to physical variability.

Field studies should concentrate on the links between physics and biological production at spatio-temporal discontinuities in the water - column, where physics control phytoplankton production and species composition, and hence the food supply for zooplankton. Such features are the key to understanding population dynamics over wider space and time scales.

A temperature dependent approach may be valid for basin-wide comparisons. If a temperature dependent model is adopted, with its implicit assumption that growth is not "food - limited" *in situ*, this suggests that a programme of studies should be directed to establishing, and defining, the microscale of food distribution in the field. To advance our quantitative understanding of the role of food in the population dynamics of zooplankton, future studies should concentrate on:

- defining what constitutes food for copepods;
- assessing how important food particle size, species, and food quality are in relation to growth;
- concentrating field studies on spatio - temporal discontinuities in water - column structure;

- quantifying micro - scale food patchiness in the ocean in relation to physical variability;
- concentrating laboratory studies on short-time scales and interactions with micro - patches;
- integrating laboratory experimentation with field studies and modelling in a highly interactive way.

6. Characteristics of copepod food (Mike Roman)

Copepods are surrounded by a diverse mixture of particulate matter (i.e. inorganic particles, bacteria, protozoa, phytoplankton, detritus) which varies in a number of parameters (particle size, concentration, chemical composition, particle motility), all of which can determine copepod ingestion and production. Although copepods exhibit complex feeding behaviours which allow them to selectively graze specific particle types, most if not all, copepods are omnivores. Copepods have been shown to ingest bacteria, protozoa, phytoplankton, detritus and copepod nauplii. The composition of copepod diets will change in space and time due to the composition of the seston as well as to ontogenetic changes in feeding behaviour. Because the diet can directly influence the growth, development, mortality and reproduction of copepods, food is a critical variable in understanding copepod population dynamics.

One way to evaluate the food available to copepods is in relation to their nutritional requirements. Although the data is rather scant, there are a number of studies which demonstrate that copepods require certain rations of proteins and

lipids; specific macro - and micro - nutrients such as amino acids, fatty acids, sterols and vitamins. One would expect that the biochemical composition of phytoplankton, protozoa and detrital types will vary in their ability to support copepod production. However, even within phytoplankton, the biochemical composition will vary within the taxonomic group, algal species within the group, phase of growth, light field and nutrient history. We know that certain species of algae support high copepod growth and reproduction. The most likely reason for this greater food "quality" is because the cells contain particular compounds (fatty acids, amino acids) which are essential for copepod production.

In recent years it has become increasingly apparent that copepods consume appreciable quantities of protozoa. Because protozoa consume small phytoplankton and bacteria which often cannot be captured by copepods, it is one means of transferring energy from the "microbial loop" to metazoans and fish. Another important role of protozoa for copepod production concerns their ability to synthesize compounds (i.e. fatty acids) which are essential elements in a copepod diet.

We know that copepods eat a variety of food types in the natural environment. From a nutritional standpoint, a varied diet may be necessary to obtain the essential compounds to sustain maximum copepod growth and reproduction. However most laboratory studies which assess copepod growth and reproduction under controlled conditions, have used single algal species. This is obviously not realistic and if the algae are not

nutritionally sufficient, copepod growth rates, development times and reproductive rates derived from these studies will be underestimates of these parameters in nature.

7. Zooplankton Models

(Paul Nival and Francois Carlotti)

1. Population dynamics:

Models describe the dynamics of the life stages which are the relevant variables to consider. Although they belong to the same species, their shape, swimming speed and behaviour differ at each stage and they play different roles in the food web. For instance in the case of fish - copepod interaction, it is clear that total biomass of each of them has no significance. Most of the interactions are concentrated on the larval stages of fish and adult stage of copepod. However different food species have to be considered for the fish so the population dynamics models should be surrounded by food web models.

In most of the models dealing with interactions of species, no population structure is considered. The simplest models are predator / prey models considering different numbers of state variables (Figure 9). Their common feature is the consideration of species or taxonomic groups, biomass instead of numbers or biomass of life stages. Ecosystem models are designed to deal with interactions of species in a complex trophic web and biomass budgets (Fasham et al., 1990).

On the contrary very few population models take into account interactions of species or trophic levels which are described in ecosystem models. The main

reason is that there is not enough knowledge on the exact nature of the predator / prey relationship between each life stage of one species and the life stages of another.

2. Variables to consider in a population dynamics model.

The pertinent variables fall into two categories:

- internal variables: those related to processes governing the life cycle dynamics (physiological variables governing the energy budget on which depend natural mortality, growth and stage to stage transfer rates). Some sub-models of individual growth have been designed and need to be developed (Astheimer et al., 1985). It becomes evident that hydrodynamics and population dynamics are effectively linked by growth characteristics (Hofmann et al. 1992).
- external variables:
 - those which control the life cycle (physical or chemical variables reducing or increasing the speed at which the life cycle progress: temperature, light).
 - those which are affecting the population structure, mainly related to the other species (predator or prey).

It is important to consider that the population of the species under consideration can be transported and dispersed in the water according to local hydrodynamics but that its prey or predators can be transported differently depending on their behaviour. It is also necessary to consider that a population is part of a trophic web. Short scale models

have been designed which consider the events at the scale of organisms.

3. Different degree of complexity in population models:

A great variety of models have been designed to simulate some real situations or to determine properties of such systems. Most of them have no spatial dimension and they address the whole population (Figure 10). Crustaceans are the simplest organisms to work with due to their well defined life stages (Figure 11).

Models with simple biology

- models which simulate cohort dynamics are adapted to parameter estimation. Egg production is forced by a gaussian function (Bossicart & Mommaerts 1979; Sonntag & Parslow, 1981; Hay et al., 1988).
- models with a simple representation of population dynamics: development time is considered as constant. Consequently the rate of transfer from one stage to the other is constant over time.

Models based on the Leslie matrix are the simplest. The generation time of the species is the time step of the model. Models based on Lefkowitz matrices allow time steps smaller than generation time (Sciandra, 1980). A simple model has been designed by Argentesi et al. (1974, 1987) for planktonic species (*Daphnia*).

4. Consideration of age instead of stages.

Most of the population dynamics models designed by mathematicians for theoretical studies consider the two dimensions of time and age. However, the biology of growth and development is oversimplified

in these models to keep them tractable (many references on age structured population dynamics models in De Angelis & Mattice, 1979). A good review of models designed for the North sea has been published by Fransz et al. (1991). Some of them include elements of population dynamics of planktonic species.

Models including growth and physiological functions

Here we include models taking into account physiology and growth as well as demography. The model developed by Slagstad (1978), Carlotti and Sciandra (1989) considered a growth model influenced by food and temperature to drive development time, mortality and transfer rate.

Models considering interactions of species and food web dynamics

A small number of models of food web consider the populations dynamics of species. The model of Steele and Frost (1977) with two trophic levels was mainly designed to simulate the effect of two copepod species on the size structure of phytoplankton prey; however, it considered some of the properties of copepod cohorts to compute ingestion.

Hofmann (1986) considered the population dynamics of a copepod and the dynamics of its food taking into account the requirements on prey size. Some attempts have been made to include the predators or competitors of the species under consideration (Kremer & Kremer, 1982; Davis, 1984, for George's Bank; Gaedke, 1990 and Gaedke & Ebenhoh, 1991 for the Ems-Dollar estuary). A multicohort age structured model proposed by Ault et al. (1991) is an

improvement on the models of fish populations.

Models with a spatial dimension

Some mathematical simulations of the spatial distribution of life stages of marine species have been published.

Davis (1985) worked on the development of a population of *Calanus* on George's Bank. Hofmann and Ambler (1988 a, 1988 b) produced a model describing the time evolution and spatial behaviour on the continental shelf of the Eastern Seaboard of the U.S. A simulation of the spreading of a copepod population in an upwelling structure was produced by Wroblewski (1982).

Woods & Onken (1982) introduced the concept of Lagrangian modelling for living organisms which is promising in the field of population dynamics. This method which allows us to consider not only the physiology of organisms but some of their behavioral characteristics has been used for zooplankton by Wolf (1990). Another example (Figure 12) is found in Hofmann et al., (1992).

Models considering rapid processes or short term events

Short term events which could modify the physiology and population dynamics of zooplankton species could go from the scale of a storm to the scale of fluctuation in food concentration on the path of a zooplankter. Most of the models consider the forcing of ingestion or reproduction by food.

Wroblewski & Richman (1987) consider the effect of wind mixing events on dynamics of anchovy larvae. A model

of egg production in a fluctuating food resource was designed for a copepod and compared to experimental data by Sciandra et al. (1990).

The interaction between zooplankton and its food on a short spatial scale was addressed by Beyer & Laurence (1981). Rothschild and Osborn (1981) have shown that the intensity of turbulence could significantly modify the amount of food gathered by a copepod. The concept developed in this paper has been used by Davis et al. (1991).

5. Problems arising in the construction of realistic population dynamics models

Population dynamics included in ecosystem dynamics

Most of the population dynamics model consider one species. However, for each species modelled it is necessary to consider also the predators and the prey. The design of an ecosystem model with the correct forcing of the population dynamics from these two levels necessitates a similar degree of complexity in each of its parts. As some stable allometric functions relate biological rates to the size of organisms, it could be easier to consider size as a pertinent variable. The idea of the size continuum was developed by Cousins (1980), Platt and Denman (1978) and Silvert and Platt (1980).

An attempt to reduce the number of variables, that is the number of taxonomic categories needed to have a description of a planktonic community has been made by Moloney and Field (1991). The forcing variables relative to the population

dynamics of a species could be considered from this point of view.

Complex behaviour of biological models

Non linear interactions provide complex behaviour (limit cycle, stable point etc.). Studies of this behaviour is usually based on two or three state variable systems. It is not clear if this complex behaviour persists when the state variables are split into developmental stages.

Population dynamics can act as a damping mechanism. Spatial forcing, especially dispersion usually stabilize the behaviour of a set of interaction variables.

Forcing with periodic functions (annual cycle of temperature or light, for example) could also induce a complex behaviour in a predator / prey system (Rinaldi et al., 1990); bifurcations, oscillations between several equilibria could occur. It is not known if the partition of the global variables into life cycle stages decreases or increases the complexity of behaviour. The biological boundary conditions are very important in hydrodynamic models with spatial dimensions. The same problem occurs with the biological components in a spatial model. The boundary conditions should be carefully set. They are critical when the species under consideration makes a vertical ontogenetic migration and when the overwintering stages are advected into the area studied. Hierarchical models could be used to define the biological boundary conditions.

8. Estimating production and mortality surfaces for zooplankton

(Joe Horwood)

[I am presenting these ideas of Simon Wood's as he cannot be here and as I believe they contribute significantly to advancing our interpretation of observed spatio-temporal distributions of organisms. I hope I am not misrepresenting him but I am sure that I am not doing him full justice].

In a series of articles Wood and colleagues (e.g. Wood et al., 1989; Wood and Nisbet, 1991) demonstrated the large errors inherent in the estimation of mortality rates from field samples subject to vagaries of sampling - as might be expected since you are seeking the difference of two error prone and possibly similar sized numbers. Even when the mortality models are assumed known the range of estimates is frequently too large to allow discrimination of differences between rates calculated at different times or localities. The propagation of error along with death of the population can additionally make estimation unstable. The problems are compounded when the underlying model is unknown (mortality may vary with time, space, size etc.).

In attempting to obtain robust and usefully precise estimates of mortality rates for copepod populations the properties of spline fitting was explored. This is a standard technique allowing fits of surfaces to time or spatially varying data. In particular however, they examined the use of cross-validated splines. Under appropriate statistical properties it can be shown that cubic (or bi-cubic) splines provide an optimal fit to data and

Cross-validated splines allow true confidence intervals to be calculated even when the underlying model is unspecified. Much of the statistical methodology was developed in the USA by Grace Wahba (e.g. Wahba, 1990).

The method is of course not the Holy Grail - solving all our problems of knowing nothing and giving us everything. There is a parameter that has to be obtained, representing the degree of smoothness of the surface (very peaky or rather smooth). This is exactly what we do not know. Is it a real sudden drop in mortality with time or a real hole in the spatial distribution? The cross-validated exercise allows this parameter to be estimated along with the error on the sample points. The concept is straightforward. A very bendy surface will fit all the points well a flat one not well. If a fit is obtained using some of the data the resulting model should predict the remainder equally well. Too structured an initial fit will inevitably fail to fit the remaining data, too flat a fit is clearly sub-optimal. The cross-validation optimises the fitting of the smoothing parameter.

Wood has used such techniques to fit production and mortality surfaces from stage or age structured populations of copepods, and insects (Wood et al., 1989; Wood and Nisbet 1991; Wood, in press). For his examples the basis is an underlying model that is credible but sufficiently flexible. For example, for an age-structured population the McKendrick-von Foerster model is suitable:

$$\frac{\delta x(a,t)}{\delta t} + \frac{\delta x(0,t)}{\delta t} + \mu(a,t) = 0$$

where:

$x(a,t)$ is the population density of age a at time t , and estimates are obtained of $\mu(a,t)$, the age and time-dependent death rate, and $x(0,t)$ the production, from observations of x .

Figure 13 shows some simulated data (Wood, in press) of, from top to bottom, populations, numbers of deaths and death rate in that order. On the right are given the results for the true population and on the left are shown the results for sampling at nine age classes at eleven times with a coefficient of 20%.

Figure 14 shows estimates of population numbers of *Pseudocalanus* in a Loch Ewe bag based on different experimental stage duration times, and Figure 15 the corresponding death rates (Wood and Nisbet, 1991; Wood, in press.). These models have also been applied to data on insect pests and to spatial and temporal data on sole eggs.

Simon has provided some answers (you have to guess the questions):

- Method usually requires estimates of stage-specific duration times, although these can be variable (with time and stage), and if data are good the requirements can be relaxed.
- From the estimated death rates and population surfaces it is possible to calculate the stage-specific rates and time-averaged rates.
- Cross-validation needs upwards of 30 points, increasing as the data become noisier.

Additionally I can add, if it is not obvious, that the model itself links information. Hence a structural stability is given by sampling the same cohorts at different times. If this sampling frequency is not achieved you are forced to grossly contract the model and to lose much of its strength.

9. Mesoscale Physical Variability and Zooplankton Spatial Structure

(Mike Fasham)

Oceanic mesoscale eddies have space scales from 50-300 km (Robinson, 1983) and it is well-known that phytoplankton distributions have similar space scales and wave-number spectrum, although the exact mechanisms linking phytoplankton production with the physical processes are still largely speculative (Strass, 1992; Weeks et al., 1993).

How might mesoscale eddies affect zooplankton distribution and dynamics?

a) If zooplankton food, phytoplankton, is correlated in some way with eddies then this would influence the spatial pattern of zooplankton. However, Steele & Henderson (1992) have shown that such a feeding coupling between phytoplankton and zooplankton does not imply that the spatial patterns will be similar. They embedded a simple predator-prey model in an environment in which eddies are simulated by a constant eddy diffusivity term. If the zooplankton death rate was subject to random variation then the spatial spectrum of zooplankton was "flatter" (more random) than that of phytoplankton. This result is supported by the observations of Weber et al. (1986) of

the spatial spectrum of krill and phytoplankton fluorescence. However, more phytoplankton-zooplankton spectra will need to be obtained before we can conclude that this is a general result.

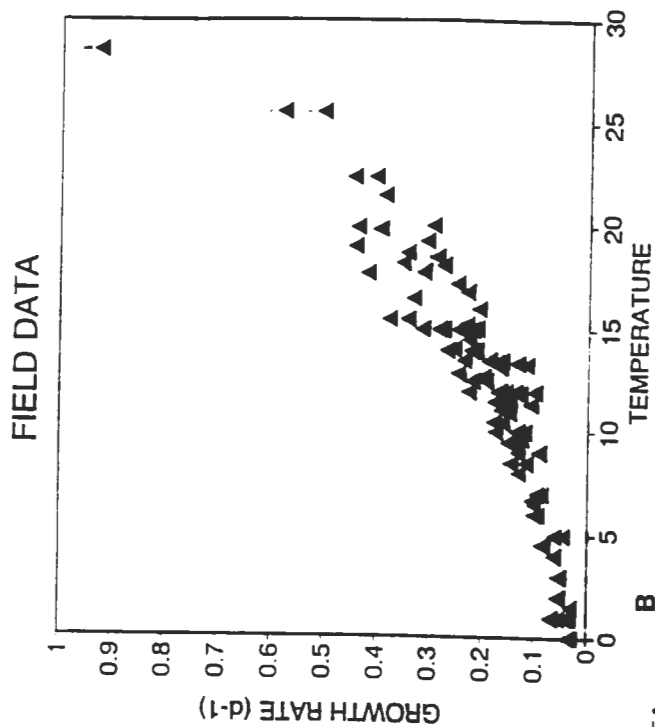
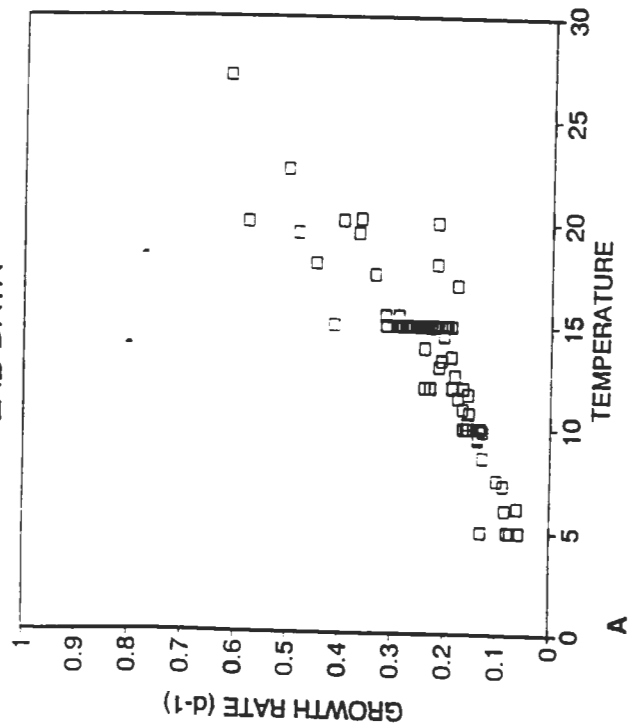
b) Direct Effects of water motion. Although convergence velocities associated with mesoscale features (10 m/d; Woods, 1988) are small compared with mesozooplankton swimming speeds (100 m/d) the combined effect of such motions coupled with zooplankton motion might produce a spatial pattern associated with the eddies; this has been studied theoretically by Franks (1992). Further study of the possibilities of such effects could be carried out by embedding ecosystem models into small-scale primitive equation models of eddies or meandering currents.

FIGURES

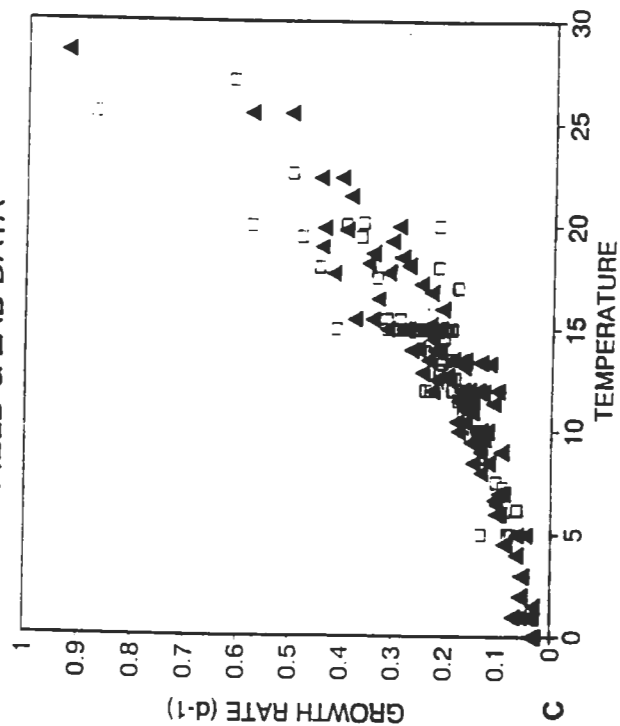
1. Maximal growth rates of zooplankton as function of temperature (Huntley and Lopez, 1992) (a) for laboratory material (b) for the field observations (c) for both.
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3. Mean fluorescence intensity of prochlorophytes over a diel cycle at a station in the Sargasso Sea in October 1989. Profiles taken during the dark are indicated with filled symbols. The fluorescence intensity is shown for the first profile only; subsequent profiles are offset by a factor proportional to the time between samples. The depth of the mixed layer (defined as the depth at which temperature was 0.02°C less than the surface temperature) is indicated by horizontal bars: it shoaled dramatically during the day due to surface heating. Note the development of a gradient in fluorescence with depth after the mixed layer shoaled, apparently because the cells were able to photoacclimate when they are no longer being rapidly mixed. From Dusenberry et al., (1990).
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5. Framework and list of the most relevant interacting factors and functions related to the study of the population dynamics of copepods.
6. Relationship between fertility of small and large size copepods and in situ concentration and threshold of food, given by chlorophyll a.
7. Importance of the nature of and inhibitory compounds of the diatom and non-diatom diets of copepods, and consequences on the hatching rate and development (viability) of eggs. From Ianora and Poulet, (1992) and from Poulet et al, (1993).
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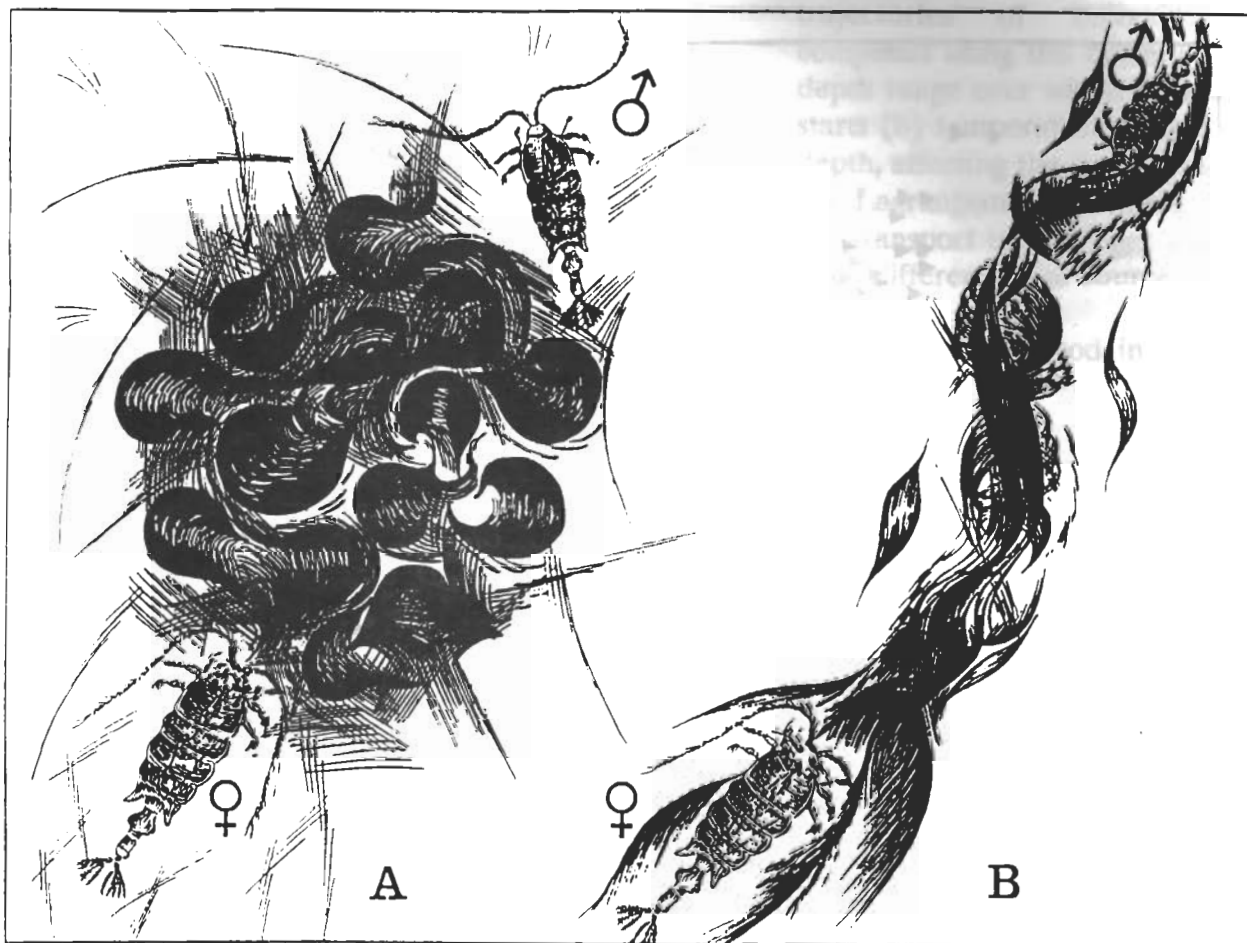
LAB DATA



FIELD & LAB DATA

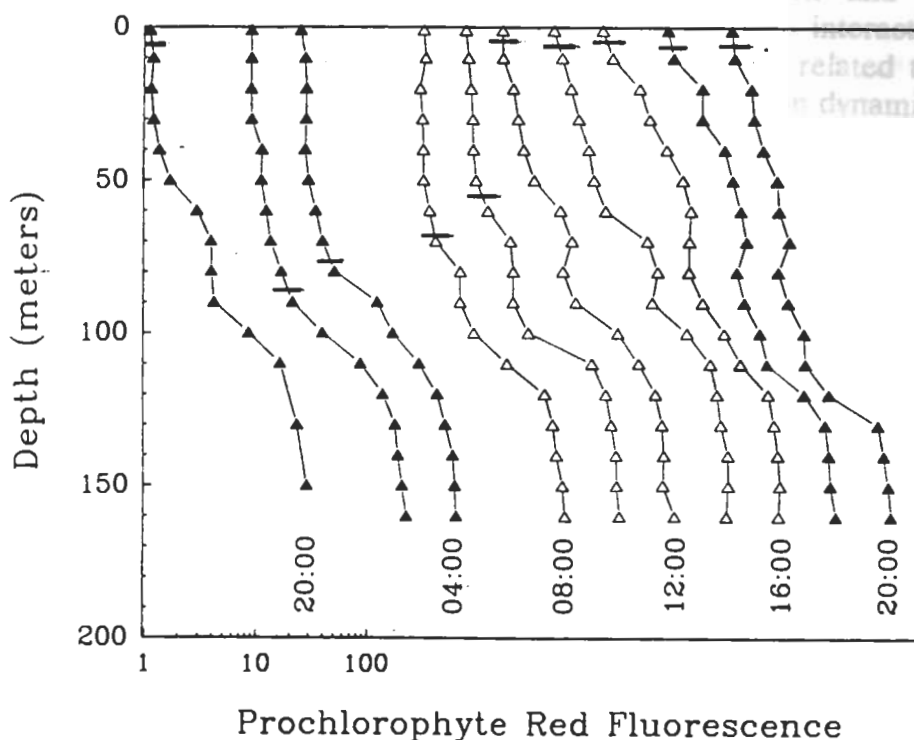


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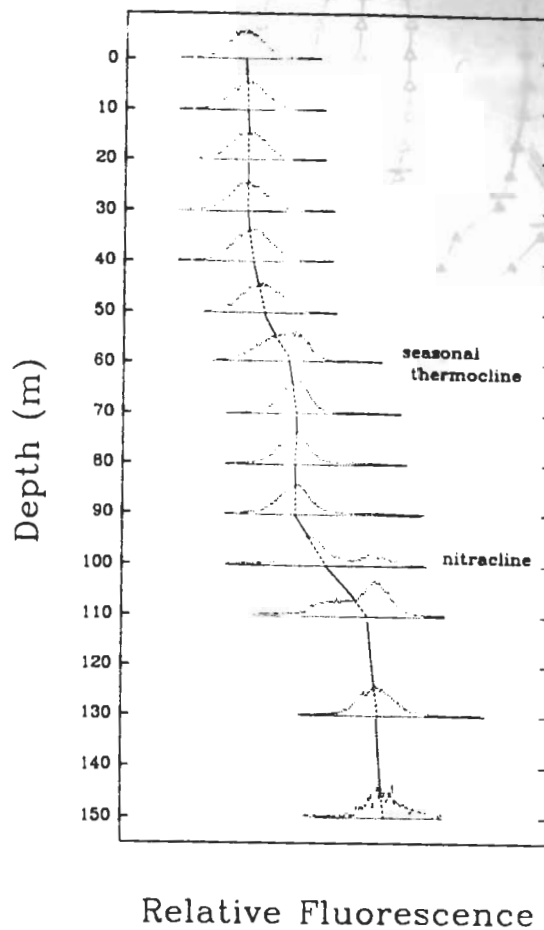


YAMAZAKI (1993)

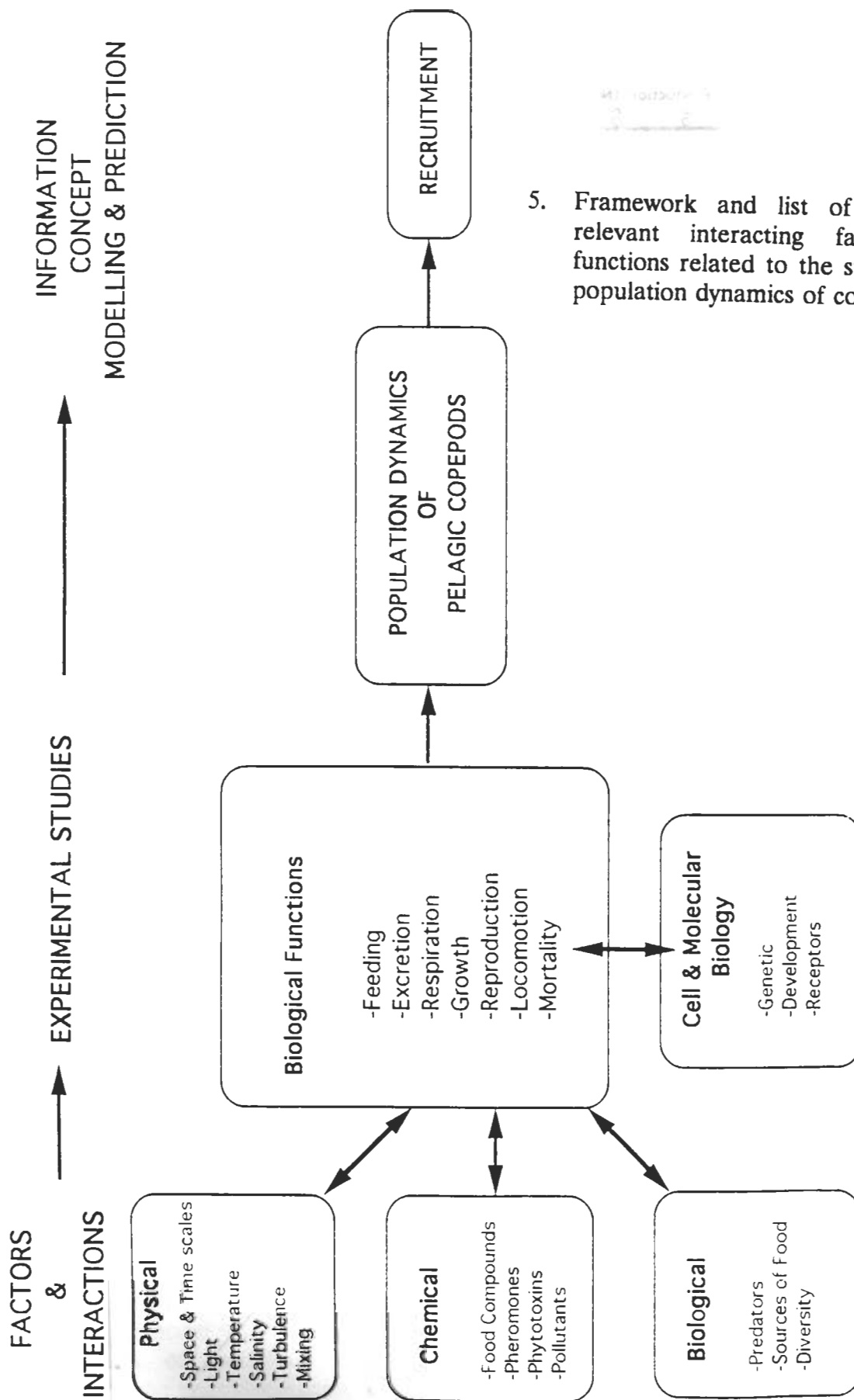
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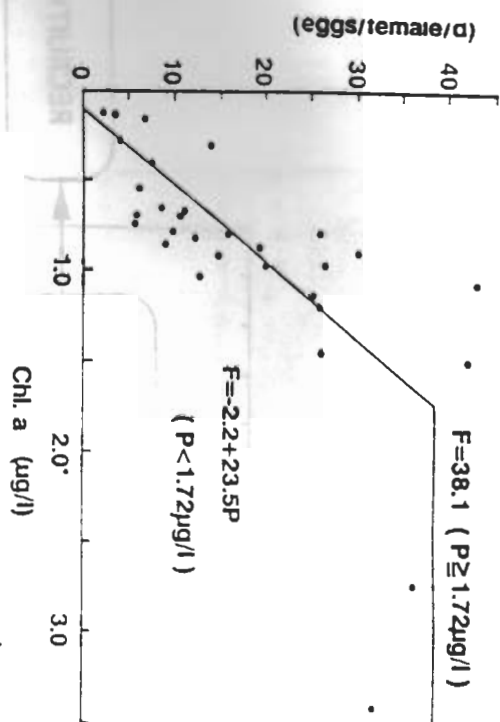


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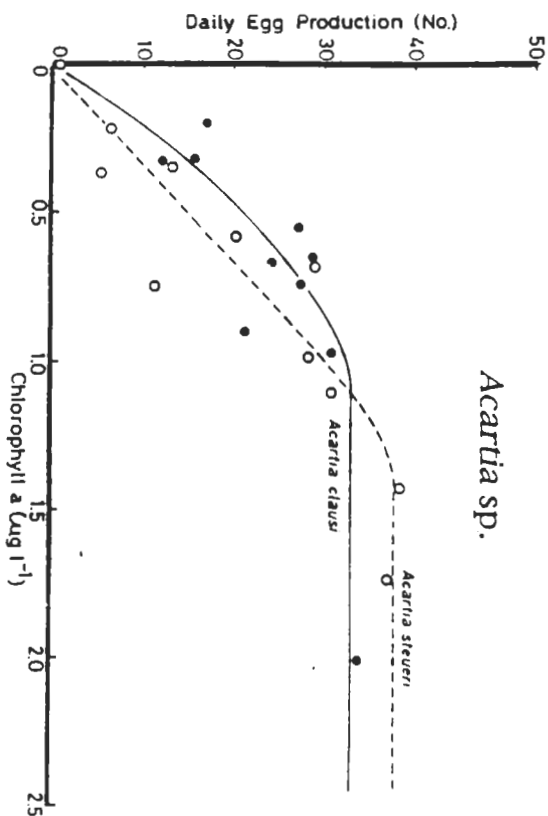


5. Framework and list of the most relevant interacting factors and functions related to the study of the population dynamics of copepods.

Paracalanus sp.

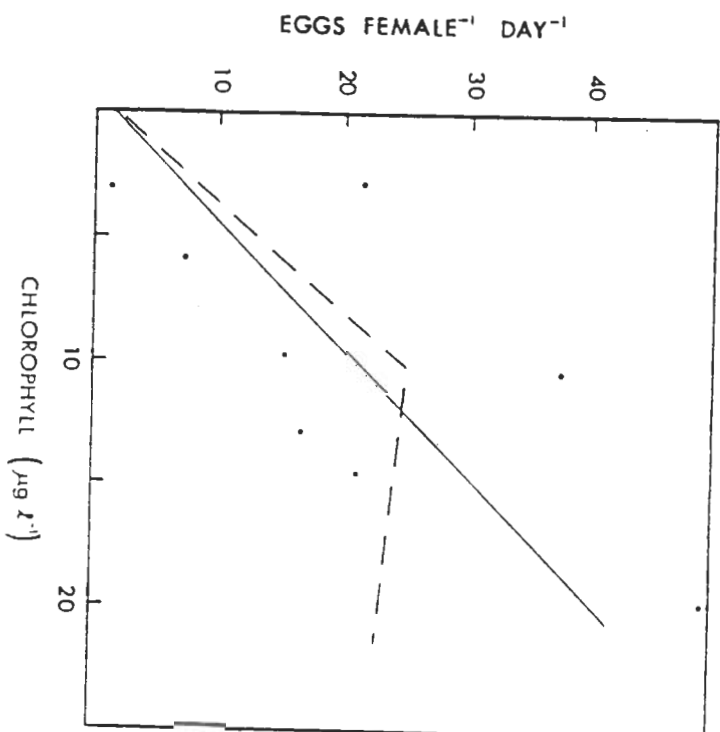


Acartia sp.



From Uye (1981); Uye et al. (1992)

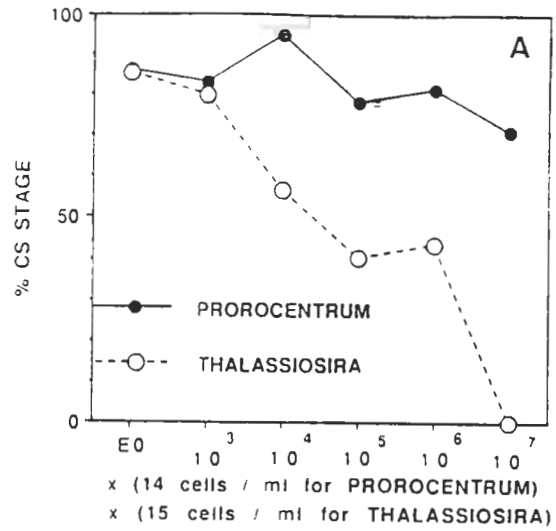
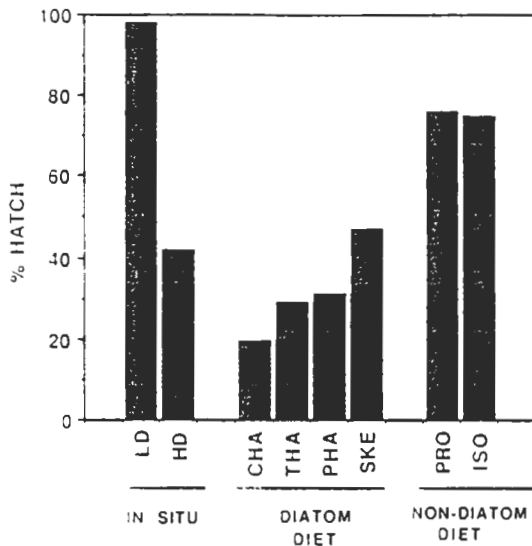
Calanus marshallae



From Peterson (1988)

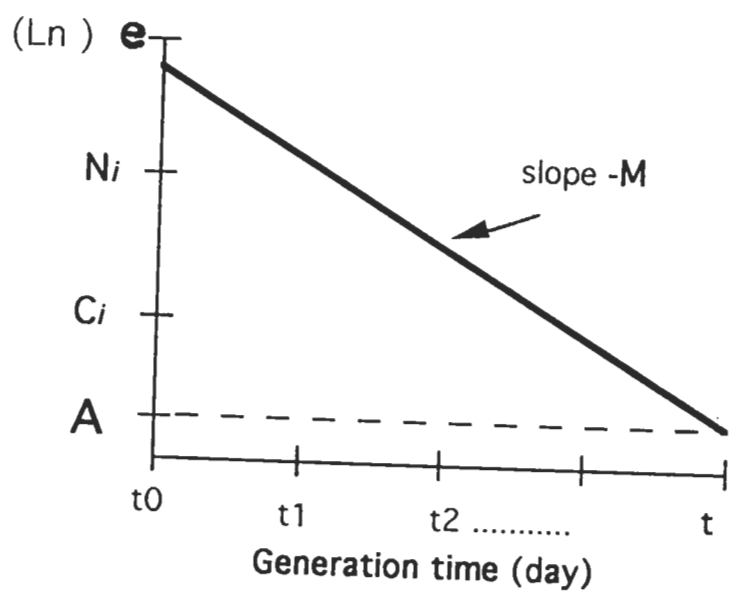
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Temora stylifera



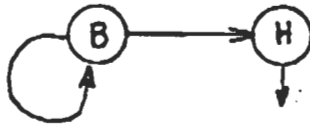
CONCENTRATION OF CELLS IN EXTRACTS

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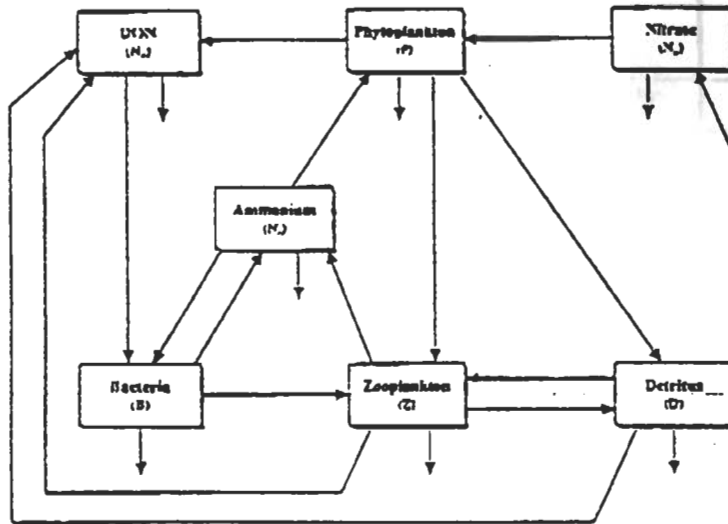
C



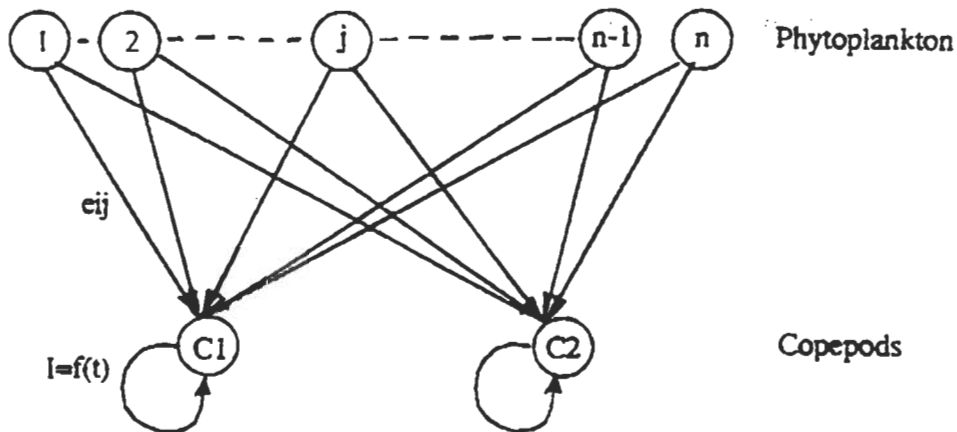
$$\frac{dB}{dt} = r \left(1 - \frac{B}{K}\right) B - \frac{a B H}{b + B}$$

$$\frac{dH}{dt} = e \frac{a B H}{b + B} - d H$$

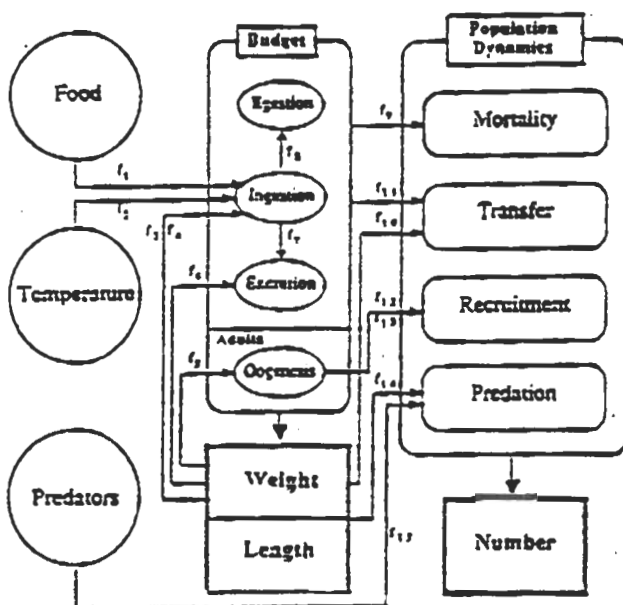
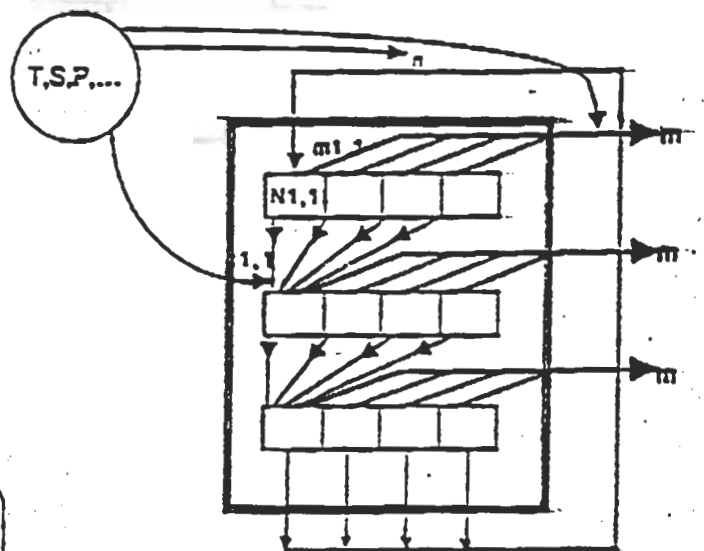
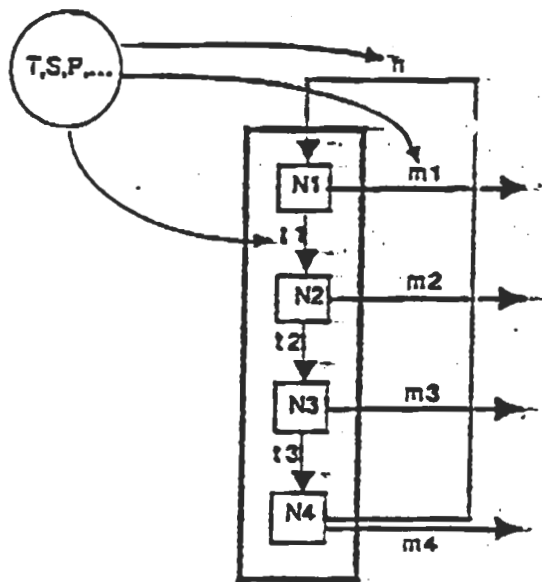
B



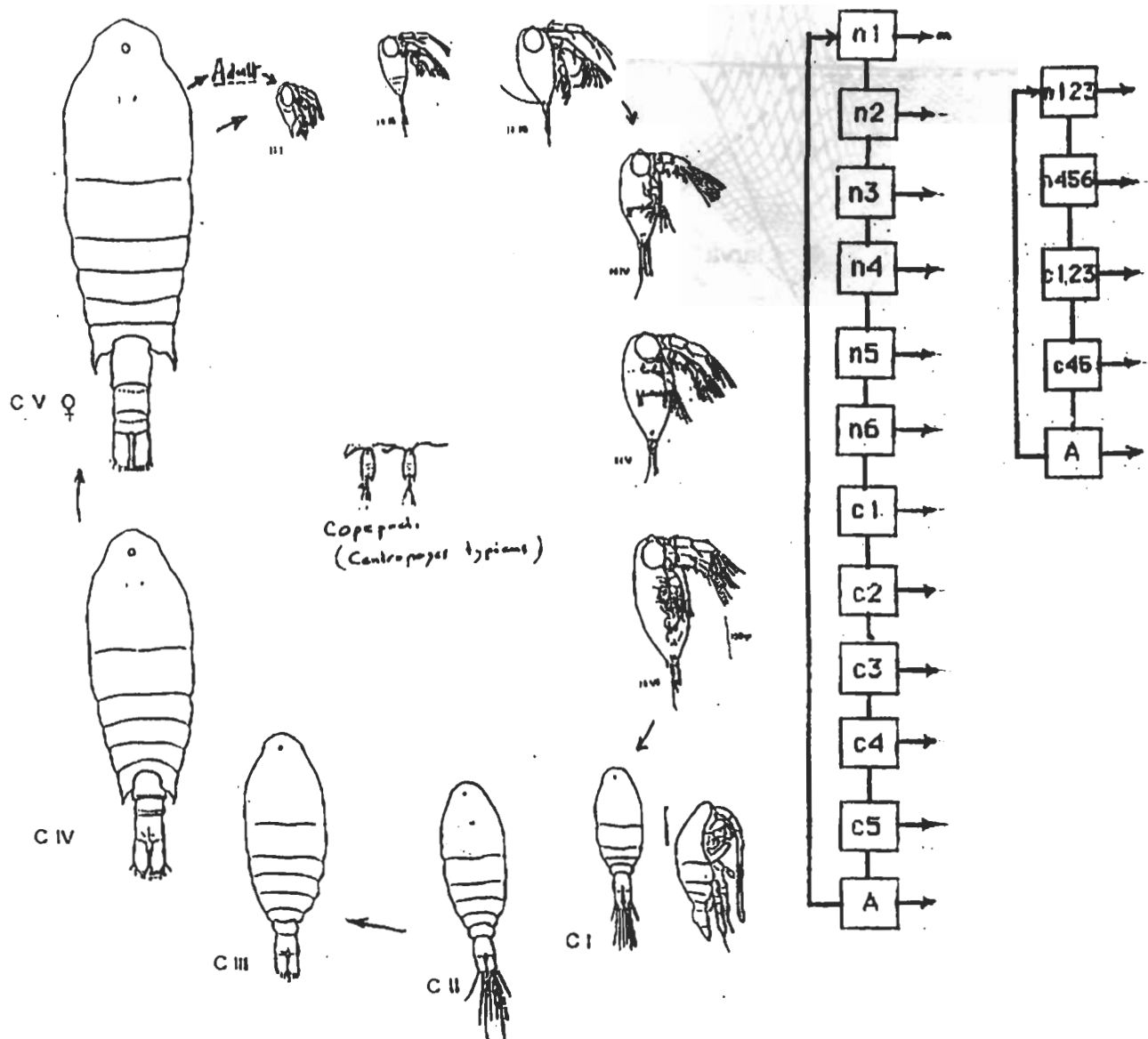
A



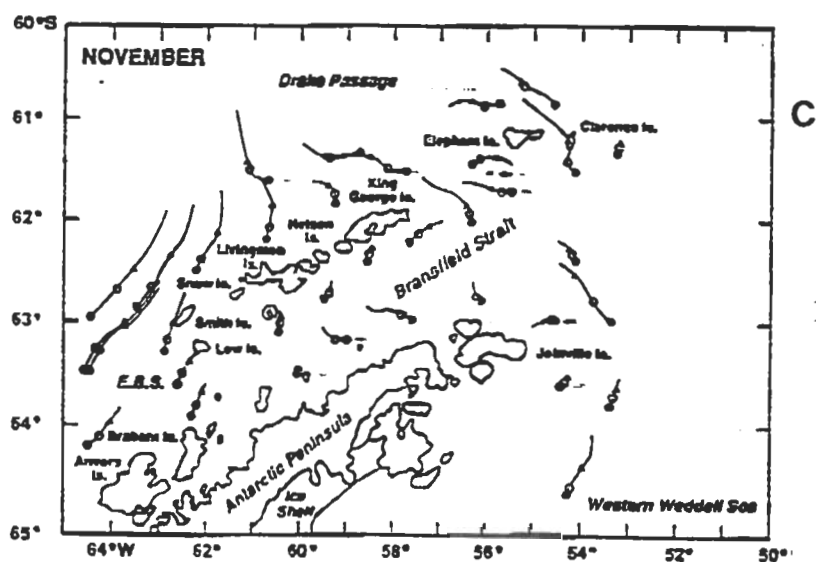
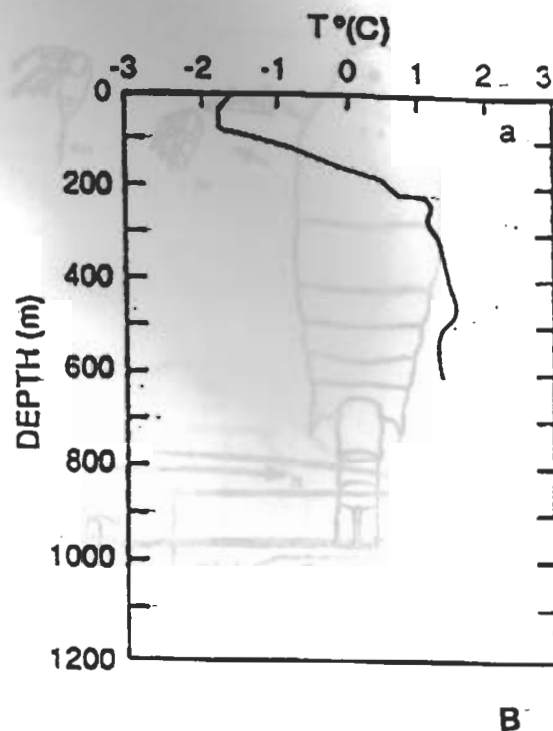
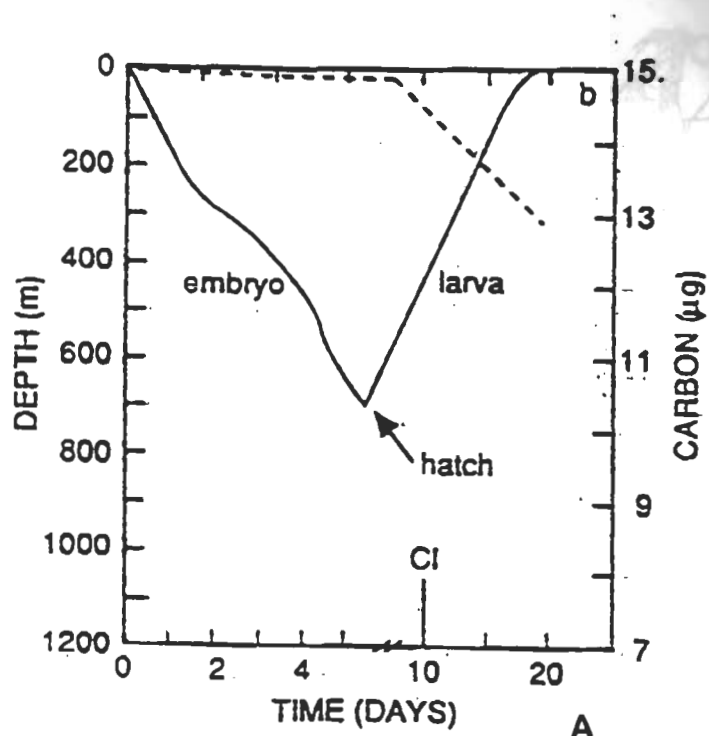
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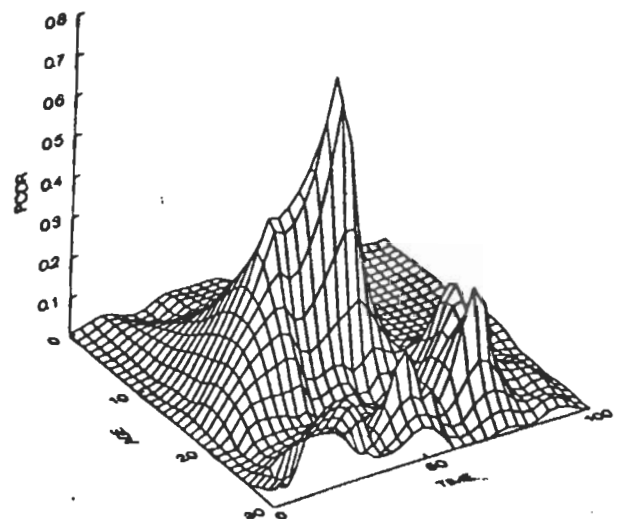
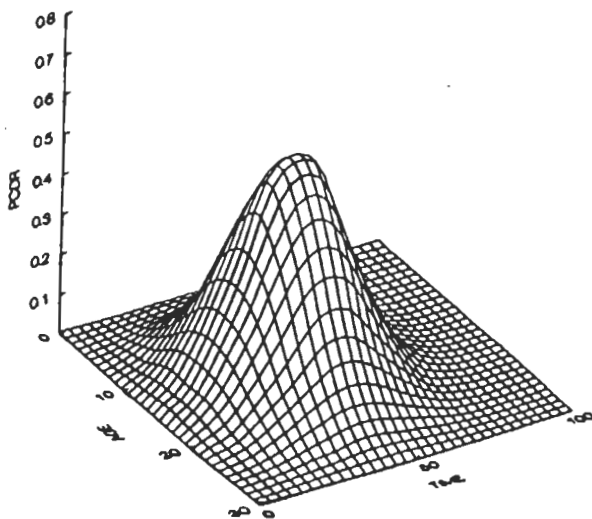
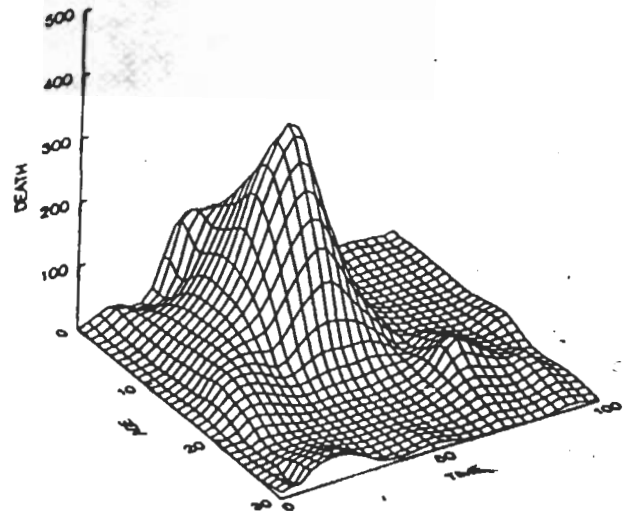
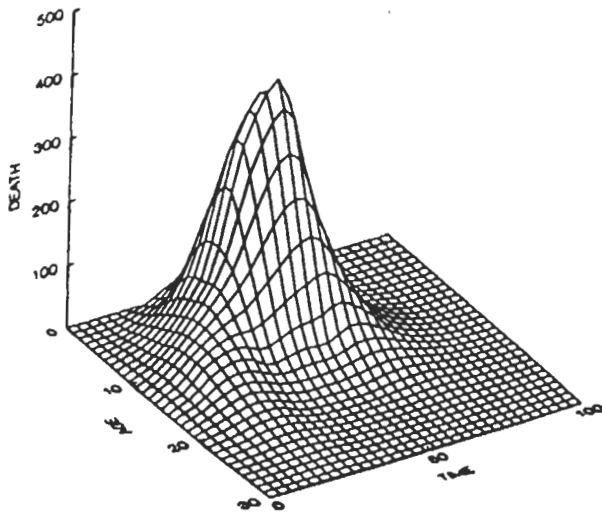
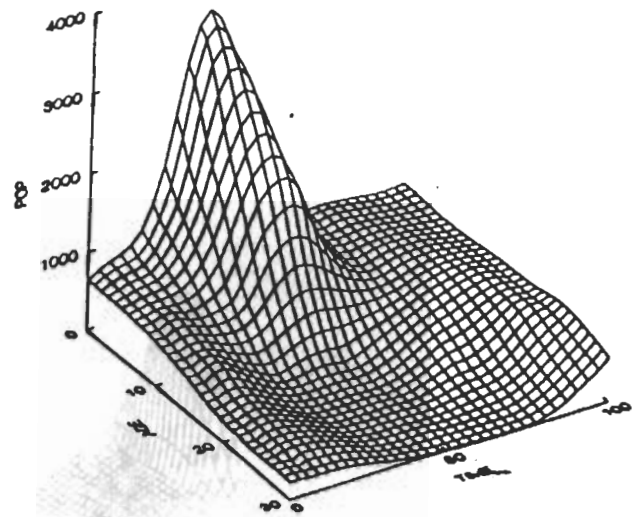
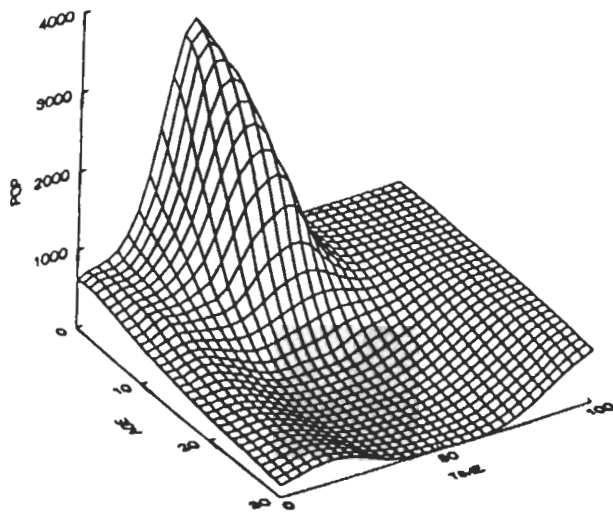
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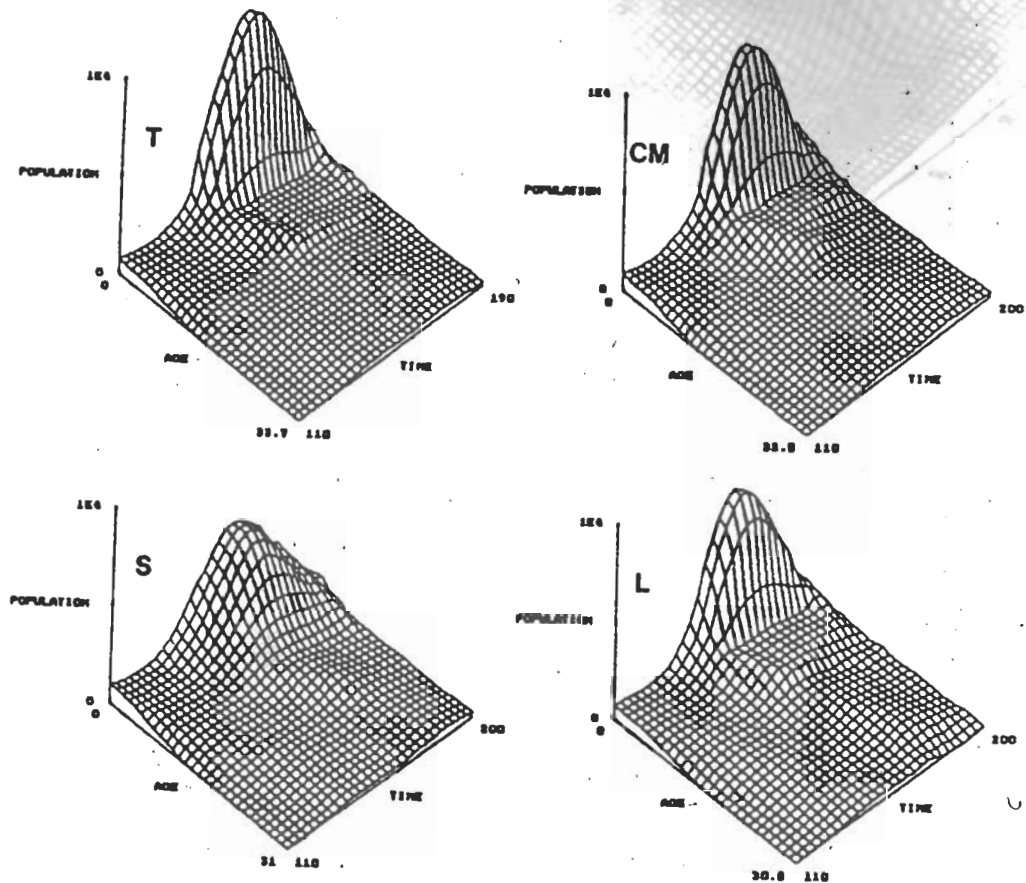
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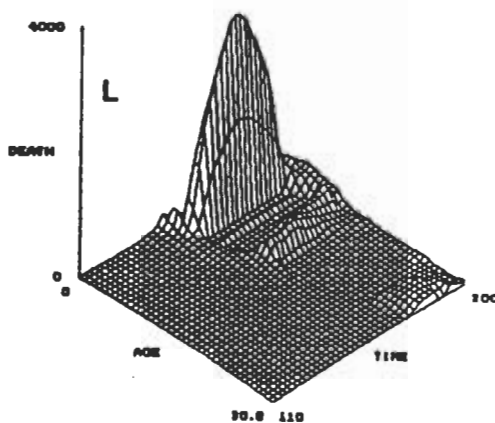
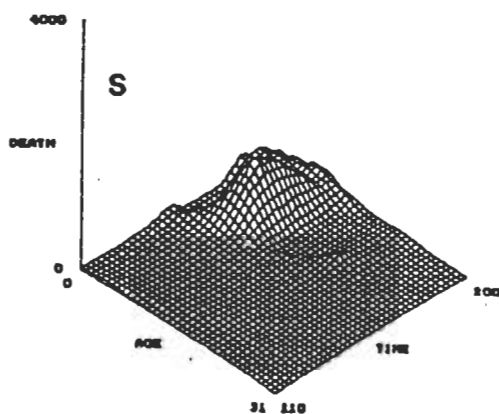
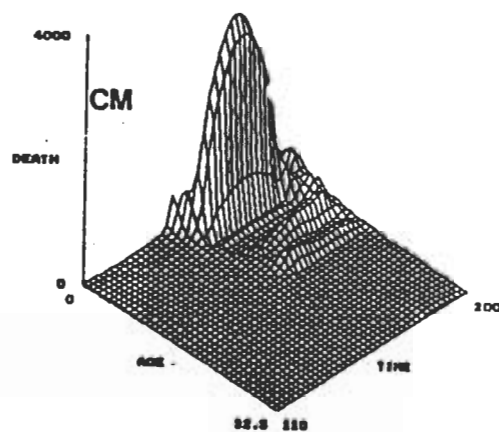
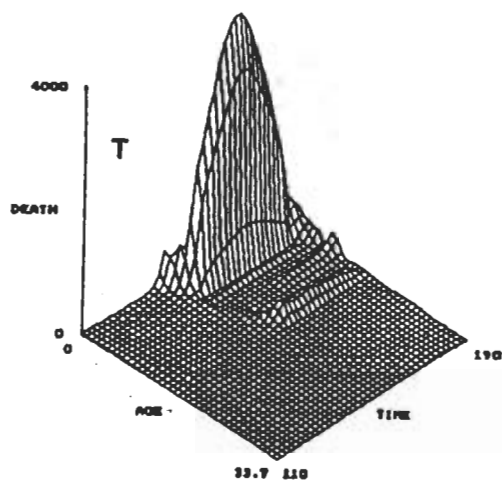
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14. Population surfaces for *Pseudocalanus* in a Loch Ewe enclosure calculated using different sets of stage durations (T is Thompson, 1982; L is Landry, 1983; S is Sazkina, 1968; CM is Corkett and McLaren, 1978).



15. Death rate surfaces corresponding to the population surfaces in Figure 14.

TABLES

Table 1

SUMMARY OF 'MAJOR ZOOPLANKTON FIELD STUDIES AROUND THE WORLD' (incomplete)

Project topic; key words	Study region	#Scien- tists (# Zooplank- tologists	Project period	Contact person
Hydrodynamics, zooplankton 2nd production and fish recruitment	Benguela current, Agulhas Bank S-Africa	19 (5)	'88-'96	Hutchings / Painting
Hydrodynamics and zooplankton population dynamics (part of RACER)	Antarctic coastal ecosystems	45 (20)	'86-'93	Huntley
Hydrodynamics and zooplankton distributions	California current	>35 (15)	'92-'97	Huntley
Physical control of biol. production, incl. zooplankton 2nd production	Celtic Sea shelf break	6 (3)	'90-'93	Harris
Physical forcing and meso- to macroscale distribution of zooplankton	Atlantic Ocean Indian Ocean Black Sea	6 (6)	'90-'93	Piontkovski
Physical forcing of zooplankton carbon cycling in Polynyas	NE Greenland	12 (2)	'92-'93	Walker-Smith
Hydrodynamics and the distribution and physiology of copepods	Mediterranean	16 (6)	'89-'95	Alcaraz / Estrada
Tidal front dynamics and zooplankton ecology	Inland Sea of Japan	11 (3)	'86-'88	Yanagi
Zooplankton interactions with seamounts (TOPO)	Eastern N. Pacific	10 (4)	'88-'93	Hauray
Zooplankton 2nd production and distribution of fish larvae	Gulf of St. Lawrence	6 (4)	'89-'93	Runge
Ice alga production, zooplankton production and fish larvae	Hudson Bay	15 (6)	'85-'89	Runge
South Atlantic Bight Recruitment Experiment (SABRE)	NW Atlantic	15 (4)	'91 ->	Checkley / Crowder
Zooplankton biomass & distribution and feeding of capelin and whales	Gulf St. Lawrence	2 (2)	'91-'94	Runge
Springtime aggregation of Calanus and whales (SCOPEX)	Gulf of Maine	7 (4)	'88-'91	Durbin
Zooplankton and fish recruitment (CalCoFi)	California Current	15 (4)	'49 ->	Mullin

Spatio-temporal distribution of zooplankton as food for larval cod (OPEN)	Scotian shelf	? (1)	'90 ->	McLaren
Monsoonal upwelling and distribution & production of zooplankton (Part of JGOFS)	Indian Ocean (Arabian Sea)	>30 (10)	'92-95	Baars / Smith
Vertical material flux and zooplankton community structure (ZOOS-WAT, JGOFS)	Sargasso Sea	11 (5)	'89-'92	Roman
Vertical material flux and Meso-zooplankton (JGOFS)	Equatorial Pacific	>20 (2)	'91-'93	Roman / Dam
Vertical material flux and micro- & macrozooplankton (JGOFS)	Equatorial Pacific	>60 (6)	'90-'93	Murray
Several more JGOFS-studies (CO ₂ -drawdown)	e.g. North Atlantic, Southern Ocean	--	--	--
Zooplankton and material fluxes	East China Sea	17 (2)	'92 ->	Iseki
Zooplankton and near-shore/offshore material flux	Tokyo & Osaka Bay	7 (1)	'89 ->	Yanagi
Role of zooplankton in POM flux	California Basin	18 (2)	'85-'91	Small
Zooplankton grazing and the 'Antarctic paradox' (SUPER)	Gulf of Alaska	7 (3)	'81-'91	Miller
Zooplankton grazing and the 'Antarctic paradox' (EPOS)	Weddel Sea	122 (15)	'88-'89	Fransz
Population dynamics Acaria; winter temperature and coupling to spring bloom	US fjord	7 (4)	?	Durbin
Population dynamics, life cycles, growth and production of copepods	Canadian high arctic	up to 4	'84-'94	Conover
Zooplankton seed populations and fate of primary production in boundary currents	off SE USA	40 (4)	6 years	Paffenhöfer
Zooplankton and food web interactions	Buzzard Bay & Boston Harbor	3-4 (2)	'88 ->	Turner
CPR studies -- Long-term trends in oceanic zooplankton	N. Atlantic	?	ca. '40->	Gamble
Biology and production of zooplankton	North Norwegian waters	4 (3)	?	Tande

Table 2

Overview of experimental methods used for estimating zooplankton production.

Ingestion (I)

- Food balance methods
 - (a) Closed chamber
 - (b) Flow-through system
- *In situ* methods
 - (a) Gut fluorescence method
 - (b) Microscopic gut content analysis
 - (c) Gut fullness
- Biochemical indices
 - (a) Activity of digestive enzymes
- Respiration change methods
 - (a) Decrease in respiration rate of field collected animals in starvation (SDA)

Assimilation (A) and Egestion (E)

- Gravimetric method
- Inert ratio methods
 - (a) Natural foods
 - (1) Ash ratio method
 - (2) Silica ratio method
 - (3) Pigment ratio method
 - (b) Prepared foods
 - (1) Chromium ratio method
- Radiotracer methods
 - (a) Quantitative recovery
 - (b) Ratio principle

Metabolism (M)

- Component balance methods (oxygen, ammonium, urea, total nitrogen)
 - (a) Closed chamber
 - (b) Flow-through chamber
- Radiotracer methods
- Biochemical indices (ETS, GDH)

Growth (G)

- Direct growth observations
- Egg production methods
- Molting rate methods
- Radiotracer methods
- Biochemical indices
 - (a) RNA/DNA ratio
 - (b) Rate of synthesis of RNA and DNA
 - (c) DNA polymerase
 - (d) Guanosine/ATP ratio
 - (e) ATC activity

Table 3

Overview of new developments of zooplankton methods.

A. Methods for determination of zooplankton rates

1. Ingestion
 - Tracers for herbivory: pigments, lipids
 - Tracers for carnivory: astaxantin, chitin
 - Video imaging for determination of feeding behaviour
 - Video imaging for quantification of feeding activity
2. Metabolism (energy producing)
 - Pyruvate kinase (PK)
 - Lactate dehydrogenase (LDH) (?)
 - Citrate synthase (CS)
3. Growth
 - Direct measure of growth using laboratory raised artificial cohorts.
 - * Silhouette photography
 - * Video images
 - * Acoustics
 - Biochemical methods involved in protein synthesis
 - * rRNA
 - * Malate dehydrogenase (MDH) (lipids to protein)
 - * Aspartate transcarbamylase (ATC)
 - * Reproducing and molting hormone activities

In: ICES Study Group on Zooplankton Production- Bergen
Report;1992- page 10.

Table 4

Characteristics of various physical structures

Physical structure	Length scale	Persistence
Antarctic circumpolar current	10 000 km	Long term
Subtropical gyres	10 000 km	Long term
Subarctic gyres	5 000 km	Long term
Shelf seas circulation	3 000 km	Long term
Large oceanic divergences	200 km	Long term
Large oceanic convergences	200 km	Long term
Seasonal coastal upwelling	100 km	Seasonal
Rings formed by frontal instability	10-300 km	Days-Year
Topographically trapped gyres	10-300 km	Seasonal-Long term
Estuarine circulation	10-200 km	Seasonal
Deep water formation, Chimneys	20 km	Seasonal
Shelf break fronts	10 km	Seasonal-Long term
Upwelling downstream of islands	10 km	Seasonal-Long term

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